THE USE OF LARYNGEAL AND BUCCOPHARYNGEAL MORPHOLOGY IN ANURAN TAXONOMY

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PREFACE

The work described in this thesis was carried out in the author's private laboratory, Pietermaritzburg, from January 1989 to December 1991, under the supervision of Professor John C. Poynton.

These studies represent original unaided work by the author, unless specifically indicated to the contrary in the text, and have not been submitted in any form to another University.

12 DECEMBER 1991

ABSTRACT

The taxonomic value of adult laryngeal and larval buccopharyngeal characters, not previously used in studies of southern African frogs, was investigated. The amphibians of Natal, recently examined using more traditional characters (Lambiris 1989), were used both for assessing the value of these characters and for testing the earlier taxonomic conclusions.

The results indicate that:

(a) Laryngeal and buccopharyngeal characters appear to be of value in anuran taxonomy;
(b) Most of the taxonomic conclusions of Poynton (1964) and of Lambiris (1989) appear to be justified;
(c) Taxonomic problems in certain of the genera and species-groups examined appear to be more easily resolved by the use of these characters than by those more generally used.

The status of six taxa has been redefined; these are *Bufo pusillus*, *Bufo poweri*, *Bufo cruciger*, *Breviceps maculatus*, *Rana umbraculata* and *Cacosternum striatum*. Five undescribed species and one new genus have been identified and await description.

ACKNOWLEDGEMENTS

I thank Professor John C. Poynton, supervisor of this thesis, for his support and discussions during the course of the work, and for the many years of guidance and friendship in which he has helped develop my interest in amphibians.

Special thanks are due to Dr. Brian Stuckenberg, Director of the Natal Museum, who not only made available full research facilities, but also accorded me the great privilege of dissecting valuable material in his care, including type specimens; and for his interest in this study.

I am also grateful to the following, for help in resolving problems requiring the dissection of material not otherwise available to me:

Mr. Wulf Haacke, Assistant Director of the Transvaal Museum, Pretoria, who allowed me to dissect larynxes from some of the paratypes of *Cacosternum striatum*, resulting in the validification of this species and the recognition of a new genus and species.

Dr. Philip Bishop (University of the Witwatersrand, Pretoria), for permitting me to dissect and examine hyolarynxes of type material from an undescribed species of *Arthroleptella*.

Dr. Paul Skelton (J.L.B. Smith Institute of Ichthyology, Rhodes University, Grahamstown), for collecting and donating tadpoles of *Rana dracomontana* and of an undescribed species of *Rana*.

Dr. Michael Cherry (South African Museum, Cape Town), who permitted me to dissect larynxes from a series of the toads here called *Bufo cruciger*.

Miss Beryl Wilson (McGregor Museum, Kimberley), for a series of *Bufo poweri*, now resurrected as a valid species.

Dr. Barry Hughes of the British Museum (Natural History), for permission to dissect a specimen of *Bufo maculatus*, here recognised as distinct from *Bufo pusillus*.

Mr. Gerald Haagner (Port Elizabeth Museum), who has donated much valuable herpetological material to my private collection in the past, some of which was used in this study; and for collecting tadpoles of several species specifically for this study.

Mr. Lynn Raw, Pietermaritzburg, who made available male *Leptopelis xenodactylus* and a series of *Kassina senegalensis* from areas of special interest.

Mr. Louis du Preez (National Museum, Bloemfontain), who donated *Pyxicephalus adspersus edulis* frogs and tadpoles for dissection.

I am also grateful to Dr. George Hughes, Chief Director, and Dr. Ortwin Bourquin, Assistant Director Species Conservation, Natal Parks Board, for their support of this study, particularly with regard to collecting permits and generous study leave conditions. Dr. Bourquin suggested the use of colour in the Plates, which has greatly facilitated interpretation.

I would also like to thank Professor Neville Passmore (University of the Witwatersrand) for the generous donation of a rotary microtome to replace my ancient Cambridge rocker; and Dr. Hugh Morris of Drs. Ferguson, Bouwer, Morris & Partners, for providing a series of slides of human tissues for testing a quad stain developed for microanatomical tadpole studies. Although not incorporated into this study in its present form, these contributions were of major importance to the approach originally adopted. Professor Passmore also provided information on the calls of *Ptychadena mascareniensis* which has been incorporated into this study, and for which I am grateful.

Mr. Peter Croeser (Arachnology Department, Natal Museum) is thanked for the many interesting and illuminating discussions on biophilosophy and on taxonomy in general, which have directly or indirectly helped clarify several of the problems arising during this study; and for making available some working space when it was needed at short notice.

Most of all, I express my profound gratitude and appreciation to my wife, June, and daughter Shirley Anne, who have supported and encouraged

this study in every way, including reading and commenting on parts of the text, and their unstinting help with the laborious task of tinting the coloured plates. Without them this thesis could never have been completed on time.

Finally, I salute the amphibians of southern Africa as a noble group that has been a lifetime source of wonder, delight and enlightenment.

To June and Shirley-Anne,
who have shared and sacrificed so much

E quant' io l'abbia in grado, mentre io vivo
convien che nella mia lingua si scerna,

Dante, *Commedia Divina*, I;xv,86-87

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CHAPTER 1

INTRODUCTION

We shall not cease from exploration
And the end of our exploring
Will be to arrive where we started
And to know the place for the first time.

T.S. Elliott - *Little Gidding*

1.1 Reasons for undertaking the study

For some years I have been troubled by the question of how an amphibian speciesmay be recognised or defined. This problem became especially apparent during a recent study on the frogs of Natal (Lambiris, 1989a), although the issue was avoided on account of the relatively limited scope of the study. A rather conservative, pragmatic morphological approach was adopted there.

In the museum it is usually possible to assign names to individual specimens, on the basis of morphological characters observable in preserved material, with relative ease and confidence. There are, however, other instances in which a preserved specimen can be named only with great difficulty and with doubt, or not be identifiable at all - yet in the field, other individuals of the same genus can be identified much more easily and surely when observed in their natural surroundings.

It therefore seems useful at this stage to examine additional morphological characters in both the adult and the larval phases and to address, from a fresh point of view, the questions "How can an amphibian species be defined" and "How can an amphibian species be recognised?" If additional characters can be found that are a useful adjunct to those already utilised, particularly in taxa that are difficult to identify by more traditional means, then it may be possible to construct better (or at least more useful) diagnoses or keys.

1.2 Principal aim of the study

Poynton & Broadley (1985:503) remarked that

> "[a] 'species' in our usage can in fact be regarded as a hypothesis; a hypothesis about the presence of a reproductively inclusive (and perhaps exclusive) group of amphibians ... patently testable by field studies, physiological investigations and more detailed or extended morphological analysis; and indeed a major value of such a hypothesis is seen to lie in whatever stimulation and facilitation it gives to further investigation of this still poorly known element of the African fauna."

The principal proximal aim of this study is to undertake a detailed morphological study of adult laryngeal and larval buccopharyngeal features that may contribute to a better definition of species boundaries in Natal amphibians.

The approach in this study is:

1. To examine the internal laryngeal morphology of anuran taxa (as currently recognised) occurring in Natal; and to assess its taxonomic usefulness in detecting intra- and interspecific variation. Extralimital taxa are included, where necessary, for comparison.

2. To examine the buccopharyngeal morphology of tadpoles identified as belonging to currently recognised taxa occurring in Natal and to assess its taxonomic usefulness in detecting intra- and interspecific variation.

3. To determine whether examination of the above features leads to taxonomic conclusions in agreement or at variance with those based on traditional morphological characters and male advertisement calls with regard both to the definition of species and identification of individual specimens; and to determine whether these characters might be of value in elucidating problems in such difficult genera as *Bufo*, *Rana*, *Ptychadena*, *Phrynobatrachus*, *Afrixalus* and *Hyperolius* where adults, or tadpoles, or both, are often extremely difficult to identify by means of conventional diagnostic characters.

The combination of larval buccopharyngeal characters (an approach developed by Wassersug 1976, 1980) and of internal laryngeal morphology in adults (original, at this level, as far as I have been able to ascertain) is intended to supplement those characters used in existing taxonomies, not to replace them; and a subsidiary aim of the investigation is to determine to what extent current taxonomic conclusions may be modified by their use. The taxonomic consequences of considering these characters are discussed in the Systematic Account (Chapter 4) and in the Conclusion (Chapter 5).

1.3 Scope of the study

I have based the present study principally on the frogs of Natal for several reasons. The province is an interesting region biogeographically, its amphibian fauna being composed of some 75 recognised taxa (Lambiris 1989a) belonging to the East African Tropical, Transitional and Cape faunal groups (Poynton, 1964; Poynton & Broadley, 1978). Furthermore, the frogs of this area provide broad taxonomic and ecological spectra which are considered fundamental to the present approach, and the recent survey cited above provides a useful summary of a conservative morphologically-based taxonomic treatment against which the present study can be tested. Finally, a geographical restriction (i.e., not considering all southern African taxa) is necessary because of the depth of the study -- a smaller geographical area, with fewer taxa, allows more effective focussing on the main questions and issues of this study.

It is not the purpose of this study to go beyond the species level or to deal with concepts and issues relating to higher classification, as is apparent from the almost total absence of any such discussion in the main body of the text. When many more taxa have been studied than have been done in this preliminary investigation, then it should be possible to use these characters to test the various conceptual approaches to higher Anuran classification more rigorously.

Although it is obviously highly desirable that adult laryngeal and larval buccopharyngeal characters also be studied in terms of behavioural, ecological and evolutionary aspects, I have considered such treatment to be

outside the principal aim of the present study -- namely, the assessment of the possible taxonomic value of morphological features. I have tried to compensate for this omission, in part, by including brief descriptions of advertisement calls and of larval diet (as revealed by microscopic study of gut contents of freshly-captured tadpoles).

Four basic questions have an important bearing on this study. It is possible that the second and third of these cannot be answered adquately, but they are questions that must be recognised and addressed as far as possible.

(i) What is a species?

A species is here considered to be a set which includes all those objects possessing a suite of attributes that we believe associates them closely (in the sense of being functionally or operatively the same) and which excludes all other objects or individuals not possessing that suite of attributes.

(ii) How is a biological species circumscribed in nature?

It may never be possible to answer this question adequately because we do not - and perhaps never will - have sufficient information to answer it. In all probability there is no single answer, for it seems that the factors that operate to render one species distinct from another vary from one major taxonomic group to another. However, we may postulate that a biological species is the product of (a) sustained and consistent survival and reproductive mechanisms of a group of organisms and of (b) the environment in which they live and with which they interact.

(iii) How does a taxonomist define a species?

Again, this is a question that probably never will be answered satisfactorily because each taxonomist has his own perception of some fragments of the world picture on which his conclusions are based. The taxonomist's concept and definition of a species must therefore of necessity be incomplete and ever-changing according to the extent of his perception of the nature of things. The definitions of Nelson & Platnick (1981:12) of species as "samples of self-perpetuating organisms that have unique sets of characters" and of Griswold (1987:6) as "a phenetically distinct set of

specimens which are morphologically distinct over a geographic area" formed the basis of my earlier study of Natal frogs (Lambiris, 1989a), and do so again in the present investigation.

(iv) How are amphibian species identified?

For all practical purposes the identification of specimens is founded on morphological attributes that can be discerned in both living and preserved material. Most of these characters are external or, if internal, sufficiently accessible to be displayed with the minimum of dissection or other preparation. The field worker has an immense advantage over his colleague in the laboratory in that he is able to observe diagnostic attributes that cannot be preserved in museum specimens, and is in a position to reinforce his diagnosis with data that more nearly reflect the biological nature of the species with which he is working. Of these, the male advertisement (or mating) call is considered to be the most diagnostic biological character of all. Nevertheless the fact remains that these biological characters, invaluable though they may be, can strictly be applied only to those living individuals exhibiting them in the field (or perhaps in the artificial confines of a laboratory), but can be related to morphologically similar individuals in a pickle jar only by extension.

It seems to me that there are only three fundamental aspects that have (within the context of a purely pragmatic approach to anuran taxonomy) any bearing on what it is that constitutes a biological species in nature and on how individual specimens may be identified - firstly, the possession of a specific mate recognition system (in this case the male advertisement call and the female response to it); secondly, the existence of strategies that allow survival of both individuals and of the circumscribed communities which engender them; and thirdly, observable morphological attributes that are present in a reasonably consistent manner; these may or not have any recognisable biological significance as far as the organism is concerned.

I have therefore attempted to find characters which I believe are of direct relevance as far as questions (i) and (ii) above are concerned and which may be used, in a practical way, in answering questions (iii) and (iv).

1.4 Statement of assumptions

This thesis rests on several assumptions, on which the approach to the present study depends. These assumptions need to be explicitly stated so that the study can be more easily evaluated. They are:

(i) That species exist as discrete taxonomic units in nature.

(ii) That biological species possess attributes directly concerned with the interaction of living organisms with each other and with their environment, which serve to maintain the identity of such biological species with reasonable consistency, yet which are sufficiently flexible to allow some measure of adaptation to changing environments and which may or may not allow speciation to occur.

(iii) That because individual organisms included within any one biological species interact with other organisms both intra- and interspecifically and with the general environment, they must possess physically expressed attributes of a biological type, such as sense organs, effector systems, reproductive and nutritional systems that permit such interactions to occur and which yet maintain the identity of the several species interacting.

(iv) That such attributes are directly observable as discrete morphological characters discernible in dead as well as in living individuals, and which are sufficiently stable to be of value in applied taxonomy.

(v) That the male advertisement call is an essential behavioural factor serving to maintain taxonomic identity at the species level in anurans. (For the purposes of this study I have deliberately excluded the female's response to the male call, without which the concept of the Specific Mate Recognition System [Paterson 1978, 1981, 1982a, 1982b. 1986] would be nonsensical, but which is nevertheless not germane to the present study. It should be recognised as an integral part of the basic approach presented here, but which demands a full study in its own right.)

(vi) That the internal morphology of the anuran male larynx reflects to a taxonomically useful extent the differences in calls that are diagnostic of the various species, and which is therefore of practical value when recordings of advertisement calls for any individual male frog are not available.

(vii) That the anuran larva is in general confined to a more restricted type of habitat (the water body in which the eggs were laid) than the adult (which can move into a wider range of terrestrial and aquatic habitats), and that feeding, niche separation, community behaviour and survival strategies may be more delicately balanced, and of greater evolutionary significance, than in the adult which is, after all, more easily able to disperse and seek alternative situations if local conditions change adversely.

(viii) That larval buccopharyngeal morphology closely reflects the essential aspects of tadpole biology, behaviour and ecology - especially feeding - and may be taxonomically more meaningful than the external features used for routine identification.

(ix) That a study of attributes relating both to reproduction and to non-reproductive survival is essential to a clearer understanding of what constitutes an amphibian species and how its individual members may be recognised. These attributes may best be studied by examining morphological characters present in the adult male and in the larval stage respectively.

(x) That the nature of an anuran species may be better understood by giving to the larval phase as much attention to morphological and biological studies as have been given to the adult phase.

(xi) That new sets of characters may be used to confirm or refute conclusions drawn in current taxonomy, based on morphological characters used for routine diagnostic or taxonomic work.

CHAPTER 2

CHARACTERS USED IN THIS STUDY

2.1 The adult hyolarynx

I have paid special attention to the internal configuration of the larynx since I feel that it is here that the fundamental qualities of the sounds uttered are produced. The extrinsic muscles responsible for air flow through the larynx, and those causing and adjusting tension on the vocal cords during vocalisation, are undoubtedly just as important in producing various species-specific characteristics of the call, but their function is dependent on the mechanics of living tissue and their morphology seems to be too circumscribed to be as taxonomically convenient at the species level. Nevertheless, such features as the relative length and position of the body of the hyoid plate as seen in medial section, the nature of the origin of the m. hyoglossus, and the general structure of the vocal sac(s) may also be of interest, apart from helping give a much clearer idea of the orientation of the larynx. The entire hyolarynx has therefore been removed and illustrated in all instances, even though extralaryngeal features have not generally been discussed in the text.

Attention in this study is directed principally towards the morphology of the larynx as seen in median sagittal section. This approach was chosen after examining a number of alternatives, including coronal and horizontal sections in various planes, or staining lightly and clearing optically in methyl salicylate. None, however, was as consistently reproducible or revealed as much detail as a simple division in the medial plane.

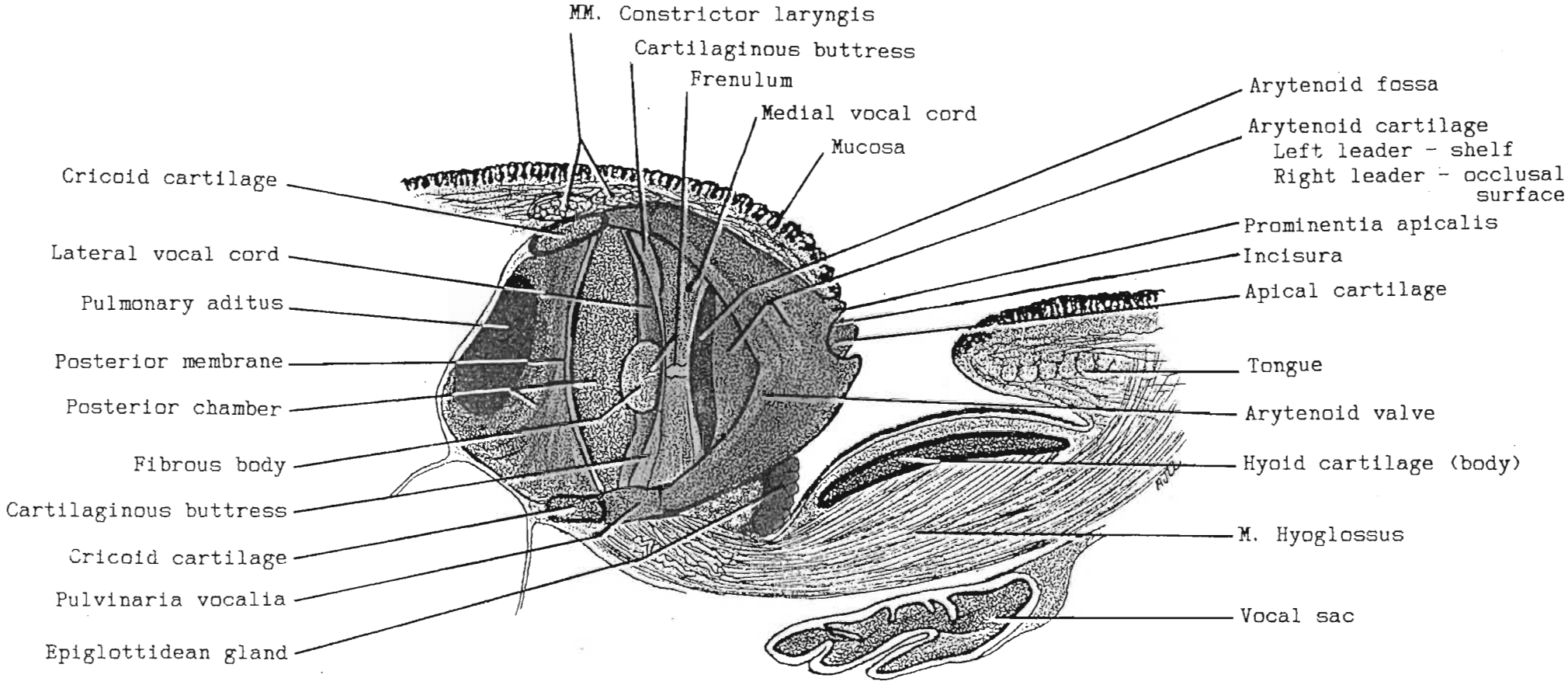
2.1.1 Historical review

Blume (1930) examined themicroscopic anatomy and surface features of the hyolarynx as illustrated by macroscopic preparations and by serial-section reconstruction models. However, internal gross morphology of the larynx was not discussed in detail or illustrated.

Trewavas (1933: 403) examined "the structures of the hyolaryngeal apparatus in a large and representative series of the Anura, in order that an idea may be gained of the range of diversity of these organs in the group, and of the extent to which resemblances in their structure are indicative of relationship." She studied 60 species belonging to 36 genera in nine families, paying special attention to the hyoid and the laryngeal skeleton, and to their associated musculature. In only a very few instances is the internal morphology of the larynx indicated, generally as brief comments on isolated structures, or as figures of transverse sections of the larynx or half-larynx; the medial surface of the arytenoid cartilage in isolation is sometimes shown. Although Trewavas demonstrated that the comparative anatomy of the hyolarynx and its related musculature as a whole is an invaluable adjunct in the consideration of phylogenetic relationships at higher levels of classification, this approach may be of limited value for differentiating between genera or species because of the rather limited range of taxonomically useful variation at this level. This may tend to support the opinion expressed above that the internal architecture of the larynx is important in species-specific sound production.

Martin (1972) discussed the evolution of vocalisation in *Bufo*, describing or commenting on the functional anatomy of larynxes in a large number of genera and species, with drawings of the interiors of the left halves of larynxes of nine leptodactylid and two bufonid species. Structures within the larynx were discussed in detail with reference to the mechanics of vibration. The importance of comparative anatomy in the production of species-specific calls (discussed at the genus, and sometimes at the species, level) as well as its significance in elucidating phylogenetic relationships at higher levels, was clearly stated. However, no attempt was made to investigate or evaluate laryngeal internal morphology as a taxonomic tool at the species level.

Duellman & Trueb (1986) described the internal structure of the larynx in some detail and referred to literature describing the diversity of structure in the anuran larynx, but also did not suggest that these differences might be of significance at the species level.



TEXT-FIG. 1: MEDIAN SAGITTAL SECTION OF AN ANURAN HYOLARYNX (GENERALISED, COMPOSITE, DIAGRAMMATIC).

Passmore (1988) found marked intraspecific and generic differences, as well as "remarkable consistency within species" in the epithelial surface at the microscopic level.

One of the principal curiosities encountered in the present study is the observation that while the relationship between laryngeal structure and the production of mating calls has been perceived (Passmore, 1988), no detailed taxonomic study based on gross morphology along these lines seems to have been done at the species level.

2.1.2 Terminology

Features described or discussed in the text are illustrated in Text-fig. 1. Terminology follows the usage of Trewavas (1933), Martin (1972) and Duellman & Trueb (1986). Trewavas uses terms "either in their original (Latin) form or their English form", a practice followed by Duellman and Trueb and by Martin in their discussions of the anuran larynx. I have followed suit, despite the obvious impropriety, because there appears to be no comparable formal anatomical nomenclature for the larval features under consideration. I have used formal nomenclature only in the few instances where convenient anglicisms do not appear to be available, but have differed from earlier usage (Blume 1930) in using *pulvinarium* rather than *pulvinar* as the singular form of *pulvinaria*. Classical authors (e.g. Cicero and Pliny) used *pulvinar* to mean a couch, and *pulvinarium* in referring to an anchorage -- this latter form seems more appropriate in the present context.

Two additional terms are introduced here:

Arytenoid shelf: That part of the internal surface of the arytenoid cartilage lying behind the occlusal surface of the cartilage and before the arytenoid fossa.

Arytenoid fossa: A fossa formed by a curvature of the arytenoid cartilage, usually vertically elliptic, lying lateral and partly anterior to the vocal cords.

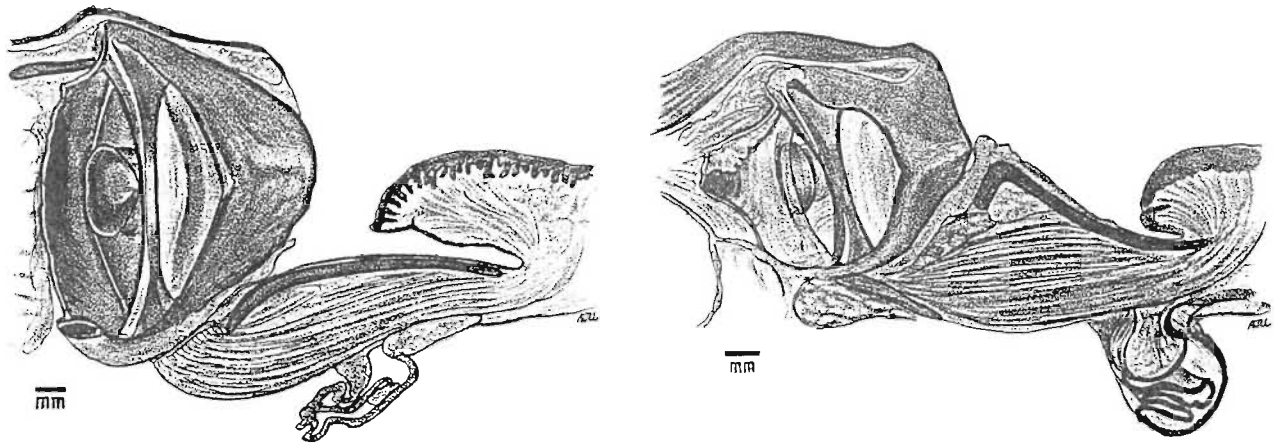


FIG. 2; Effects of hyoglossal contraction. (a) *Bufo garmani*, relaxed. (b), *Bufo rangeri*, contracted. Note buckling of hyoid body.

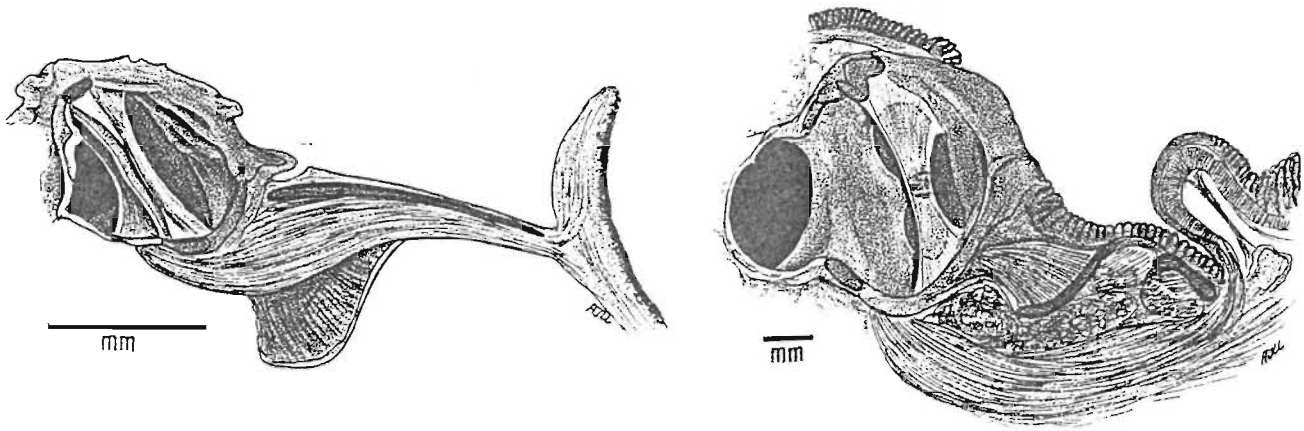


FIG. 3; Distortion of organs. (a) *Microbatrachella capensis*, Tongue protruded. (b) *Hemisus guttatus*, Posterior part of tongue flattened, but larynx unaltered.

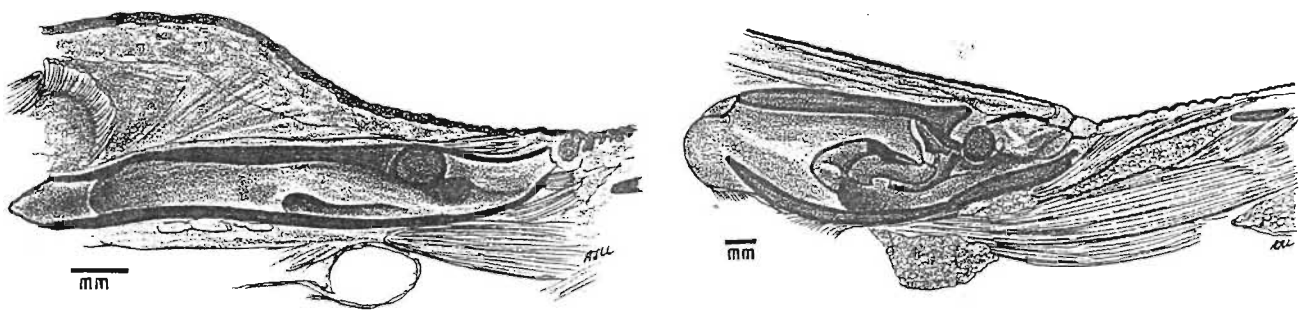


FIG. 4; Extreme laryngeal contraction in *Xenopus laevis laevis*. (a) Larynx relaxed. (b) Larynx contracted.

2.1.3 Patterns of variation

Several important points concerning intra- and interspecific variation in general that are clearly demonstrable may conveniently be summarised here (Text-figs. 2 - 10).

2.1.3a Preparation artefacts

Three principal types of artefacts were discerned in this study.

The degree of contraction or relaxation of the m. hyoglossus had a marked effect on the shape and apparent length of the muscle, the distance between the tongue, and on the sectional profile of the hyoid plate (Text-figs. 2 & 3). However, comparison between specimens in which the m. hyoglossus was contracted and relaxed showed that there was no discernible effect on laryngeal shape. This type of artefact was considered not to be significant in the examination of laryngeal morphology *per se*, though it would be crucial in any use of the hyoid plate as a diagnostic character.

Distortion of organs by compression or extension was found in several specimens. The tongue would sometimes be protruded or, if the mouth was held open with a wad of cotton wool during fixation, be somewhat flattened (Text-figs 3a, b). The larynx was usually not affected, as was demonstrated by comparison with undistorted specimens. Some specimens were found in which the stomach had been prolapsed anteriorly by the forcible injection of large volumes of fixative into the body cavity. In these cases the larynx was usually somewhat distorted and such specimens were not used in this study. In some species the heart lies close against the posteroventral surface of the posterior chamber. This appears not to be a preservation artefact, since little difference could be discerned in specimens injected with varying amounts of fixative.

Alteration of laryngeal morphology by contraction of extrinsic muscles was avoided by using specimens known to be killed in a relaxed condition as far as possible. That such distortion is both possible and significant is shown by the comparison of relaxed and contracted *Xenopus* larynxes (Text-fig. 4a, b). Such distortions are readily recognised when preparations from animals killed in a relaxed state are available for comparison.

TEXT-FIGS. 5 - 7: SEXUAL DIMORPHISM IN LARYNXES

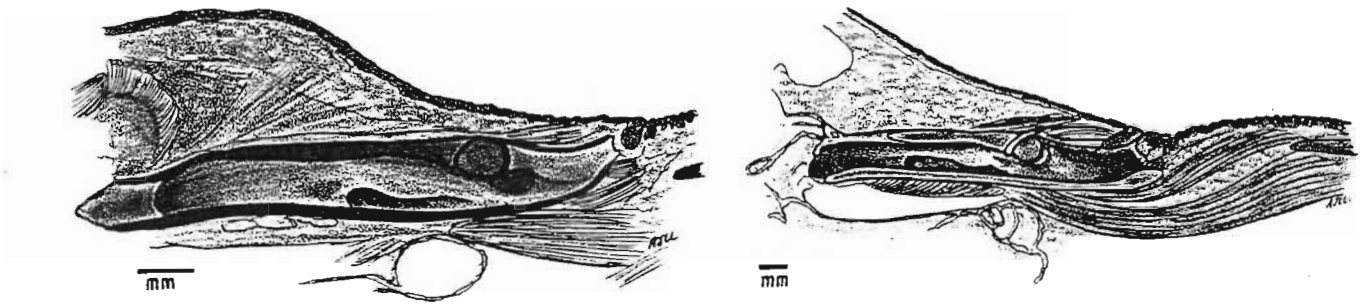


FIG. 5: Slight sexual dimorphism, *Xenopus laevis laevis*, (a) Male, (b) Female.

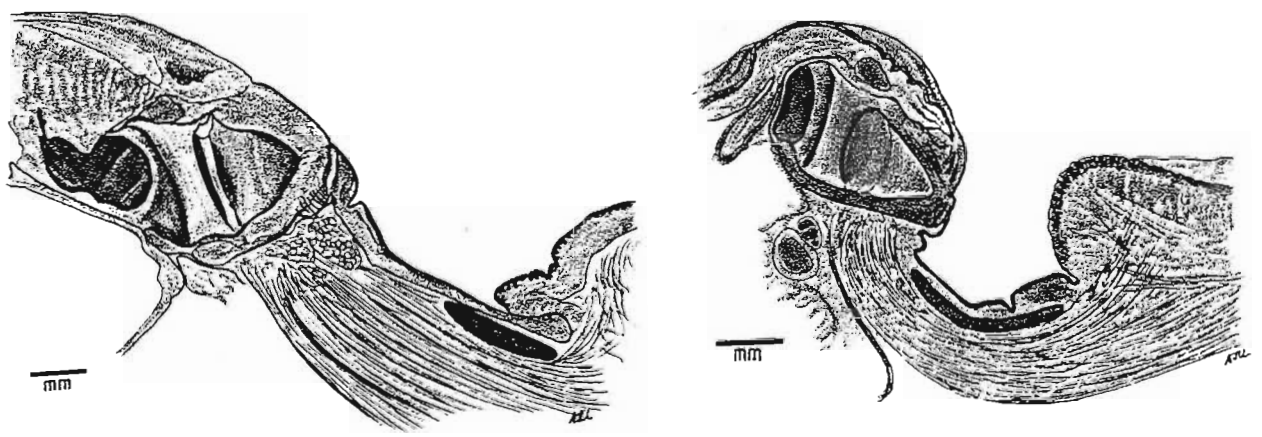


FIG. 6: Moderate sexual dimorphism, *Heleophryne natalensis*, (a) Male, (b) Female.

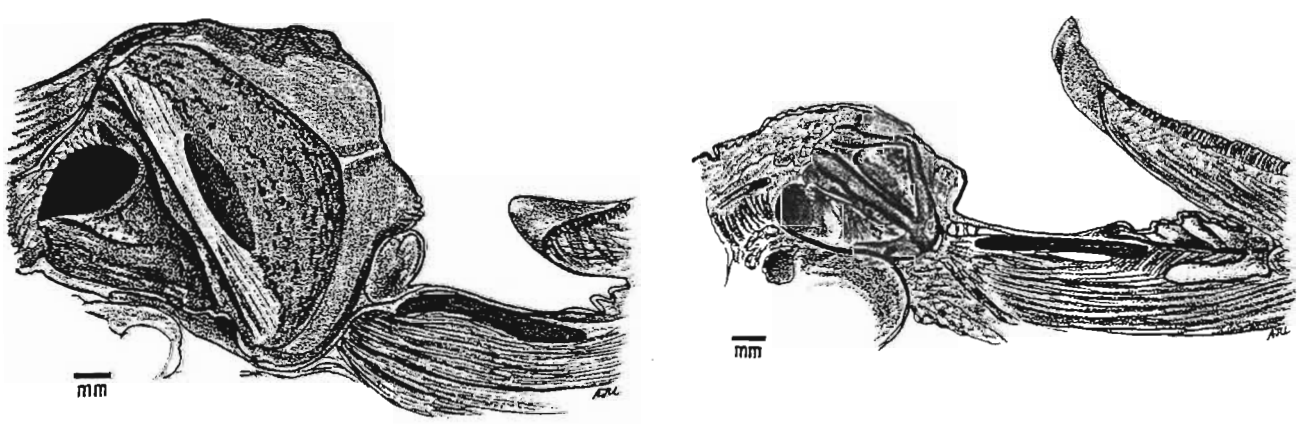


FIG. 7: Marked sexual dimorphism, *Rana fuscigula*, (a) Male, (b) Female.

2.1.3b Intraspecific variation

Sexual dimorphism in internal laryngeal structure is distinct in most of the taxa examined. Only in *Xenopus* (Text-fig. 5a, b) does the female larynx closely resemble that of the male. In most other genera the female larynx is smaller and structurally simpler than that of the male. The differences may be moderate, as in *Heleophryne* (Text-fig. 6a, b), or pronounced, as in *Rana* (Text-fig. 7a, b).

Apart from sexual dimorphism, intraspecific variation is very slight. There appear to be no appreciable differences in larynxes taken from breeding and non-breeding adults, or from subadults of either sex (see Appendix I, p. 348). In some species juveniles have larynxes almost identical to those of adults, but in others there appears to be some measure of allometric variation. This latter aspect was not investigated in detail, as being extraneous to the principal aims of this study.

2.1.3c Interspecific variation

There are distinct and consistent differences in laryngeal morphology at the species/subspecies and genus levels. These are illustrated in male larynxes both here and in the species accounts (Chapter 4).

Differences between species may be relatively slight as, for example, in *Pyxicephalus* (Text-fig. 8a, b); or more pronounced, as in *Breviceps* (Text-fig. 9a, b) and in *Cacosternum* (Text-fig. 10a, b).

These illustrations also serve to demonstrate the nature of intergeneric variation. There is insufficient material to comment on patterns at the family level, but they assuredly exist, as examination of Pipid, Leptodactylid and Bufonid and Hyperoliid larynxes will show.

2.1.3d Usefulness of laryngeal characters

The internal laryngeal characters examined appear to possess sufficient intraspecific stability and sufficient interpsecific differences to make them worthwhile using to test existing classifications.

TEXT-FIGS. 8 - 10: INTERSPECIFIC VARIATION IN MALE LARYNXES

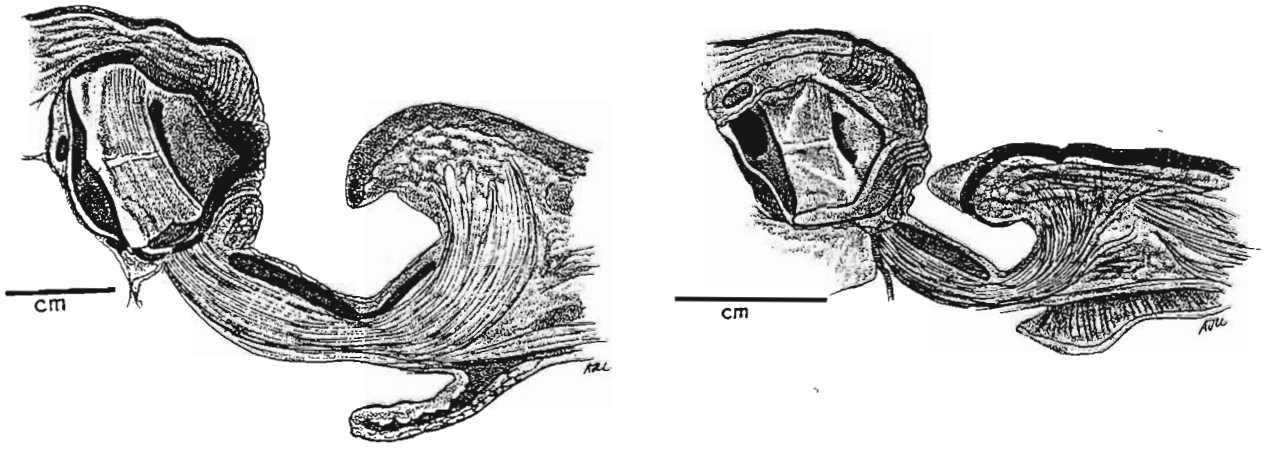


FIG. 8: (a) *Pyxicephalus adspersus adspersus*. (b) *Pyxicephalus adspersus edulis*.

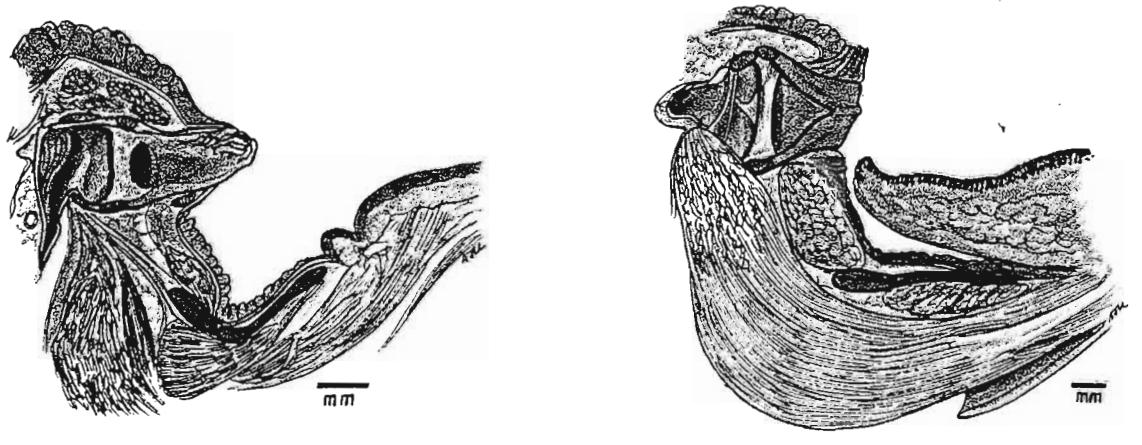


FIG. 9: (a) *Breviceps maculatus*. (b) *Breviceps mossambicus*.

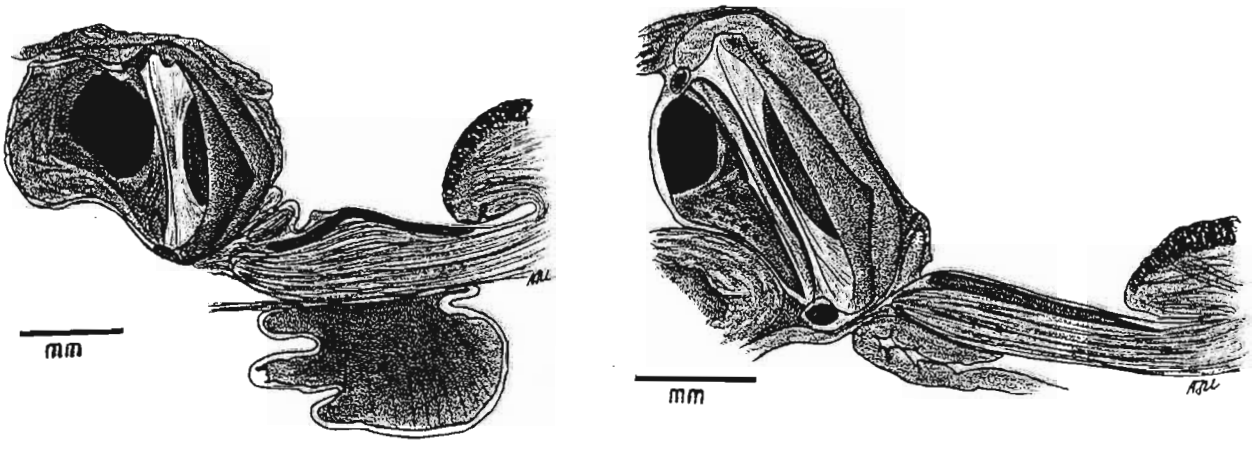


FIG. 10: (a) *Cacosternum parvum*. (b) *Cacosternum nanum*

A brief account of the characters utilised, and of interspecific variation, is presented before the species account for each genus treated in this investigation. Such accounts should not be considered definitive, since in many instances genera are incompletely represented and series are generally short.

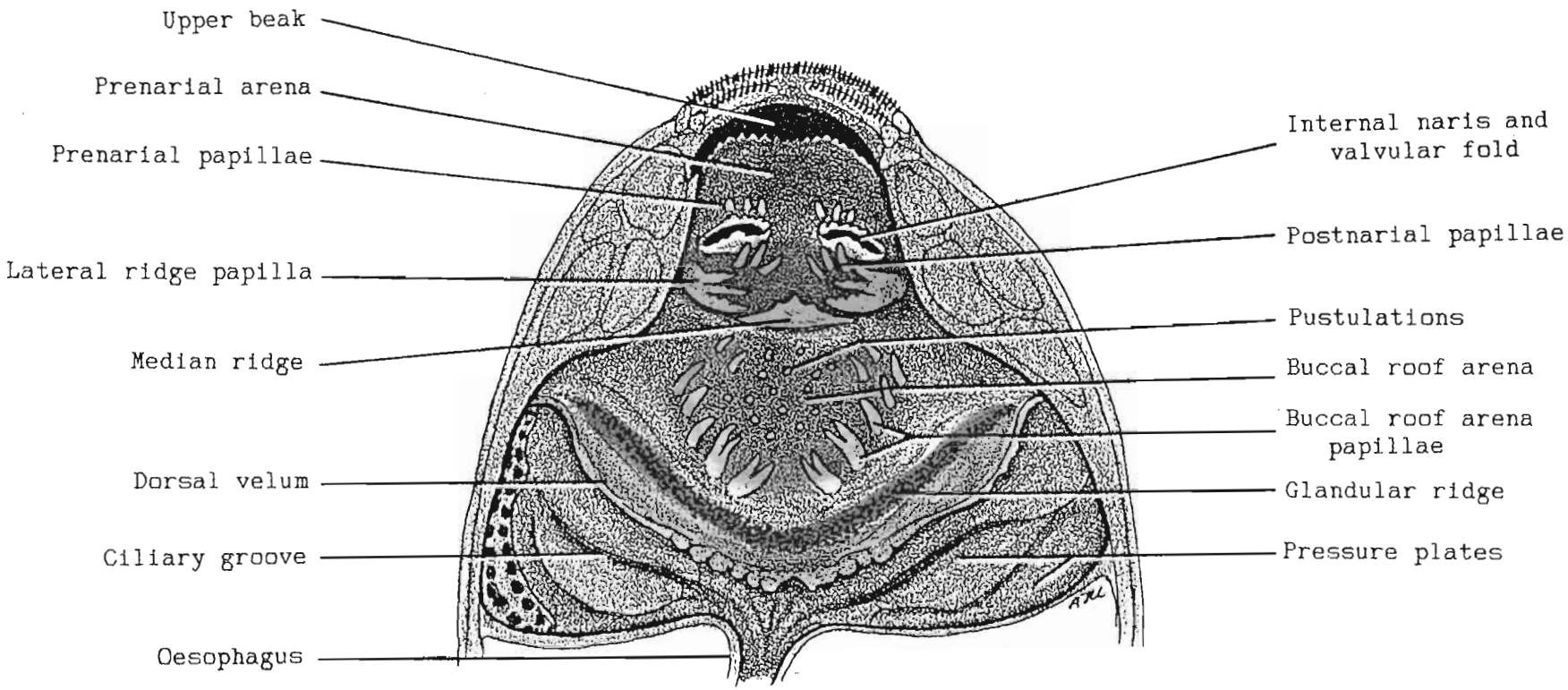
2.2 Advertisement calls

Where possible, I have described the advertisement call verbally so that laryngeal morphology may be approximately associated in the reader's mind with the kind of sound uttered by the frogs. I have not included sonagrams in the accounts since this somewhat secondary aspect of the study is concerned more with generalities than with rigorous correlation.

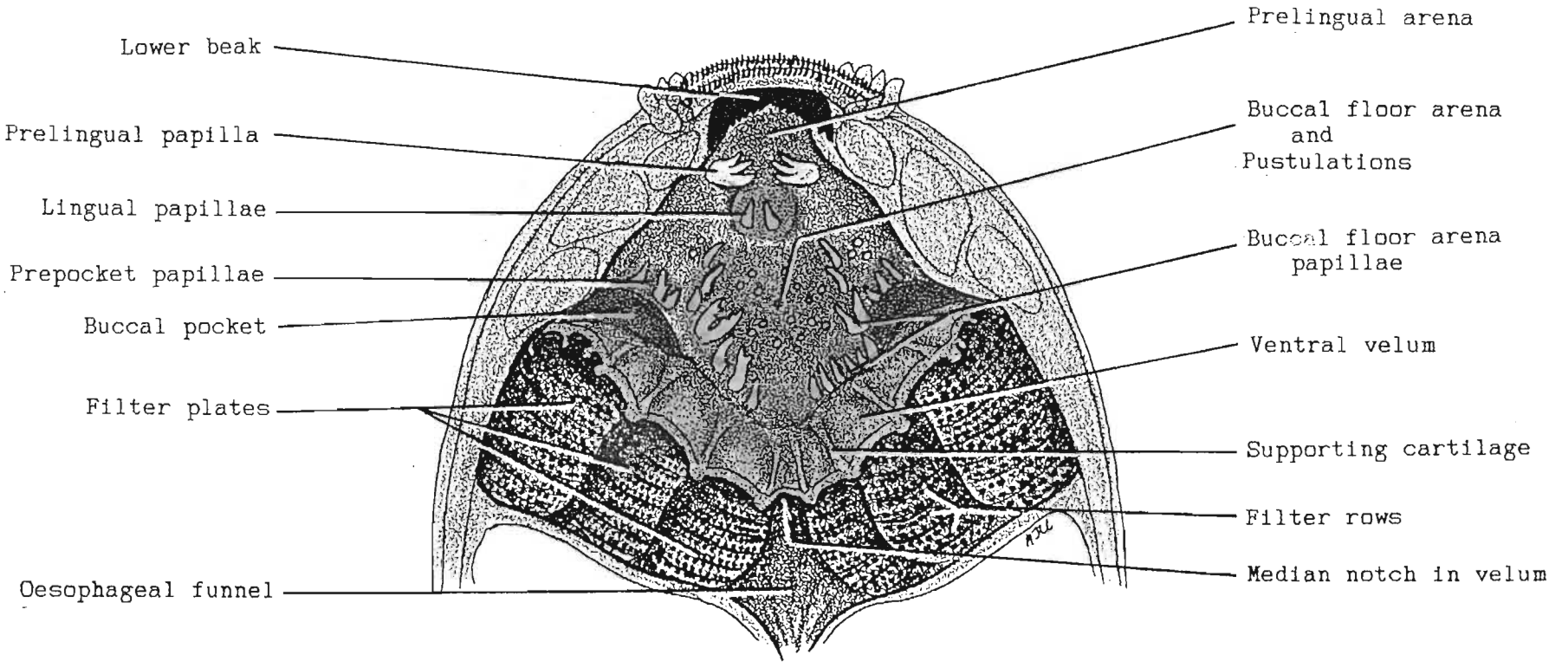
2.3 The larval buccopharynx

2.3.1 Historical review

Although the taxonomic value of anuran larval characters was recognised by Lataste as early as 1876, little attention was subsequently paid to them. Noble (1927a, 1927b) urged the importance of larval characters (principally external ones) as well as of life history data in evolutionary studies but his contributions in this field were also largely ignored. Orton (1953, 1957) and Starrett (1973) made use of larval internal anatomy for systematic and phylogenetic studies, without considering the structure of the buccopharynx in detail. Wassersug (1976, 1980) seems to have been the first to have carefully studied buccopharyngeal morphology with special attention not only to systematic considerations but also to functional, evolutionary and ecological aspects, and can fairly be regarded as having pioneered a major advance in anuran systematics. The value of larval buccopharyngeal morphology in amphibian taxonomy was further emphasised by Inger (1985) in his descriptions of tadpoles from Borneo. The treatment of larval morphology in the present study is considerably indebted to the work of these two authors.



TEXT-FIG. 11: BUCCOPHARYNGEAL ROOF OF AN ORTON TYPE 4 TADPOLE (GENERALISED, COMPOSITE, DIAGRAMMATIC).



TEXT-FIG. 12: BUCCOPHARYNGEAL FLOOR OF AN ORTON TYPE 4 TADPOLE (GENERALISED, COMPOSITE, DIAGRAMMATIC).

2.3.2 Terminology

Features described or discussed in the text are illustrated in Text-figs. 11 and 12. Terminology follows that of Wassersug (1975) for the most part, but I follow Inger (1985) in using the terms **prenarial** and **prelingual** instead of **infralabial**, and have introduced an additional term:

Lingual area: The tongue anlage and the lateral prominences on either side, when present.

2.3.3 Patterns of variation

Only short series have been examined in the majority of cases and the extent and nature of intraspecific and interspecific variation must be considered as yet imperfectly known.

2.3.3a Preparation artefacts

There seemed to be no appreciable differences in the appearance of the buccopharynx in tadpoles anaesthetised with Benzocaine before fixation, and those preserved directly.

Many museum specimens collected by earlier workers were packed in glass tubes closed with a wad of cotton wool. They were usually badly compressed and distorted, and most were quite unsuitable for dissection and examination. Several species whose tadpoles are known could not be described in the present study for this reason, as indicated in the text.

Tadpoles fixed and preserved in formalin were easy to dissect and never showed evidence of distortion caused by this reagent. Tissues of formalin specimens were found to be more robust and less susceptible to compression artefacts than those processed in alcohol. These specimens also gave better results with silver impregnation and thionine stains than many alcohol preparations.

Tadpoles "fixed" and preserved in alcohol were very variable in quality. Well-prepared specimens were comparable to formalin-fixed specimens but many others showed shrinkage, distortion of delicate structures such as

papillae, and softening of the tissues that made neat, precise dissection very difficult. Alcohol tadpoles were, in general, much more damaged by compression during storage than formalin specimens.

2.3.3b Intraspecific variation

The material examined showed remarkable constancy between Gosner stages 32/33 to 39/40 regarding overall morphology.

Intraspecific variation was noted principally in the number of papillae bordering the buccal roof and buccal floor arenas. The total range of variation tends to be least in buccal roof and floor arenas bounded by few papillae, and most where the number of papillae is very large. In general, the difference in number of papillae on the left and right sides of the arenas is but slightly less than the total range of variation shown in the series examined.

Variation in papilla morphology appears to be slight. Where buccal arena papillae are numerous, the numbers of simple and bifurcate papillae appear to be somewhat more variable than when they are fewer in number.

Similarly, pustulations appear to be less variable in number and disposition when they are few than when they are very numerous.

Buccal pockets seem to be rather variable with regard to definition and to the number and disposition of prepocket papillae, but nevertheless show sufficient constancy to be of some diagnostic value. They may be hidden by the lateral walls of the buccal cavity if the line of dissection is not well placed, and small pockets and papillae may appear to be absent when they are actually present.

The tongue anlage and lingual papillae seem to be more dependent on the developmental stage examined than other structures and should probably only be given their full taxonomic weight if characterised between about Gosner stages 35 - 39.

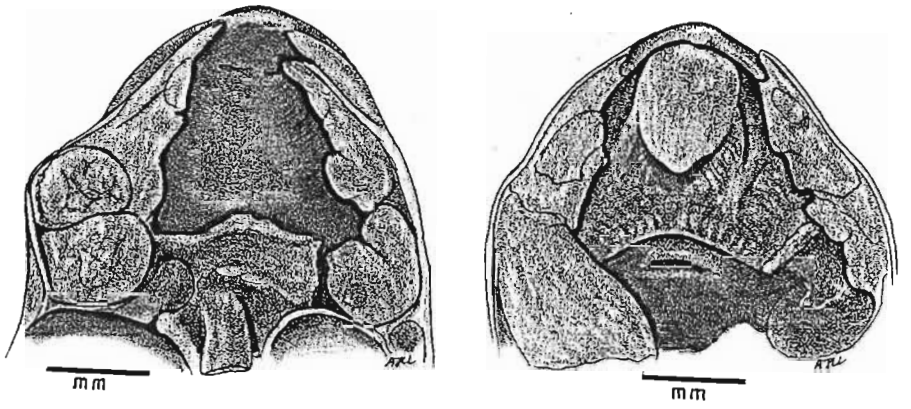


FIG. 13: *Breviceps pentheri*.

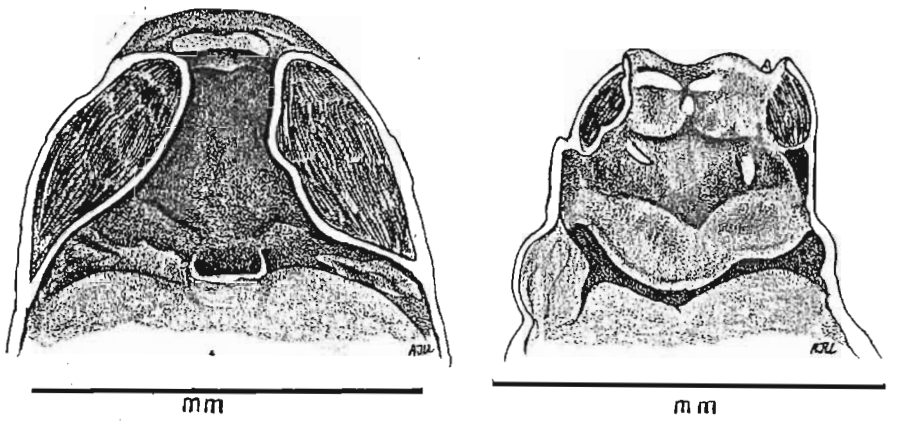


FIG. 14: *Arthroleptella lightfooti*.

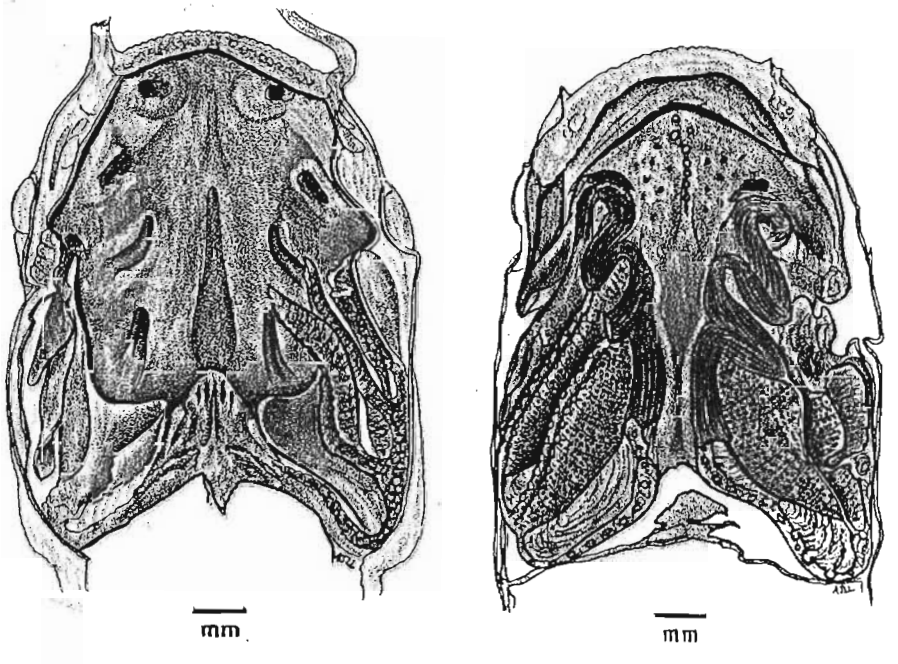


FIG. 15: *Xenopus laevis laevis*.

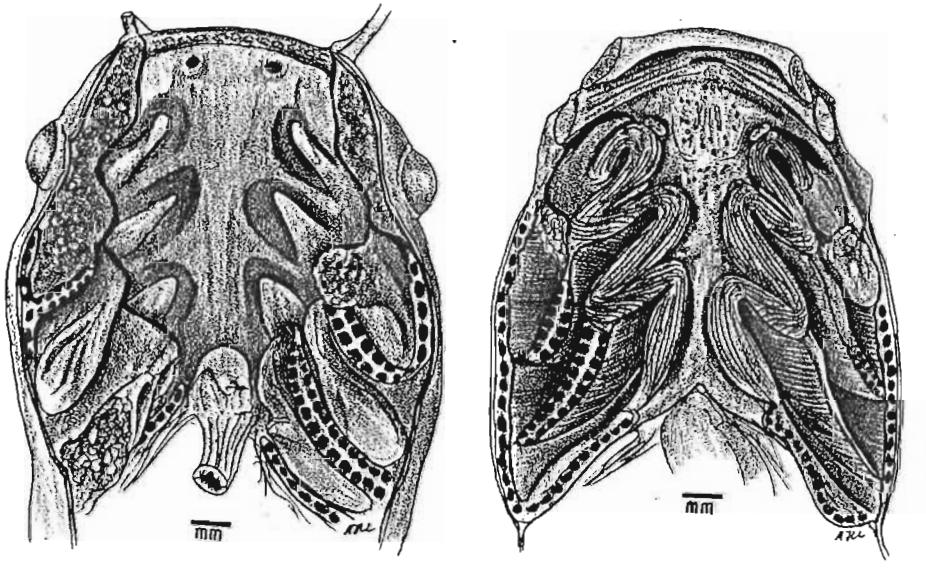


FIG. 16: *Xenopus muelleri*.

The filter plates and, especially, the pressure pads are particularly susceptible to damage during dissection, and variation in these structures is not easily assessed. I have therefore accorded less attention to them than to other structures in this investigation.

2.3.3b Interspecific variation

There are distinct and consistent differences in buccopharyngeal morphology at the species/subspecies and genus levels, as illustrated in the accompanying text-figures and in the species accounts (Chapter 4). Differences at family level are also obvious, as may be seen by consulting the plates, but are not treated in this study.

Direct development larvae probably show the least degree of interspecific variation. Although insufficient material has been examined to be certain, the almost total lack of buccopharyngeal structures in *Breviceps pentheri* tadpoles (Text-fig. 13) suggests that the same condition is true of other members of the genus. In *Arthroleptella lightfooti* (Text-fig. 14), however, a few simple papillae are present on the buccal floor and there is a ventral velum, suggesting that in this genus there may prove to be some interspecific variation.

Nektonic tadpoles (*Xenopus*, *Phrynomerus*) have rather simple buccopharynxes and in *Xenopus*, at least, interspecific differences are relatively slight (Text-figs. 15, 16).

Most other taxa examined show a greater measure of interspecific variation, as exemplified in *Bufo* (Text-fig . 17, 18) and *Rana* (Text-figs. 19, 20).

2.3.3d Usefulness of buccopharyngeal characters

The usefulness of larval buccopharyngeal characters demonstrated by Wassersug (1980) and by Inger (1985) is confirmed in the present study.

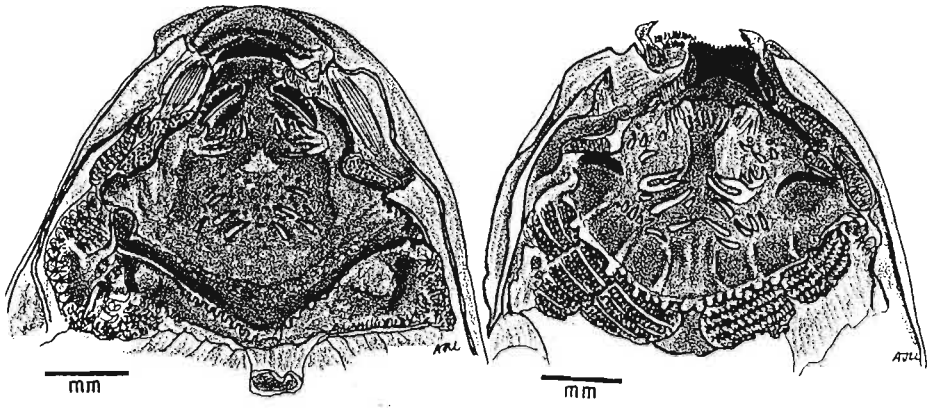


FIG. 17: *Bufo gutturalis*.

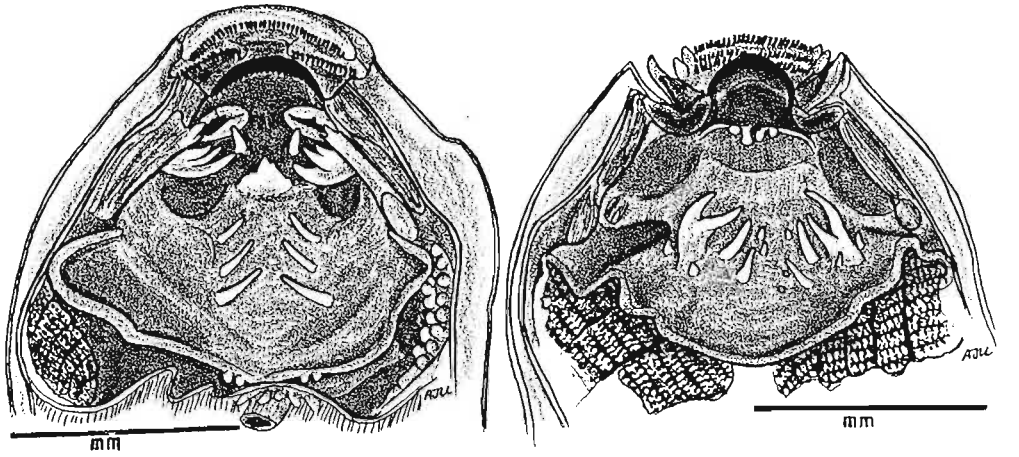


FIG. 18: *Bufo fenoulheti fenoulheti*.

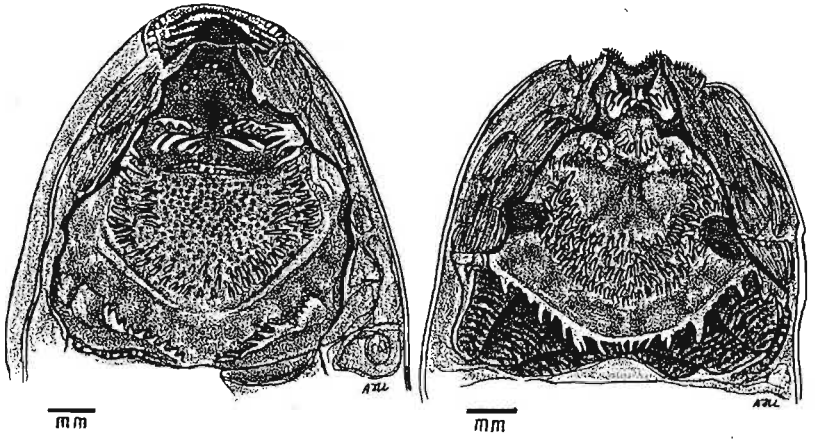


FIG. 19: *Rana angolensis*.

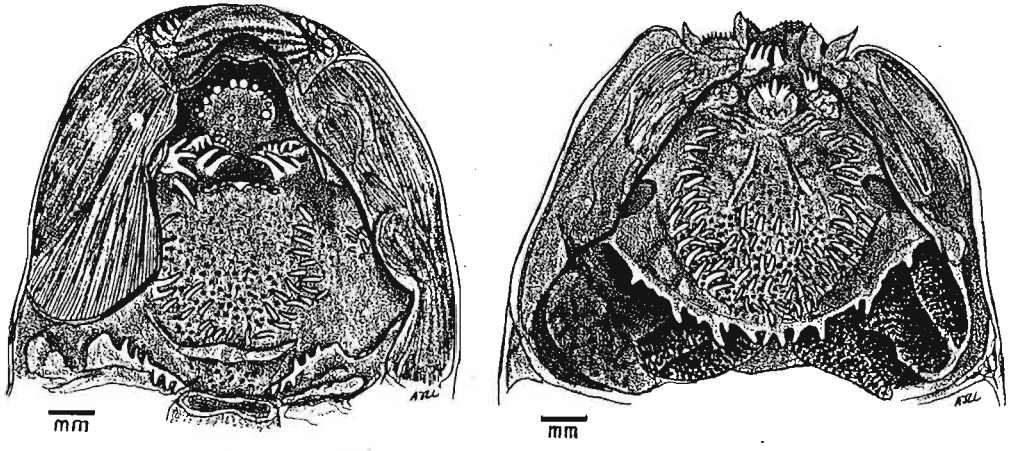


FIG. 20: *Rana dracomontana*.

TEXT-FIGS. 17 - 20: INTERSPECIFIC VARIATION IN LARVAL BUCCOPHARYNXES.
(Roof on left, floor on right)

2.4 Published illustrations

The external morphology of adults discussed in this study is illustrated in Poynton (1964), Passmore & Carruthers (1979) and Lambiris (1988, 1989b).

Many of the larvae discussed are illustrated (left lateral view of the entire animal, and external mouthparts in ventral view) in Lambiris (1988, 1989b).

Sonagrams of advertisement calls of most of the taxa discussed are figured in Passmore & Carruthers (1989).

2.5 Character matrices

Where three or more taxa are treated, I have summarised adult laryngeal and larval buccopharyngeal characters in a matrix of the kind devised by Peters & Donoso-Barros (1970). Not only is this format amenable to computer analysis, as remarked by Peters & Donoso-Barros, but also permits subsequent emendations to taxa listed and characters used, much more easily than is the case with the more usual dichotomous keys. The use of such a flexible format has indeed been a great help in determining and listing salient characters in the present study.

CHAPTER 3

MATERIALS AND METHODS

3.1 Sources and use of material

Most of the specimens dissected and examined in this study are from the author's collection (AJL), supplemented by additional material from the British Museum (Natural History) (BMNH), the McGregor Museum (MMK), the Natal Museum (NM), the private collection of Mr. L.R.G. Raw, Pietermaritzburg (LR) and the South African Museum (SAM). Certain details pertaining to advertisement calls were taken from Passmore & Carruthers, as indicated in the text; all other descriptions of calls and call sites, and of larval habitats and feeding behaviour, are drawn from personal field observations (mostly unpublished, but partially summarised in Lambiris 1989a, 1989b) from 1960-1991.

Although taxonomic studies based on external morphological characters should be based on the longest possible series of material available, in the present case there are serious difficulties with such a requirement.

Catalogued museum specimens are preserved in trust for the use of posterity but no matter how carefully done, dissection always results in a lesser or greater degree of irreparable destruction of the specimen. This imposes a great responsibility not only on the researcher, but also on the collection manager, who has a duty to make the material entrusted to his care available for legitimate research and who must always be mindful of the needs of others yet to come. Although carefully prepared and curated dissections may still form a valuable part of a research collection, there is a real and justifiable reluctance on the part of most curators to allow long series of specimens to be dissected -- in the final analysis, catalogued specimens are a non-renewable resource and the needs of one worker must always be balanced against the peremptory demands of the scientific community as a whole.

Entomologists frequently dissect out the genitalia of specimens in their collections, to prepare them for light or scanning electron microscopy and

the curators of such collections seem to have no problems with such procedures. Herpetologists should at least be prepared to consider whether such an approach might not be justified, at least to a limited extent, in their own discipline.

I have dissected a relatively large proportion of the series of several taxa represented in my collection with a view to assessing the degree of intraspecific morphological variation occurring therein, but in view of the considerations outlined above, samples for the majority of taxa discussed in this study have been kept to very short series, whether drawn from my own or from other collections. The present investigation being an exploratory study, the principal aim has been to show that there exist characters worthy of further attention, and which can be tested by the examination of longer series subsequently.

3.2 Selection of material

3.2.1 Adult hyolarynxes

Hyolarynxes were excised from adult or subadult males and females. For assessing sexual and non-sexual variation, two larynxes (one each from an adult male and from an adult female) were accurately drawn, and other dissections compared with the drawings. Examination of bufonid larynxes showed no apparent differences between breeding and non-breeding specimens of either sex (see Appendix I) and no attempt was made to select only adults in breeding condition for the study as a whole. The findings are discussed in Chapter 2 (2.1.3). For the principal purpose of this study the emphasis is on the male larynx as the more important element of a Specific Mate Recognition System, and the larynxes of females have only been illustrated for selected taxa to indicate the general nature of sexual dimorphism.

When specimens could not reliably be sexed by the presence or absence of sexually dimorphic characters (e.g. presence or absence of nuptial pads or spines, external vocal sacs, gular discs, etc), a small incision was made in the flank and the viscera examined with an endoscope (a modified Gowlands auriscope) to determine whether testes or ovaries were present. Such a

procedure does not significantly damage the specimen. Minute specimens could sometimes be sexed by internal transillumination (a further modification of the auriscope) via the oesophagus or rectum.

Where possible, specimens were selected that were well fixed and preserved, with no observable dehydration or hydration, and which were not physically distorted or damaged. Frogs that had been fixed in a position as closely approximating the natural sitting posture as could be found, were preferred.

3.2.2 Larval buccopharynxes

Tadpoles were taken principally from the author's collection. This material usually has fairly detailed habitat and microhabitat notes, made at the time of collection; and tadpoles are routinely sorted into developmental stages (Gosner, 1960) before cataloguing, which greatly facilitated selection of suitable specimens. Distortion of material in this collection is reduced as far as possible by avoiding compression at all times during fixation and subsequent storage. A considerable amount of material in museum collections, especially that fixed and stored in alcohol, tends to become macerated or crushed, and was not suitable for this kind of examination.

Tadpoles selected for dissection were at (or as close to as possible to) Gosner's stage 38. The range of variation permitted was usually from stages 35 to 40; in rare instances, earlier developmental stages were used if nothing else was available.

Identification of tadpoles was based as far as possible on preserved series of developmental stages including transformates possessing characters in common with, and diagnostic of, adults. Where such series were not available identification was based on the keys of Van Dijk (1966) or Lambiris (1989); from small samples of tadpoles where some specimens were raised to identifiable froglets without intermediate developmental stages being preserved; or, in a few instances, by exclusion where tadpoles were taken from localities where other members of the genus are known not to occur (for example, *Phrynomerus b. bifasciatus*), or where tadpoles of all the other

members of a genus have been identified and only one remains to be definitively diagnosed, as in the case of tadpoles of what are probably *Bufo f. fenoulheti* from Zululand. In each case the basis of identification is clearly indicated in the text.

3.3 Preliminary preparation of material

The processing of herpetological material in many museum collections is not always consistently documented. However, most of the MMK, NM and SAM material examined is known to have been fixed and preserved in 70% ethanol, although the quality of the specimens tends to be rather variable.

All specimens in the author's collection are routinely killed with an intraperitoneal injection of pentobarbitone sodium or, if very small, by immersion in a dilute solution of benzocaine hydrochloride. Both give excellent muscular relaxation. Specimens are fixed in unbuffered 10% formalin for a period appropriate to their size, and stored in neutral 10% formalin or in neutral isotonic formal-saline. Specimens from the author's collection which were dissected for this study had been preserved for periods ranging from one month to 27 years, and none showed observable distortion arising from killing or fixation. The effects of alcohol fixation/preservation as applied in many museums, especially on poorly curated material, has still to be assessed in detail, but in many instances I have found specimens "fixed" and stored in alcohol to be far inferior to formalin specimens (Lambiris 1990). In the present study this proved particularly true for material that I tried to stain with thionine, and, as noted above, anatomical detail was often inadequately preserved in many larvae.

3.4 Adult hyolaryngeal preparations

3.4.1 Dissection

The entire floor of the mouth, the distal portion of the buccopharynx and the proximal portion of the oesophagus, the heart and the lungs (or at least the roots of the lungs) are excised in one piece for examination as follows (Text-figs. 21 - 27):

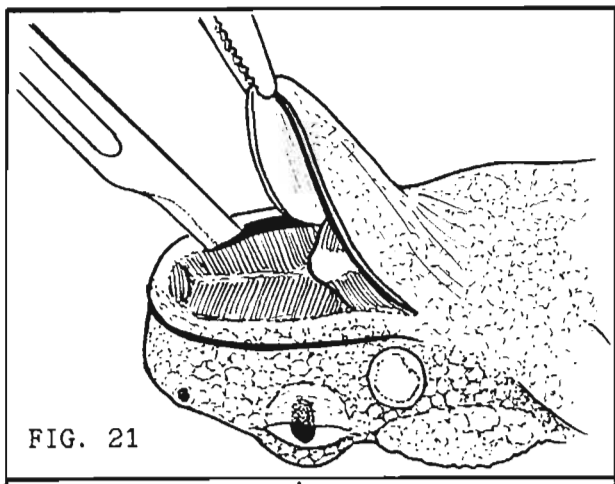


FIG. 21

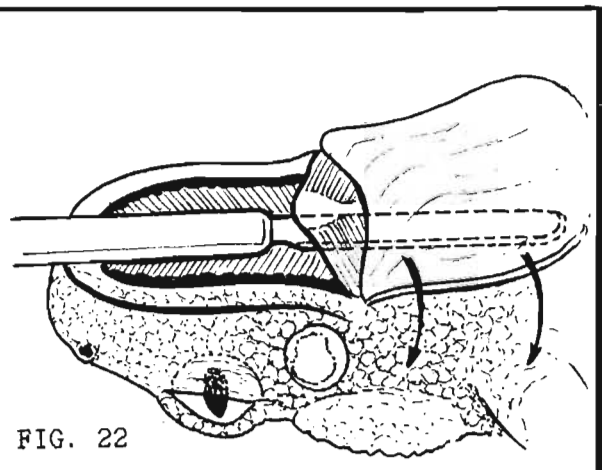


FIG. 22

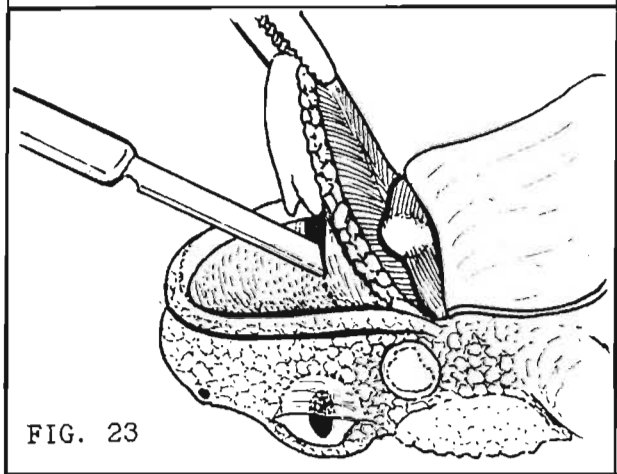


FIG. 23

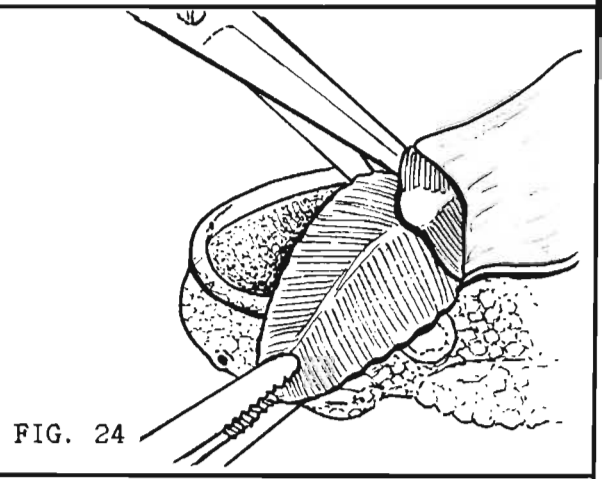


FIG. 24

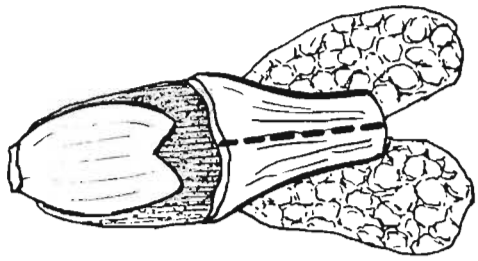


FIG. 25

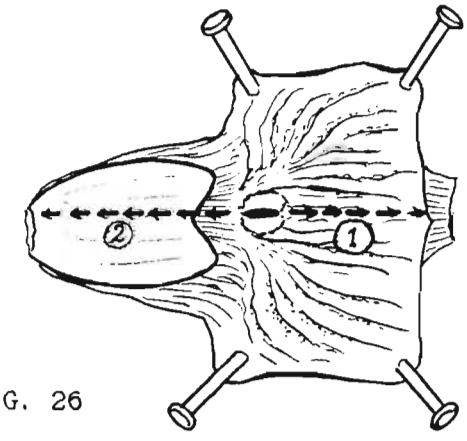


FIG. 26

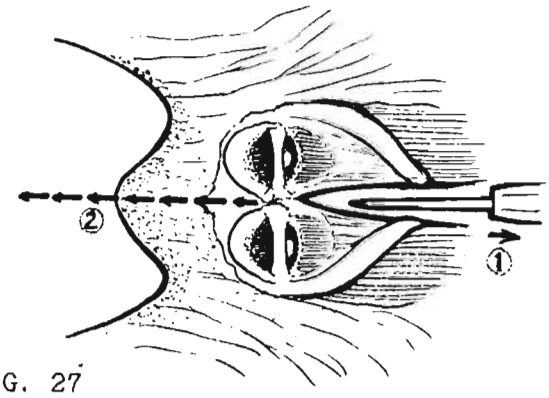


FIG. 27

TEXT-FIGS. 21 - 27: STAGES IN THE DISSECTION OF THE ADULT HYOLARYNX

Explanation in the text.

1. Incise the skin of the lower jaw, close to the medial borders of the mandibles, extending the incision on each side to the chest. (Where markings on the lower jaw are of diagnostic importance, e.g. dwarf *Phrynobatrachus*, care should be taken to preserve these.) Reflect the U-shaped flap thus produced backwards over the chest, freeing it from the vocal sac and connective tissue over the pectoral girdle with a few light strokes of the scalpel blade (Fig. 21). Where a gular disc or similar structure is present in males (e.g. as in *Hyperolius*), this must be preserved with the skin flap and in such cases it is easier to invert the skin flap so that the bottom of the "U" traverses the pectoral region. However, such a flap has a weaker point of attachment and should only be used where necessary.

2. Incise the muscles of the floor of the mouth , again keeping as close to the medial margins of the mandibles as possible (Fig. 21). It is easier to work from the m. interhyoideus to the m. submentalis than in the other direction.

3. Carefully free the muscles and connective tissues attached to the internal surfaces of the ventral portion of the pectoral girdle, then carefully work the blade laterally on each side in turn, to about the level of the glenoid fossa (Fig. 22). It is essential that the tissues be freed completely all round, and as far back as the distal end of the xiphisternum. When the episternum is known to extend forward under the m. intermandibularis, this muscle should first be divided medially and the episternum freed before undertaking this manoeuvre. A long-bladed knife, e.g. a cataract knife, is ideal for this procedure.

4. Grasping the root of the tongue with forceps, lift the whole floor of the mouth upwards to expose the roof of the buccal cavity. Cut through all the tissues forming the roof of the buccal cavity, from the severed mandibular muscles on one side of the head, to the other, immediately behind the eustachian tubes (Fig. 26).

5. Carefully free the roof of the posterior portion of the buccal cavity thus severed, and the oesophagus, from the surrounding tissues as far backwards as in step 3.

6. Gently pull the freed floor of the mouth and the attached posterior buccopharynx, oesophagus, heart and lungs forward and to one side. A pair of fine scissors is insinuated behind the lungs and heart to sever the oesophagus, and the whole mass can be removed from the frog in one piece (Fig. 24).

7. Cut through the short portion of the roof of the mouth and the proximal portion of the oesophagus in the middle line, using fine scissors (Fig. 25), and pin down the flaps thus formed, under slight tension. This exposes the larynx clearly (Fig. 26).

8. Cut through the dorsum of the larynx, exactly in the middle line, with a scalpel. If the flaps referred to in step 7 have been pinned down with sufficient tension, the larynx is pulled slightly apart and one has a clear view into it (Fig. 27). It is then possible to cut through the floor of the larynx, again exactly in the mid-line, with no chance of inadvertently injuring any part of one side or the other. If the specimen is very small, it is helpful to stain it lightly with iodine and to divide it under the dissecting microscope, or at least with the aid of a jeweller's loupe.

9. When the larynx and the structures posterior to it have been divided, the floor of the mouth anterior to the larynx, and the tongue, are also divided medially.

3.4.2 Staining methods

The half-hyolarynx was stained for 5 - 10 minutes in dilute (about 0.1%) aqueous thionine, acidified with a few drops of dilute hydrochloric acid, then rinsed in tap water. In a few instances longer staining (up to 20 minutes) was required.

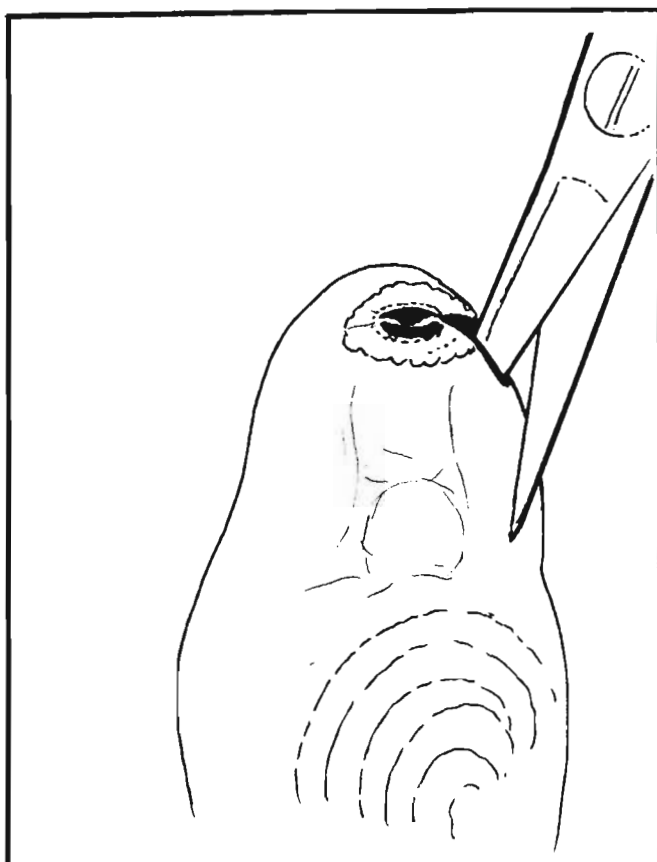


FIG. 28

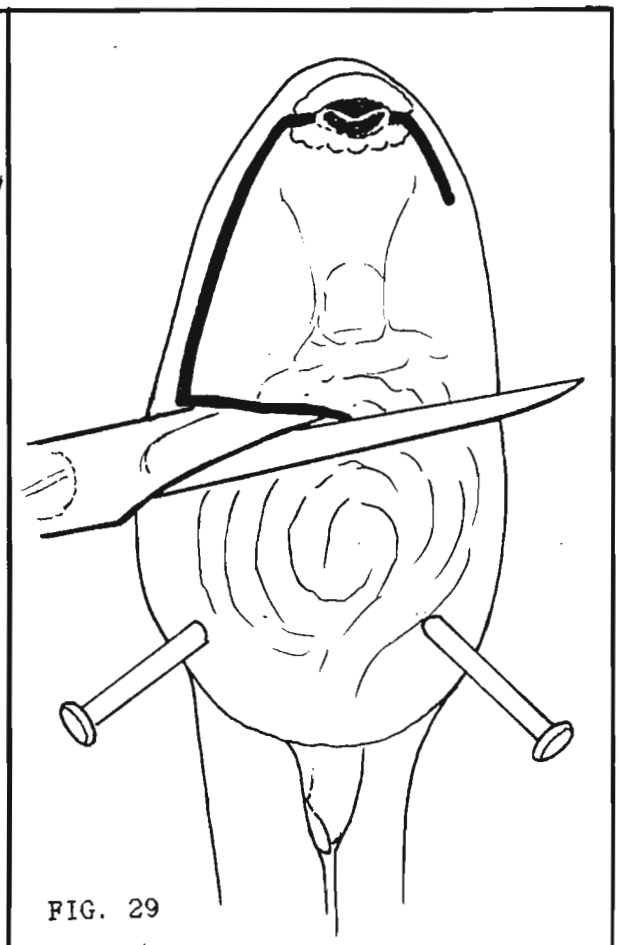


FIG. 29

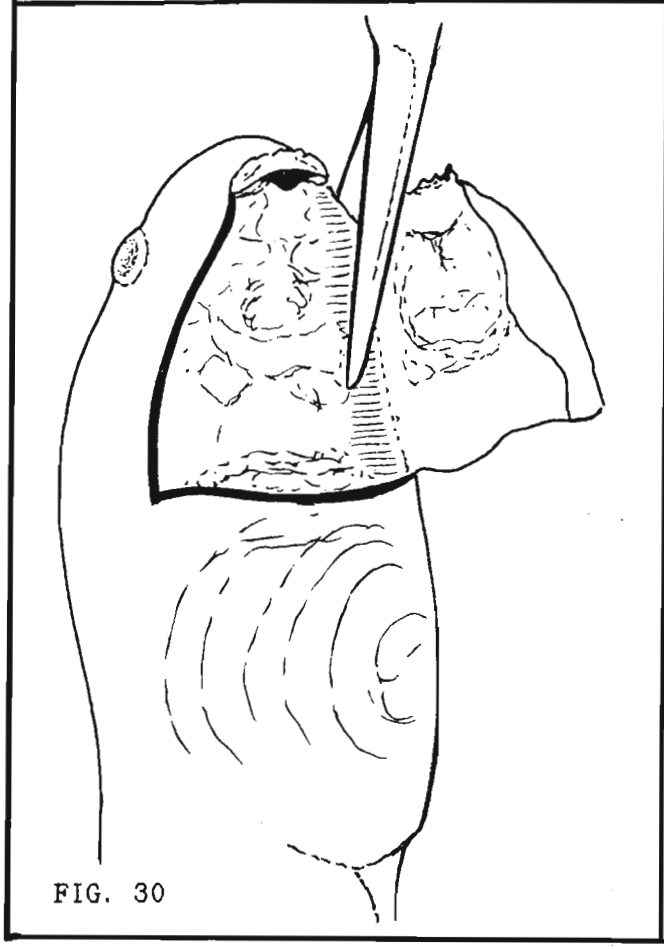


FIG. 30

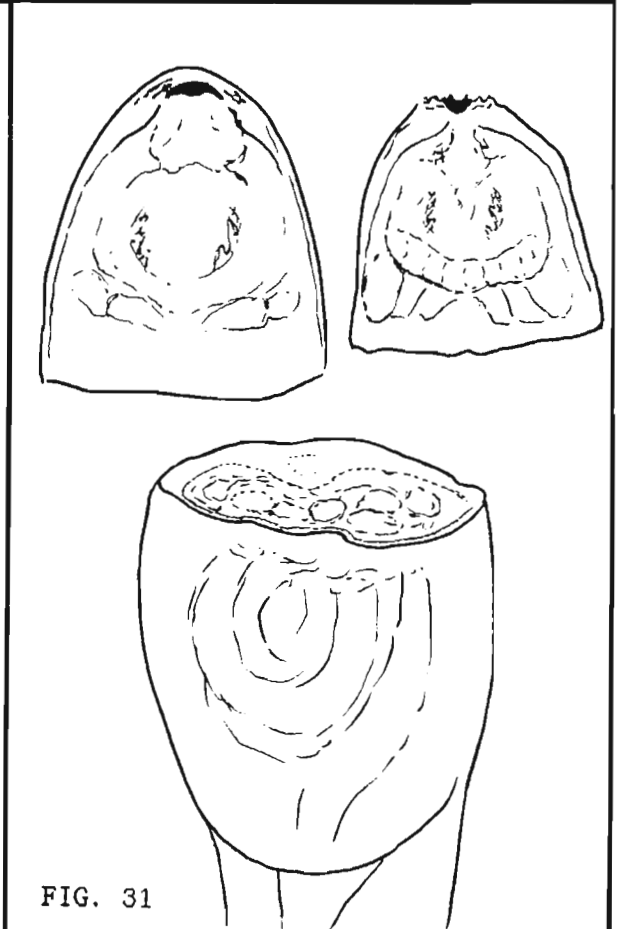


FIG. 31

TEXT-FIGS. 28 - 31: STAGES IN THE DISSECTION OF THE LARVAL BUCCOPHARYNX

Explanation in the text.

3.5 Larval buccopharyngeal preparations

3.5.1 Dissection

Separate buccopharyngal roof and floor preparations are made as follows (Text-figs. 28 - 31):

1. Pin down the tadpole, ventral side uppermost, in the dissecting bowl. The pins should transfix the body on either side of the midline, at a point about two-thirds of the way down between the spiracle and the base of the caudal muscles. Care should be taken not to damage the distal portion of the trunk or the tail, which bear important structures and should subsequently be preserved with the dissected moieties.

2. Cut through the oral angle for a short distance beyond the oral disc on one side (Fig. 28).

3. Cut through the oral angle on the contralateral side and extend the incision along the flank to a point just before the pins holding the tadpole down (Fig. 29). The entire thickness of the body wall should be divided in one manoeuvre, without damaging the contents of the buccopharynx. The line of the incision should pass dorsad to the muscles associated with Meckel's cartilage and the branchial arches, and along the middle of the flank.

4. Cut transversely across the ventrum of the trunk, dividing not only the body wall but also the viscera in the line of the cut (Fig. 29).

5. Carefully remove the portions of abdominal viscera anterior to the transverse incision, identifying and severing the oesophagus a little behind the posterior pharyngeal wall.

6. Return to the original short incision through the oral angle on the side not yet longitudinally divided and extend it, as before, to meet the transverse incision (Fig. 30). The dissection is materially helped if gentle traction is applied with fine forceps to the freed ventral portion of trunk.

7. Lift the distal portion of freed ventrum on one side, using forceps, and carefully snip through the wall of posterior wall of the branchial

chamber. Carefully separate the intermeshing dorsal and ventral vela at the same time (Fig. 30). The entire ventral portion is now completely free. (Note: this step is rendered easier if the buccopharynx is first irrigated with iodine solution to render the almost transparent tissues more visible.)

8. Using fine dissecting scissors, cut transversely through the tadpole immediately anterior to the supporting pins, to separate the buccopharyngeal roof preparation from the rest of the trunk (Fig. 31).

NOTE: Where limited material is available, it may be desirable not to prepare buccopharyngeal roof and floor dissections separate from the trunk. In such instances, the following technique is preferred:

Proceed to Step 6, but do not extend the second flank incision as far as the transverse ventral incision. Continue with Step 7 as before, but leave the dissection as it appears in Fig. 30.

After staining and examination the tadpole may be closed to retain its normal external appearance.

The dorsal and ventral moieties of the buccopharyngeal preparation may be further processed immediately, as described below, or stored in a suitably labelled specimen tube together with the remainder of the trunk and tail.

3.5.2 Staining and impregnation methods

3.5.2a Routine stains

Some tadpoles from each series were stained with dilute aqueous solutions of Methyl Violet 2B (C.I. 42535) or of Crystal Violet (C.I. 42555), to demonstrate mucus-secreting tissue. Staining time was usually 2-3 minutes, but longer times were occasionally needed.

3.5.2b Silver impregnation

Routine histological stains, e.g. thionine, crystal violet or methyl violet, are useful in demonstrating mucus-secreting tissue that is not

otherwise easily seen, but do not make surface features sufficiently distinct for detailed examination. A silver impregnation technique was therefore devised that would combine the relative simplicity of routine histological staining procedures with the enhanced surface detail of a scanning electron microscope preparation, but for use with a standard dissecting microscope.

Fixation: Formalin, Bouin, or formal-saline. Alohol-fixed tadpoles give good impregnation results also but tissues tend to be more distorted.

Reagents:

Disodium Ethylene-diamine-tetraacetic acid, 1% aq.
Silver nitrate, 0.01% aq.
Sodium hydroxide, 4% aq.
Ammonia solution, 35% (S.G. about 0.880).
Formalin, 10% aq.
Sodium thiosulphate, 5% aq.

Technique:

1. Rinse dissections in tap water (2-3 minutes).
2. Transfer to EDTA for 3 minutes.
3. Rinse in two changes of distilled water, 1½-2 minutes each.
4. Transfer to silver nitrate for 3 minutes.
5. Rinse briefly (a few seconds) in distilled water.
6. Transfer to sodium hydroxide for 1 minute.
7. Rinse briefly in tap water.
8. Transfer to ammonia for 1 minute.
9. Rinse briefly in tap water.
10. Reduce in formalin (3-5 minutes).
11. Wash in tap water.
12. Fix in sodium thiosulphate (5-10 minutes), and rinse in tap water before storing the impregnated preparation in formalin. (NOTE: This step is optional, and is not necessary unless the impregnation was very light.)

Notes:

1. The intensity of impregnation can be varied by reducing the length of time in silver nitrate. Light impregnation gives a rather translucent result

which permits structures deep to the mucosa to be seen, but which does not render surface topography as clear as might be desirable for illustration or photography. Light impregnation may differentiate, to some extent, some mucus-secreting tissues that would not be distinguished by deep impregnation.

2. The reagents may be used several times over, especially if specimens are rinsed between stages. Sufficient silver may be recovered from used reagents to make recycling worthwhile, but the usual precautions should be taken for handling potentially explosive ammoniacal silver solutions.

3. Dissections are best transferred from one reagent to another in short lengths of glass tubing of suitable diameter with a piece of nylon stocking stretched tightly and tied across one end. Excess reagent may be gently blown out of the transfer tube to avoid excessive loss and cross-contamination of reagents, but a mouth-piece of plastic tubing should be used for safety.

4. Dissections may be mounted on microscope slides (ringed preparations) for permanent storage, with less risk of damage. Glycerol-jelly is a suitable medium, but transfer through graded concentrations must be done gradually if distortion is to be avoided.

3.6 Examination and illustration of specimens

Preparations were examined with a KYC stereo dissecting microscope equipped with a squared eyepiece micrometer, at magnifications of 10x, 20x or 40x.

Because many preparations were too large to be included entirely within the field of view, a Zeiss mechanical stage was modified and fitted to the dissecting microscope, to facilitate precise positioning of the specimen while it was being examined and drawn.

Illumination was provided from two paraxial dissecting lamps with focusable lenses, mounted on universal swivel arms fixed to the foot of the microscope. This arrangement gave excellent lighting, the intensity and angle of which could be varied to suit the exact requirements of each preparation.

Illustrations were made on drawing card ruled with a grid of appropriate dimensions, and were checked on at least two separate occasions for accuracy before final inking and completion.

I have used colours in the plates to facilitate recognition of, and comparison between, the major features described in the text. The use of colour in the illustrations of larval buccopharyngeal roofs and floors has been further employed to emphasise approximate topographical relationships between the two.

298 adult male and female hyolarynxes were examined, representing 90 species and subspecies in 27 genera and 13 families and subfamilies; they are depicted in 123 illustrations.

96 larval buccopharyngeal preparations were examined, representing 53 species and subspecies in 25 genera and 12 families and subfamilies; they are depicted in 106 illustrations of the roof and floor.

3.7 Abbreviations used in the text

Museum acronyms:

AJL : Lambiris Herpetological Collection, Pietermaritzburg, Natal, South Africa.

BMNH : British Museum (Natural History), London, England.

LR : Private collection of Mr. L.R.G. Raw, Pietermaritzburg, Natal, South Africa.

MMK/F: McGregor Museum, Kimberley, South Africa.

NM : Natal Museum, Pietermaritzburg, Natal, South Africa.

SAM : South African Museum, Cape Town, Western Cape, South Africa.

General terminology:

(m) : male

(f) : female

SVL : snout-vent length as defined for adults and larvae in Lambiris 1989a.

CHAPTER 4

SYSTEMATIC ACCOUNT

Family PIPIDAE Gray, 1825

Subfamily XENOPODINAE Fitzinger, 1843

Genus *Xenopus* Wagler, 1827

Xenopus Wagler, 1827, *Isis von Oken*, 20, col. 726. Type species by monotypy: *Xenopus boiei* Wagler = *Bufo laevis* Daudin.

CHARACTERS

ADULT LARYNX (Pl. 1)

The larynx is elongate and cylindrical in both sexes, and differs considerably from the basic pattern of all glossal taxa examined. The arytenoid cartilages are strongly curved around the fleshy lips of the m. constrictor laryngis (Pl. 1, fig. 1); only the dorsal occlusal surface is prominent in the dissections, appearing roughly discoid in section. The cricoid cartilage (= cricotracheal cartilage of Blume 1930) forms by far the greater part of the laryngeal wall. Vocal cords are absent. There is no separation into anterior and posterior chambers, but cricoid and arytenoid moieties may be distinguished.

There appears to be no sexual dimorphism in the larynx *Xenopus l. laevis* (Pl. 1, figs. 2 & 3), and few appreciable differences between the larynxes of male *Xenopus l. laevis* and of *X. muelleri* (Pl. 1, fig. 4), apart from the smaller arytenoid disc and more elongate arytenoid cartilage of *Xenopus muelleri*. There is virtually no intraspecific variation in the male larynx of either species.

LARVAL BUCCOPHARYNX (Pl. 2)

The cavity is not divided into discrete buccal and pharyngeal moieties as is true of the glossal anurans, and lacks certain structures occurring in Orton's Type 2 and Type 3 tadpoles (Orton, 1953). Buccopharyngeal morphology of the two species under consideration is very similar.

Internal nares lack valvular folds (present in the larvae of all free-swimming glossal taxa examined). The narial diameter/internarial distance does not give ratios that can be used to separate the two species.

Buccopharyngeal roof arena ridges are present instead of the papillae characteristic of most other tadpoles. There are three pairs. In *Xenopus l. laevis* they are slender, of subequal diameter, and the first pair is much shorter than the second and third; they do not arise from distinct depressions in the buccal roof. In *X. muelleri* they are robust, much thicker basally, and subequal in length; they arise from clearly-defined depressions in the buccal roof.

The **buccopharyngeal floor** is bounded laterally by elaborate folds overlying the filter plates. The floor is slightly wider in *Xenopus l. laevis* than in *X. muelleri*, and buccal floor pustulations tend to be concentrated medially in *X. l. laevis*, more widely spread in *X. muelleri*.

In all other respects larval buccopharyngeal morphology of the two species is essentially similar.

SPECIES ACCOUNT

Xenopus laevis laevis (Daudin, 1802)

Bufo laevis Daudin, 1802, Fig. 3, *Hist. Nat. Rain. Gren. Crap.*; 80, pl. 30, fig. 1. No type locality. Holotype no longer in existence, according to Poynton (1964:31).

Xenopus laevis (Daudin); Van Dijk 1966:225.

Xenopus laevis laevis (Daudin); Poynton 1964:30, fig. 3. Passmore & Carruthers 1979:44, figs. Poynton & Broadley 1985a:507. Lambiris 1988:13, figs., pl. 1 figs. 1a-c; 1989a:42; 1989b:44, figs. 7 & 8, pl. 1 figs. 1a-c.

ADULT LARYNX (Pl. 1, figs. 1 & 2)

Material examined: SOUTH AFRICA: NATAL - AJL 2678 (m, SVL 72,6 mm), 25 WSW Port Shepstone. AJL 3062 (f, SVL 100,0 mm), Paddock. AJL 1957 (f, SVL 86,6 mm), Mtunzini. AJL 3441, (f, SVL 63,3 mm), 13 km NE Cato Ridge. AJL 3490 (m, SVL 54,5 mm), Forest Hills. E. CAPE - AJL 311 (m, SVL 88,5 mm), Cockscomb Mts. AJL 313 (f, SVL 85,0 mm), and AJL 315 (f, SVL 80,5 mm), Grahamstown.

Advertisement call: Soft buzzes, at about 1.6 kHz and about 0.2 second duration, uttered under water (Passmore & Carruthers, 1979:44).

Male larynx:

Pharyngeal mucosa: Sectional surface smooth; forming distinct and somewhat thickened but simple glottal margins.

Arytenoid cartilage: The ala is about one third of the total length of the larynx. The occlusal surface (disc) is dorsad and posterad and fits into a small, shallow fossa on the dorsal anterior margin of the cricoid cartilage.

Cricoid cartilage: Internal surface thrown into elaborate folds. A prominent semilunar fold (the curvature directed posterad) encircles two more laterally placed, horizontally sigmoid processes. Two shallow fossae are associated with these processes near their posterior margins -- one dorsal to, and one ventral to them.

LARVAL BUCCOPHARYNX (Pl. 2, fig. 1a & b)

Identification of larvae: Based on a series from Mare Dam, Nyanga National Park, Zimbabwe (AJL 1382-1386, stages 27-44; 10 January 1980),

where no other species of *Xenopus* is known to occur, and showing the short subocular tentacle diagnostic of adults at stage 44.

Material examined: ZIMBABWE - AJL 1383; Mare Dam, Nyanga National Park; stage 37, SVL 22,5 mm; silver impregnation. SOUTH AFRICA: NATAL - AJL 3100; St. Lucia Estuary; stage 38/39, SVL 18,0 mm; silver impregnation. AJL 3496(b); Confluence of Naneni and Mooi Rivers; stage 38, SVL 24,3 mm; thionine stain.

Larval habitat: Shallow to moderately deep pools or pans, or quiet backwaters of streams where water flow is minimal. Substratum may be sand or silt, less commonly rock. The presence or absence of aquatic macrophytes is a variable feature (Lambiris 1989a:43).

Buccopharyngeal roof

General shape: Roughly rectangular, maximum width about 0.75 of length. General surface shallowly and regularly concave.

Prenarial arena: Roughly triangular; basal width about 5x medial length. Weakly excavate. No papillae or pustulations.

Internal nares: Small, circular or weakly ellipsoid, lacking valvular flaps, and level with the feebly raised general surface of the nasal capsules.

Postnarial arena: Not demarcated in any way, merging insensibly into the buccopharynx.

Buccal roof arena: Broad and rectangular, about twice as long as wide, and bounded laterally by three pairs of prominent ridges, all lateral to the posterior nares. All are slender, subequal in diameter, and arise from feebly-defined basal eminences on the buccopharyngeal roof. The first (post-narial) pair, whose bases are level with the anterior margin of the eye, are only about twice as long as broad, straight, directed anteromedially at an angle of about 45°, and about half the length of either of the other two pairs. The middle pair, whose apices are roughly level with the posterior margin of the eye, are also directed anteromedially at an angle of about 45°, but the apical portion is curved forwards. The posterior (pre-oesophageal) pair are directed more nearly sagitally than the others.

Other pustulations and papillae are lacking, as are glandular areas and a dorsal velum.

Pressure cushions: The lateral cushions are folded and narrower than the larger, triangular medial cushions. **Ciliary grooves** could not be clearly discerned in the preparations examined.

Buccopharyngeal floor

General shape: Narrowly triangular, the somewhat curved base at the mouth and the apex at the oesophagus, and shallowly excavate. A deep transverse crease is present behind the lower lip.

Prelingual papillae and **lingual papillae** are absent.

The **buccal floor arena** passes insensibly into the pharynx; the buccopharyngeal floor is bounded laterally by elaborate secretory folds arranged in three arches, overlying the medial ventral margins of the filter plates; they have fine longitudinal, slightly spiral, striations. The anteriormost arch is capped by a short, curved, transverse ridge.

Pustulations are few and concentrated in the middle line of the buccal floor, not extending beyond the first pair of lateral arches.

Buccal pockets lie lateral to the first lateral arch, and are poorly defined.

Ventral velum:: Absent.

Branchial baskets: About twice as long as broad; the filter cavities are wide.

Filter plates: Large, about 0.75 of the length of the buccopharynx, in four rows on either side, and diverging posterolaterally. They lack elaborate folds. The mesh is moderately dense and the filter canals are narrower than the filter rows.

Xenopus muelleri (Peters, 1854)

Dactylethra mülleri Peters, 1844, *Mber. Königl. Akad. Wiss. Berlin*: 37. Type locality: Angola and Mozambique (restricted to Tete [Mozambique] by Loveridge, 1957). Holotype in the Zoologisches Museum Berlin.

Xenopus calcaratus (Buchholz & Peters): Blume 1930:407, figs. 119-123.

Xenopus muelleri (Peters): Poynton 1964:33, fig. 4. Van Dijk 1966:252. Passmore & Carruthers 1979: 46, figs. Poynton & Broadley 1985a:511. Lambiris, 1989a:43; 1989b:48, figs. 10 & 11, pl. 1 figs. 3a-c.

ADULT MALE LARYNX (Pl. 1, fig. 3)

Material examined: MOZAMBIQUE: NM 1580 (m, SVL 66.0 mm), Beira. SOUTH AFRICA: TRANSVAAL - AJL 3474 (m, SVL 46.3 mm), Main Camp, Manyeleti Game Reserve. NM 5368 (m, SVL 59.3 mm), Pafuri. NATAL - AJL 2659 (m, SVL 54.4 mm), Mpumpuna Pan, Ndumu Game Reserve. NM 6668 (m, SVL 50.3 mm), Ndumu Game Reserve. NM 1584 (m, SVL 66.0 mm), Nyalazi Store, Zululand.

Advertisement call: A series of tapping sounds, at about 0.8 kHz and 0.05 second duration, uttered about twice per second (Passmore & Carruthers 1979: 46).

General remarks: The larynx is similar in most respects to that of *Xenopus laevis laevis*; there appear to be few differences of diagnostic significance. The ala of the arytenoid cartilage is about half the total length of the larynx (only about one third the total length in *Xenopus l. laevis*) and the occlusal surface (disc) is smaller than that of *Xenopus l. laevis*, being barely wider than the dorsal sectional surface of the cricoid cartilage.

LARVAL BUCCOPHARYNX (Pl. 2, fig. 2)

Identification of larvae: Based on a series from Manyeleti Game Reserve (AJL 3455-3472, stages 27-45; January 1991), showing the longer subocular tentacle diagnostic of adults from stage 44.

Material examined: SOUTH AFRICA: TRANSVAAL - AJL 3461: Main Camp, Manyeleti Game Reserve; stage 33, SVL 24.0 mm; methyl violet stain. AJL 3467a-d; Main Camp, Manyeleti Game Reserve; stage 38, snout-vent lengths 27.6 - 29.5 mm; silver impregnation.

Larval habitat: Shallow to moderately deep pools and pans, with sand or silt substratum; presence of aquatic macrophytes is a variable feature, but appear to be fewer than is the case for *X. laevis* (unpublished observations).

Buccopharyngeal roof

Similar in most respects to that of larval *Xenopus l. laevis*, but differing as follows:

Prenarial arena very narrow, basal width 8-10x medial length, and barely excavate.

Buccal roof arena: The lateral ridges are much thicker and straighter than those of *Xenopus l. laevis* and the terminal portions are not inflected.

Buccopharyngeal floor

Similar in most respects to that of larval *Xenopus l. laevis*, differing in having more widely-scattered pustulations over the buccopharyngeal floor, and in having smaller prepocket ridges.

DISCUSSION

The close similarity of the larynxes of adult males in the two species examined is in strong contrast to the situation in the glossal taxa studied and is difficult to account for. Duellman & Trueb's remark (1986:91) that "the cartilaginous disc slips or pops anteriorly, and so produces the sharp, metallic clicking noise that characterises vocalisation in these frogs" [ie *Pipa*] could apply to the call of *Xenopus muelleri*, but is difficult to imagine operating in the same way during the much longer call of *X. l. laevis*.

Similarly, the similarity in larval buccopharyngeal morphology in these two taxa accords with the observation that they have not yet been observed to breed in the same body of water, although in parts of their respective ranges the two species may occupy adjacent, or even the same, quarter-degree squares (Poynton, 1964, map 4). At Mutare, Zimbabwe, *X. muelleri* "seems to occur only in the sewerage pond works, while the adjacent streams are occupied by *l. laevis* (Poynton & Broadley, 1985:511). Allopatry seems to be maintained here by external factors influencing habitat selection, and reproductive isolation by differences in advertisement call. Apparent intergrades are rare (Poynton & Broadley, 1985:511).

It is interesting to note that isolating mechanisms seem to fail in the Western Cape, where *Xenopus l. laevis* invades water bodies favoured by the smaller endangered species *X. gilli*, which characteristically favours waters with a low pH and rich in polyphenols (Picker, 1988). The advertisement call of *Xenopus gilli* is very different from that of *X. muelleri*, and somewhat resembles that of *X. l. laevis* in that it is a buzz of about 0.2 second duration, although of higher frequency, more distinctly pulsed, and uttered more frequently (based on sonagrams and descriptions in Passmore & Carruthers, 1979).

PLATE 1
ADULT HYOLARYNXES
XENOPUS –

Median sagittal section. View into left half. Anterior to right.

FIG. 1: *Xenopus laevis laevis* (Daudin, 1802)
AJL 3490 (male), Forest Hills, Natal, South Africa.

FIG. 2: *Xenopus laevis laevis* (Daudin, 1802)
AJL 315 (female), Grahamstown, E. Cape, South Africa.

FIG. 3: *Xenopus muelleri* (Peters, 1844)
AJL 2659 (male), Ndumu Game Reserve, Natal, South Africa.

PLATE 2
XENOPUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

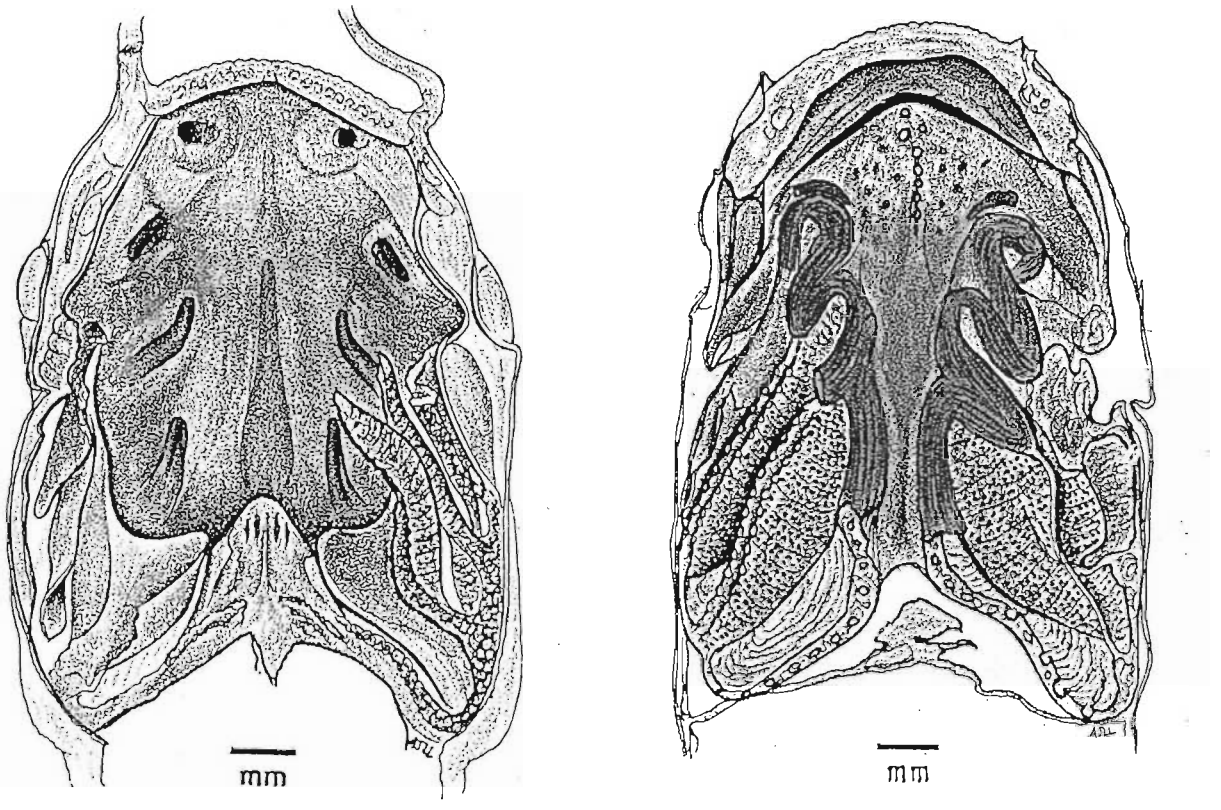


FIG. 1; *Xenopus laevis laevis* (Daudin, 1802)
AJL 1383, Stage 37, Mare Dam, Nyanga National Park, Zimbabwe.

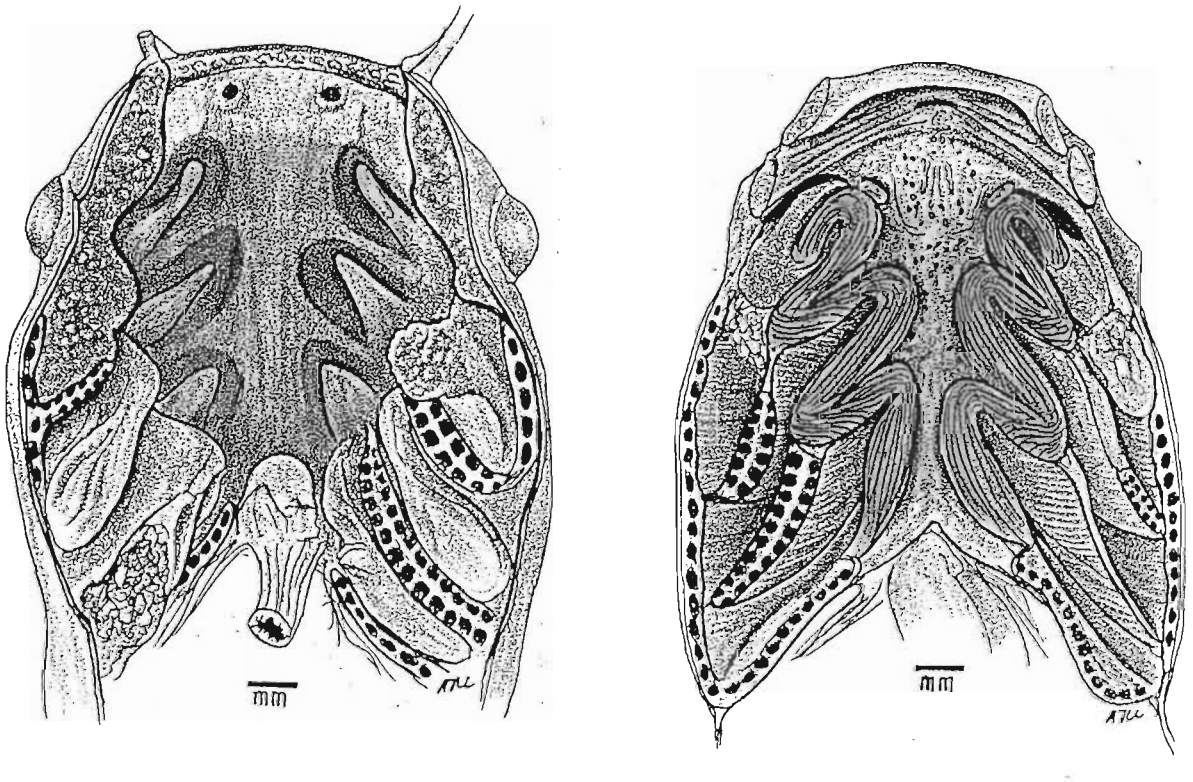


FIG. 2; *Xenopus muelleri* (Peters, 1844)
AJL 3467, Stage 38, Manyeleti Game Reserve, Transvaal, South Africa.

Family HELEOPHRYNIDAE Noble, 1931

Genus *Heleophryne* Sclater, 1899

Heleophryne Sclater, 1899, *Ann. S. Afr. Mus.*, 1:110. Type species by monotypy: *Heleophryne purcelli* Sclater.

CHARACTERS

Only one species of *Heleophryne* occurs in Natal. A detailed comparison of adult laryngeal and larval buccopharyngeal characters with those of the six currently recognised Western Cape taxa was not made, as being considered beyond the proximal aims of this study; treatment is limited to simple description of these structures for *Heleophryne natalensis*. However, the adult larynx and larval buccopharynx of *H. rosei* (Pl. 3, fig. 3 and Pl. 4, fig. 2 respectively) are included to illustrate the nature of interspecific variation in the genus, as indicated in the Discussion, below.

ADULT LARYNX (Pl. 3)

The male larynxes examined showed no appreciable intraspecific variation, those differences observed (compression of pharyngeal mucosa, pericardial region and m. hyolaryngeus) manifestly being preservation artifacts in carelessly processed specimens.

Sexual dimorphism in the larynx of *Heleophryne natalensis* is quite pronounced - note especially the more elongate arytenoid cartilage of the female (Pl. 3, fig. 2) with its more acutely V-shaped occlusal surface and the absence of the lateral vocal cord.

LARVAL BUCCOPHARYNX (Pl. 4)

Only one tadpole of either species was dissected for examination, precluding any assessment of intraspecific variation. Intrapecific variation is pronounced, as inspection of the illustrations will show.

SPECIES ACCOUNT

Heleophryne natalensis Hewitt, 1913

Heleophryne natalensis Hewitt, 1913, *Ann. Natal Mus.*, 2:477, pl. 34, figs 1, 3, 5-7. Type locality: "a tributary of the Krantz Kloof river" ["probably in the Krantzkloof Nature Reserve, 12 miles northwest of Durban" (Poynton 1964:40).] Holotype in the Mariannhill Monastery Museum, Natal. Poynton 1964:41, fig. 8. Van Dijk 1966:225. Lambiris 1988:14, figs., pl. 1 figs 2a-c; 1989a:45.

ADULT LARYNX (Pl. 3, Fig. 1)

Material examined: TRANSVAAL - NM 5376 (m), Horo Bush. NATAL - AJL 2518 (m, SVL 44,5 mm), Injasuti Outpost, Giant's Castle Game Reserve. AJL 3389 (f, SVL 41,8 mm), Highmoor State Forest. NM 6379 (m, SVL 67,2 mm), and NM 6381 (m, SVL 63,2 mm), St. Heliers, Hillcrest. NM 6368 (m, SVL 53,4 mm), "Colbourne", Karkloof.

Advertisement call: A clear note at about 2 kHz, less than 0.1 second duration, uttered about twice per second.

Male larynx:

Pharyngeal mucosa: Thick, narrowing rapidly towards the base of the arytenoid cartilage, the anterior superior surface of which is invested with a fine layer of mucosa barely discernible at medium magnification.

Arytenoid cartilage: Occlusal surface rather broad, moderately widely V-shaped; apical width about 0.5 length of arytenoid shelf. No valvular fold. No incisura, prominentiae apicales or apical cartilage. Arytenoid fossa narrowly elliptic.

Pulvinaria vocalia: No distinct pulvinaria vocalia are discernible.

Vocal cord: Lateral portion narrow, anterior to and separate from the medial cord, overlying the arytenoid fossa. Medial cord broad (width about 0.25 length), inclined somewhat superoposterad; lacking a frenulum chordae vocalis and cartilaginous buttresses.

Posterior chamber: A well-developed semilunar fold defines the pulmonary aditus.

M. hyoglossus: Originates broadly on the inferior surface of the arytenoid cartilage.

LARVAL BUCCOPHARYNX (Pl. 4, fig. 1a & b)

Identification of larvae: Only one species known to occur in Natal.

Material examined: NATAL - AJL 3491; Incandu Forest Reserve; stage 38/39; SVL 41,3 mm; silver impregnation.

Larval habitat: Shallow, rocky-bottomed streams with clean, cool to cold water and at least a moderate rate of flow. Breeding sites are usually associated with a fairly dense canopy cover. Tadpoles require crevices in bedrock, or loose rocks on the bottom, for shelter, and feed on algae or organic sediment on rock surfaces (Lambiris, 1989a:46).

Buccopharyngeal roof

General shape: Roughly triangular, base about 1.1x length. General surface complex, with a distinct median longitudinal prominence flanked by narrow, rather deep depressions medial to the internal nares and extending more broadly and less deeply towards the glandular ridge.

Prenarial arena: Very narrow, about 6x wider than deep at the level of the anterior margins of the internal nares, but extending far back lateral to the nares; deeply excavate anteriorly, and with elaborate, digitate papillae on the labial border.

Internal nares: Elongate slits about one-sixth of the buccal roof length, oriented roughly longitudinally but diverging posteriorly. The medial margin abuts a deep, narrow depression and possesses a prominent valvular flap. Two small papillae lie on the medial line between the anterior margins of the nares.

Postnarial arena: About twice as broad as deep. Postnarial papilla bifid. Six moderate-sized papillae (three on either side of the medial buccal roof ridge) at the level of the postnarial papillae, with a much larger median one posterior to them, which is probably homologous with the median ridge. A single, large, digitate lateral ridge papilla on either side, the posterad element largest and rather warty.

Buccal roof arena: Roughly pentagonal in shape, about 1.5x broader than deep, and with a narrow, poorly defined depression on either side of the elevated medial portion. Small papillae of subequal size

scattered over the arena without any regular pattern, but tending to be more numerous laterally. No pustulations observed.

Glandular area: A rather broad, gently wrinkled area distinctly delimiting the whole posterior border of the buccal roof arena.

Dorsal velum: Not discernible as a separate entity, probably as one with the glandular area.

Pressure cushions: Relatively narrow, transversely oriented, with a prominent flexure at about mid-point on either side.

Buccopharyngeal floor

General shape: Triangular, apex anterad; base about 1.3x length.

Labial papillae are present on the lower lip at about the position that would be occupied by the infrarostrodont; they are small, simple, closely-spaced and arranged in groups of four or five on either side of the midline.

Prelingual arena: A conspicuous, narrowly trapezoid area, bearing a large, palpoid, rather warty lateral papilla anteriorly on either side; but otherwise devoid of papillae or pustules.

Buccal floor arena: Roughly pentagonal, about 1.3x broader than deep, bounded posterolaterally by a single row of closely-spaced simple papillae, smallest medially and largest laterally. The arena floor is prominently raised and lacks papillae or pustulations. The anterolateral margins are clearly demarcated by deep clefts.

Buccal pockets: Only the right pocket is intact in the specimen dissected; it is an oblique, narrow, deep cleft adjacent to the antero-lateral border of the ventral velum and lacks prepocket papillae.

Other pustulations: A triangular zone of rather closely-spaced pustulations is present between the buccal floor arena papillae and the ventral velum.

Ventral velum: Extends across the entire width of the buccopharyngeal floor. Extreme lateral depth twice medial depth. Supporting spicules not clearly discernible in this preparation. Posterior margin of velum narrowly thickened and broadly crenulate, with prominent lobular projection on the crenular junctions approximately

indicating the medial margins of the underlying filter plates; median notch small and shallow.

Branchial baskets: Roughly triangular, base about half of transverse width; each about half the buccal area; filter cavities large.

Filter plates: Not strongly imbricate. About 14 filter rows on each plate; filter rows single on the outer plates, but alternating with partial filter rows on the inner plates. Filter mesh dense, with tertiary folds, and filter canals narrower than the filter rows.

Glottis: Clearly visible under the median notch, and possesses distinct fleshy lips.

Oesophageal funnel: Not intact in this preparation.

DISCUSSION

Although insufficient taxa and specimens have been examined to permit any meaningful discussion of variation within the genus, it is perhaps permissible within the scope of the present investigation to comment on some of the differences observed between the adult larynxes and larval buccopharynxes of *Heleophryne natalensis* and *H. rosei*.

Laryngeal morphology

Although not easily described verbally, inspection of the illustrations clearly shows the essential simplicity of the *Heleophryne* larynx in the taxa examined. The significance of this simplicity is not yet clear, but it is so striking that it deserves comment.

Laryngeal morphology shows an overall similarity between the two species, most notably in the peculiar narrow lateral vocal cord which lies anterior to the much broader medial cord which is presumably principally responsible for producing sounds. The anterior curvature of the posterior membrane is another unusual feature of the genus which emphasises the close relationship of the two species.

The principal differences between the male larynxes of the two species are in the shapes of the arytenoid cartilages and in the origin of the M. hyoglossus. In *H. natalensis* the arytenoid cartilage is relatively short and the occlusal surfaces are of roughly uniform width; the M. hyoglossus arises from a broad aponeurosis on the antero-inferior surface of the arytenoid cartilage. In *H. rosei* the arytenoid cartilage is elongate and the occlusal surfaces are of varying width, and the M. hyoglossus arises from a long, narrow aponeurosis originating below the inferior pulvinaria vocalia.

The shape of the epiglottidean gland may also be of significance. It is short and lies just below the apex of the arytenoid cartilage in *Heleophryne natalensis*, but is long and lies against the entire inferior surface ofthe arytenoid cartilage in *H. rosei*.

The larynx of female *Heleophryne natalensis* resembles that of male *H. rosei* in possessing an elongate arytenoid cartilage, but differs in that the occlusal surfaces are of roughly uniform width, as in male *H. natalensis*, and lacks both a lateral vocal cord and an epiglottidean gland.

Buccopharyngeal morphology

Apart from the striking difference in size, the most conspicuous differences between the two taxa examined are seen in the floor of the buccopharynx. The whole musculature and jaw apparatus are remarkably different in shape, *Heleophryne natalensis* having a proportionately much narrower mouth than *H. rosei*, as well as a narrower and longer prelingual arena (that of the latter species possessing numerous papillae) and a shorter, broader and more U-shaped buccal floor arena. The buccal floor arena papillae are much shorter, more uniform in size and less elaborate in structure than those of *H. rosei*, although the ventral velum is more elaborate. Although the two species exploit superficially similar breeding habitats (cold, shallow, fast-flowing streams with rocky bottoms), these anatomical differences suggest ecological and behavioural differences of considerable importance.

A close examination of adult larynxes and of larval buccopharynxes of the Western Cape taxa could prove to be of considerable value in determining the taxonomic status of the various populations in this rather enigmatic genus.

PLATE 3

HELEOPHRYNE – ADULT HYOLARYNXES

Median sagittal section, View into left half, Anterior to right.

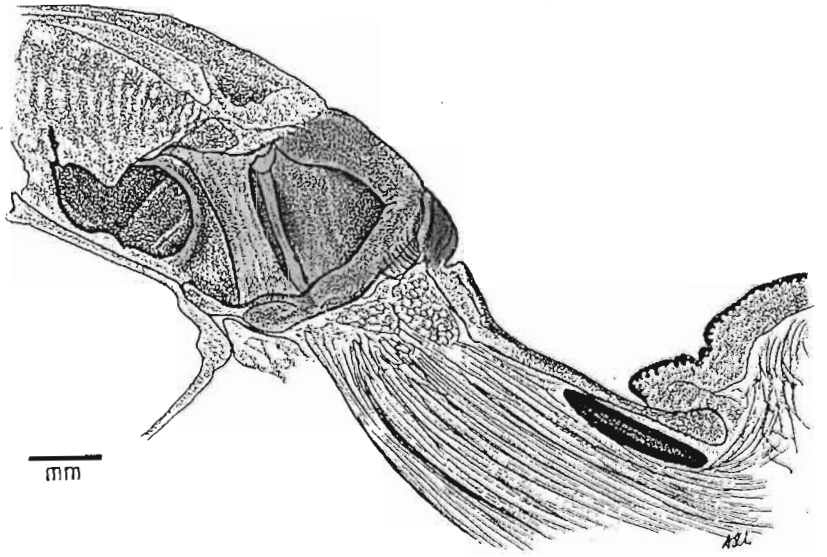


FIG. 1; *Heleophryne natalensis* Hewitt, 1913
NM 6379 (male), St. Heliers, Hillcrest, Natal, South Africa.

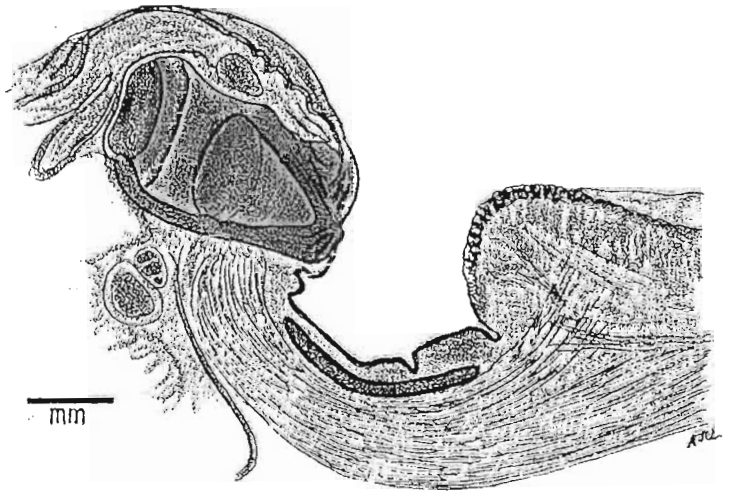


FIG. 2; *Heleophryne natalensis* Hewitt, 1913
AJL 3389 (female), Highmoor State Forest, Natal, South Africa.

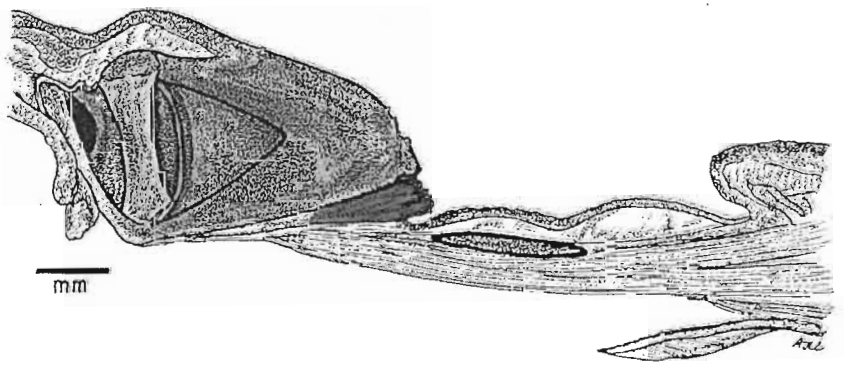


FIG. 3; *Heleophryne rosei* Hewitt, 1925
NM 1951 (male), Skeleton Gorge, Table Mountain, Cape Town, Western Cape, South Africa.

PLATE 4
HELEOPHRYNE – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

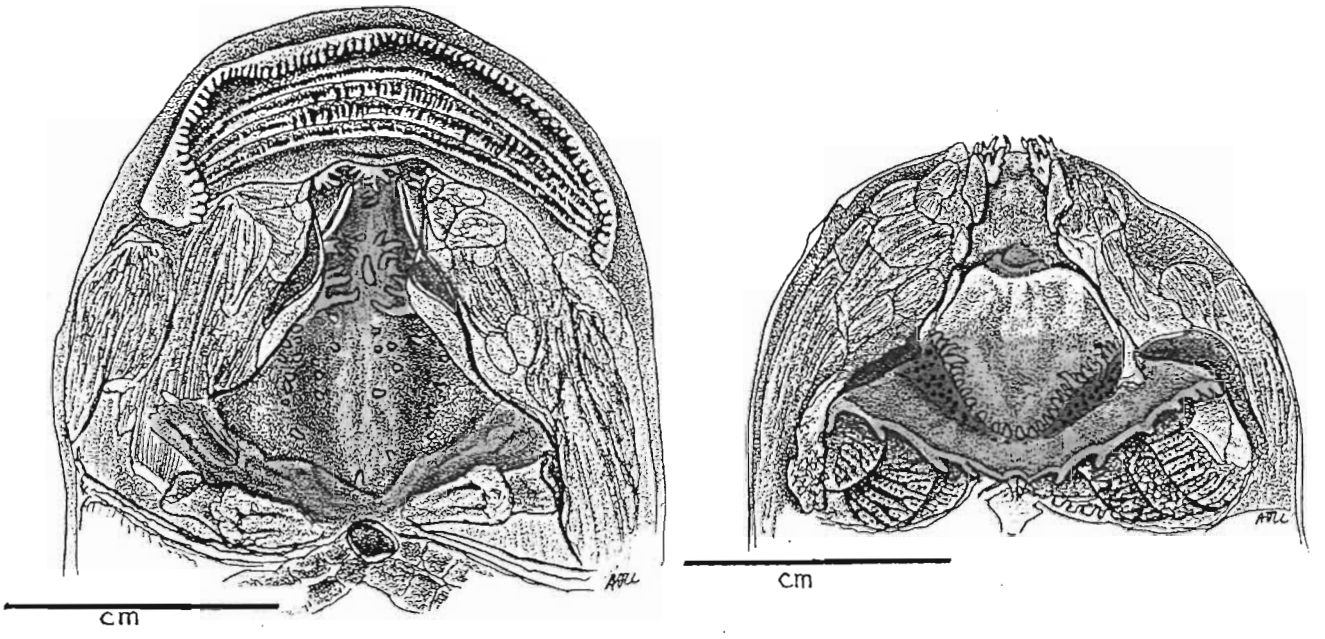


FIG. 1; *Heleophryne natalensis* Hewitt, 1913
AJL 3491, Stage 38/39, Incandu Forest Reserve, Natal, South Africa.

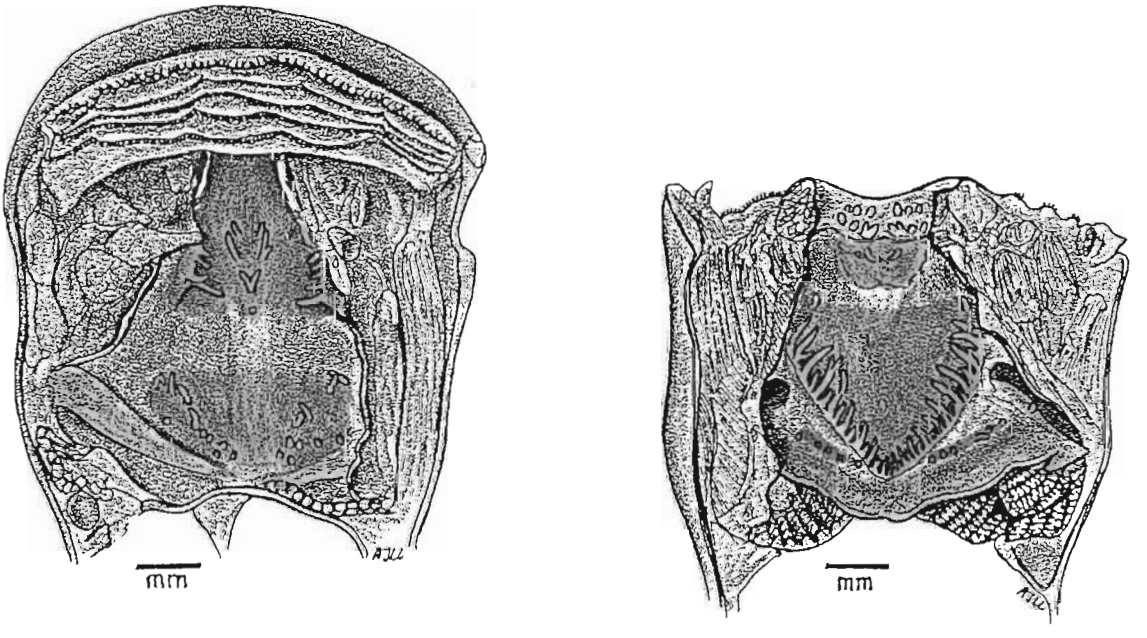


FIG. 2; *Heleophryne rosei* Hewitt, 1925
AJL 277, Stage 36, Skeleton Gorge, Table Mountain, Cape Town, Western Cape, South Africa.

TABLE 1. Laryngeal characters: *Bufo* and *Schismaderma*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

* = extralimital taxa included for comparison

	INTERNAL MARGIN OF ARYTENOID U-SHAPED	ARYTENOID VALVE PRESENT	ARYTENOID VALVE ON INTERNAL MARGIN OF OCCLUSAL SURFACE	RIDGES ON OCCLUSAL SURFACE OF ARYTENOID	VOCAL CORD BROAD AT MID-POINT	VOCAL CORD STRONGLY CURVED IN SECTION	VOCAL CORD MARGINS DISTINCTLY FLANGED	CARTILAGINOUS SUPPORT RODS PRESENT	FIBROUS BODY LARGE	FIBROUS BODY DISTINCTLY BILOBED	FIBROUS BODY EXTENDS BEYOND ANTERIOR MARGIN OF VOCAL CORD	FIBROUS BODY IN CLOSE CONTACT WITH ANTERIOR MARGIN OF POSTERIOR MEMBRANE	POSTERIOR MARGIN OF FIBROUS BODY LIES MEDIAL TO MARGIN OF POSTERIOR MEMBRANE	FRENULUM PRESENT
*Bufo gariepensis gariepensis**	3	3	1	1	3	1	1	1	3	3	1	1	3	1
gariepensis nubicolus	3	3	4	1	1	3	1	3	1	3	1	3	4	3
gutturalis	1	1	1	1	3	3	3	1	1	3	3	1	1	3
pusillus	3	3	1	1	1	3	3	1	3	3	3	1	1	3
*maculatus**	* 1	1	1	3	3	3	1	1	1	1	3	1	1	3
garmani	3	1	1	3	3	3	1	1	1	1	3	1	1	3
*poweri**	1	1	1	1	1	1	1	1	1	1	3	1	1	3
rangeri	3	1	1	3	1	3	3	1	1	1	3	1	3	3
pardalis	1	1	1	1	3	1	1	1	1	3	3	1	3	3
*cruciger**	1	1	1	1	3	3	3	1	1	3	1	1	1	3
fenoulheti fenoulheti	3	1	1	1	3	3	3	3	1	3	3	1	3	3
Schismaderma carens	3	1	3	1	3	3	3	1	3	3	3	3	4	3

Family BUFONIDAE Gray, 1825

CHARACTERS

The genera *Bufo* and *Schismaderma* are considered jointly in this section, and in the Discussion.

ADULT LARYNX (Table 1; Pls. 5 - 9, 14)

Analysis is restricted to characters of the male larynx only, which possesses a number of features that show clear interspecific differences yet which have little intraspecific variation (Table 1). The extralimital taxa *Bufo maculatus, poweri* and *B. cruciger* (see Discussion, below, for attribution of names) were examined for this study as they have a bearing on the taxonomy of Natal forms. Sexual dimorphism in the taxa examined is pronounced, as shown in the plates; the female larynx is not considered further here, although possessing features as taxonomically useful as those of the male.

Shape of the arytenoid cartilage

The anterior margin is generally U-shaped throughout and shows no useful variations in outline. The posterior margin of the occlusal surface of the arytenoid cartilage may be either U-shaped (*Bufo gutturalis, garmani, poweri, pardalis* and *cruciger*, or V-shaped (*Bufo pusillus, rangeri, f. fenoulheti, g. gariepensis* and *Schismaderma carens*. *Bufo cruciger* is the only taxon examined whose arytenoid cartilage has an incisura and prominentiae apicales.

Arytenoid valve and ridges

An arytenoid valve is present in all the taxa examined except *Bufo g. gariepensis, B. g. nubicolus* and *B. pusillus*.

In the genus *Bufo* the arytenoid valve occurs as a shallow rounded ridge or lip following the internal margin of the arytenoid cartilage, and it is most clearly defined in *Bufo gutturalis, B. f. fenoulheti* and *B. cruciger*, less so in *B. pardalis* and least distinct in *B. garmani*, where it is no more than a slight lip. In *B. poweri* and *B. rangeri* it is weakly developed but clearly discernible as a roughly triangular area.

Longitudinal folds are present on the occlusal surfaces of the arytenoid cartilages of most taxa examined, generally clearest on those in which the arytenoid valve is poorly developed; an exception is *Bufo cruciger*, which possesses a distinct arytenoid valve and conspicuous folds.

In *Schismaderma carens* the arytenoid valve lies on the anterior margin of the cartilage and is deeply ridged longitudinally. There are also well-defined ridges on the internal border of the cartilage, but these are much smaller in extent.

Vocal cord

The vocal cord possesses a number of taxonomically useful features.

Medial width: The width at mid-point expressed as a proportion of the greatest width. A broad cord has a medial width greater than two-thirds of the greatest width; a narrow cord has a medial width half, or less, than that of the greatest width.

Cross-sectional shape: Flat (or weakly concave), or strongly concave.

Marginal flanges: A flange is present on one or both free margins of the vocal cord in some species. They are most pronounced in the extralimital *B. g. gariepensis* (Pl. 5, fig. 1), where they extend along the entire length of both margins as extensions of the supporting rods; they are much less conspicuous in the other taxa examined.

Supporting cartilaginous rods are present on at least the posterior margins of the vocal cords in all taxa examined, but vary from little more than mere thickening of the cord (*B. gutturalis*, *pusillus*, *pardalis* and *B. cruciger* to well-developed, conspicuous elements (*B. garmani*, *poweri*, *rangeri* and *pardalis*, and *Schismaderma carens*.

Fibrous body

Present in the male larynx of all taxa examined, but absent in female *Bufo g. nubicolus*, *garmani*, *rangeri* and *B. f. fenoulheti*; and but feebly developed in female *B. pardalis*. In males, the size, shape and position in relation to the vocal cord and posterior membrane appear to be taxonomically useful characters.

The fibrous body lies lateral to, and across the full width of the cord, in *Bufo g. gariepensis*, *B. g. nubicolus* and *B. cruciger*; it lies

TABLE 2. Buccopharyngeal characters: *Bufo* and *Schismaderma*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

[1] Single median papilla
[2] Transverse ridge
[3] Intra-pocket palp

	PRENARIAL PAPILLAE PRESENT	MARGIN OF NARIAL VALVE DENTICULATE	POSTNARIAL PAPILLAE BIFID TERMINALLY	LATERAL RIDGE PAPILLAE WARTY OR ROUGH	FREE BORDER OF MEDIAN RIDGE SERRATED	SOME BUCCAL ROOF ARENA PAPILLAE BIFID OR TRIFID TERMINALLY	BUCCAL ROOF ARENA PUSTULATE	DORSAL VELUM PAPILLATE ALONG HALF OR MORE OF ITS FREE EDGE	PREPOCKET PAPILLAE PRESENT	DISTINCT BUCCAL POCKETS PRESENT	SOME BUCCAL FLOOR ARENA PAPILLAE ENLARGED AND COMPOUND	BUCCAL FLOOR ARENA PAPILLATE OR PUSTULATE	CLOSELY-SPACED PAPILLAE ON AT LEAST PART OF FREE EDGE OF VENTRAL VELUM
Bufo gariepensis nubicolus	3	0	3	3	3	3	1	3	1	1	3	1	3
gutturalis	3	1	3	1	1	3	1	1	1	1	1	3	1
pusillus	3[1]	3	1	3	3	3	1	0	4	3	3	3	3
garmani	1[2]	3	3	3	3	3	3	3	4	1	3	3	3
rangeri	1	1	3	1	3	1	1	1	1	1[1]	3[2]	1	3
pardalis	3	1	1	1	1	3	3	3	4	3	1	1	1
fenoulheti fenoulheti	3	3	3	3	2	3	3	3	3	1	1	3	3
Schismaderma carens	3[1]	1	1	3	3	1	1	1	1	1	1	3	1

behind and closely applied to the posterior margin of the cord, in the other taxa examined.

It is ovoid in *Bufo gutturalis, pusillus, pardalis* and *B. f. fenoulheti*; it is distinctly bilobed in the other species of *Bufo* examined.

In *Schismaderma carens* the fibrous body is small and feebly developed.

The posterior border of the fibrous body lies medial to the medial margin of the posterior membrane in *Bufo gutturalis, pusillus, garmani, poweri* and Sp. A; and lateral to the medial margin in the remaining species examined. In *Schismaderma carens* alone it is remote from the posterior membrane.

Epiglottidean gland

Present in all taxa examined, but only weakly so in *Bufo g. gariepensis, garmani, poweri, pardalis* and *f. fenoulheti*. It is particularly well developed in *Bufo pusillus, B. cruciger* and *Schismaderma carens*.

LARVAL BUCCOPHARYNX (Table 2; Pls. 10 - 13, 15)

Character variation in *Bufo* and *Schismaderma* is summarised in Table 2.

Prenarial papillae

Of the taxa examined only *B. rangeri* has a prenarial papilla closely associated with each naris; these are large and trifid. *Bufo garmani* has a double-curved transverse median prenarial ridge which may represent fused prenarial papillae, while *B. pusillus* and *Schismaderma carens* both have a single median papilla anterior to the nares.

Narial valve

In all taxa examined the narial valve is well developed. In *B. gutturalis, rangeri* and *pardalis*, and in *Schismaderma carens*, the margin is denticulate on the anterior margin; it is smooth in the other taxa.

Postnarial papillae

Postnarial papillae are absent in *Bufo gariepensis nubicolus* but present in all other taxa examined. *Bufo f. fenoulheti* possesses a single rather large pair; the other *Bufo* species and *Schismaderma* have two or more pairs. In *B. pusillus*, *B. pardalis* and *Schismaderma carens* they are bifurcate or denticulate terminally.

Lateral ridge papillae

Large, digitate lateral ridge papillae are present in all the taxa examined except for *Bufo gariepensis nubicolus*, where they take the form of two simple papillae on a broad pedicel on either side, and *B. garmani*, where they are short and triangular, with feebly denticulate margins. In *Bufo gutturalis*, *rangeri* and *pardalis* the digitations are warty or weakly papillate, and are trifid in all except *B. pusillus*, where they are quadrifid.

Median ridge

The median ridge shows considerable interspecific variation in size and shape. It is roughly triangular in all the *Bufo* examined, but narrow, almost lorate, in *Schismaderma*.

In *Bufo gariepensis nubicolus* it is small, little more than a rather broad papilla closely flanked by the lateral ridge papillae. In *B. pusillus* the apex is finely tricuspid, and in *B. garmani* the apex is deeply notched, giving a bicuspid appearance. In the remaining taxa the free edge of the ridge is serrated or denticulate to a greater or lesser degree.

Buccal roof arena papillae

The buccal roof arena is defined by papillae that are generally regularly and symmetrically disposed along the lateral boundaries. Average numbers on either side range from two *Bufo pardalis* to four (*B. gutturalis* and *B. garmani*, with three (someetimes four on one side) in *B. pusillus*, *rangeri* and *fenoulheti*, and in *Schismaderma carens*.

In most taxa examined the papillae are simple, but in *B. rangeri* each bears a small papilla suggestive of an incipient bifurcation, and in *Schismaderma carens* the ends are weakly bifurcate or trifurcate.

Pustulations

The buccal roof arena is pustulate in *Bufo pusillus* and *B. rangeri*, and in *Schismaderma carens*.

Dorsal velum

The dorsal velum is feebly defined in *Bufo gariepensis fenoulheti*. In *B. gutturalis* and *B. pardalis* it is broadly V-shaped, with papillae (small, subequal in *gutturalis*), large medially and becoming smaller laterally in *pardalis*) along the middle half of the trailing edge. In *B. rangeri* it is gently curved, with tiny papillae along most of the free edge, while in *B. f. fenoulheti* there are only two small, rounded papillae on either side, close to the mid-line. In *B. garmani* the velum is a simple, unadorned, transverse, slightly convex fold. In *S. carens* the velum is curved, with short, rounded papillae along the middle half of the free edge.

Prelingual papillae

Simple prelingual papillae are present in *B. gutturalis, pusillus, garmani* and *rangeri*. *Bufo rangeri* also possesses an additional pair of papillae very close to the base of the infrarostrodont. In *B. pardalis* the outermost papillae are terminally bifid, whilst in *B. f. fenoulheti* they are short, rounded, and arise from a transverse ridge. In *Schismaderma carens* they are enalrged palps, and there are a few pustulations between these and the infrarostrodont.

Prepocket papillae

Prepocket papillae are clearly identifiable in *Bufo gutturalis*, *B. rangeri* and *Schismaderma carens*; they are present as a large palp on either side in *B. gariepensis nubicolus*, not identifiable in *B. f. fenoulheti*, and absent in *B. pusillus* and *B. pardalis*, which lack buccal pockets. *Bufo rangeri* is exceptional among the taxa examined in that large, digitate palps are actually within the buccal pockets.

Buccal pockets

Buccal pockets are variable in shape and orientation. They bare narrow and longitundinally elongate in *Bufo gariepensis nubicolus* and *B.*

garmani, transversely ovoid in the other taxa examined; *Bufo rangeri* appears to possess two pairs of pockets.

Buccal floor arena papillae

These tend to be less regularly and symmetrically arranged than those of the buccal roof arena; they are most regular in *Bufo pusillus* and *B. garmani*, and much more randomly scattered in the other taxa examined. The arena itself is, with the exception of the two taxa just mentioned, liberally scattered with papillae and pustulations; these are particularly abundant in *Schismaderma carens*.

Simple papillae are present *Bufo gariepensis nubicolus, pusillus, garmani* and *rangeri*. *Bufo gutturalis, pardalis* and *B. f. fenoulheti* have, in addition, a large bifurcate papilla on either side; these are smallest in *B. gutturalis* and *B. pardalis*, very much larger in *B. f. fenoulheti*. *Schismaderma carens* also possesses several bifurcate or trifurcate papillae, which are larger than the simple papillae.

Ventral velum

The ventral velum is a simple fold with a feebly crenate margin in *Bufo gariepensis nubicolus*. In *B. pusillus* and *B. f. fenoulheti* it is broadly scalloped or undulant, without distinct supporting cartilages, and devoid of marginal ornamentation. In *Bufo garmani* the free portion of the velum is fine, delicate, lacking marginal ornamentation, and supported on long, conspicuous cartilaginous rods. In the remaining taxa examined the velum is moderately broad, supported by much less conspicuous cartilaginous elements, and is papillate to a greater or lesser extent along the trailing edge.

SPECIES ACCOUNT

Genus *Bufo* Laurenti, 1768

Bufo Laurenti, 1768, *Synops. Rept.*: 25. Type species by tautonomy: *B. vulgaris* Laurenti = *Rana bufo* Linnaeus.

Schismaderma A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App.: 28 (part).

Bufo gariepensis nubicolus Hewitt, 1927

Bufo gariepensis nubicola Hewitt, 1927, *Rec. Albany Mus.*, 3:412, pl. 24, fig. 5. Type locality: Summit of Mont-Aux-Sources. Holotype in the Port Elizabeth Museum, Port Elizabeth, South Africa. Van Dijk 1971:72.

Bufo gariepensis nubicolus Hewitt: Poynton 1964:48, fig. 13. Passmore & Carruthers 1979:64, figs. Lambiris 1988:16, figs., pl. 1 figs. 3a-c; 1989a:48.

ADULT LARYNX (Table 1; Pl. 5, figs. 2 & 3)

Material examined: SOUTH AFRICA: NATAL - NM 6558 (m, SVL 47,4 mm), and NM 6559 (m, SVL 43,2 mm), Bannerman's Hut, Giant's Castle Game Reserve. NM 640 (m, SVL 45,8 mm), Nkandla Forest (sic! - obviously erroneous, but correct locality not traced). AJL 2457 (f, SVL 43,3 mm), Injasuti Outpost, Giant's Castle Game Reserve, Natal.

Advertisement call: A rasping squawk, somewhat trilled, at about 1.5 kHz, about 0.5 second long; uttered about once a second, from swampy areas or from the edges of shallow temporary pans.

Male larynx:

Pharyngeal mucosa: Thick, and deeply folded over the superior surface of the arytenoid cartilage.

Arytenoid cartilage: External margin V-shaped; internal margin broadly V-shaped, but with an acute notch. Incisura, prominentiae apicales and apical cartilage are absent. There is no arytenoid valve. The occlusal surface of the arytenoid cartilage is weakly ridged anteriorly. The arytenoid shelf is low but distinct, with a median backwardly-directed point on the posterior margin. The inferior puvinarium vocale is well developed; the superior pulvinarium vocale is barely definable.

Arytenoid fossa: Deeply excavate.

Vocal cord: Broad, the midpoint being almost as wide as the flared insertions, but not strongly curved in section. It is transparent and

delicate. The anterior margin is distinctly but delicately flanged, and strongly constricted above and below the fibrous body. The posterior margin is delicately flanged and lacks cartilaginous buttresses. There is no frenulum, but the vocal cord is fused to the medial surface of the fibrous body.

Fibrous body: Large and roughly cardioid, the apex directed posterad, and extending the full width of the vocal cord. The anterior margin of the fibrous body blends with that of the vocal cord by a fine band of tissue; the posterior margin of the body projects freely beyond the posterior margin of the vocal cord.

Posterior membrane: Robust, rather thick, and with a gently curved anterior margin well separated from the fibrous body.

M. hyoglossus: Arises from a point below the inferior cricoid cartilage.

LARVAL BUCCOPHARYNX (Table 2; Pl. 10, fig. 1a & b)

Identification of larvae: Identified from Van Dijk 1971, and Lambiris 1989a.

Material examined: NATAL - AJL 3404; Highmoor State Forest; stage 29/30; SVL 5,7 mm; silver impregnation. AJL 3406; Highmoor State Forest; stage 39/40; SVL 6,0 mm; silver impregnation.

Larval habitat: Waterlogged depressions with emergent grassy vegetation (Lambiris 1989a); or in very shallow, rocky-bottomed, slow-flowing streams with cold, clear water and short marginal grass. Tadpoles appear to feed on algae growing on bare rock and on accumulations of silted matter.

Buccopharyngeal roof

General shape: An antero-posteriorly elongate trapezoid.

Prenarial arena: Somewhat arched, about twice as broad as deep, with a markedly tricuspid posterior margin.

Internal nares: Large, length about 0.45x width of floor at level of posterior margins; about twice as long as wide; and obliquely set.

Anterior internarial distance about equal to narial length, posterior internarial distance about 2.5x narial length. Anterior margin smooth.

Narial valve: Distinct but shallow.

Postnarial arena: Shallowly and evenly excavate, and devoid of papillae or pustulations. The **lateral ridge papillae** are two simple papillae arising from a common ridged base on either side of, and closely flanking, the almost papillate **median ridge**, a simple triangular flap 1.5x deeper than broad.

Buccal roof arena: About half the width of the whole roof, delimited by two simple papillae on either side (three on the right side of AJL 3406), slightly converging posteriorly. 10 - 11 pustulations are scattered over the arena. No other papillae or pustulations are present on the buccopharyngeal roof.

Glandular ridge: Feebly developed and barely discernible in the specimens examined.

Dorsal velum: A thin, weakly-developed fold without supporting spicules or marginal ornamentation.

Pressure cushions and ciliary ridges are damaged in the specimens dissected.

Buccopharyngeal floor

General shape: Roughly triangular. The lateral borders of the buccal floor are deeply grooved in AJL 3406, in which the tongue is beginning to develop, and less so in AJL 3404.

Prelingual arena: Small and narrow. In AJL 3404 there is a paramedian pair of rather large, broad prelingual papillae immediately behind the infrarostrodont; the tips are somewhat pustulate.

Lingual papillae: AJL 3404 has four simple papillae, arranged in a transverse row; the medial pair is about twice the height of the lateral ones.

Buccal floor arena: Roughly circular, almost as wide as the buccopharyngeal floor, and with 4 - 6 long, simple papillae concentrated roughly on either side of the arena; one closely-spaced pair on either side is much longer than the others. A pair of short papillae lie on the posterior border, and the arena is irregularly scattered with 8 - 10 pustulations.

Prepocket papillae: A large palp on either side.

Buccal pockets: Narrow, deep, longitudinally oriented, and imperforate.

The **ventral velum** is broad, moderately thick, of even width throughout, with a row of six or seven evenly-spaced pustulations along its anterior margin, and free along its entire posterior border, which is feebly crenulate. Supporting spicules are not apparent.

Ventral pharynx: Details are not clear in the specimens dissected, but in AJL 3404 the right filters are obliquely oriented, somewhat arched, with tertiary folds, and open.

Bufo gutturalis Power, 1927

Bufo regularis gutturalis Power, 1927, *Trans. Roy. Soc. S. Afr.*, 14:416, pl. 21, fig. 2. Type locality: Lobatsi and Kuruman [Botswana-Transvaal border]. Syntypes in the McGregor Museum, Kimberley, South Africa.

Bufo regularis (non Reuss, 1834): Poynton 1964:51, fig. 15. Van Dijk 1971:73.

Bufo gutturalis Power: Passmore & Carruthers 1979:68, figs. Poynton & Broadley 1988:452. Lambiris 1988:18, figs., pl. 2 figs. 1a-c; 1989a:49; 1989b:52, figs. 14 & 15, pl. 2 figs 2a-c.

ADULT LARYNX (Table 1; Pl. 6, figs. 1 & 2)

Material examined: ZIMBABWE: AJL 676 (m, SVL 85,0 mm), Harare. AJL 716 (m, SVL 78,0 mm), Kutama Mission. AJL 818 (m, SVL 72,5 mm), Rhodes Estate Preparatory School, Matopos. SOUTH AFRICA - NATAL: AJL 1969 (m, SVL 68,4 mm), Waterfall. AJL 1952 (f, SVL 86,5 mm), Mtunzini. AJL 2458 (f, SVL 80,3 mm), Makhamisa Pan, Umfolosi Game Reserve. AJL 2592 (f, SVL 90,2 mm), Spioenkop Dam.

Advertisement call: A trilled snore at about 1 kHz and about one second long, repeated about once in three seconds (Passmore & Carruthers 1979:68), from partly concealed or exposed positions at the water's edge. The choral structure is usually antiphonal.

Male larynx:

Pharyngeal mucosa: A thick layer covering the dorsal surface of the arytenoid cartilage only, and clearly demarcated from it.

Arytenoid cartilage: External margin broadly rounded, internal margin U-shaped; the anteroventral margin is slightly ridged. Incisura, prominentiae apicales and apical cartilage are lacking. An arytenoid valve is present, the dorsal element prominent and rounded, the ventral element narrower and less conspicuous. Pulvinaria vocalia are not discernible.

Arytenoid fossa: Wide, the arytenoid shelf being reduced to a short narrow lip, and deeply excavate.

Vocal cord: Moderately narrow at mid-point, flaring widely at its insertions on the arytenoid cartilage. The anterior margin is slightly flanged, and cartilaginous buttresses are present on the posterior margin; the dorsal one is more robust than the weakly-developed ventral one. There is no frenulum.

Fibrous body: Large, oval, and almost entirely visible. The posterior margin lies medial to the anterior border of the posterior membrane.

Posterior membrane: Forms a broad, well defined septum.

Epiglottidean gland: Well-developed but simple in shape.

M. hyoglossus has a rather short origin on the ventral portions of the arytenoid and cricoid cartilages.

LARVAL BUCCOPHARYNX (Table 2; Pl. 10, fig. 2a & b)

Identification of larvae: Based on a series from Milton Park, Harare, Zimbabwe (AJL 1464-1485, stages 20-46; 9 Sept.-10 Nov. 1980), from eggs laid by identified adults, and showing the porous parotid glands locally diagnostic of postmetamorphics from stage 43 onwards.

Material examined: ZIMBABWE; AJL 1478 a & b, stage 36/37, SVL 10,6 & 10,5 mm; AJL 1479 a & b, stage 37, SVL 10,5 & 10,8 mm; AJL 1480, stage 37, SVL 10,9 mm; Milton Park, Harare; silver impregnation.

Larval habitat: More or less permanent open pools, dams and streams of shallow to moderate depth, with sandy or silt bottoms, and usually with both submerged and emergent aquatic macrophytes. Tadpoles feed on algae growing on plants or stones, and on decaying plant matter such as water-lily petioles.

Buccopharyngeal roof

General shape: Triangular, the base about 1.4x the height.

Prenarial arena: About 3.5x broader than deep, moderately excavate, and devoid of papillae or pustulations.

Internal nares: Large, about 0.5x width of roof at level of posterior margins, about 3x as long as broad, obliquely set; medial margin deeply grooved. Anterior internarial distance 0.5x narial length, posterior internarial distance about 1.8x narial length. Anterior margin denticulate.

Narial valve: A moderately deep flap of uniform width.

Postnarial arena: Triangular, base 1.5x wider than height. Two small papillae lie in the centre of the arena. There are three simple

postnarial papillae on either side, the medial one being largest. The **lateral ridge papillae** are large palps with pustulate digitate lobes and the triangular **median ridge** has a serrate margin.

Buccal roof arena: About 1.5x broader than deep, bounded laterally by posteriorly converging rows of 3 - 4 equally spaced subconical papillae which increase regularly in size posteriorly; each row is flanked laterally at about mid-point by a single papilla. The floor of the arena is covered by about 25 - 30 closely scattered pustulations.

Glandular ridge: Not apparent in these specimens.

Dorsal velum: A rather narrow V-shaped fold with regularly-spaced subequal denticulations along the medial half on either side of the apex.

Pressure cushions: There appears to be a single triangular cushion with a rather broad ciliary groove, on either side.

Buccopharyngeal floor

General shape: Broadly oval, slightly wider than deep, with a median longitudinal depression in the buccal portion.

Prelingual arena: Small, triangular, and devoid of ornamentation.

Lingual papillae: Four equally-spaced, simple, subequal papillae of moderate length, in a slightly anteroconvex transverse row.

Buccal floor arena: About twice as broad as deep, bounded laterally by posteriorly convergent rows of major papillae, of which the first two on either side are largest, slightly pustulate, and arise from a common base; the distal papillae are simple and decrease in size posteriorly. (In AJL 1478 three minor papillae arising from a common base are present lateral to the first major pair on the left side only.) The posterior border of the arena is delimited by a row of 3 - 4 minor papillae on either side, which are rather short and subconical; the medial papilla of each series is longer than the others.

Prepocket papillae: 3 - 4 short, simple conical papillae grouped together with 2 - 3 pustulations, set far forward on either side.

Buccal pockets: Oval to rounded, of moderate depth, and imperforate.

Ventral velum: Broad, U-shaped, of subequal width throughout, rather thick, and supported by distinct spicules, each of which is

associated with a short, rounded major projection. The middle third of the velum has about 6 additional short rounded marginal papillae on either side of a slightly larger closely-spaced median pair overlying the larynx.

Branchial baskets: Triangular, major axis transverse; combined areas about two-thirds that of buccal area.

Filter plates: Curved, imbricate, more or less covering the cavities; filter rows with short secondary and tertiary folds and narrow canals.

Bufo pusillus Mertens, 1937

Bufo maculatus (non Hallowell, 1854): Passmore & Carruthers 1979:70, figs. Poynton & Broadley 1988:460.

Bufo regularis pusillus Mertens, 1937, *Abh. Senckenb. naturf. Ges.*, 435:17, fig. 1. Type locality: Letaba Camp, Kruger National Park. Holotype in the Senckenberg Museum, Frankfurt.

Bufo pusillus Mertens: Poynton 1964:53, fig. 16. Channing 1972:509, fig. 1. Lambiris 1989a:50; 1989b:55, figs. 16 & 17, pl.2 fig. 3a & b.

ADULT LARYNX (Table 1; Pl. 6, figs. 2 & 3)

Material examined: ZIMBABWE: AJL 1559 (m, SVL 59.0 mm), Atlantica Ecological Research Station, 23 km W. of Harare. AJL 1168 (f, SVL 64.0 mm), Maori Ranch, 17.9 km SE. of Umvukwes.

Advertisement call: A strident croak, not as distinctly trilled as that of *B. gutturalis*. The call is about 0.5 second long, at about 1.8 kHz (Passmore & Carruthers 1979:70) and is uttered about once a second from partly concealed positions on land at the water's edge, at night. Choral structure is usually antiphonal.

Male larynx:

Pharyngeal mucosa: Covers the dorsal surface of the arytenoid cartilage only, from which it is clearly demarcated, and thickest anteriorly; the surface lacks elaborate folds.

Arytenoid cartilage: External and internal margins broadly rounded. Incisura, prominentiae apicales and apical cartilage are absent. The arytenoid valve is a narrow rim along the internal margin of the occlusal surface, which is not ridged. A ventral pulvinaria vocalia is evident. The width of the arytenoid shelf is about one-third the medial width of the occlusal surface.

Arytenoid fossa: Greatest width equal to that of the arytenoid shelf; deeply excavate.

Vocal cord: Moderately narrow at mid-point, flaring widely at it's insertions. The anterior margin is not flanged. Cartilaginous buttresses are present on the posterior margin only; they are narrow but prominent, and united by a narrow marginal flange. There is no frenulum.

Fibrous body: Large and bipartite, the medial portion very broadly ovate, the lateral portion more rounded. The posterior margin of the

medial lobe lies internal to the anterior margin of the posterior membrane.

Posterior membrane: Prominent. The superior and inferior margins are much wider than the mid-point.

Epiglottidean gland: An inconspicuous narrow fold of mucosa closely applied to the inferior margin of the arytenoid cartilage, in the specimen examined.

M. hyoglossus: Originates moderately broadly on the arytenoid cartilage and ventral pulvinaria, entirely anterior to the level of the inferior cartilaginous buttress.

LARVAL BUCCOPHARYNX (Table 2; Pl. 11, fig. 1a & b)

Identification of larvae: Tadpoles from eggs laid by identified adults, and compared with Channing 1972.

Material examined: ZIMBABWE: AJL 1841 a & b; Atlantica Ecological Research Station, 23 km W. of Harare; stage 37, SVL 7,5 and 7,6 mm; silver impregnation.

Larval habitat: Pools and quiet streams, in open savanna or grassland, with sandy or silted bottoms and with submerged and marginal emergent macrophytes.

Buccopharyngeal roof

General shape: Truncately triangular, base about 1.5x greater than height. General surface more or less regularly concave.

Prenarial arena: Large, roughly trapezoid, greatest width about twice depth, with prominent folds on the lateral margins, and with a small, pustulate central papilla.

Internal nares: Large, narrowly elliptical, obliquely set. Length slightly greater than half width of roof at level of posterior margins of nares. Anterior internarial distance about 0.4x and posterior internarial distance about 1.9x the length of a naris. A very shallow groove is discernible along the medial border. The anterior margin is smooth.

Narial valve: A prominent, shallowly triangular flap.

Postnarial arena: Four cylindrical, transversely-arranged **postnarial papillae** at about the level of the posterior margin of the nares in two closely-spaced pairs on either side of the mid-line; the lateral ones simple, the medial ones notched apically. The **lateral ridge papillae** are large and palpoid, with smooth digitate lobes. The **median ridge** is a trapezoid flap, surmounted on a broad raised base, and with a tridentate superior margin.

Buccal roof arena: An inverted trapezoid, the base about 1.5x the height, and bounded laterally by posteriorly convergent rows of long, subequal, simple conical papillae, four on each side (three on the right side of AJL 1481a. The anterior border is demarcated by 6 - 8 pustulations across the base of the median ridge, and the floor is scattered with 8 - 10 pustulations. 3 - 4 additional pustulations lie external to the major papillae on either side.

Additional pustulations: A very large pustulation (or very short, broad papilla) lies on the anterior lateral border of the dorsal velum on either side.

Glandular ridge: Not discernible.

Dorsal velum: A feebly-developed flap of mucosa devoid of supports or ornamentation.

Pressure cushions and ciliary ridges: Damaged in the specimens dissected.

Buccopharyngeal floor

General shape: Roughly triangular, base about 1.6x height.

Prelingual arena: A deep, narrow trapezoid. A median triangular papilla is present immediately behind the infrarostrodont, and there is a group of three closely-set, simple, subequal, cylindrical papillae in an oblique, backwardly-directed row on either side of the floor, immediately anterior to the lingual papillae.

Lingual papillae: Four long , simple, subequal cylindrical papillae roughly equally-spaced in an anteriorly-directed curve, on a slightly ridged base, and lying anterior to the tongue anlage.

Buccal floor arena: About 1.5x broader than deep, and demarcated laterally by oblique, strongly convergent rows of 5 - 6 cylindrical or subconical major papillae interspersed with 3 or 4 minor papillae on

either side (one pair surmounted on small prominences anterior and internal to the distalmost major papillae). There are no pustulations in the arena. There are two or three minor papillae on the velum, on either side of the mid-line.

Prepocket papillae: There are no definite prepocket papillae or pustulations.

Buccal pockets: Narrow, transverse, shallow and imperforate.

Ventral velum: Narrow, rather thick, with broadly scalloped and thickened margins devoid of ornamentation, converging to a widely V-shaped apex. Supporting spicules are not evident.

Branchial baskets: Narrow, transversely oriented triangles a little less than half the area of the buccal floor.

Filter plates: Large, curved and largely covering the filter chambers; mesh fine, with short secondary and tertiary folds, and channels narrower than the filter rows.

Bufo garmani Meek, 1897

Bufo garmani Meek, 1897, *Field Mus. Nat. Hist. Zool. Ser.*, 1:176. Type locality "Haili" [foot of Gobis range, about 48 km SE of Berbera, Somaliland]. (Corrected to "Halleh, British Somaliland" by Poynton 1964:55.) Syntypes in the Chicago Museum of Natural History, and in the Museum of Comparative Zoology, Harvard. Poynton 1964:55, fig. 17. Van Dijk 1971:73. Passmore & Carruthers 1979:72, figs. Poynton & Broadley 1988:455. Lambiris 1989b:57, figs 18 & 19, pl. 2 figs. 4a & b. Channing 1991:81, fig. 1.

ADULT LARYNX (Table 1; Pl. 7, figs. 3 & 4)

Material examined: ZIMBABWE: AJL 1073 (m, SVL 89,0 mm), Kwekwe. AJL 934 (f, SVL 66,0 mm), Nyanyana River Mouth, Lake Kariba. SOUTH AFRICA: TRANSVAAL - AJL 673 (m, SVL 78,0 mm), Olifants River, 40 km SW of Hoedspruit.

Advertisement call: A loud [untrilled] bray, about half a second long, repeated about once a second, at a frequency of about 1 kHz (Passmore & Carruthers 1979:72). Calls are uttered at night from exposed positions on land at the water's edge, in a definite choral sequence.

Male larynx:

Pharyngeal mucosa: Covers the dorsal surfaces of the arytenoid cartilages only, thickest anteriorly and lacking elaborate folds.

Arytenoid cartilage: External margin broadly U-shaped, internal margin widely V-shaped. Incisura, prominentiae apicales and apical cartilage are absent. The arytenoid valve is present as a very weakly developed fold along the internal superior and inferior margins of the occlusal surface of the cartilage, which lacks ridges. The inferior pulvinarium vocale is clearly defined, the superior pulvinarium feebly so. The arytenoid shelf is a little less than one half the medial width of the occlusal surface.

Arytenoid fossa: Width about equal to that of the arytenoid shelf; deeply excavate.

Vocal cord: Narrow at mid-point, flaring widely at the insertions. The anterior margin lacks flanges and the cord is not strongly curved in section. Long, relatively slender cartilaginous buttresses are present on the posterior margins and are united by a narrow marginal flange. There is no frenulum.

Fibrous body: Large and bipartite; the medial portion is ovate and not obscured by the vocal cord, the lateral portion squarer. The

posterior margin of the medial lobe lies internal to the anterior margin of the posterior margin.

Posterior membrane: Well developed and moderately broad towards the extremities, narrowest medially.

Epiglottidean gland: A free narrow fold lying along the greater part of the inferior surface of the arytenoid cartilage.

M. hyoglossus: Inserts broadly on the inferior surface of the arytenoid cartilage, anterior to the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX (Table 2; Pl. 11, fig. 2a & b)

Identification of larvae: Based on a series from Manyeleti Game Reserve, Transvaal, South Africa (AJL 2914-2922, stages 38-45, collected in December 1988), showing the divided interorbital bars and reddish infusions of the thighs diagnostic of postmetamorphic frogs.

Material examined: SOUTH AFRICA: TRANSVAAL - AJL 2914a & b, stage 38, SVL 13.0 and 11.5 mm; AJL 2195a & b, stage 39, SVL 14.0 and 13.5 mm; Manyeleti Game Reserve; silver impregnation.

Larval habitat: Shallow temporary water bodies with a sandy bottom and few aquatic macrophytes, frequently rather exposed, in bushveld or grassland or open woodland. Quiet backwaters of rivers are sometimes used. My few field records indicate feeding behaviour broadly similar to that of *Bufo gutturalis* although the load of finely particulate material in waters occupied by *B. garmani* tadpoles appears to be lower than that of *B. gutturalis*.

Buccopharyngeal roof

General shape: Triangular, the base about 1.2x the height.

Prenarial arena: Roughly square, very slightly broader than deep, deeply excavate, and with a large, well-developed bicuspid prenarial ridge just anterior to the nares, and extending almost across the arena.

Internal nares: Large, their length about 0.4x the width of the roof at the level of the posterior margins, about 4x as long as broad, and obliquely set. The medial margin is deeply grooved over the posterior half. Anterior internarial distance 0.5x narial length,

posterior internarial distance about twice narial length. Anterior margins of nares smooth.

Narial valve: A deep flap of uniform width.

Postnarial arena: Very narrow, width about 7x depth. Three (two on one side in AJL 2914a) rather robust conical **postnarial papillae** are arranged obliquely on either side in a row parallel to each naris, the middle one in each row being much larger than the outer ones. The **lateral ridge papillae** are short, broad, stubbily digitate palps and the rather deep **median ridge** has a strongly bicuspid free margin.

Buccal roof arena: About as broad as deep, one third the width of the roof, and bounded laterally by 3 - 4 short, simple conical papillae, regularly spaced and slightly increasing in size posteriorly; the posteriormost papilla on either side tends to be more slender than its fellows. There are no pustulations within or outwith the arena.

Glandular ridge: Not clearly discernible.

Dorsal velum: A feebly developed transverse fold, only slightly inflected posteriorly, with a short, moderately wide oesophageal funnel.

Pressure cushions and ciliary ridges: Details are not clear in the preparations available.

Buccopharyngeal floor

General shape: Roughly triangular, base about 1.1x height.

Prelingual arena: Small and square. There are two series, a single long cylindrical papilla on either side arising from the posterior end of the lateral wall of the narrow, rather square, prelingual arena; and two pairs of closely apposed long, cylindrical papillae anterior to, and on either side of, the tongue anlage.

Lingual papillae: Absent.

Buccal floor arena: About 3x broader than deep, bounded posteriorly by a transverse row of 9 - 11 subequal simple, subconical, moderately elongate papillae spaced more closely laterally than medially, and with a single similar papilla on either side indicating the anterior level of the arena. There are no pustulations or other papillae.

Prepocket papillae: Absent.

Buccal pockets: Shallow, feebly defined, oriented in a slightly posterolateral direction.

Ventral velum: A broad fixed portion (about twice the width of the free portion) with a somewhat wrinkled but otherwise unadorned surface, is present. The free portion of the velum is supported by strongly developed transverse bars and 3 - 4 longitudinal spicules (the latter sometimes asymmetrical in number and disposition) and with a large median notch bearing an elaborate flap.

Ventral pharynx: Details are not clear in the available specimens.

Bufo rangeri Hewitt, 1935

Bufo regularis rangeri Hewitt, 1935, *Rec. Albany Mus.*, 4:285. Type locality: "Glennifer", Kei Road, Cape Province. Holotype in the Port Elizabeth Museum, South Africa.
Bufo rangeri Hewitt: Poynton 1964:57, fig. 18. Van Dijk 1971:73. Passmore & Carruthers 1979:74, figs. Lambiris 1988:19, figs., pl. 2 figs. 2a, b; 1989a:53.

ADULT LARYNX (Table 1; Pl. 8, figs. 1 & 2)

Material examined: SOUTH AFRICA: NATAL - AJL 1237 (m, SVL 85.0 mm), Camp Site, Royal Natal National Park. AJL 2151 (f, SVL 85.3 mm), Mount Currie Nature Reserve.

Advertisement call: A short rasping quack, at about 2 kHz and about 0.2 second long (Passmore & Carruthers 1989:74), uttered about twice a second from exposed positions at or near the water's edge, at night. Calling tends to be continuous, and there is a well-developed choral structure.

Male larynx:

Pharyngeal mucosa: Moderately thick, and blending insensibly into the antero-superior margin of the arytenoid cartilage.

Arytenoid cartilage: External margin V-shaped, but outline modified superiorly by the mucosa; internal margin with a small V-shaped notch medially. Incisura, prominentiae apicales and apical cartilage absent. Occlusal surfaces smooth. Arytenoid valve a feeble fold, barely discernible. Pulvinariae vocales well developed.

Arytenoid fossa: Broad and deeply excavate; arytenoid shelf greatly narrowed.

Vocal cord: Moderately broad at mid-point, flaring towards the insertions. The anterior margin is not flanged. Cartilaginous buttresses are well developed and prominent; the straight superior cartilage is about 1.5x longer than the curved inferior cartilage, and both lie well inside the posterior margin of the cord.

Fibrous body: Large and strongly bipartite; the major portion is oval and lies lateral to the anterior margin of the posterior membrane.

Posterior membrane: Broad, but rather fine and translucent.

Epiglottidean gland: Poorly developed.

M. hyoglossus: Originates rather narrowly on the artyenoid and cricoid cartilages.

LARVAL BUCCOPHARYNX (Table 2; Pl. 12, fig. 1a & b)

Identification of larvae: Based on a series from Hillcrest, Natal, AJL 1936-1946, stages 31-46, 7 Feb. 1984, showing markings from stage 43 onwards in common with, and diagnostic of, postmetamorphics.

Material examined: SOUTH AFRICA: NATAL - AJL 1936: Hillcrest; stage 31, SVL 9.4 mm; silver impregnation. AJL 1938: Hillcrest; stage 33, SVL 9.8 mm; silver impregnation.

Larval habitat: Ponds, rivers or streams, in grassland or woodland, with aquatic macrophytes and a sandy or silted bottom, especially where algae and soft or decaying plant matter is available. The tadpoles tend to occupy a position within the water body intermediate between those of *Bufo gutturalis* (shallower and more peripheral) and of *B. pardalis* (deeper and more central).

Buccopharyngeal roof

General shape: Roughly triangular, base about equal to height.

Prenarial arena: About 1.8x broader than deep, moderately excavate, and with a large prenarial palp, each with three smooth digitate lobes of increasing size, arising from the lateral wall on each side. The arena lacks papillae or pustulations.

Internal nares: Large, about 0.6x width of roof at level of posterior margins, about twice as long as broad, obliquely set; medial margin rather deeply grooved. Anterior internarial distance about 0.4x narial length, posterior internarial distance about twice narial length. Anterior margin denticulate, with three equally-spaced rounded lobes.

Narial valve: A moderately deep flap of uniform width.

Postnarial arena: About 3x broader than deep. There are three **postnarial papillae** on either side, two simple minor (only one on the left side of AJL 1938), and one much larger subconical major, set well behind each naris; and a small, pustulate medial papilla between them. The **lateral ridge papillae** are massive palps with three or four denticulate or pustulose digitations. The **median ridge** is a large triangular flap with a strongly denticulate free margin.

Buccal roof arena: About twice as broad as deep, bounded laterally by posteriorly converging rows of three large, subequal conical

papillae, the second and third each bearing a distinct pustulation on the terminal half or third. The floor of the arena has about 16 irregularly scattered pustulations, which are continuous with others between the arena and the median ridge, and between the arena papillae and the velum and glandular ridge.

Glandular ridge: Clearly defined on either side of the buccal roof arena, along the proximal lateral borders of the ventral velum, but with a large medial discontinuity.

Dorsal velum: A weakly developed fold.

Pressure cushions and ciliary ridges: The pressure cushions are not clearly differentiated into medial and lateral portions.

Buccopharyngeal floor

General shape: Roughly triangular, width about 1.6x height.

Prelingual arena: Large, trapezoid. A large pustulose cylindrical papilla arising from either lateral wall, projecting inwards.

Lingual papillae: Four simple, equally spaced subconical papillae arranged in a transverse row, the inner two somewhat shorter than the outer.

Buccal floor arena: About twice as broad as deep, bounded laterally by irregularly spaced and arranged simple conical papillae of various sizes, interspersed with about 15-17 pustulations, also irregularly but more or less anteroposteriorly arranged, and continuous with a few other pustulations beyond the limits of the arena.

Prepocket papillae: A short, conical papilla immediately anterior to each buccal pocket.

Buccal pockets: Oblique, oval, and perforated by a large palpoid papilla with three or four digitations.

Ventral velum: A broad, thick, convex flap of subequal width throughout, supported by two distinct spicules on either side of the midline. The thickened margin has 7 short, rounded, equally spaced projections and no distinct median notch.

Branchial baskets: Triangular, major axis transverse.

Filter plates: Curved, imbricate, partially covering the filter cavities. Filter rows with short secondary and tertiary folds and narrow canals.

Bufo pardalis Hewitt, 1935

Bufo regularis pardalis Hewitt, 1935, *Rec. Albany Mus.*, 4:288, Type locality: Kei Road, Cape Province, Holotype in the Port Elizabeth Museum, South Africa.

Bufo pardalis Hewitt: Poynton 1964:59, fig. 19 (part), Van Dijk 1971:73 (part), Passmore & Carruthers 1979:76, figs. (part), Lambiris 1989a:54.

ADULT LARYNX (Table 1; Pl. 8, figs. 3 & 4)

Material examined: SOUTH AFRICA: EASTERN CAPE - AJL 376 (m, SVL 120.0 mm), Grahamstown, AJL 312 (f, SVL 98.0 mm), Grahamstown, NATAL - AJL 2679 (f, SVL 82.7 mm) Albert Falls.

Advertisement call: A deep, slowly pulsed snore at about 1.75 kHz, and about 1.3 seconds long (Passmore & Carruthers 1979:76), uttered every three or four seconds in deep water, usually partially concealed by emergent vegetation, at night. There is a loose but definite choral structure.

Male larynx:

Pharyngeal mucosa: A thick layer covering the dorsal and anterior surfaces of the arytenoid cartilage, and continuing as a thin, unstructured layer over the antero-inferior surface of the arytenoid cartilage.

Arytenoid cartilage: External margin truncate V-shaped, internal margin very broadly U-shaped. Incisura, prominentiae apicales and apical cartilage are absent. The arytenoid valve is a fleshy ypsiloid prominence along the internal margins of the cartilage, with a median horizontal extension to the anterior margin, and with a conspicuous short rim in the bifurcation. The occlusal surface of the cartilage is finely ridged. Pulvinaria vocalia are not very distinct. The arytenoid shelf is virtually absent.

Arytenoid fossa: Deeply excavate.

Vocal cord: Moderately narrow at mid-point, about 0.25 width at insertions, and curved in section. Anterior margin slightly but distinctly flanged. Prominent cartilaginous buttresses are present on the posterior margin, and are united by a marginal flange. The flared portions of the cord have curved, transverse folds. There is no frenulum.

Fibrous body: Massive, oval, with the posterior border lying lateral to the anterior margin of the posterior membrane.

Posterior membrane: Moderately broad, more widely flared inferiorly than superiorly.

Epiglottidean gland: Not distinguishable from the mucosa.

M. hyoglossus: Arises broadly from an aponeurosis on the anteroinferior surface of the arytenoid cartilage.

LARVAL BUCCOPHARYNX (Table 2; Pl. 12, fig. 2a & b)

Identification of larvae: Van Dijk 1971; Lambiris 1989a.

Material examined: SOUTH AFRICA: EASTERN CAPE - AJL 2981a & b, stage 35, SVL 11,5 and 12,0 mm; Grahamstown; silver impregnation.

Larval habitat: Deep permanent ponds and dams with sand/silt bottoms; away from the banks, especially among fairly dense emergent aquatic macrophytes. Tadpoles feed on algae and on soft or decaying macrophyte material.

Buccopharyngeal roof:

General shape: Roughly pentangular; width about 1.4x height.

Prenarial arena: Rectangular, about 3x wider than deep, more strongly excavate anteromedially than laterally, and devoid of papillae or pustulations.

Internal nares: Large, about 0.5x width of roof at posterior level of margins, about 3.5x as long as broad, obliquely set; medial margin not deeply gooved. Anterior internarial distance about 0.5 narial length, posterior internarial distance about 2.2x narial length. Anterior margin denticulate, 2 - 3 closely-spaced lobes widely laterad to a single more mediad lobe.

Narial valve: A moderately deep flap of uniform width.

Postnarial arena: Narrowly rectangular, about 8x wider than deep. There are two **postnarial papillae** on either side, a moderate-sized spatulate papilla with a shortly tricuspid tip behind the posteromedian border of the naris, and a much larger one set more posterolaterally. The **lateral ridge papillae** are large palps with strongly pustulate

digits, and the large triangular **median ridge** has a denticulate free margin.

Buccal roof arena: About twice as deep as broad, delimited laterally by converging rows of long, subequal, simple conical papillae, and about 0.3x the width of the roof. There are no pustulations or minor papillae.

Glandular ridge: Discernible as a crescentic thickening along tha naterior border of the dorsal velum.

Dorsal velum: Rather narrow, but well developed, and with a conspicuously thickened free border (especially laterally), with 6 - 8 short papillae, increasing in length medially, on the middle half.

Pressure cushions were damaged in the specimens dissected.

Buccopharyngeal floor

General shape: Roughly pentagonal, and rather flat.

Prelingual arena: Narrowly rectangular. A broad, flat, bicuspid papilla on either posterolateral border.

Lingual papillae: A subconical papilla on either side of the tongue anlage.

Buccal floor arena: About 3x wider than deep, and about 0.6x the width of the floor. Bounded laterally by a large robust bifid or trifid palpoid papilla on either side, and posteriorly by an irregularly spaced and arranged series of major and minor simple, subconical papillae with 10 - 11 pustulations scattered roughly along the medial axis.

Prepocket papillae and **Buccal pockets** are absent.

Ventral velum: A moderately broad convex flap of subequal width throughout, lacking distinct supporting spicules; there is a a single large scallop with two or three large blunt papillae on the outer ends of the velum, and the middle fifth has about 8 short, blunt coarse papillae on the free margin.

Branchial baskets: Triangular, major axis transverse; combined area about two-thirds that of buccal area.

Filter plates: Curved, imbricate, covering the cavities. Filter rows with rather short secondary and tertiary folds, and narrow canals.

Bufo fenoulheti fenoulheti Hewitt & Methuen, 1913

Bufo fenoulheti Hewitt & Methuen, 1913, *Trans. R. Soc. S. Afr.*, 3:108. Type locality: Newington and Woodbush, north-eastern Transvaal. Syntypes in the Transvaal Museum, Pretoria, and in the Port Elizabeth Museum.

Bufo vertebralis fenoulheti Hewitt & Methuen: Poynton 1964:63, fig 22. Passmore & Carruthers 1979:80, figs.

Bufo fenoulheti fenoulheti Hewitt & Methuen: Poynton & Broadley 1988:466. Lambiris 1989a:55; 1989b:61, fig. 22, pl. 3 figs. 1a-d.

ADULT LARYNX (Table 1; Pl. 9, figs. 3 & 4)

Material examined: ZIMBABWE: AJL 1153 (m, SVL 28,2 mm), 16 km SSW of Chakari, AJL 1167 (m, SVL 28,0 mm), Maori Ranch, 17,9 km SE of Umvukwes, AJL 624 (f, SVL 33,5 mm), Dombashawa Hill.

Advertisement call: A coarse nasal rasp, at about 3.4 kHz and about 0.5 second long (Passmore & Carruthers 1989:80), uttered about twice per second for several seconds, from exposed or semi-exposed sites near water (usually temporary water-filled depressions on dwalas, or large rock outcrops), at night or in the late afternoon.

Male larynx:

Pharyngeal mucosa: Very thick, and recurved over the dorsum of the larynx, but not thrown into folds.

Arytenoid cartilage: External margin U-shaped; internal margin V-shaped. Incisura, prominentiae apicales and apical cartilage absent. The very broad occlusal surface is somewhat folded on either side of the midline. Arytenoid valve a narrow but distinct ridge along the internal surface. Inferior pulvinarium vocale well-developed, the superior pulvinarium less so.

Arytenoid fossa: Moderately excavate, without a definite shelf.

Vocal cord: Slender and only slightly flared at the insertions, with a small, rounded prominence on the posterior margin at about the mid-point. Flanges, supporting cartilages and frenulum are absent.

Fibrous body: Relatively large and ovoid, the posterior portion lying medial to, and concealed by, the posterior membrane.

Posterior membrane: Broad, and closely applied to the posterior portion of the fibrous body. The anterior margin is thick and strongly defined, and looks as if it could act as a secondary vocal cord.

Epiglottidean gland: Feebly developed.

M. hyoglossus: Arises from a short aponeurosis originating anterior to the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX (Table 2; Pl. 13, fig. 2a & b)

Identification of larvae: Identification is not certain, as none of the tadpoles in the single series examined had been reared to frogs, but these small bufonid tadpoles (a broad mental gap in the oral papillae) cannot be attributed to any other taxon known to occur in the area.

Material examined: SOUTH AFRICA; NATAL - AJL 2984 a-e; Between Ubombo and Mbazwana, Zululand; all stage 25, SVL 3,9 - 4,0 mm; silver impregnation.

Larval habitat: Shallow, exposed water-filled depressions or pools on rock outcrops or granite dwalas, devoid of any aquatic macrophytes. The larvae appear to feed on rather sparse growths of small algae and on organic silt on the bottom of the pools.

Buccopharyngeal roof

General shape: Roughly triangular, base about 1.3x the height.

Prenarial arena: About 3.5x broader than deep, moderately excavate, and lacking papillae or pustulations.

Internal nares: Large, about 0.4x the width of the roof at the level of the posterior margins, about twice as long as broad, and obliquely set. Medial margin not grooved. Anterior internarial distance about equal to narial length, posterior internarial distance about 4.5x narial length. Anterior margin fleshy, notched at about the mid-point.

Narial valve: A simple flap of uniform width.

Postnarial arena: Narrowly rectangular, about 5x broader than deep. There is a single large conical postnarial papilla on either side, the length about equal to the anterior internarial distance. The **lateral ridge papillae** are large and palpoid, with three strong, smooth lobes and the large triangular **median ridge** has a slightly denticulate free margin.

Buccal roof arena: About as deep as broad, delimited laterally by parallel rows of long, simple, conical papillae, three on either side.

The papillae increase in size posteriorly, the posterior one being about 0.3x longer than the anterior one. There are no minor papillae, and only the faintest suggestion of two or three pustulations in the arena.

Glandular ridge: Discernible as an indistinct ridge along the anterior border of the dorsal velum.

Dorsal velum: Narrower medially than laterally, with a conspicuously thickened free border. Two short, rounded, closely set papillae on either side of the mid-line.

Pressure cushions are not clearly displayed in the specimens dissected.

Buccopharyngeal floor

General shape: Roughly pentagonal. The infralabial arena is deeply excavate, and the depressed lateral portions of the buccal floor are divided by a transverse ridge on either side.

Prelingual arena: Deeply arcuate, with a low curved ridge a little behind the root of the beak.

Lingual papillae: Four short, rounded, closely-set papillae arranged in a transverse row anterodorsally, flanked by a curved narrow transverse ridge on either side.

Buccal floor arena: About 2.5x wider than deep, and about 0.4x the width of the floor. Bounded laterally by a very large bifurcate palpoid papilla on either side, each straddled by a pair of minor papillae basally, and a pair of simple conical papillae (the anterior one larger) internal to the palpoid papillae. 4 - 5 minor papillae are irregularly scattered in the middle of the arena.

Prepocket papillae are absent, although large, somewhat oblique, closed **buccal pockets** are present.

Ventral velum: A broad convex flap of subequal width, lacking distinct supporting spicules. The medial third is convex, the lateral thirds are somewhat undulant. The free margin is slightly thickened but lacks any ornamentation.

Branchial baskets: Triangular, major axis transverse. Combined area more than two-thirds that of buccal area.

Filter plates: Curved, open. Filter rows with short secondary and tertiary rows, and narrow canals.

Genus *Schismaderma* A. Smith, 1849

Schismaderma A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App.: 28. Type species by monotypy: *S. lateralis* A. Smith, 1849 (substitute name for *Bufo carens* A. Smith, 1848).

Schismaderma carens (A. Smith, 1848)

Bufo carens A. Smith, 1848, *Illus. Zool. S. Afr., Rept.*, pl. 68, fig. 1. Type locality: Interior of Southern Africa. Syntypes in the British Museum (Natural History), London. Trewavas 1933:456, Poynton 1964:60, fig. 20, Passmore & Carruthers 1979:78, figs.
Schismaderma carens (Smith): Van Dijk 1966:255, Poynton & Broadley 1988:484, Lambiris 1989a:56; 1989b:64, figs. 24 & 25, pl. 3 figs. 3a-e.

ADULT LARYNX (Table 1; Pl. 14, figs. 1 & 2)

Material examined: ZIMBABWE: AJL 1074 (m, SVL 79,0 mm), Kwekwe. SOUTH AFRICA: NATAL - AJL 2015 (m, SVL 78,2 mm), Weenen Nature Reserve. AJL 2157 (m, SVL 77,5 mm), Kranskloof Farm, Port Shepstone. TRANSVAAL - AJL 2687 (f, SVL 76,0 mm), Tzaneen.

Advertisement call: A deep, muffled booming sound at about 0.2 kHz and about 1 second duration (Passmore & Carruthers 1979:78), rather bovine in character, uttered repeatedly every three or four seconds; in deep, permanent water bodies with no or minimal water flow; usually at night. There is a loose but definite choral structure.

Male larynx:

Pharyngeal mucosa: Moderately thick and folded, extending beyond the apex of the arytenoid cartilage onto the antero-inferior surface.

Arytenoid cartilage: External margin bluntly V-shaped, internal margin V-shaped with an acute apical angle. Incisura, prominentiae apicales and apical cartilage are absent. Prominent folds form a valve on the anterior margins of the arytenoid cartilage. There is a ventral pulvinaria vocalia only. The arytenoid shelf is distinct but short, restricted to the middle third of the internal margin of the occlusal surface, and conspicuously ridged.

Arytenoid fossa: Deeply excavate. There is a prominent rounded protruberance immediately behind the arytenoid shelf.

Vocal cord: Narrow at mid-point, about 0.3x the width of the insertions, and curved in section. Anterior margin not flanged.

Cartilaginous buttresses are well-developed and prominent. There is a strongly unguiform superior anterior buttress; the long, tapering superior and inferior posterior buttresses are linked by a short flange. There is no frenulum.

Fibrous body: Very small and feebly developed. It does not make contact with the posterior membrane.

Posterior membrane: Broad but delicate, and gently concave.

Epiglottidean gland: Large and prominent, with a fimbriated anterior margin.

M. hyoglossus: Arises beneath the inferior pulvinaria vocalia.

LARVAL BUCCOHPHARYNX (Table 2; Pl. 15, fig. 1a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 3507a-d, stage 30, SVL 10,0 - 10,5 mm; Windy Hill, 20 km NE of Pietermaritzburg; silver impregnation.

Larval habitat: Deep permanent pools and streams with minimal water flow, witrh silty or fine sandy bottoms, and peripheral emergent aquatic macrophytes. Tadpoles feed largely on soft macrophyte material as well as on organic matter in the silt. Unpublished field studies seem to indicate that the characteristic swarming motions of *Schismaderma* tadpole shoals may cause fine particulate matter to be swirled off the bottom of the pool, and possibly ingested. The elaborate architecture of the buccopharynx may lend a measure of credibility to such a speculation.

Buccopharyngeal roof

General shape: Roughly pentangular, and rather regularly concave.

Prenarial arena: Rectangular; width about twice height. A single small, triangular, flap-like papilla lies on the mid-line a little anterior to the internal nares.

Internal nares: Large, about 0.33x width of roof at posterior level of margins, about twice as long as broad, and obliquely set. Medial margin not deeply grooved. Anterior internarial distance about equal to

narial length, posterior internarial distance about 3x internarial length. Anterior margin finely denticulate.

Narial valve: Triangular.

Postnarial arena: Rectangular, about 3x wider than deep. There are two **postnarial papillae** on either side - a small conical papilla close to the base of the narial valve, and a much larger, medially-curving major papilla with a finely pustulate lateral border, diagonally midway between the narial valve papilla and the median ridge. The **lateral ridge papillae** are large and palpoid, bifurcate or trifurcate. The **median ridge** is a small, roughly triangular flap with a lateral constriction on either free side.

Buccal roof arena: About twice as broad as deep, and about one-third the width of the buccal roof. It is delimited laterally by sharply converging rows of robust major papillae of subequal length, and with pustulose (usually shortly bifid, sometimes trifid) tips. 9 - 12 pustules, rather regularly arranged, lie between the anterior border of the arena and the median ridge.

Glandular ridge: A crescentic ridge along the anterior border of the dorsal velum.

Dorsal velum: Rather narrow, of subequal width, and with a thickened posterior margin bearing about 10 short, rounded, closely spaced papillae along the middle third. The more median papillae are well defined, but the lateral ones are more feebly differentiated.

Pressure cushions: Lateral and median pressure cushions are short and broad, arranged linearly, and without any distinct ciliary groove.

Buccopharyngeal floor

General shape: Roughly pentagonal, noticeably excavate medially in the form of a clearly defined posteriorly directed triangle from the infrarostrodont to the centre of the buccal floor arena.

Prelingual arena: Somewhat rectangular. A large, shortly trifid or quadrifid papilla on either posterolateral margin, directed medially. Four papillae within the arena are arranged in a trapezoid, the apex directed posteriorly.

Lingual papillae: A pair of small subconical papillae arranged on either side of the midline, each arising from a distinct base.

Buccal floor arena: The greater part of the buccal floor is so thickly covered with papillae of varying sizes and shapes that it is difficult to define a definite arena clearly. Major papillae are conical or terminally bifid, usually single but sometimes two or three arise from a common base. Minor papillae are shortly conical and simple. Pustulations are absent. The triangular depression in the buccal floor referred to above is bounded laterally by short ridges, and is devoid of papillae.

Prepocket papillae: A group of 4 - 5 very short, almost pustulose minor papillae.

Buccal pocket: Transversely ovoid, closed.

Ventral velum: Moderately broad, strongly convex, and of subequal width throughout. Three supporting spicules are discernible on either side of the midline. The free edge is slightly thickened and bears about 12 - 14 feebly developed, closely-spaced pustulate papillae along the middle third, and 2 - 3 similar papillae at about the midpoint of the outer thirds of the margin.

Branchial baskets: Triangular; major axis postero-transverse. Combinedarea greater than two-thirds that of buccal area.

Filter plates: Curved, imbricate but open. Filter rows with short secondary and tertiary folds, and narrow canals.

DISCUSSION

Adult laryngeal morphology shows a considerable degree of sexual dimorphism in the taxa examined, but intrasexual variation is as slight as intraspecific variation and the female larynx would appear to be as taxonomically useful as that of the male. A definitive atlas of male and female larynxes is beyond the scope and aims of the present study, although it is hoped that the illustrations of larynxes of both sexes of taxa studied in this genus will serve to illustrate the point.

Larval buccopharyngeal morphology also shows a gratifying range of interspecific variation that appears to accord closely with that of adult laryngeal morphology. It also reflects differences in niche selection of tadpoles, so often observed in the field and summarised in the species accounts presented in this study.

It is particularly interesting to note that those tadpoles that are generally found in clear waters over coarsely sandy, stony or rocky bottoms have a simple buccopharyngeal structure with relatively few papillae, arranged in a rather open plan. These include *Bufo gariepensis nubicolus*, *B. garmani* and *B. f. fenoulheti*. Those that live in streams or pans with finer sand or silted bottoms and more aquatic macrophytes have more elaborate and compact structures increasing in complexity according to the nature of their microhabitats. These include *B. gutturalis*, *B. pusillus*, *B. rangeri* and *Schismaderma carens*. *Bufo pardalis* is interesting in that the larva lives typically in deep pools with aquatic macrophytes growing at least peripherally, on silted bottoms. However, it spends most of its time near the surface or in the middle depths, where finely particulate loads are lower than those at the bottom of the pool and probably lives in an environment functionally closer to that of the first group than to the other members of the *gutturalis* group.

Morphology of the adult male larynx and, where known, of the larval buccopharynx support most of the taxonomic conclusions reached by Poynton (1964) and of Poynton & Broadley (1988) as far as Natal taxa are

concerned. Where these authors have indicated problems in the taxa that they recognise (e.g. *Bufo garmani*), laryngeal and buccopharyngeal features seem to clarify issues that have defied resolution by means of more traditional external character analysis. The status of the more problematic taxa are re-assessed below in the light of these characters.

Bufo gariepensis nubicolus

In his discussion of *Bufo gariepensis nubicolus* Poynton (1964:48) remarked that in Lesotho specimens of the nominate form

> "the differential characters show both merging and independent assortment, making the allocation of such specimen to one form or another somewhat arbitrary. The distinctness of the Drakensberg material from typical *gariepensis* justifies taxonomic separation, but the merging of the two forms indicates that this separation can only be made at the subspecific level."

This opinion appears to be justified at least as far as laryngeal morphology is concerned, for the male larynxes of the two taxa are very similar in many respects, particularly with regard to the configuration of the vocal cord and fibrous body. This similarity emphasises the close relationship between the two taxa. The arytenoid and cricoid cartilages and the pharyngeal mucosa are consistently different, as is the posterior membrane, indicating differences best expressed at the subspecific level.

Although *Bufo g. nubicolus* lives and breeds only in alpine habitats, the environmental requirements of the tadpole show some similarity to that of *B. g. gariepensis* in that both live in shallow temporary sandy or stony-bottomed pools with few or no aquatic macrophytes. A detailed comparison of the tadpoles would be most interesting.

Bufo pusillus and *Bufo maculatus*

Tandy (1972) and Tandy & Keith (1972) relegated *Bufo pusillus* Mertens 1937 to the synonymy of *Bufo maculatus* Hallowell, 1854 on the grounds that they found no significant differences between the mating calls of the two forms. Passmore & Carruthers (1979) and Poynton &

Broadley (1988) followed Tandy & Keith, though Lambiris (1989a, 1989b) disagreed with this practice.

Adult laryngeal (both sexes) and larval buccopharyngeal morphology reflect the close affinity of *Bufo pusillus* with those taxa examined of Poynton's (1964: 42) *regularis* [= *gutturalis*] group. On the other hand, the larynx of a male Liberian toad collected and identified by Tandy as *Bufo maculatus* differs in several important details (Plate 7, fig. 1) from that of male *B. pusillus* (Plate 6, fig. 3) from southern Africa -- most notably in the shape of the arytenoid cartilage, the vocal cord, the fibrous body and the greatly reduced posterior membrane. This specimen further differs from *Bufo pusillus* in lacking a light cross on the head; there is only a dark interocular bar.

These differences appear to indicate that the West African and the southern African populations are taxonomically distinct. The name *Bufo maculatus* is a *nomen dubium*, in that the type is lost and that Hallowell's description is insufficiently detailed to indicate clearly the differences between the two taxa. While such an action is clearly not within the scope of the present study, it should be remarked that the designation of a neotype for *Bufo maculatus* in order to stabilise the situation, in terms of Article 75, Recommendation 75E of the International Code, should be considered after a more comprehensive study of this group.

Bufo maculatus Hallowell, 1854
(Table 1; Pl. 7, fig. 1) MATERIAL EXAMINED: BMNH 1984.163 (m, SVL 65.8 mm), Monrovia, Liberia, Collected by J. and M. Tandy.

The *Bufo garmani* complex

Poynton & Broadley (1988:455) have dealt in some detail with the problems arising in trying to define and separate specimens variously identified as *B. garmani* Meek, *B. pseudogarmani* Hulselmans or *B. poweri* Hewitt. This matter is beyond the scope of the present study, but I have examined the larynxes of a series of adult males and a female from Kimberley, the type locality of *B. poweri* (Pl. 7, fig. 2) and from other

localities from the northern Cape within the range of this taxon; they differ from those of *B. garmani* (Pl. 7, figs. 3 & 4) in sufficient degree to warrant recognition of *B. poweri* as a valid species. Tadpoles of *B. poweri* were unfortunately not available for study.

The principal differences are in the arytenoid cartilages (smooth and with a feeble valve in *B. garmani*, strongly ridged or folded on the antero-inferior margin in *B. garmani*); the shape of the bipartite fibrous body (cardioid in *B. garmani*, oval in *B. poweri*); and in the vocal cord (long, narrow buttresses on the posterior border only in *B. garmani*, shorter, robust and much more abruptly tapered buttresses on both anterior and posterior margins in *B. poweri*).

These differences appear to be supported by the findings of Channing (1991), who has examined sonagrams of the calls of *Bufo garmani* from Kenya to South Africa, and of *Bufo poweri* from Zimbabwe, Botswana and South Africa, and who has found differences which he considers species specific.

Bufo poweri Hewitt, 1935
(Table 1; Pl. 7, fig. 2) MATERIAL EXAMINED: NM 1797 (m, SVL 81.3 mm), Kimberley. NM 1809 (m, SVL 95.4 mm), Vryburg. MMK/F/457 (m, SVL 83.5 mm), Kimberley. MMK/F/467 (f, SVL 72.0 mm), Kimberley. MMK/F/475 (m, SVL 63.3 mm), Riverton. MMK/F/476 (m, SVL 66.4 mm), Upington.

Bufo pardalis and *Bufo cruciger*

In a preliminary study of Natal amphibians (Lambiris 1989a:55) it was noted that small but consistent differences between Eastern and Western Cape populations of *Bufo pardalis* required further investigation. These differences included ground colour, details of markings, parotid glands, skin texture, tubercles of the hands and feet, and the tympanum. An examination of larynxes from Eastern Cape toads (Pl. 8, figs. 3 & 4) and Western Cape toads (Pl. 9, figs. 1 & 2) show additional consistent differences. Tadpoles of Eastern Cape populations were available for study (Pl. 13, fig. 2a & b), but none could be obtained from the Western Cape. The differences in both external and in

laryngeal characters are sufficient to justify recognition of the Western Cape population as a separate species.

The name *Bufo cruciger* Oken, 1816 is on the Official Index of Rejected and Invalid Names in Zoology (Opinion 651), but Poynton (*in* Branch *et al.*, 1988:2) notes that the name *Bufo cruciger* P. Schmidt, 1852, is available. This name is accordingly here resurrected for the Western Cape populations, since the type locality of *Bufo pardalis* Power, 1935 (Kei Road) is in the Eastern Cape.

The larynxes differ in the following major respects: The arytenoid cartilage is somewhat V-shaped in *Bufo pardalis* and broadly U-shaped in *B. cruciger*; the latter also possesses an incisura and prominentiae apicales, features not present in other taxa examined. *Bufo cruciger* possesses a well-developed arytenoid valve, lacking in *B. pardalis*. Cartilaginous buttresses are robust and prominent in *B. pardalis*, less strongly developed in *B. cruciger*. The fibrous body of *B. pardalis* is ovoid and does not extend across the width of the vocal cord, as it does in *B. cruciger*. The female larynx also shows a number of differences, the most conspicuous being the prominent superior and inferior fleshy lobes on the anterior margin of the arytenoid cartilage in *B. pardalis*, and the extraordinarily large inferior pulvinaria vocalia in *B. cruciger*.

Bufo cruciger P. Schmidt, 1852
(Table 1; Pl. 9, figs. 1 & 2) MATERIAL EXAMINED: SAM 955 (f, SVL 50,0 mm), and SAM 4253 (f, SVL 37,3 mm), Cape Flats. SAM 2143 (f, SVL 103,5 mm), Cape Town. SAM 43373 (m, SVL 83,8 mm), Varkenvlei, Ottery, Cape Flats. SAM 43377 (f, SVL 104,6 mm), Varkenvlei Road, near Ottery, Cape Flats. SAM 45747 (m, SVL 98,3 mm), and SAM 45750 (f, SVL 104,2 mm) Empire Ave., Hout Bay.

Bufo f. fenoulheti

The larynx of this taxon (Pl. 9, figs. 3 & 4) differs remarkably from those of the other taxa examined in several respects. The pharyngeal mucosa is very thick and the underlying sheet of connective tissue is recurved over the superior surface of the arytenoid cartilage in a manner quite unlike that seen elsewhere. The arytenoid fossa is not so

sharply excavate and lacks any trace of an arytenoid shelf. The vocal cord is narrow and completely different in shape from those of the other taxa examined, especially with respect to the prominence on its posterior border. The posterior membrane is so strongly developed as to suggest a function as an accessory vocal cord. It is possible that these features are characteristic of the *vertebralis* group recognised by Poynton (1964:42), but this has to be confirmed by further study.

Schismaderma carens

The adult larynx (Pl. 10, figs 1 & 2) and the elaborate larval buccopharyngeal floor, with its dense array of papillae and central depression (Pl. 15, fig. 1b), are quite unlike that of any *Bufo* tadpole examined and would appear to add to the evidence supporting recognition of *Schismaderma* as a separate genus.

PLATE 5

BUFO – ADULT HYOLARYNXES

Median sagittal section. View into left half. Anterior to right.

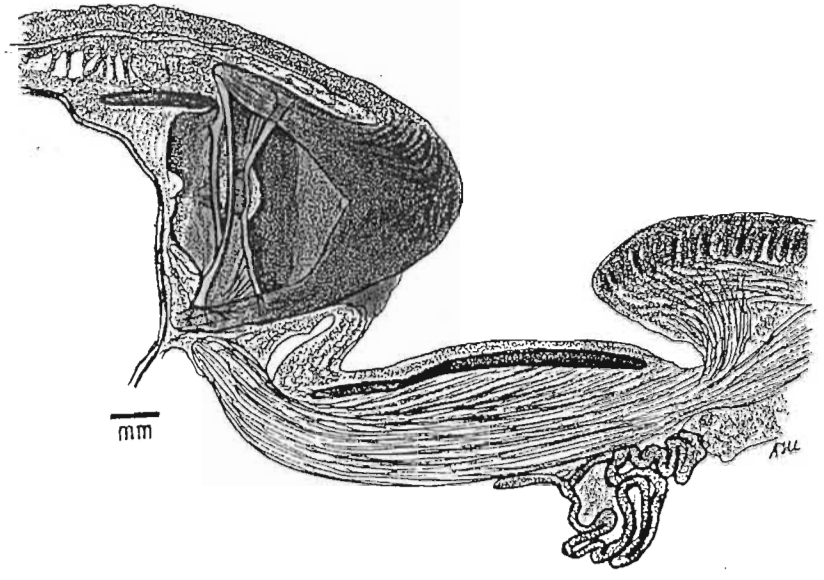


FIG. 1: *Bufo gariepensis gariepensis* A. Smith, 1848
AJL 381 (male), Grahamstown, Eastern Cape, South Africa.

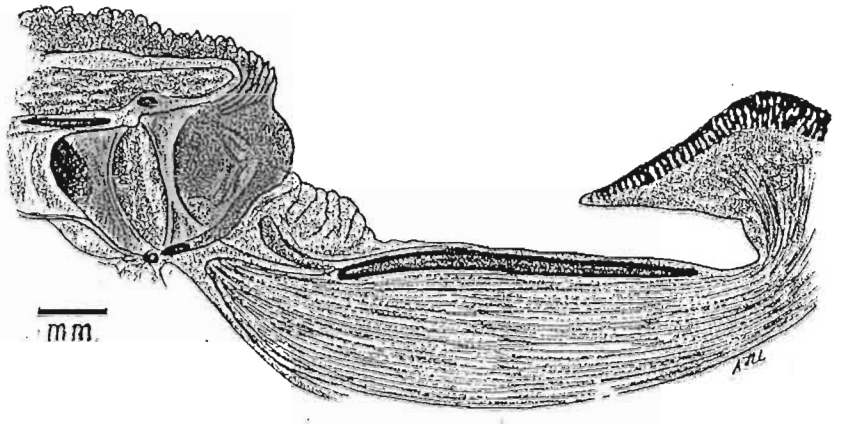


FIG. 2: *Bufo gariepensis gariepensis* A. Smith, 1848
NM 7559 (female), Mountain Zebra National Park, Cradock, Eastern Cape, South Africa.

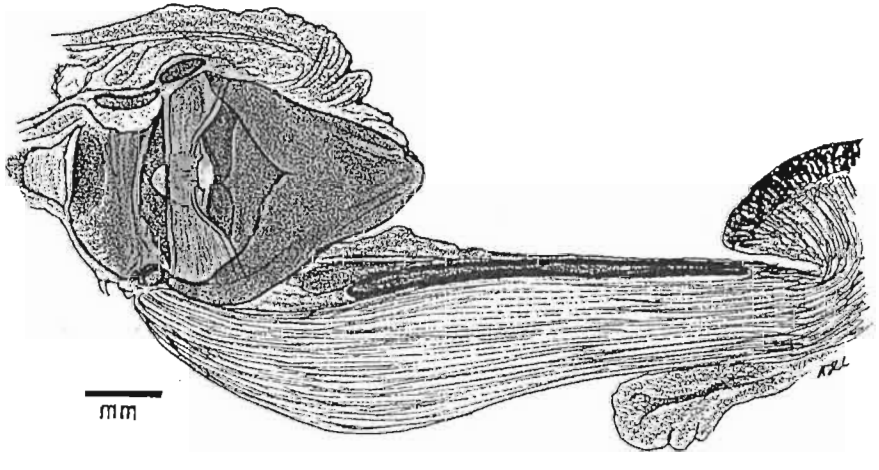


FIG. 3: *Bufo gariepensis nubicolus* Hewitt, 1927
NM 6558 (male), Bannerman's Hut, Giant's Castle Game Reserve, Natal, South Africa.

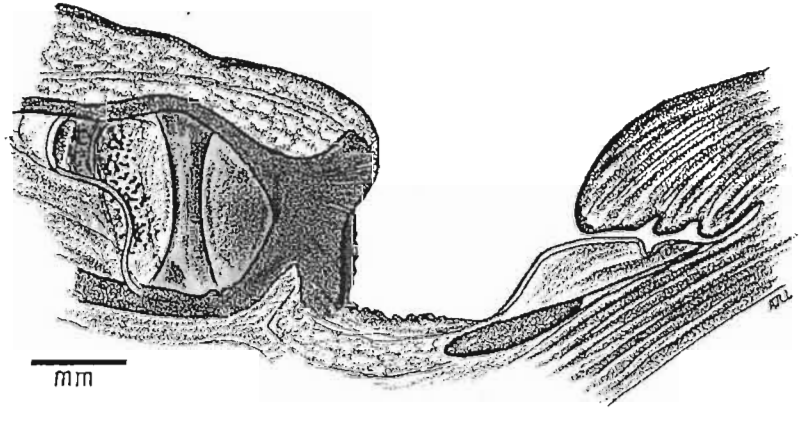


FIG. 4: *Bufo gariepensis nubicolus* Hewitt, 1927
AJL 2454 (female), Injasuti Outpost, Giant's Castle Game Reserve, Natal, South Africa.

PLATE 6
BUFO – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

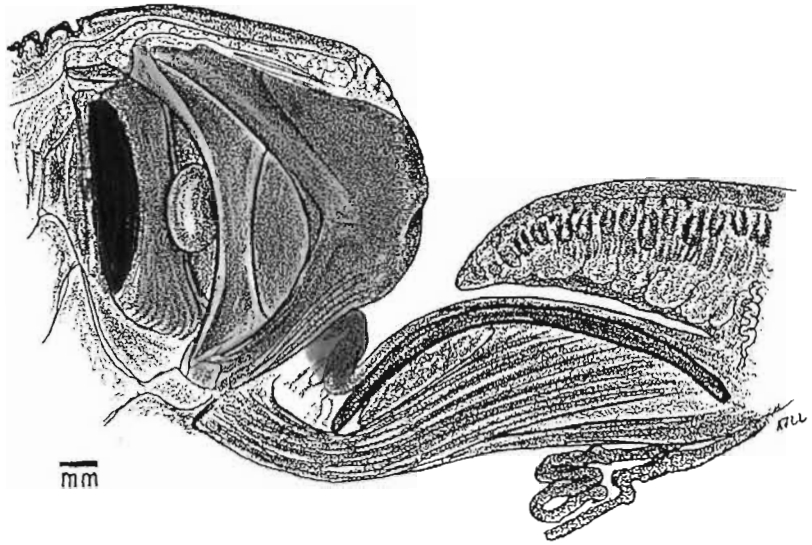


FIG. 1; *Bufo gutturalis* Power, 1927
AJL 716 (male), Kutama Mission, Zimbabwe.

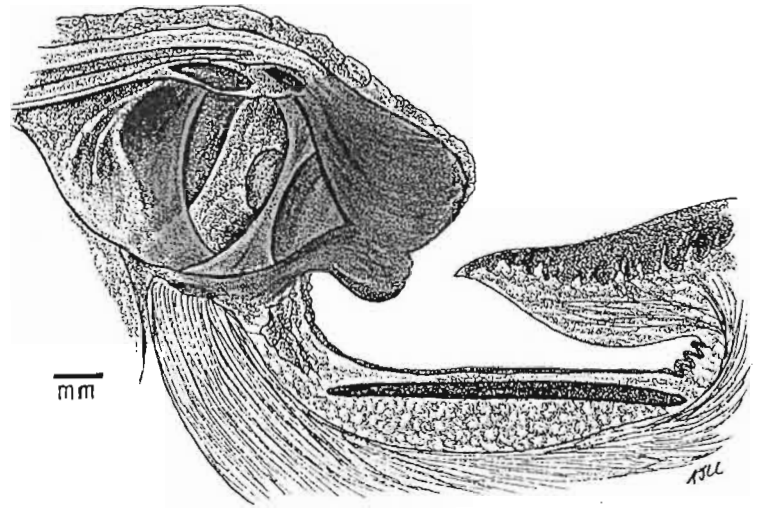


FIG. 2; *Bufo gutturalis* Power, 1927
AJL 2458 (female), Makhamisa Pan, Umfolozi Game Reserve, Natal, South Africa.

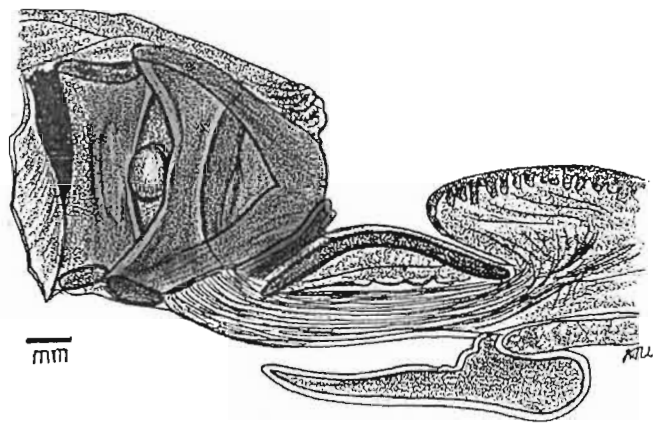


FIG. 3; *Bufo pusillus* Mertens, 1937
AJL 1559 (male), Atlantica Ecological Research Station, 23 km west of Harare, Zimbabwe.

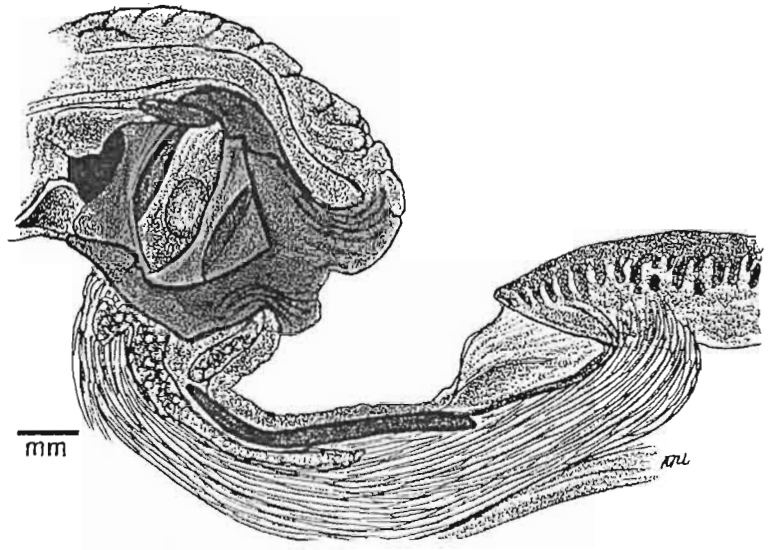


FIG. 4; *Bufo pusillus* Mertens, 1937
AJL 1168 (female), Maori Ranch, 17,9 km SE of Umvukwes, Zimbabwe.

PLATE 7
BUFO – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

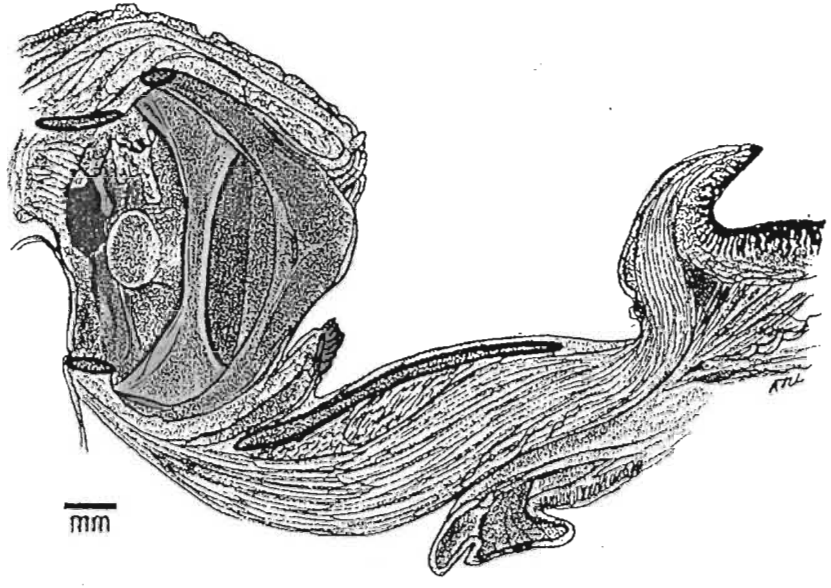


FIG. 1: *Bufo maculatus* Hallowell, 1854
BMNH 1984.163 (male). Monrovia, Liberia.

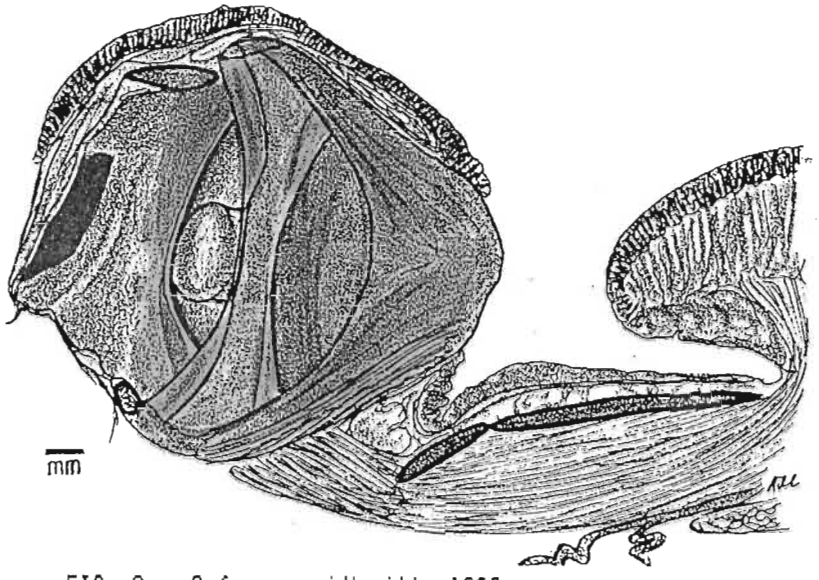


FIG. 2: *Bufo poweri* Hewitt, 1935
NM 1797 (male). Kimberley, Northern Cape, South Africa.

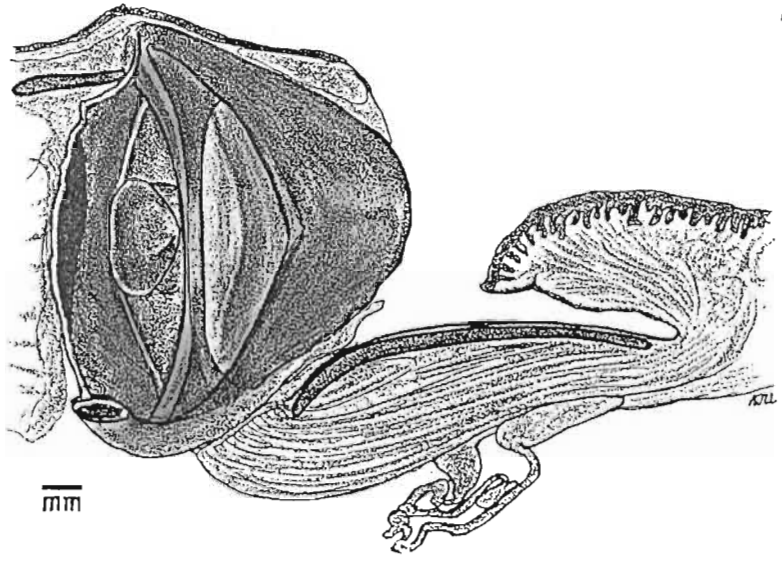


FIG. 3: *Bufo garmani* Meek, 1897
AJL 673 (male). Olifants River, 40 km WSW of Hoedspruit, Transvaal, South Africa.

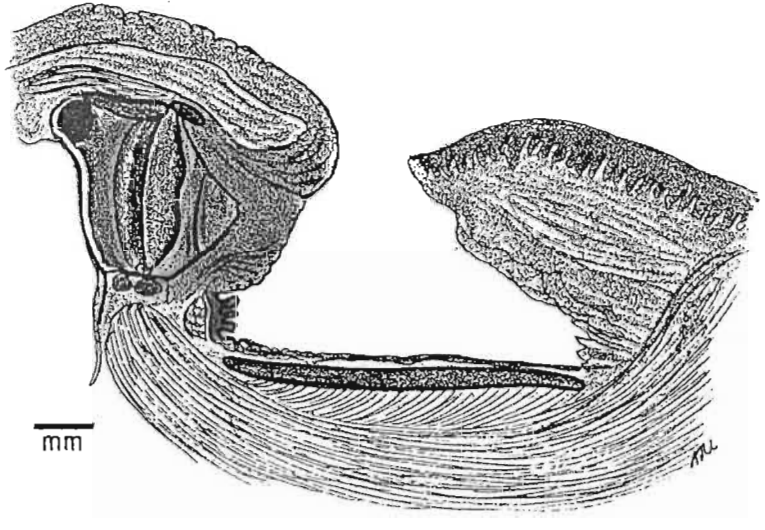


FIG. 4: *Bufo garmani* Meek, 1897
AJL 934 (female). Nyanyana River mouth, Lake Kariba, Zimbabwe.

PLATE 8
BUFO – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

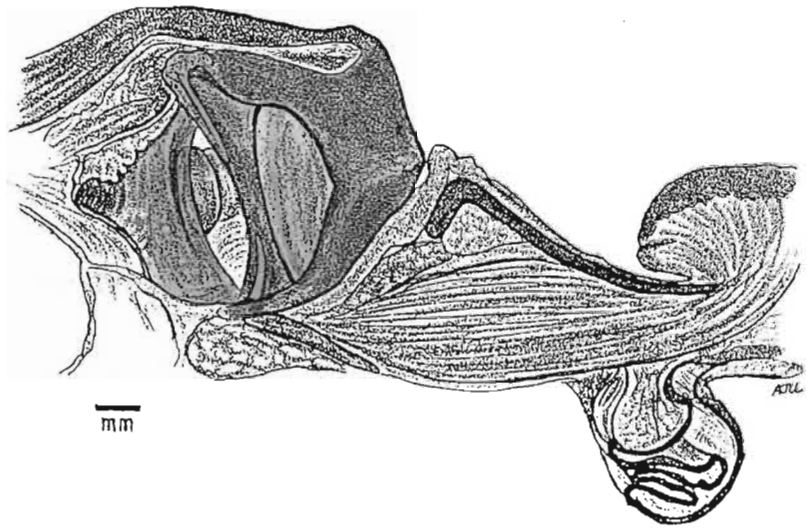


FIG. 1: *Bufo rangeri* Hewitt, 1935
AJL 1237 (male), Camp site, Royal Natal National Park, Natal, South Africa.

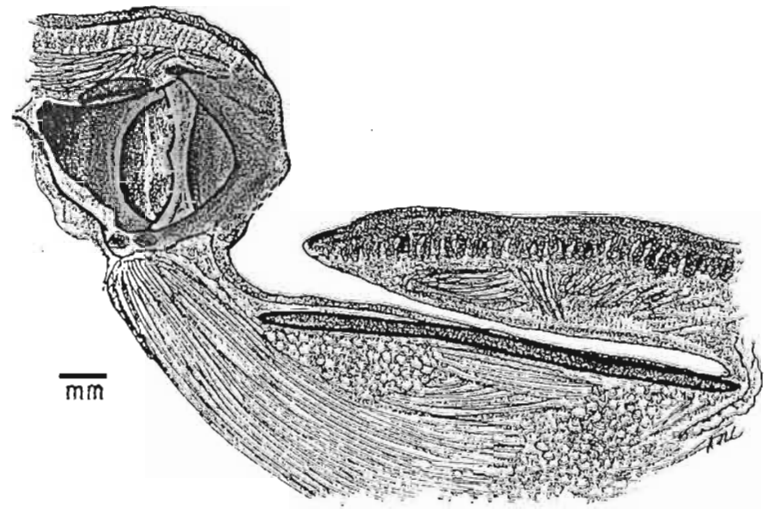


FIG. 2: *Bufo rangeri* Hewitt, 1935
AJL 2151 (female), Mount Currie Nature Reserve, Natal, South Africa.

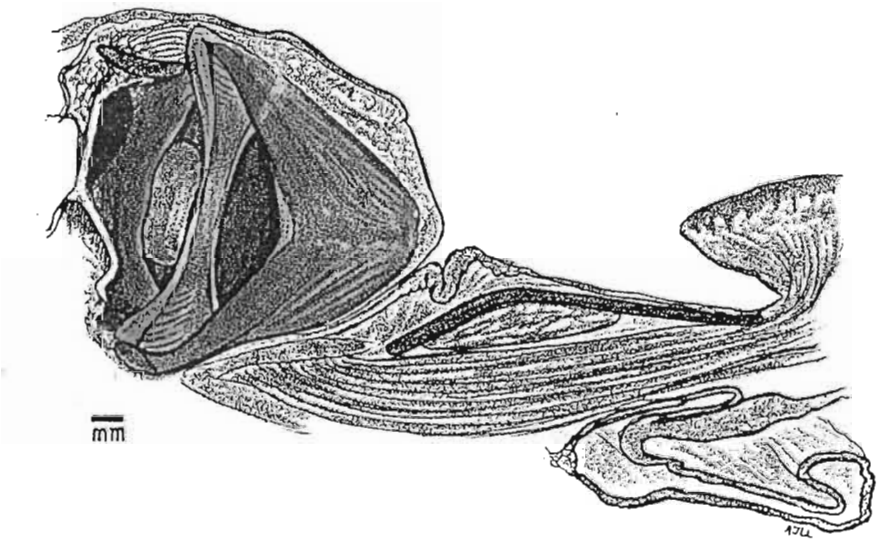


FIG. 3: *Bufo pardalis* Hewitt, 1935
AJL 376 (male), Botanical Gardens, Grahamstown, Eastern Cape, South Africa.

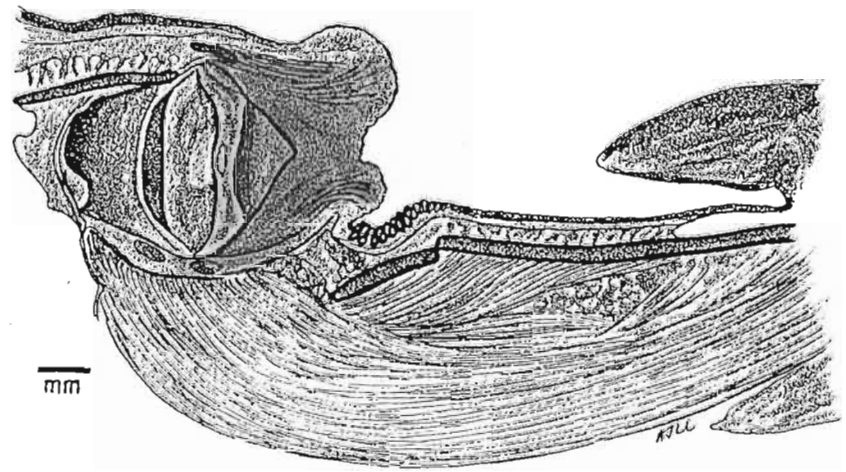


FIG. 4: *Bufo pardalis* Hewitt, 1935
AJL 312 (female), Rhodes University, Grahamstown, Eastern Cape, South Africa.

PLATE 9
BUFO – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

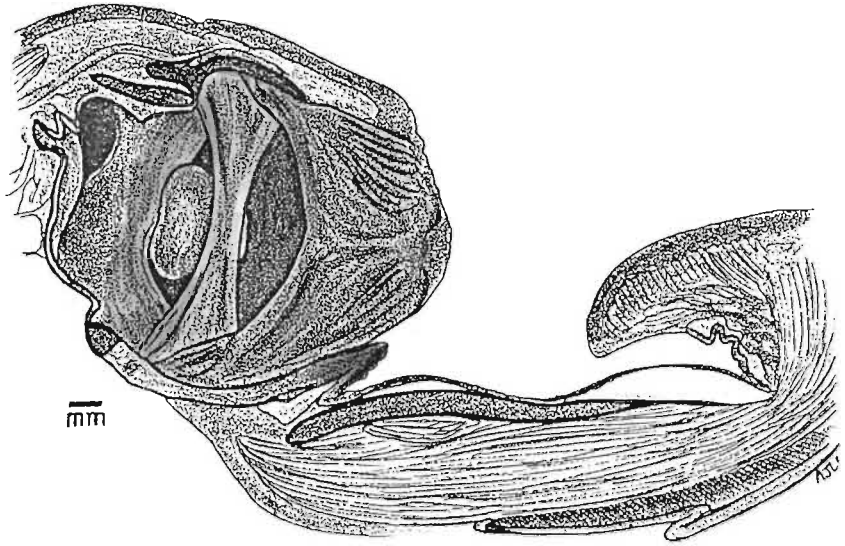


FIG. 1; *Bufo cruciger* Schmidt, 1852
SAM 45758 (male), Strandfontein, Cape Flats, Western Cape, South Africa.

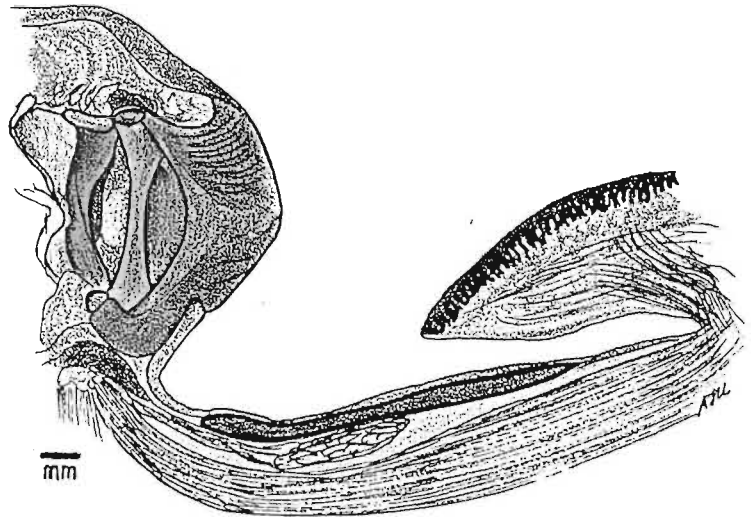


FIG. 2; *Bufo cruciger* Schmidt, 1852
SAM 43377 (female), Varkenvlei Road, near Ottery, Cape Flats, Western Cape, South Africa.

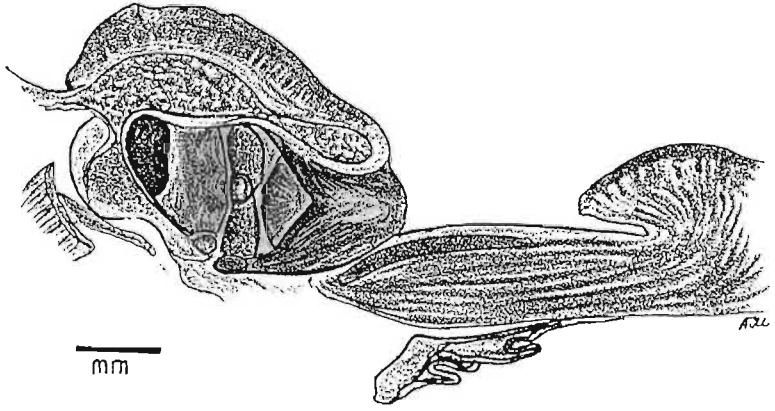


FIG. 3; *Bufo fenoulheti fenoulheti* Hewitt & Methuen, 1913
AJL 1167 (male), Maori Ranch, 17,9 km SE of Umvukwes, Zimbabwe.

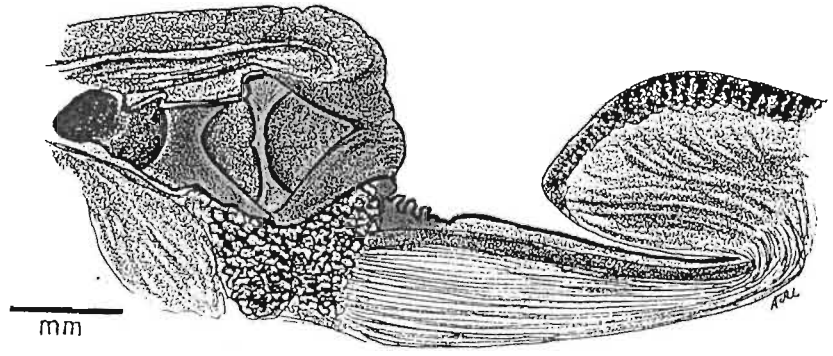


FIG. 4; *Bufo fenoulheti fenoulheti* Hewitt & Methuen, 1913
AJL 624 (female), Dombashawa Hill, Chinamora Communal Land, Zimbabwe.

PLATE 10
BUFO – LARVAL BUCCOPHARYNXES
Roof on left, floor on right

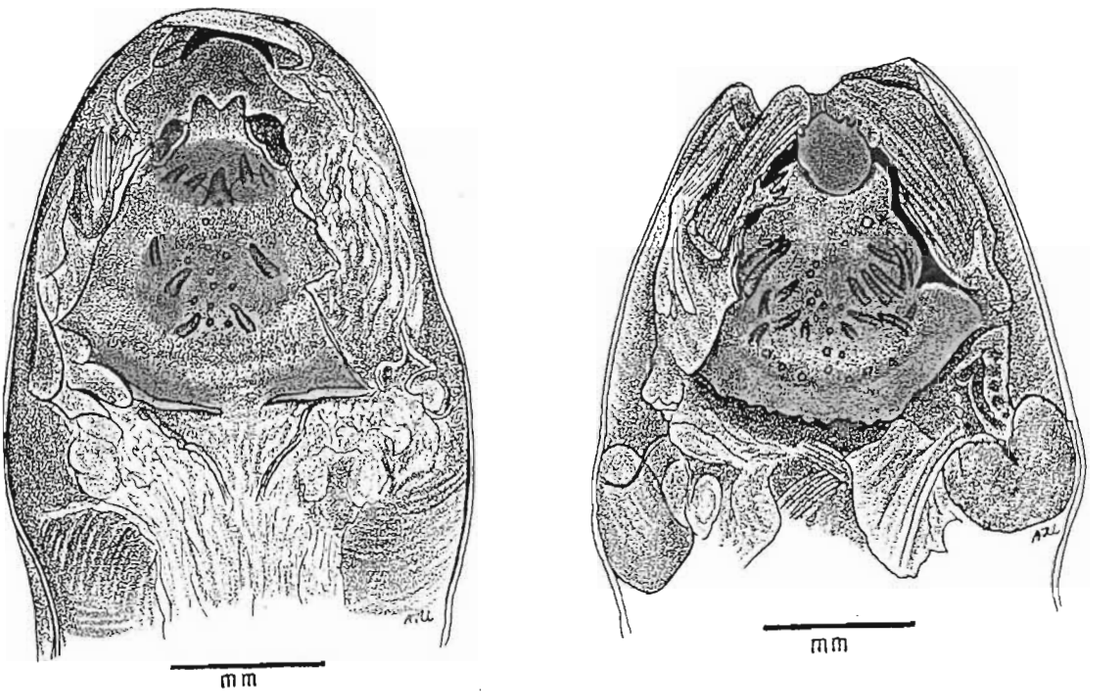


FIG. 1: *Bufo gariepensis nubicolus* Hewitt, 1927
AJL 3406, Stage 39/40, Highmoor State Forest, Natal, South Africa.

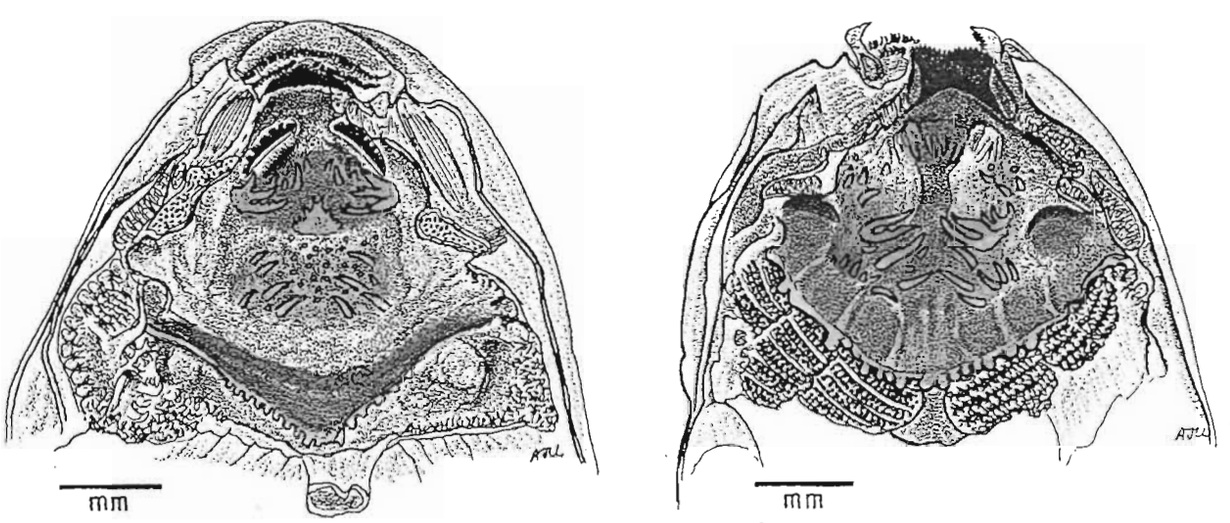


FIG. 2: *Bufo gutturalis* Power, 1927
AJL 1478, Stage 36/37, Milton Park, Harare, Zimbabwe.

PLATE 11
BUFO – LARVAL BUCCOPHARYNXES
Roof on left, floor on right

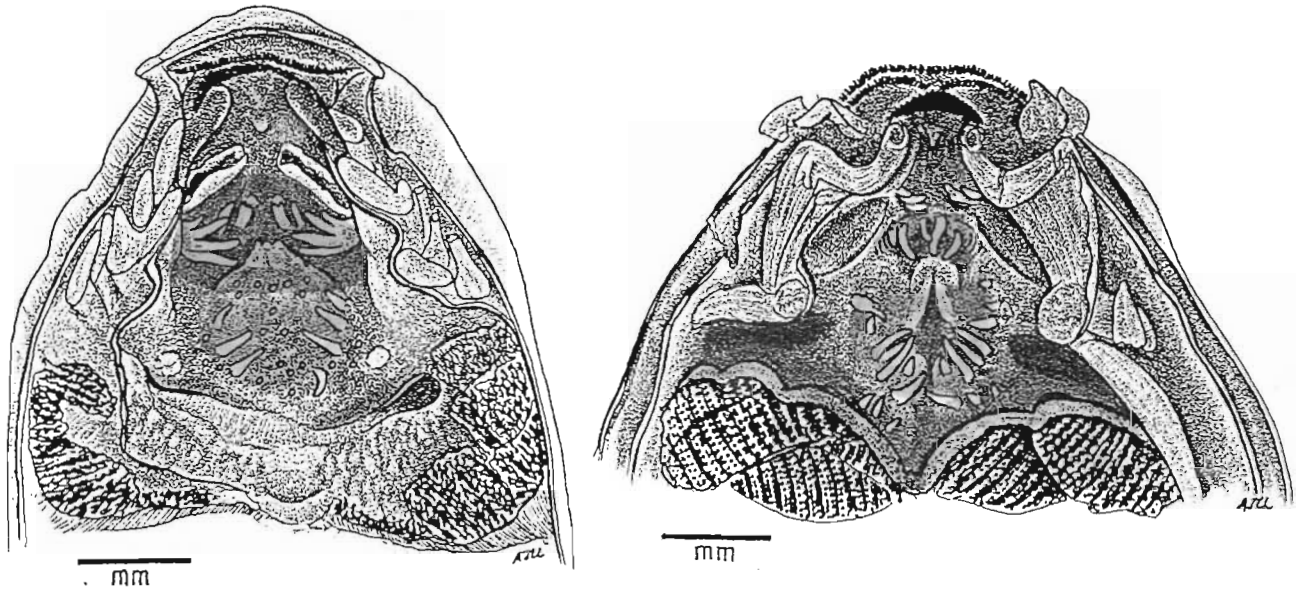


FIG. 1; *Bufo pusillus* Mertens, 1937
AJL 1841a, Stage 37, Atlantica Ecological Research Station, 23 km west of Harare, Zimbabwe.

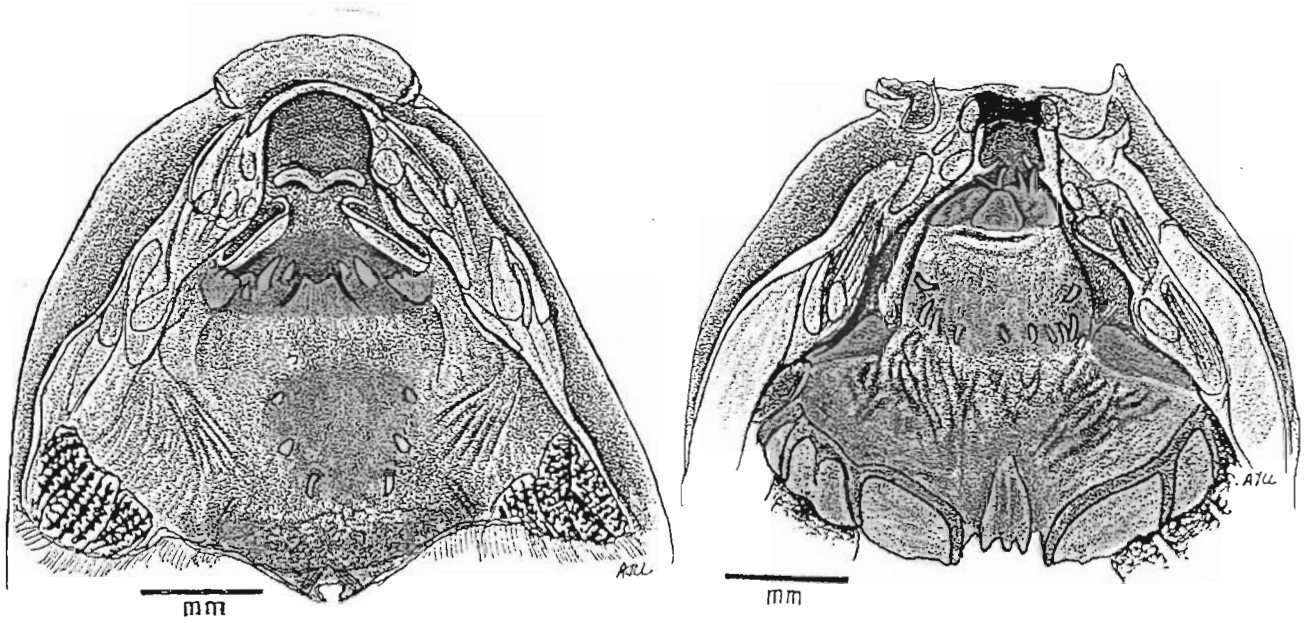


FIG. 2; *Bufo garmani* Meek, 1897.
AJL 2914, Stage 37, Manyeleti Game Reserve, Transvaal, South Africa.

PLATE 12
BUFO – LARVAL BUCCOPHARYNXES
Roof on left, floor on right

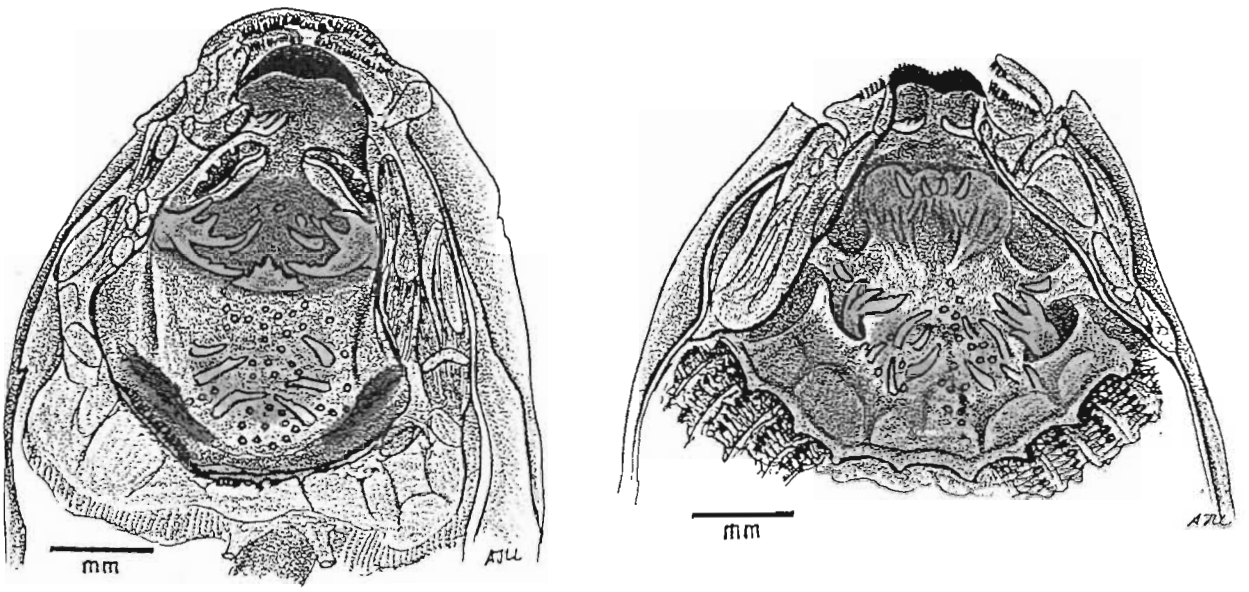


FIG. 1; *Bufo rangeri* Hewitt, 1935
AJL 1938, Stage 33, Hillcrest, Natal, South Africa.

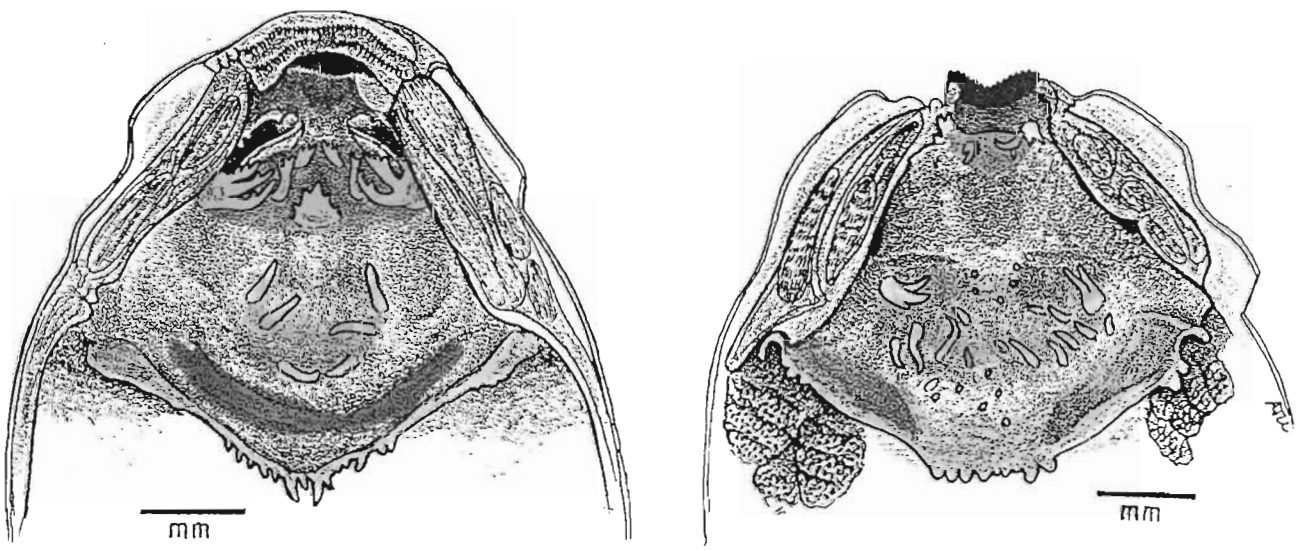


FIG. 2; *Bufo pardalis* Hewitt, 1935
AJL 2981, Stage 35, Grahamstown, Eastern Cape, South Africa.

PLATE 13
BUFO – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

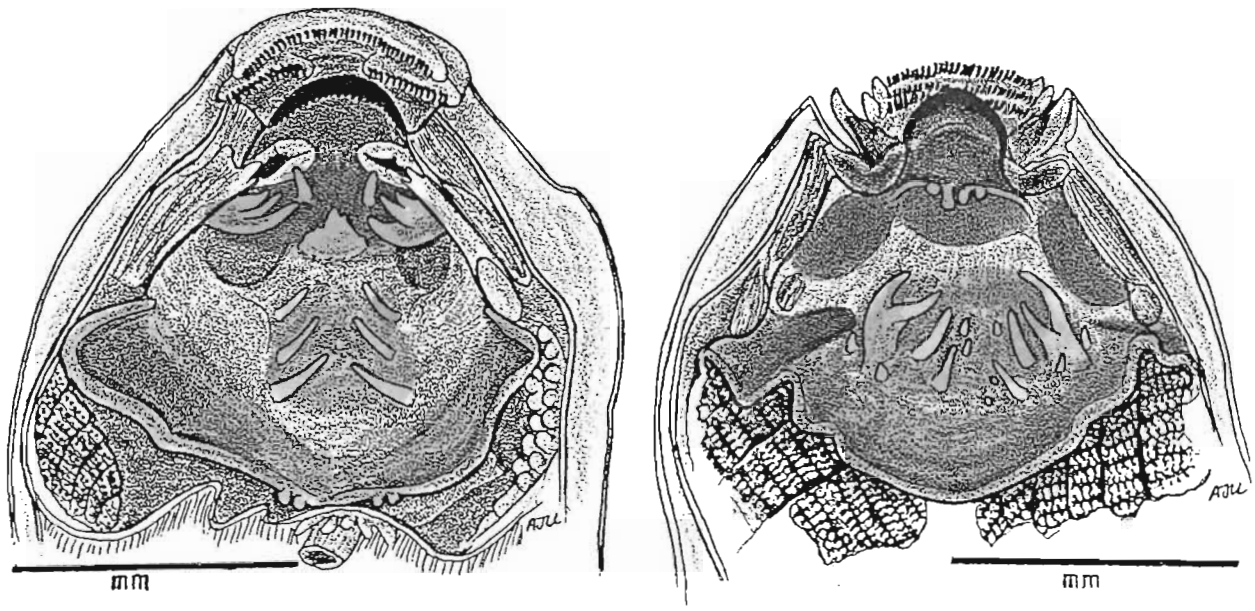


FIG. 2: ? *Bufo fenoulheti fenoulheti* Hewitt & Methuen, 1913
AJL 2894, Stage 25, Between Ubombo and Mbazwana, Natal, South Africa.

PLATE 14
SCHISMADERMA – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

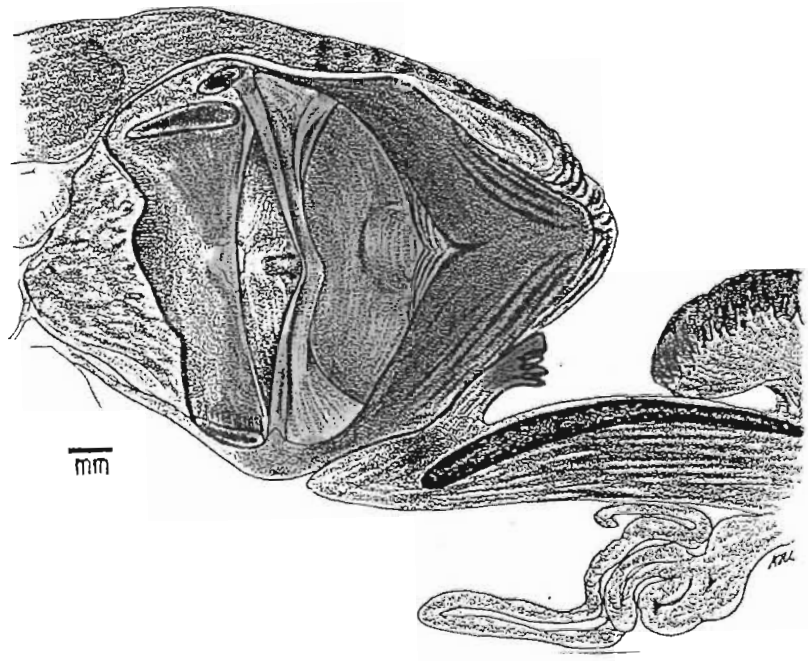


FIG. 1: *Schismaderma carens* (A. Smith, 1848)
AJL 2015 (male), Weenen Nature Reserve, Natal, South Africa.

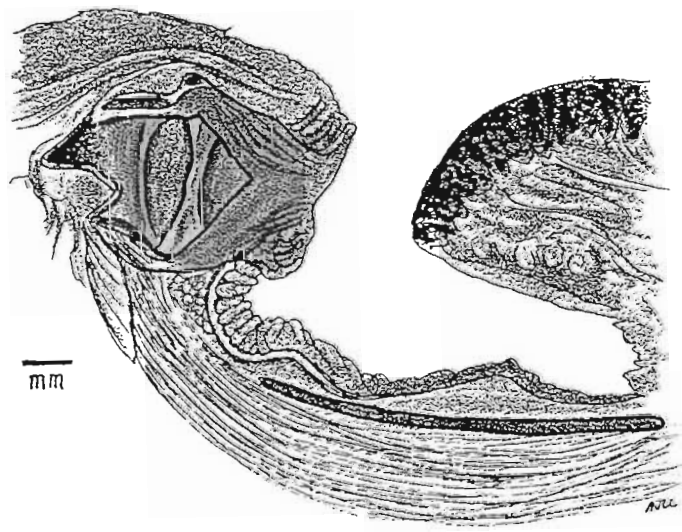


FIG. 2: *Schismaderma carens* (A. Smith, 1848)
AJL 2687 (female), Tzaneen, Eastern Transvaal, South Africa.

PLATE 15
SCHISMADERMA – LARVAL BUCCOPHARYNX
Roof on left, floor on right

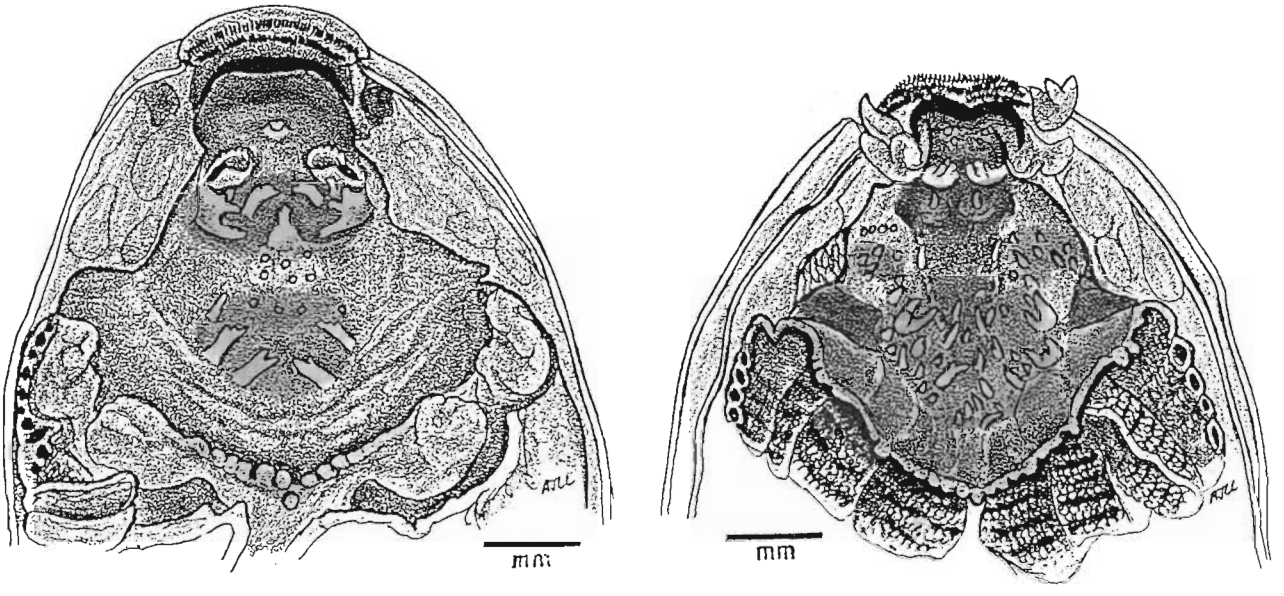


FIG. 1: *Schismaderma carens* (A. Smith, 1848)
AJL ==== Stage 30, Windy Hill, 20 km NE of Pietermaritzburg, Natal, South Africa.

Family MICROHYLIDAE Günther, 1859 "1858"

Subfamily PHRYNOMERINAE Noble, 1931

Genus *Phrynomerus* Noble, 1926

Brachymerus Smith (not Dahlbom), 1847, *Illus. Zool. S. Afr., Rept.*: 63. Type species by monotypy: *Brachymerus bifasciatus* Smith, 1847.

Phrynomantis Peters (part), 1867, *Mber. Königl. Akad. Wiss. Berlin*: 35 (replacement name for *Brachymerus* Smith, 1847 [preoccupied; type species: *Phrynomantis fusca* Peters]).

Phrynomerus Noble, 1926, *Amer. Mus. Novit.*, 237:20 (replacement name for *Brachymerus* Smith, 1847 [preoccupied] after dividing *Phrynomantis* Peters, 1867; type species: *Phrynomerus bifasciatus* (Smith, 1847).)

CHARACTERS

Only one species of *Phrynomerus* occurs in Natal. No comparison with the other two currently recognised southern African taxa was made. Characters of the adult larynx (Pl. 16, figs. 1 & 2) and of the larval buccopharynx (Pl. 17, figs. 1a, b) are described fully in the Species Account, below; only a few salient features are noted here.

ADULT LARYNX (Pl. 16)

Sexual dimorphism is pronounced, especially with regard to the size of the larynx and morphology ofthe pharyngeal mucosa, the arytenoid cartilage and of the vocal cords. The vocal cords comprise a large, well-developed medial cord and a smaller lateral cord. There is no fibrous body, and no posterior membrane.

LARVAL BUCCOPHARYNX (Pl. 17)

Phrynomerus tadpoles are filter-feeders and the buccopharyngeal morphology is accordingly modified, but not to the same degree as in *Xenopus*. The overall morphology is nevertheless quite remarkable in many respects. The buccal cavity has a greatly narrowed postnarial arena, a divided dorsal velum, a deep channel in the buccal floor arena, a long row of well-developed post-lingual papillae on either side, and buccal floor arena papillae defining the posterior border only. The ventral velum has a curious median flap arising from the dorsal surface.

SPECIES ACCOUNT

Phrynomerus bifasciatus bifasciatus (A. Smith, 1847)

Phrynomerus bifasciatus A. Smith, 1847, *Illus. Zool. S. Afr., Rept.*, pl. 63, Type locality: "Country to the east and north-east of the Cape Colony", Syntypes in the British Museum (Nat. Hist.), London.

Phrynomerus bifasciatus (Smith): Van Dijk 1966:271, Passmore & Carruthers 1979:108, figs.

Phrynomerus bifasciatus bifasciatus (Smith): Poynton 1964:85, fig. 44, Poynton & Broadley 1985a:513, Lambiris 1989a:59; 1989b:75, figs. 32 & 33, pl. 4 figs. 4a-c.

ADULT LARYNX (Pl. 16, figs. 1 & 2)

Material examined: ZIMBABWE: AJL 1227 (m, SVL 41,0 mm), Gem Farm, 34 km NW of Beitbridge, AJL 1489 (f, SVL 57,9 mm), Atlantica Ecological Research Station, 23 km W. of Harare, SOUTH AFRICA: NATAL - AJL 2461 (f, SVL 43,7 mm), and AJL 2462 (m, SVL 39,6 mm), Makhamisa Pan, Umfolozi Game Reserve, AJL 2074 (f, SVL 50,2 mm), eGodeni, Hluhluwe Game Reserve.

Advertisement call: A rich melodious trill at about 1.2 kHz (Passmore & Carruthers 1979:108), about two seconds long, uttered every five or six seconds. Calls are made at night, from exposed positions at the edges of shallow pans, pools or dams. They are single or antiphonal; only infrequently is there any definite choral structure.

Male larynx:

Pharyngeal mucosa: Rather thin and mostly smooth, but somewhat fimbriated over the apex of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surfaces narrow and broadly U-shaped, with a slight apical notch in the internal margin. The arytenoid shelf is broad, about 3x wider than the occlusal surface and the narrow fossa is deeply excavate. The pulvinaria vocalia are well developed.

Vocal cord: The medial cord is moderately broad, the midpoint width about half that of the superior insertion, which is more strongly flared than that of the inferior insertion. The margins are slightly flanged, and the anterior margin has a secondary ridge and a small thickening suggestive of a greatly reduced fibrous body incorporated within the

cord itself. The lateral cord is broadly undulant and partially concealed by the medial cord.

Posterior chamber: The common ventricle into which the lungs open is large and the anterior surface is strongly ridged. The posterior wall has a falciform fold between the roots of the lungs.

LARVAL BUCCOPHARYNX (Pl. 17, fig. 1a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a.

Material examined: SOUTH AFRICA: TRANSVAAL - AJL ==== a & b, stage 39, SVL 16.5 mm; Manyeleti Game Reserve; silver impregnation. NATAL - AJL 4410b, stage 38/39, SVL 15.5 mm; Mboneni Pan, Mkuzi Game Reserve; thionine stain.

Larval habitat: Shallow pans or pools; if in deeper dams, then found only in the shallower marginal waters. Those with silted bottoms and fairly dense peripheral stands of emergent, submerged and small floating macrophytes, with areas of open water, are preferred. A fairly high load of suspended finely particulate matter is usually present.

Buccopharyngeal roof

General shape: Buccal cavity funnel-shaped, with a strongly domed labial boundary, and weakly excavate. The pharyngeal chambers are very large and triangular.

Prenarial arena: Roughly triangular, the base about twice the height. There is a small triangular median papilla flanked laterally by two fairly widely-spaced pustulose papillae on either side; behind these is a short, gently convex row of about 6 closely-spaced pustulose papillae between the anterior borders of the internal nares.

Internal nares: Moderately large, about 0.2x width of roof at the level of the posterior margins, about twice as long as broad, and divergently oblique. Anterior internarial distance about 1.3x narial length, posterior internarial distance about 4.4x narial length.

Narial valve: Not developed.

Postnarial arena: Reduced to a transverse row of papillae immediately abutting the posterior borders of the internal nares. There is a large cylindrical **postnarial papilla** with a pustulose tip

immediately behind each naris, flanked laterally by a pair of long subconical **lateral ridge papillae**. The **median ridge** is reduced to a small triangular papilla between the postnarial papillae.

Buccal roof arena: The arena is not defined by papillae and is entirely devoid of ornamentation. If defined by the dorsal velum, it is a large triangular area, the apex directed towards the oesophagus.

Dorsal velum: Divided into two halves, converging posteromedially onto the oesophageal funnel. The free edges are ornamented with numerous small papillae.

Pressure cushions: The very large medial cushion is flanked anterolaterally by the much smaller (about one third the size) lateral cushion. There is no obvious ciliary groove.

Buccopharyngeal floor

General shape: The buccal cavity is roughly ovate, with broad divergent ridges behind the tongue, and with a deep median channel in the buccal floor arena.

Prelingual arena: Laterally compressed, very narrow, and devoid of papillae or pustulations.

Post-lingual papillae: A row of 7 - 8 fairly closely-spaced conical papillae, shortest lingually and longest laterally, arise on either side from broad, posteriorly divergent ridges on the anterolateral walls of the buccal cavity.

Buccal floor arena: Roughly defined posterolaterally by a curved row of 17 - 20 conical papillae, shortest laterally and longer medially; the largest ones have a distinctly thickened base. Some large papillae encroach the arena posteromedially, and the arena itself is transected by a deep median channel narrowest retrolingually, widening posteriorly.

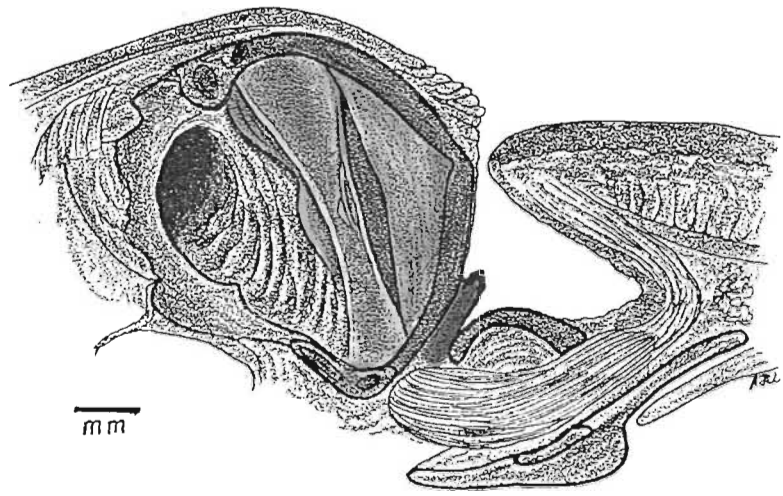
Buccal pockets: Poorly-defined closed depressions between the lateral edges of the ventral velum and the postlingual papillae?

Ventral velum: Broad, curved, of subequal width throughout. It is supported by distinct spicules, but lacks any marginal ornamentation. A calyculate structure arises medially from the dorsal surface of the velum.

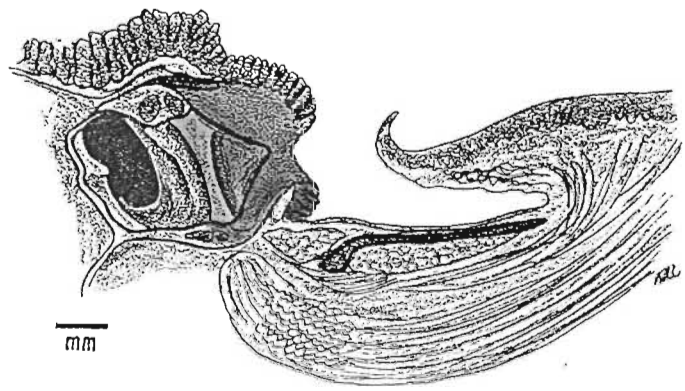
Branchial baskets: Triangular; equal in area to the buccal cavity.

Filter plates: Curved, weakly imbricate, not covering the cavities.

PLATE 16
PHRYNOMERUS – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right,



FIG, 1; *Phrynomerus bifasciatus bifasciatus* (A, Smith, 1847)
AJL 1227 (male), Gem Farm, 34 km NW of Beitbridge, Zimbabwe,



FIG, 2; *Phrynomerus bifasciatus bifasciatus* (A, Smith, 1847)
AJL 2074 (female), eGodeni, Hluhluwe Game Reserve, Natal, South Africa,

PLATE 17
PHRYNOMERUS – LARVAL BUCCOPHARYNX
Roof on left, floor on right

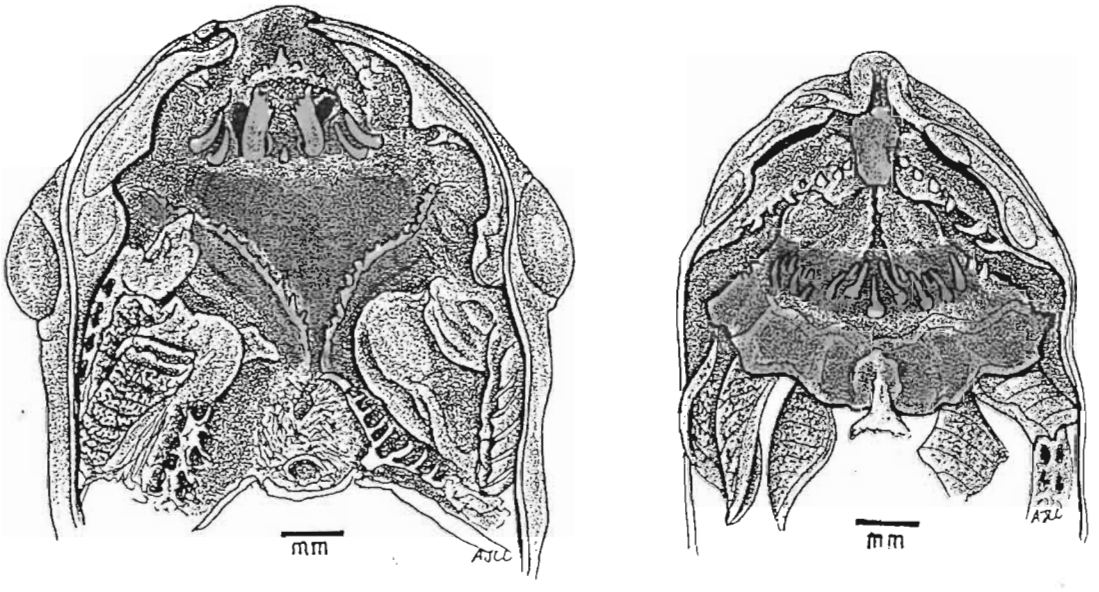


FIG. 1: *Phrynomerus bifasciatus bifasciatus* (A. Smith, 1847)
AJL ====, Stage 39, Manyeleti Game Reserve, Transvaal, South Africa.

TABLE 3. Laryngeal characters: *Breviceps*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

* = extralimital taxon included for comparison

	PROMINENTIA APICALIS INFERIORIS LARGE AND ELABORATE	A WELL-DEFINED ARYTENOID VALVE PRESENT	PROMINENTIA APICALIS INFERIORIS PRESENT	VOCAL CORD HAS MARGINAL THICKENINGS OR PROTRUBERANCES	DISCRETE CARTILAGINOUS BUTRESS(ES) PRESENT	FRENULUM BROAD AT LEAST ROSTRALLY	POSTERIOR CHAMBER WITH A CLEARLY DEFINED FOLD OR FOLDS
Breviceps verrucosus verrucosus	3	3	3	3	3	1	3
verrucosus tympanifer	3	3	3	1	3	3	1
maculatus	3	3	3	3	3	3	3
sp. A*	3	3	3	1	1	3	1
adspersus	3	1	1	3	3	3	3
pentheri	1	3	1	1	3	1	1
mossambicus	3	3	1	3	3	1	1
mossambicus X adspersus	3	3	1	1	3	1	3

Subfamily BREVICIPTINAE Bonaparte, 1850

Genus *Breviceps* Merrem, 1820

Breviceps Merrem, 1820, *Tentam. Syst. Amphib.*: 177. Type species by monotypy: *Rana gibbosa* Linnaeus.

CHARACTERS

ADULT LARYNX (Table 3; Pls. 18 & 19)

Interspecific differences in male larynxes of the taxa examined are summarised in Table 3.

Pharyngeal mucosa

The pharyngeal mucosa, which overlies a thick bed of connective tissue, is thin and smooth in *Breviceps*, sp. A; thin but folded in *B. v. verrucosus* and *B. pentheri*. It is thick and folded in *B. adspersus*, *mossambicus* and *B. adspersus* X *mossambicus* hybrids.

Shape of the arytenoid cartilage

The rostral margin is elaborated with bizarre prominentiae apicales in all the taxa examined. *Breviceps pentheri* has a large prominentia apicalis inferior; the other taxa have only the prominentia apicalis superior, which has its own characteristic shape for each taxon (see Plates 18, 19).

Occlusal surfaces are strongly ridged only in *Breviceps v. verrucosus*, barely ridged in *B. adspersus* and *Breviceps* sp. A.

The arytenoid shelf is clearly defined in *Breviceps adspersus*, *B. pentheri* and *B. mossambicus*. It is weakly defined in *B. v. verrucosus*, sp. A, and *B. adspersus* X *mossambicus* hybrids.

Vocal cord

The vocal cord shows a considerable degree of interspecific variation, better depicted in the plates than by words. The simple,

slightly flared basic pattern exemplified in *Breviceps v. verrucosus* is modified by variations in thickness of the cord and in the degree of flaring of the superior or inferior insertions. In *Breviceps adspersus* there is a low, broadly conical projection on the posterior surface of the cord and in *B. pentheri* a tiny tubercle on the anterior surface at about the junction of the superior and middle thirds of the cord. Only in *Breviceps* sp. A does the cord possess a cartilaginous buttress (internal to the superior posterior border) and flanged margins.

Frenulum

A broad frenulum uniting the vocal cord with the posterior chamber is present in *Breviceps v. verrucosus* and *B. pentheri*; a narrow, well developed frenulum is present in *B. mossambicus*, a less less strongly developed frenulum in *Breviceps v. tympanifer*, *Breviceps* sp. A, and *B. adspersus*. *Breviceps maculatus* lacks a frenulum.

M. hyoglossus

The origin of this muscle does not appear to show any taxonomically useful features.

LARVAL BUCCOPHARYNX (Pl. 20)

Only larvae of *Breviceps pentheri* were available for examination. Since larval development in *Breviceps* is completely extra-aquatic and encapsular, nutrition is derived entirely from an embryonic yolk sac, and the buccopharyngeal structures essential for a free-living aquatic larval stage are redundant.

The specimen dissected is completely lacking in buccal structures other than the tongue and the dorsal and ventral vela, both simple folds devoid of ornamentation. Functional branchial chambers are not apparent.

There seems no reason to believe that other *Breviceps* larvae are likely to possess buccopharyngeal structures of taxonomic value and the specimen examined is described in the Species Account purely for because these larvae are so poorly known.

SPECIES ACCOUNT

Breviceps verrucosus verrucosus Rapp, 1842

Breviceps verrucosus Rapp, 1842, *Arch. Naturgesch.*, 8:291, pl. 6, fig. 5. Type locality: Natal. Type not traced (Poynton 1964:70).
Breviceps verrucosus verrucosus Rapp: Poynton 1964:70. Passmore & Carruthers 1979:84, figs. Lambiris 1989a:61, fig. 10a, b.

ADULT MALE LARYNX (Table 3; Pl. 18, fig. 1)

Material examined: SOUTH AFRICA: TRANSVAAL - NM 1449 (m, SVL 29.6 mm), Barberton, NATAL - NM 1225 (m, SVL 27.5 mm), Swartkops, Cedara.

Advertisement call: A thin, shrill whistle about 0.4 second long, at about 2 kHz (Passmore & Carruthers 1979:84) repeated every three or four seconds, usually antiphonally, from the concealed entrance of a burrow, at night or (less commonly) in the open, on grass tussocks.

Pharyngeal mucosa: Thin, but overlying a thick bed of connective tissue, and terminating on the superior prominentia apicalis.

Arytenoid cartilage: Broad and horizontally elongate, with an obliquely flattened apex rising to a large, rather recurved, elaborately fimbriated prominentia apicalis superior. The superior and inferior margins of the occlusal surface are strongly ridged. The arytenoid shelf is weakly defined but the fossa is large and broadly elliptical.

Vocal cord: Simple, slightly flared at the insertions, and lacking any ornamentation.

Frenulum: A broad frenulum (about one third the length of the vocal cord) links the lower half of the posterior border of the cord to the floor of the posterior chamber, where a faint fold is discernible.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

Breviceps verrucosus tympanifer Hewitt, 1925

Breviceps tympanifer Hewitt, 1925, *Ann. Natal Mus.*, 5:190, pl. 10, figs. 1, 2. Type locality: Pirie, eastern Cape Province. Holotype in the Port Elizabeth Museum.
Breviceps verrucosus tympanifer Hewitt: Poynton, 1964:72. Passmore & Carruthers 1979:84, figs. Lambiris 1989a:62, fig. 10c, d.

ADULT MALE LARYNX (Table 3; Pl. 18, fig. 2)

Material examined: SOUTH AFRICA: NATAL - NM 1899 (m, SVL 35,4 mm), Sweetwaters, E. CAPE - NM 1900 (m, SVL 38,2 mm), Bedford.

Advertisement call: Not known to me.

Pharyngeal mucosa: Moderately thick and crenulated, becoming thinner towards the rostral margin of the arytenoid cartilage, and appearing to blend with the prominentia apicalis superior.

Arytenoid cartilage: Horizontally elongate, somewhat V-shaped, with a thickly lobed prominentia apicalis superior on the anterodorsal margin. The occlusal surfaces are somewhat ridged. The arytenoid shelf is weakly defined but the fossa is large and broadly elliptical.

Vocal cord: Broad and flared at both insertions. The anterior and posterior margins are thickened at the insertions, the thickened portions uniting over the main portion of the cord.

Frenulum: A very narrow, weakly defined frenulum links the cord to a narrow, feebly defined fold on the floor of the posterior chamber.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

Breviceps maculatus FitzSimons, 1947

Breviceps maculatus FitzSimons, 1947, *Ann. Natal Mus.*, 11:134, pl. 3, figs. 1-3, Type locality: Bushman's Peak, Drakensberg, Natal. Holotype in the Natal Museum, Pietermaritzburg. Paratypes in the Natal Museum and in the Transvaal Museum, Pretoria. Poynton 1964:73, fig. 30. Lambiris 1988:21, figs., pl. 2 fig. 3a-c. 1989a:64.

Breviceps verrucosus verrucosus (non Rapp, 1842): Passmore & Carruthers (part, Natal Drakensberg) 1979:84, figs.

ADULT MALE LARYNX (Table 3; Pl. 18, fig. 3)

Material examined: SOUTH AFRICA; NATAL - NM 656b (male paratype; SVL 35.4 mm), Bushman's Peak, Natal Drakensberg.

Advertisement call: A thin, shrill whistle about 0.5 seconds long, at about 2 kHz (Passmore & Carruthers 1989:84, and sonagram).

Pharyngeal mucosa: Very thick and crenulate, overlying a deep layer of connective tissue, and not blending with the prominentia apicalis superior.

Arytenoid cartilage: Very elongate horizontally, about 1.5x longer than high, and narrowly V-shaped. The prominentia apicalis superior is large and papillate, extending over about half of the dorsal surface of the arytenoid cartilage. The occlusal surfaces, which are very feebly defined, are smooth. The arytenoid shelf is very shallow and feebly defined. The fossa is deep and broadly oval.

Vocal cord: Broad, barely flared, and simple.

Frenulum: Absent.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

Breviceps sp. A

Breviceps maculatus (non FitzSimons, 1947): Poynton 1964:73, fig. 30 (part), Lambiris 1988:21, figs., pl. 2 fig 3a-c (part), 1989a:64 (part).

Breviceps verrucosus verrucosus (non Rapp, 1842): Passmore & Carruthers 1979:84, figs. (part, Natal Drakensberg).

ADULT MALE LARYNX (Table 3; Pl. 18, fig. 4)

Material examined: LESOTHO: NM 187 (m, SVL 22,8 mm), "Basutoland".

Advertisement call: Not known.

Pharyngeal mucosa: Thin, but overlying a thick bed of connective tissue narrowing towards the apex of the arytenoid cartilage.

Arytenoid cartilage: Broad and horizontally elongate, triangular, and with a large fimbriated prominentia apicalis superior. The occlusal surfaces are very weakly ridged. The arytenoid shelf is shallow and weakly defined, sloping gently into a moderately broad, elliptical fossa.

Vocal cord: Broad, and flared at the insertions. Both margins are flanged, the posterior more so than the anterior. A long (almost half the length of the vocal cord), narrow, tapering superior cartilaginous buttress lies just posterior to the midline of the cord.

Frenulum: A narrow, poorly defined frenulum links the posterior border of the vocal cord to a well defined bi-arcuate fold in the lateral wall of the posterior chamber.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

Breviceps adspersus Peters, 1882

Breviceps adspersus Peters, 1882, *Reise nach Mossambique*; 177. Type locality; Damaralande (Westafrika), als aus Transvaal, zwischen dem 25. und 26°S.Br. Types in the Zoologisches Museum, Berlin. Trewavas 1933:489, fig. 68. Poynton & Broadley 1985a:523; fig. 5.

Breviceps adspersus adspersus Peters; Poynton 1964:89, fig. 40. Passmore & Carruthers 1979:102, figs. Lambiris 1989a:65. 1989b:72, fig. 30, pl. 4 figs. 3a & b.

ADULT LARYNX (Table 3; Pl. 19, fig. 1)

Material examined: SOUTH AFRICA; NATAL - AJL 1980 (m, SVL 33,7 mm), Nagle Dam. NM 6414 (m, SVL 38,6 mm), Weenen Nature Reserve. NM 1972 (m, SVL 38,7 mm), Pietermaritzburg. AJL 1904 (f, SVL 42,0 mm), Waterfall.

Advertisement call: A short discordant chirp, about 0.1 second long, at about 2 kHz (Passmore & Carruthers), repeated two or three times a second, with short rests between brief series of calls; usually uttered from just inside the opening of a concealed burrow or, less often, on the surface, at night.

Male larynx:

Pharyngeal mucosa: Thick and narrowly folded, overlying a deep bed of connective tissue. It does not blend into the prominentia apicalis superior.

Arytenoid cartilage: Essentially V-shaped, but with a broad, rather square, anterodorsally directed prominentia apicalis superior with a shallowly crimped superior surface. The occlusal surface is marked by a distinct arytenoid valve, and the rather shallow arytenoid shelf is well defined. The fossa is deep and narrowly elliptic.

Vocal cord: Broad, moderately flared at the insertions, and with a light bulge at the midpoint of the posterior margin; it lacks any other ornament.

Frenulum: Triangular, apex directed posterad and continuous with a crescentic thickening on the lateral wall of the posterior chamber.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

Breviceps pentheri Werner, 1899

Breviceps pentheri Werner, 1899, *Zool. Anz.*, 22:116. Type locality "Capland, warscheinlich Grahamstown". Type not traced (Poynton 1964:82).

Breviceps parvus Hewitt, 1925, *Ann. Natal mus.*, 5:192, pl. 10, figs. 6-8. Type locality: Grahamstown. Syntypes in the Port Elizabeth Museum. De Villiers 1929:142, figs. 1-8.

Breviceps adspersus pentheri Werner; Poynton 1964:82, fig. 41. Passmore & Carruthers 1979:102, fig. Lambiris 1988:22, figs., pl 2 fig. 4a-c. 1989a:66. 1989b:74 fig. 31.

ADULT LARYNX (Table 3; Pl. 19, fig. 2)

Material examined: SOUTH AFRICA: NATAL - NM 1974 (m, SVL 23.5 mm), Champagne Castle, below Cathkin Peak. NM 1975 (m, SVL 27.0 mm), Mooi River. NM 269 (m, SVL 23.0 mm), Newcastle (Muller's Pass). NM 190 (m, SVL 27.6 mm), Polela, Bulwer. E. CAPE - AJL 216 (f, SVL 41.0 mm), Grahamstown.

Advertisement call: Short discordant chirp about 0.1 second long, at about 2.2 kHz (Passmore & Carruthers 1979:102), uttered singly at short intervals from the mouth of a burrow (often concealed by a tuft of grass or by a stone), at night.

Male larynx:

Pharyngeal mucosa: Thin, overlying a thick sheet of connective tissue, and terminating behind the prominentia apicalis superior.

Arytenoid cartilage: Occlusal surface smooth and broad. The superior and inferior prominentiae apicales very large, the superior prominentia apicalis elaborately fimbriated, the inferior one less so; the anterior surface of the cartilage between the two prominentiae more or less vertical. Apex of internal margin U-shaped. Arytenoid shelf broad and sharply defined. The arytenoid fossa is narrowly elliptic.

Vocal cord: Broad and robust. The superior insertion is moderately flared, the inferior insertion only slightly so. There is a small rounded tubercle on the anterior margin at the junction of the upper and second quarters.

Frenulum: A well-developed frenulum, broadly flared at its origin on the central posterior margin of the vocal cord and constricted medially, unites the cord with the lateral wall of the posterior chamber, which possesses a pair of well-defined arcuate folds.

LARVAL BUCCOPHARYNX (Pl. 20, fig. 1a & b)

Identification of larvae: From a series collected by FitzSimons & Van Dam, and described by De Villiers (1929); specimen donated by the Transvaal Museum. The series includes stages from early embryos to Gosner's stage 46 showing the minute 5th toe, warty skin and ventral marbling diagnostic of adults.

Material examined: SOUTH AFRICA: TRANSVAAL - AJL 2866 (from TM 11139); Stage 37; SVL 7,6 mm; Kastrol Nek, 16 km NE of Wakkerstroom.

Larval habitat: Encapsular. Eggs laid in an underground chamber overlaid by a stone.

Buccopharyngeal roof

General shape: Conical, with a rounded apex labially. The roof is regularly concave.

Internal nares: Small transverse slits level with the general surface, devoid of any margins or valves.

Papillae and pustulations are totally absent.

Dorsal velum: A poorly-defined fold which would appear to be completely non-functional.

Buccopharyngeal floor

General shape: Roughly triangular, but without any definite base.

Appendages: There are no papillae or pustulations. The only structures present are a large, well-developed tongue and a rudimentary but distinct ventral velum which is no more than a simple fold of tissue.

Breviceps mossambicus Peters, 1854

Breviceps mossambicus Peters, 1854, *Mber. Königl. Akad. Wiss. Berlin*, 1854:628. Type locality: Mozambique Island and Sena. Types in the Zoologisches Museum, Berlin. Poynton 1964:83, fig. 43. Passmore & Carruthers 1979:104, figs. Lambiris 1989a:67, 1989b:70, fig. 29, pl. 4 figs 2a, b.

ADULT LARYNX (Table 3; Pl. 19, fig. 2)

Material examined: MALAWI: AJL 1390 (m, SVL 37.0 mm), and AJL 1300 (f, SVL 47.0 mm), Blantyre.

Advertisement call: "A short sparrow-like chirp. About two calls per second." [About 0.05 second long, at 2.5 kHz.] "Males are known to call from the mouths of burrows." (Passmore & Carruthers 1979:104.)

Male larynx:

Pharyngeal mucosa: Thick and folded. The portion overlying the apex of the arytenoid cartilage is especially deep and thown into villiform folds.

Arytenoid cartilage: External margin squarely U-shaped, internal margin V-shaped. Occlusal surfaces smooth, but with a slight median ridge. Arytenoid shelf shallow, moderately well-defined. Fossa narrowly elliptical.

Vocal cord: Simple, slightly flared at the insertions.

Frenulum: Arises from a broad insertion on the posterior margin of the vocal cord, is strongly flexed dorsad, and tapers sharply along its attachment to the medial wall of the posterior chamber, which bears a pair of narrow vertical ridges.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

DISCUSSION

The morphology of adult male larynxes in the taxa examined shows very little intraspecific, and consistently distinct interspecific differences that have helped clarify some problems in this troublesome genus.

The tadpole of only one taxon, *Breviceps pentheri*, was available for examination and it is clear from an examination of the buccopharynx of this direct-development type that no features of taxonomic value can be expected to be found in *Breviceps* larvae.

The taxonomic conclusions of Poynton (1964) and of Lambiris (1989a) are largely supported, but with some amendments.

Breviceps sp. A:

Poynton (1964:73) provisionally referred two Lesotho specimens to *Breviceps maculatus* FitzSimons, 1947, but Lambiris (1989a:65) considered the single surviving specimen (NM 187) to represent an undescribed taxon, on the basis of differences in hand and foot morphology. This opinion appears to be reinforced by differences in the larynx, and the Lesotho specimen is here removed from *Breviceps maculatus* and referred to as *Breviceps* sp. A pending formal description.

Breviceps pentheri

Although treated as a subspecies of *Breviceps adspersus* by most authors, examination of material from north-western Natal, where the ranges of the two taxa overlap, shows no evidence of hybridisation. The larynxes show considerable differences, particularly in the vocal cord, arytenoid cartilage and prominentiae apicales. *Breviceps pentheri* is accordingly here considered a full species.

The *Breviceps verrucosus / maculatus* complex

Lambiris (1989a:65) discussed the status and occurrence of *Breviceps verrucosus tympanifer* in Natal, basing his conclusions on the external morphological characters then generally in use. Larynxes of

Natal material agree closely with those of Eastern Cape populations, despite the considerable disjunction along the Transkei, tending to confirm that *B. v. tympanifer* does occur in Natal. I have continued to treat *tympanifer* as a subspecies of *Breviceps verrucosus* not only because of the close similarity of the larynxes, but also because of the somewhat gradistic nature of the diagnostic markings of *tympanifer* (Lambiris 1989a:62).

Breviceps maculatus was referred to the synonymy of *B. verrucosus* by Passmore & Carruthers (1979:84) on the basis of close similarities in the advertisement call, but Lambiris (1989a:64) considered it to be a valid species. The larynx of one of the male paratypes (Pl. 18, fig. 3) is so unlike those of *Breviceps v. verrucosus* (Pl. 18, fig. 1) and *B. v. tympanifer* (Pl. 18, fig. 2) that I now consider the taxonomic validity of *B. maculatus* to be confirmed.

The single surviving specimen (fortunately a male) of the two Lesotho specimens provisionally referred to *Breviceps maculatus* by Poynton (1964:73) but considered by Lambiris (1989a:65) not to be referable to this species, also proves to have a distinctive larynx unlike that of any other taxon examined. The markings are similar to those of *Breviceps maculatus*, but the hand and foot show differences in shape, proportions of the digits, and the various tubercles. The larynx shows a certain superficial similarity to those of the two *Breviceps verrucosus* subspecies, especially in the shape of the prominentia apicalis superior, but differs from those of all other taxa examined in the possession of distinct marginal flanges to the vocal cord and a conspicuous superior cartilaginous buttress. Taking all these points into account, it would appear that this specimen does in fact represent an undescribed species, and it is so treated here.

The *Breviceps adspersus / mossambicus* complex

Breviceps pentheri has generally been considered a subspecies of *Breviceps adspersus* because of of the close external similarities. However, the considerable differences in laryngeal morphology (Pl. 19,

figs. 1 and 2) strongly suggest that they should be considered distinct species.

Pure *Breviceps mossambicus* is a rarity in southern African collections but the limited material available shows distinctive features in the arytenoid cartilage, vocal cord, frenulum and posterior chamber that clearly identify such specimens (Pl. 19, fig. 3). Hybrids between *B. adspersus* and *B. mossambicus* are not uncommon in Zululand and although some are clearly distinguishable as such, others are less so. The larynx does, however, show differences that clearly separate such hybrids from parents of pure stock (Pl. 19, fig. 4). A comprehensive survey of laryngeal morphology in such hybrids, though desirable, would involve the study of material from Natal, the Transvaal, Mozambique, Zimbabwe and Malawi; this is clearly beyond the scope of the present study, which is intended merely to assess the potential value of these structures in taxonomic work. The consequences of such grossly different laryngeal morphology and altered calls in terms of specific mate recognition systems and female responses would also be worthy of more detailed study and consideration than is possible here.

PLATE 18
BREVICEPS – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

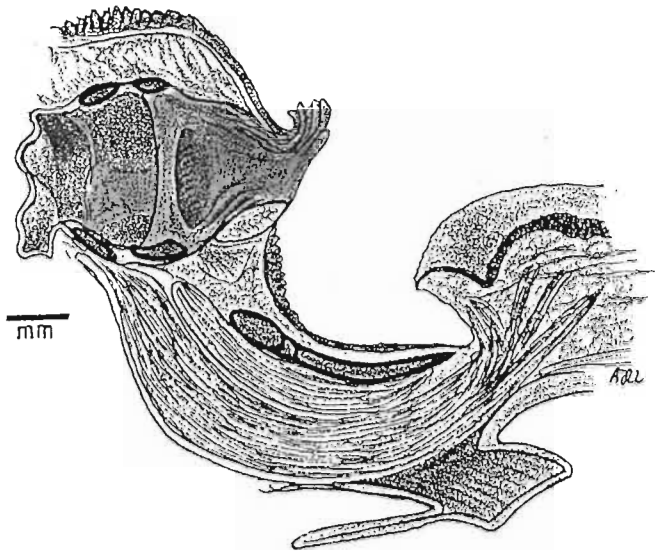


FIG. 1: *Breviceps verrucosus verrucosus* Rapp, 1842
NM 1225 (male), Swartkops, Cedara, Natal, South Africa.

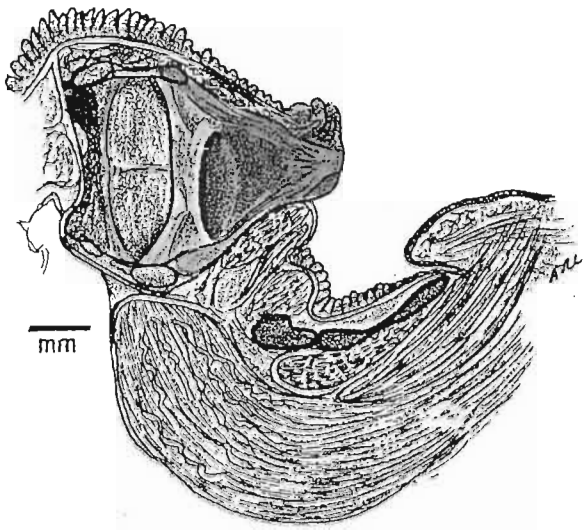


FIG. 2: *Breviceps verrucosus tympanifer* Hewitt, 1925
NM 1899 (male), Sweetwaters, Natal, South Africa.

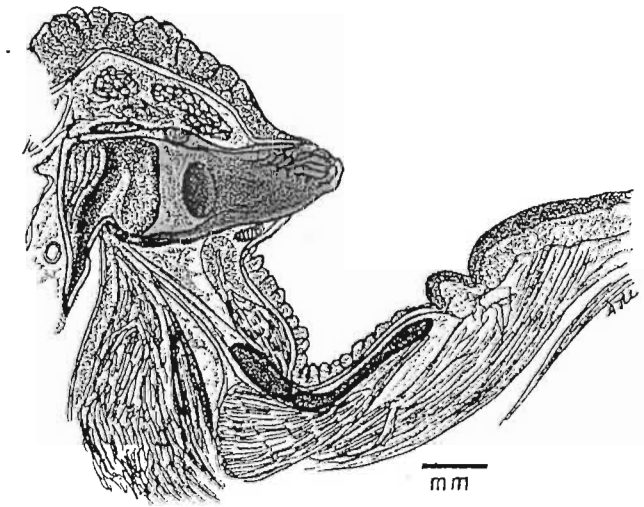


FIG. 3: *Breviceps maculatus* FitzSimons, 1947
NM 656 (male), Bushman's Peak, Natal Drakensberg, South Africa, PARATYPE

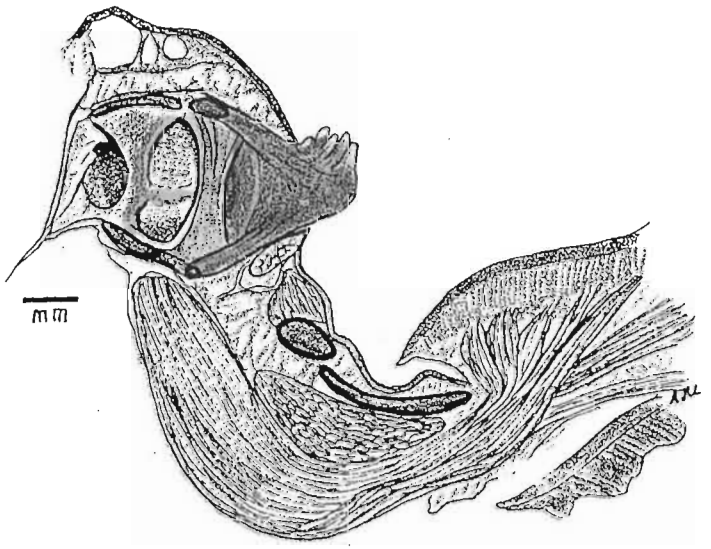


FIG. 4: *Breviceps* sp. A
NM 187 (male), "Basutoland" [=Lesotho]

PLATE 19
BREVICEPS - ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

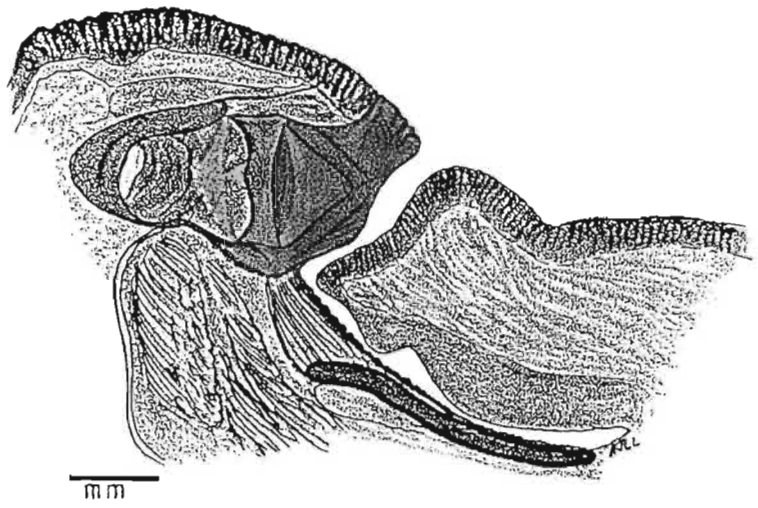


FIG. 1: *Breviceps adspersus* Peters, 1882
AJL 1980 (male), Nagle Dam, Natal, South Africa.

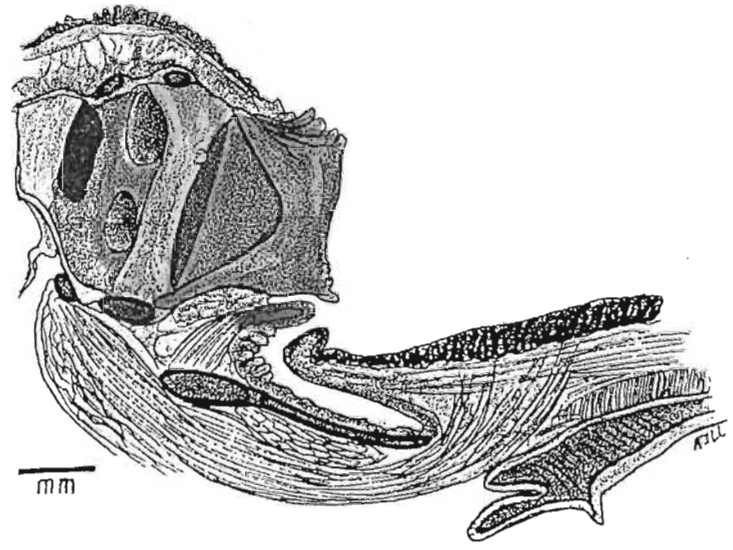


FIG. 2: *Breviceps pentheri* Werner, 1899
NM 1975 (male), Mooi River, Natal, South Africa.

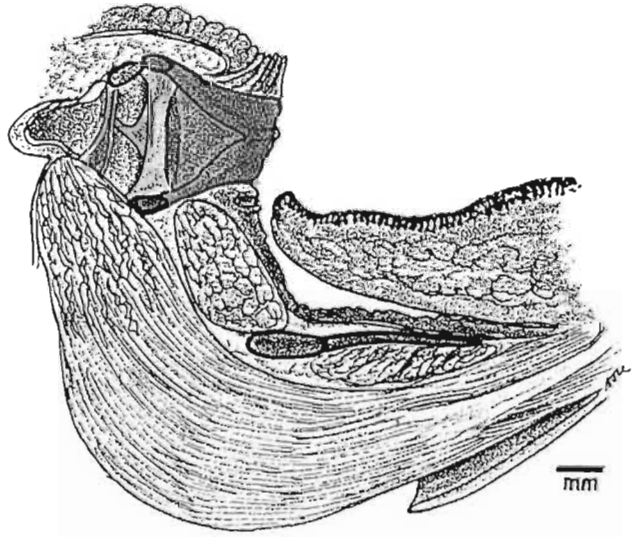


FIG. 3: *Breviceps mossambicus* Peters, 1854
AJL 1390 (male), Blantyre, Malawi.

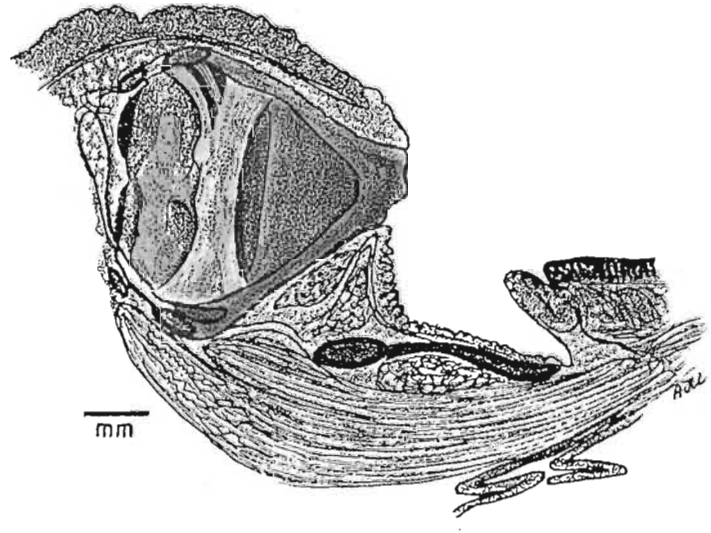


FIG. 4: *Breviceps adspersus* X *Breviceps mossambicus*
NM 5471 (male), Pafuri, Transvaal, South Africa.

PLATE 20
BREVICEPS – LARVAL BUCCOPHARYNX
Roof on left, floor on right

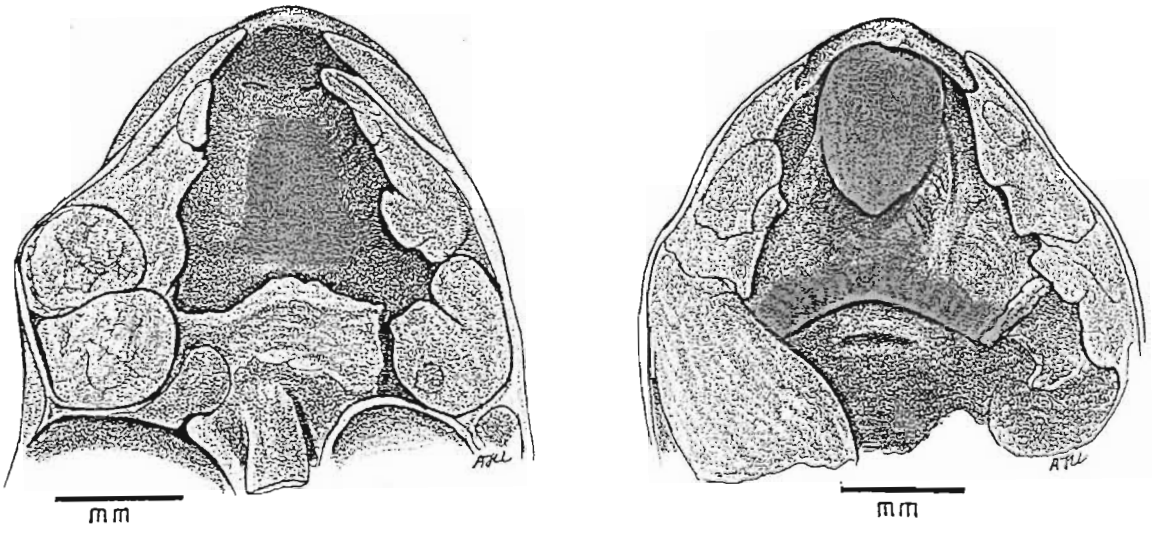


FIG. 1: *Breviceps pentheri* Werner, 1899
AJL 2866, Stage 37, Kastrol Nek, 16 km NE of Wakkerstroom, Transvaal, South Africa.

Family RANIDAE Gray, 1825

The large number of genera and species contained in the Ranidae, even within the geographical limits of the area chosen for this study, renders an overview of adult hyolaryngeal and larval buccopharyngeal characters too unwieldy for practical purposes. Such a treatment is given genus by genus as a matter of expediency, for it is felt that a more broadly-based approach is not justified in view of the even greater number of taxa not examined in this study.

It may briefly be noted here that the principal results of the present study, within the Raninae and the Phrynobatrachinae, are:

1. The taxonomic distinctness of the two subspecies of *Pyxicephalus adspersus* recognised by Parry (1982) is confirmed.
2. Differences in adult laryngeal morphology clearly separate *Tomopterna krugenensis* from *T. cryptotis* and *T. marmorata*.
3. *Ptychadena m. mascareniensis*, as currently recognised, appears to consist of at least two sibling species.
4. *Ptychadena poyntoni* is conspecific with *P. porosissima*.
5. *Rana angolensis*, *R. dracomontana* and *R. fuscigula* are clearly separable on adult laryngeal and larval buccopharyngeal characters.
6. *Rana vertebralis* and *R. umbraculata* are taxonomically distinct, and a third cryptic species, as yet unnamed, appears to be present in this group.
7. The *Strongylopus* sp. A tadpole noted by Lambiris (1987, 1989a) is confirmed to be distinct from *S. hymenopus* tadpoles.
8. *Cacosternum nanum parvum* is here treated as a full species.
9. *Cacosternum striatum* FitzSimons, 1947 is shown to be a valid species, which appears to be known only from the type series taken in Durban. (The termination of the species-name must be changed to conform with Article 31(b), International Code of Zoological Nomenclature.
10. Frogs from Boston, Natal, and from Sehlabathebe, Lesotho, called *Cacosternum striatus* by Lambiris 1989a are an undescribed species which should probably be referred to a new genus.

Subfamily RANINAE Gray, 1825

Genus *Pyxicephalus* Tschudi, 1838

Pyxicephalus Tschudi, 1838, *Classif. Batr.*, pp. 46, 83. Type species by designation of Fitzinger 1843: *Pyxicephalus adspersus* Tschudi, 1838.

CHARACTERS

ADULT LARYNX (Pl. 21)

The male larynxes of the two taxa examined show close similarities in overall morphology.

Arytenoid cartilage

The principal differences are in the shape of the occlusal surface (narrow, and lacking a discrete arytenoid valve in *Pyxicephalus a. adspersus*; broader, and possessing a distinct arytenoid valve in *P. a. edulis*); and in the size and shape of the arytenoid fossa (a narrow, elongate ellipse in *P. a. adspersus*, short and oval in *P. a. edulis*).

Vocal cord

The anterior margin is slightly flanged in *Pyxicephalus a. adspersus*, but not in *P. a. edulis*. The posterior margin is conically thickened superiorly and inferiorly, and bears a midpoint protruberance in *P. a. adspersus*, but lacks these in *P. a. edulis*. There are no cartilaginous buttresses in either taxon.

LARVA BUCCOPHARYNX (Pl. 22)

The taxa examined show greater differences in buccopharyngeal morphology than in adult laryngeal morphology. These appear to be correlated with differences in preferred breeding habitats. Only the principal features are discussed here.

Most of the structures associated with the buccopharyngeal roof are more elaborate in *Pyxicephalus adspersus edulis* than in *P. a. adspersus*.

The internal nares, their valves and associated papillae are very much larger; the buccal roof arena papillae are both larger and more numerous in *edulis* than in *adspersus*; and the dorsal velum is more elaborate in the former taxon. *Pyxicephalus a. adspersus* has a better developed median ridge, and more obviously recognisable lateral ridge papillae, than *P. a. edulis*, and the buccal roof arena is more sharply defined.

Pyxicephalus adspersus edulis again shows a more complex general arrangement of the buccopharyngeal floor than does *P. a. adspersus*, particularly in the more elaborate prelingual papillae and the much more numerous buccal floor arena papillae.

SPECIES ACCOUNT

Pyxicephalus adspersus adspersus Tschudi, 1838

Pyxicephalus adspersus Tschudi, 1838, *Classif. Batr.*, pp. 46, 84. Type locality: "Promontorium Bona Spei." Syntypes in the Muséum Natural d'Histoire Naturelle, Paris. Poynton 1964:93, fig. 47 (part). Van Dijk 1966:258 (part). Passmore & Carruthers 1979:115, figs. (part).

Pyxicephalus adspersus adspersus Tschudi: Parry 1982:285, fig. 2. Poynton & Broadley 1985b:122. Lambiris 1989a:73; 1989b:80, figs. 34 & 35, pl. 5 figs. 1a-e.

ADULT MALE LARYNX (Pl. 21, fig. 1)

Material examined: Zimbabwe: AJL 405 (m, SVL 184.0 mm), Harare. SOUTH AFRICA: TRANSVAAL - NM 2009 (m, SVL 141.5 mm), Pretoria.

Advertisement call: A deep "whoop" about 0.3 second long, at about 0.3 kHz, repeated once a second three or four times, from shallow water. Call sites are rather exposed. The choral structure is rather loose.

Pharyngeal mucosa: Thin and simple, overlying a deep submucosa which covers the entire surface of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface narrow, somewhat V-shaped, and lacking striations or folds. Prominentiae are absent. There is no distinct arytenoid valve. The arytenoid shelf is broad and shallow. The pulvinaria vocalia are well developed.

Arytenoid fossa: Narrow, arcuate, and extending almost fully the width of the shelf.

Vocal cord: A very broad band, as wide as the arytenoid shelf. The anterior margin is slightly flanged. The posterior margin lacks distinct cartilaginous buttresses but is markedly thickened towards its insertions. It has an ovoid median marginal body continuous with the superior marginal thickening. A feebly-defined band traverses the cord at about mid-point.

Posterior chamber: Narrow. The pulmonary aditus is relatively small.

M. hyoglossus: Originates below the cricoid cartilage and the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX (Pl. 21, fig. 1a & b)

Identification of larvae: Lambiris 1989b.

Material examined: SOUTH AFRICA; TRANSVAAL - AJL 3508b & c; Stage 35, SVL 17,0 and 16,8 mm; Pretoria; silver impregnation.

Larval habitat: Ephemeral ponds or shallow dams with emergent marginal vegetation (grasses, sedges and reeds) interspersed with open areas, on sandy or moderately silted substrata.

Buccopharyngeal roof

General shape: Truncately triangular, base about 1.1x greater than height. General surface more or less regularly concave, prenarial arena moderately excavate.

Prenarial arena: Large, roughly trapezoid, base about 1.7x height; with three small pustulate papillae arranged in a triangle approximately in the centre of the arena.

Internal nares: Large, narrowly elliptical, transversely set. Length about 0.4x width of naris. Margins not grooved.

Narial valve: Well-defined flaps on the anterior and posterior borders of the naris; the anterior flap has a short (about 0.3x width of naris) cylindrical papilla arising at about the mid-point.

Postnarial arena: A large, conical **postnarial papilla** with a slightly pustulate anterior surface, behind either naris, the base slightly lateral to the narial mid-point, and curving medially. The **lateral ridge papilla** on either side is large, broad, and terminally fimbriate. (One is shown attached to the left wall of the floor of the buccopharynx in fig. 1b, pl. 21). The **median ridge** is an arcuate flap about 0.23x the width of the roof at that level, with a finely pustulate free margin.

Buccal roof arena: U-shaped, bounded laterally by a posteriorly convergent row of 4 - 6 simple conical papillae on either side, diminishing regularly in size posteriorly. Numerous small pustulations in the arena extend beyond its anterior boundary, to the median ridge.

Glandular ridge; Not clearly discernible in these preparations.

Dorsal velum: A very feebly developed flap, broadly discontinuous medially, and lacking any ornamentation.

Pressure cushions: Do not appear to be separable into lateral and medial moieties.

Buccopharyngeal floor

General shape: Triangular, base about 1.2x height. A posteriorly bifurcating depression extends from the lingual area into the buccal floor arena.

Prelingual papillae: Three moderately large, stout sub-cylindrical papillae on either lateral wall of the prelingual arena.

Lingual papillae; Two narrow, cylindrical, close-set papillae of moderate length on the tongue anlage.

Buccal floor arena: Transversely oval, about 1.8x broader than deep. Demarcated laterally by 3 or 4 large, stout, close-set conical papillae diminishing somewhat in size posteriorly; bounded posteriorly by a gently arcuate line of smaller, subequal cylindrical papillae tending to be bunched in groups of 3 or 4. The centre of the arena has some half-dozen small pustules on either side of a median ridge.

Buccal pockets and prepocket papillae: Not discernible in these specimens.

Ventral velum: Well developed, slightly narrower medially than laterally, and with a somewhat creased or folded appearance between the marginal projections. Three blunt, equally-spaced marginal projections on either side of the midline, which is marked by a close-set pair of projections. No conspicuous supporting spicules.

Branchial baskets: Roughly triangular, major axis transverse.

Filter plates: Curved, more or less closed. Filter rows rather short and finely folded, with narrow channels.

Pyxicephalus adspersus edulis Peters, 1854

Pyxicephalus edulis Peters, 1854, *Mber. Akad. Wiss. Berlin*, p. 626. Type locality: Boror, Tete and Mozambique Island. Type destroyed (formerly in the Zoologisches Museum, Hamburg -- Poynton & Broadley, 1985b:123).

Pyxicephalus adspersus (non Tschudi, 1838): Poynton 1964:93 (part, fig. 47). Van Dijk, 1966:252, 258 (part?). Passmore & Carruthers 1979:114 (part, photos of subadults).

Pyxicephalus adspersus edulis Peters: Poynton 1980:246. Parry 1982:286, figs. 3, 6. Poynton & Broadley 1985b:123. Lambiris 1989a:74; 1989b:81, fig. 37, pl. 5 figs. 2a-d.

ADULT LARYNX (Pl. 21, fig. 2)

Material examined: BOTSWANA: NM 7393 (m, SVL 103.6 mm), and NM 7394 (m, SVL 111.7 mm), 8 miles S. of Mababe Gate (entrance to Chobe National Park). SOUTH AFRICA: NATAL - AJL 2872 (f, 86.0 mm), Futululu, Zululand. AJL 2077 (f, SVL 69.5 mm), Chibilembube, Hluhluwe Game Reserve.

Advertisement call: A deep "whoop" about 0.3 second long, at about 0.3 kHz, repeated once a second three or four times, from emergent grasses in shallow water.

Male larynx:

Pharyngeal mucosa: Thin and lacking folds, overlying a deep submucosa that is indistinctly demarcated from the surface of the arytenoid cartilage.

Arytenoid cartilage: Both margins of the occlusal surface broadly U-shaped. There is a slight incisural notch, but no distinct prominentiae and no apical cartilage. The broad occlusal surface is distinctly ridged and there is a distinct arytenoid valve on the inner margin. Pulvinaria vocalia are large and well-developed.

Arytenoid fossa: Small (only about 0.4x length of the vocal cord), elliptic, and moderately deeply excavate.

Vocal cord: Very broad, with a trifurcate fibrous inclusion -- a middle horizontal member at about the middle of the cord, and diagonal superior and inferior members arising from its posterior end. There are no cartilaginous buttresses.

Posterior chamber: Small, with a moderately large pulmonary aditus.

M. hyoglossus: Originates from a relatively narrow aponeurosis anterior to the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX (Pl. 22, fig. 2a & b)

Identification of larvae: Lambiris 1989b, and a series from Manyeleti Game Reserve, Transvaal (AJL 3475 - 3489, stages 28 - 45; December 1987 - January 1988; collected by G.V. Haagner), showing the white tympanic spot diagnostic of postmetamorphics, at Stage 45.

Material examined: SOUTH AFRICA; TRANSVAAL - AJL 3481a; stage 37, SVL 18,0 mm, AJL 3482a; stage 38, SVL 20,0 mm, AJL 3483a; stage 39, SVL 20,5 mm, All from Manyeleti Game Reserve; silver impregnation, ORANGE FREE STATE - AJL ====; Bloemfontein; stage 40, SVL 35,5 mm; silver impregnation.

Larval habitat: Shallow pans or dams with some emergent grasses or sedges, or inundated grassy wetlands, usually on poorly drained clays.

Buccopharyngeal roof

General shape: Truncately triangular, base about 1.2x greater than height. General surface more or less regularly concave; prenarial arena moderately excavate.

Prenarial arena: Large, almost square, about 1.1x broader than deep, with a central transverse ridge about 0.3x the width of the arena.

Internal nares: Large, narrowly elliptical, transversely set. Length about 0.5x width of roof at level of nares. Internarial distance about 0.2x width of naris. Margins not grooved.

Narial valve: Well-defined flaps on the anterior and posterior borders of the naris. Anterior flap with a long (subequal to narial width) cylindrical papilla arising near the lateral angle.

Postnarial arena: A large, smooth, conical **postnarial papilla** behind either naris, the base slightly medial to the narial mid-point, and curving laterally. The **lateral ridge papilla** is similar but slightly smaller. The **median ridge** is a tiny papillate projection about 0.15x the width of the roof at that level.

Buccal roof arena: U-shaped, bounded laterally by a posteriorly convergent row of 5 - 6 simple, subequal conical papillae on either side. Numerous small pustulations are confined to the arena.

Glandular ridge: A broad, curved band immediately behind the buccal roof arena, extending the width of the roof.

Dorsal velum: A narrow but well-defined flap, with a serrated free margin, broadly interrupted medially.

Pressure cushions: Do not seem to be separable into lateral and medial moieties.

Buccopharyngeal floor

General shape: Triangular, base about 1.4x height.

Prelingual papillae: Three large conical papillae on either side (one cylindrical and with a pustulose tip, in one specimen), all closely set and occupying much of the posterior part of the prelingual arena.

Lingual papillae: Two narrow, cylindrical, close-set papillae of moderate length on the tongue anlage.

Buccal floor arena: Transversely oval, about 1.8x broader than deep. Demarcated laterally by numerous moderate to large, close-set conical papillae tending to diminish in size posteriorly. There are numerous tiny pustulations in the arena.

Buccal pockets and prepocket papillae: Not discernible in these specimens.

Ventral velum: Well developed, of subequal width throughout. Four to six projections (some rather small, but mostly large) on either side of the midline, which is marked by a close-set smaller pair. There are no conspicuous supporting spicules.

Branchial baskets: Roughly triangular, major axis transverse.

Filter plates: Curved, more or less closed. Filter rows rather short and finely folded, with narrow channels.

DISCUSSION

Differences in laryngeal and buccopharyngeal morphology support recognition of the two forms discussed here as separate taxa, but the limited material available for dissection does not permit any judgement as to whether the distinction should be at the species or subspecies level. This would require examination of longer series from all parts of both taxons ranges. Indeed a thorough examination of all the taxa currently recognised in the genus would be desirable, since diagnoses based on external characters are not always satisfactory. The subspecific status of these taxa accorded by Parry (1982) is retained in the interests of taxonomic stability.

The considerable differences between the larynxes of *Pyxicephalus* (Plate 21) and of *Tomopterna* (Plate 23) support separation at the genus level.

PLATE 21
PYXICEPHALUS – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

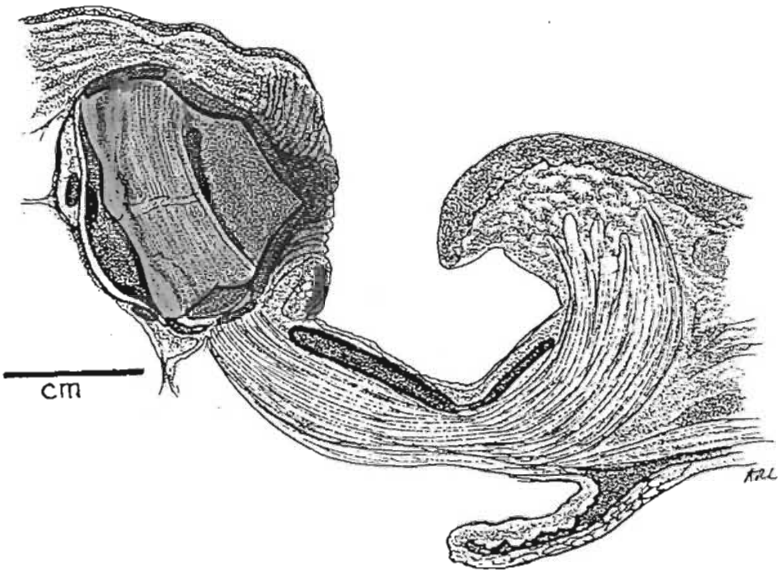


FIG. 1; *Pyxicephalus adspersus adspersus* Tschudi, 1838
AJL 405 (male), Harare, Zimbabwe.

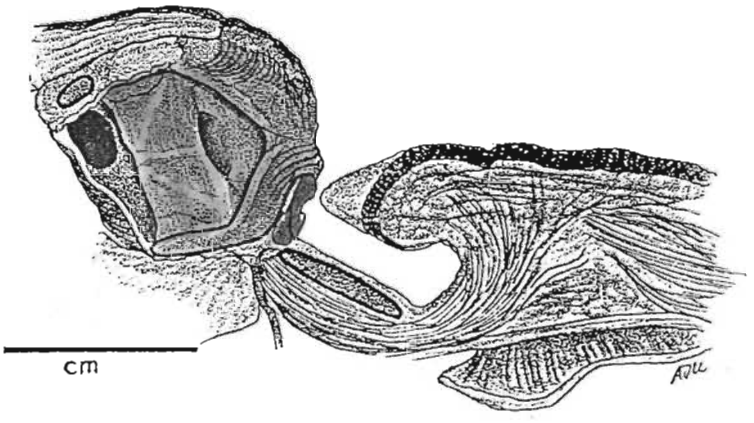


FIG. 2; *Pyxicephalus adspersus edulis* Peters, 1854
NM 7394 (male), 8 miles south of Mababe Gate (Entrance to Chobe National Park), Botswana.

PLATE 22
PYXICEPHALUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

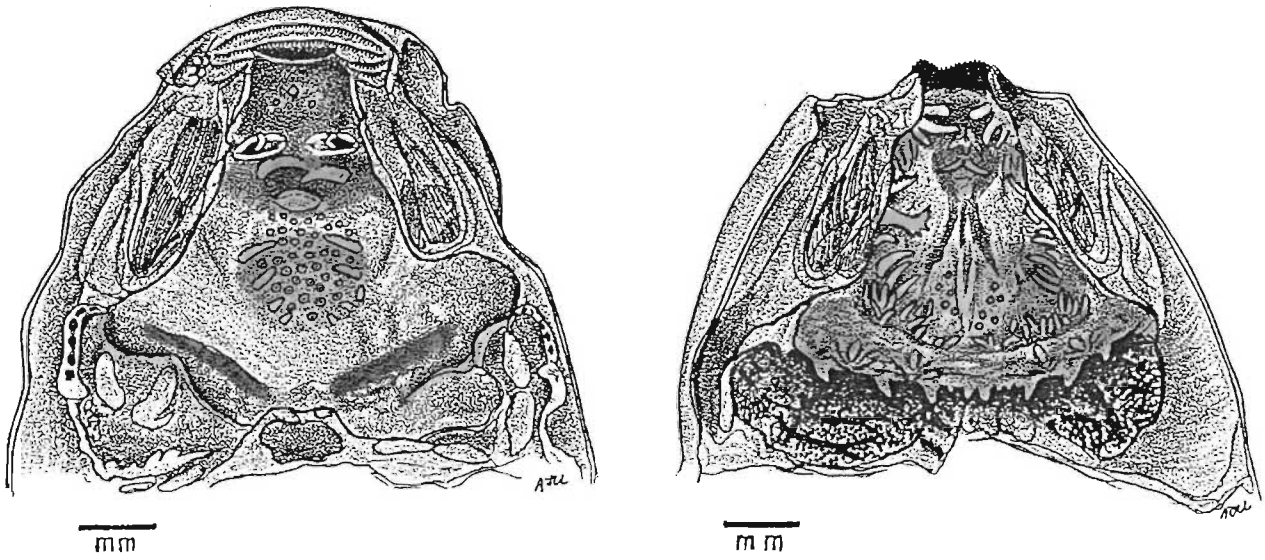


FIG. 1; *Pyxicephalus adspersus adspersus* Tschudi, 1838
AJL 3508, Stage 35, Pretoria, Transvaal, South Africa.

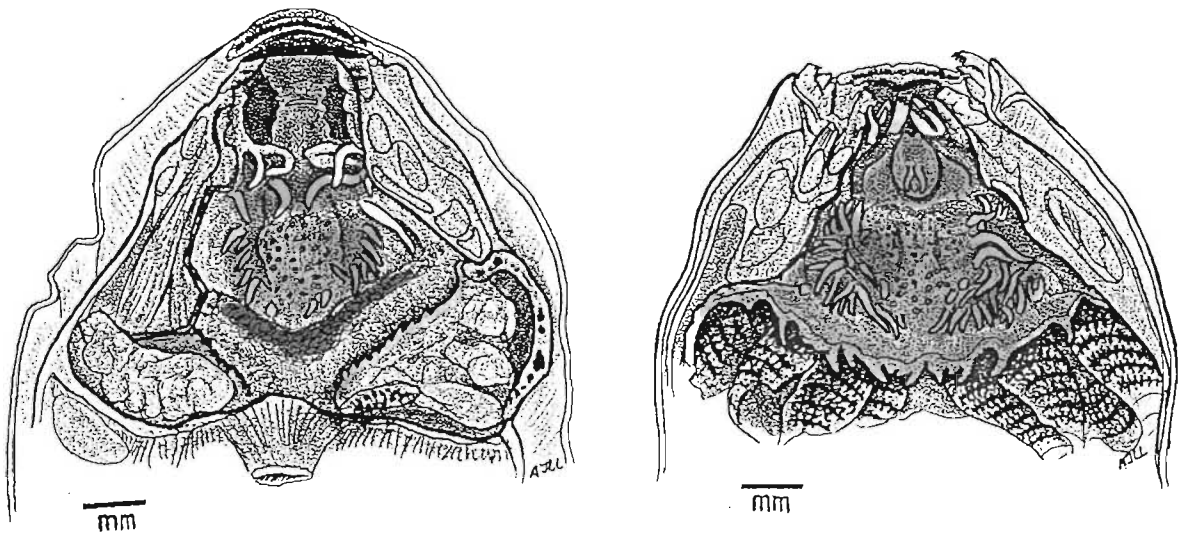


FIG. 2; *Pyxicephalus adspersus edulis* Peters, 1854
AJL ====, Stage 37, Manyeleti Game Reserve, Transvaal, South Africa.

TABLE 4. Laryngeal characters: *Tomopterna*

0 = Unknown
1 = True
2 = Variable
3 = False
4 = Inapplicable

	PROMINENTIAE APICALES PRESENT	INTERNAL MARGIN OF ARYTENOID CARTILAGE U-SHAPED	ANTERIOR MARGIN OF ARYTENOID LUMEN CONVEX	MEDIAL VOCAL CORD WITH PAIRED PROJECTIONS ON POSTERIOR MARGIN	LATERAL VOCAL CORD PRESENT	LATERAL VOCAL CORD STRUCTURALLY COMPLEX
Tomopterna cryptotis	1	3	1	1	1	1
krugerensis	3	3	1	1	1	1
marmorata	1	1	3	3	1	3
natalensis	1	1	1	1	3	4

Genus *Tomopterna* Duméril & Bibron, 1841

Pyxicephalus Tschudi, 1838, *Classif. Batr.*, pp. 46, 83. Type species, by designation of Fitzinger 1843: *Pyxicephalus adspersus* Tschudi, 1838.

Tomopterna Duméril & Bibron, 1841, *Erpét. Gén.*, 8:443. Type species, by designation of Boulenger 1918: *Pyxicephalus delalandei* Tschudi, 1838.

CHARACTERS

ADULT LARYNX (Table 4; Pl. 23)

Interspecific differences in the male larynxes of the taxa examined are summarised in Table 4.

Shape of the arytenoid cartilage

The external occlusal margin of the arytenoid cartilage is squared-off, with large, fimbriated superior and inferior prominentiae (but lacking an incisura) in *Tomopterna cryptotis*, *T. marmorata* and *T. natalensis*. It is more or less regularly convex only in *T. krugerensis*. The internal occlusal margin is V-shaped in *T. cryptotis* *T. krugerensis*, and U-shaped in *T. marmorata* and *T. natalensis*.

None of the taxa examined has an arytenoid valve, and only *T. krugerensis* shows faint suggestions of weak striations on the occlusal surface of the cartilage.

The arytenoid shelf is moderately distinct in the taxa examined. Only in *T. marmorata* is the curved margin of the shelf biarcuate.

Pulvinaria vocalia are absent (very weakly developed?) in *T. marmorata*, but present in the other taxa examined.

Vocal cords

Lateral and medial vocal cords are present in all but *Tomopterna natalensis*.

In *T. cryptotis* and *T. krugerensis* the lateral cord is large, prominent, and possesses a frenulum-like band at the mid-point. In *T. marmorata* the lateral cord is smaller, shorter, and linked to the medial cord by a short frenulum.

The medial cord possesses a single (*T. marmorata*) or paired (*T. cryptotis*, *krugerensis* and *natalensis*) prominenences on the posterior

margin; in *T. krugerensis* they are small and rounded, but are much more pointed in the other taxa examined.

Posterior chamber

The posterior chamber is relatively small, and simple. Only in *Tomopterna natalensis* is there a trace of a semilunar fold anterior to the pulmonary aditus.

LARVAL BUCCOPHARYNX (Pl. 24)

Only tadpoles of *Tomopterna cryptotis* and *T. natalensis* were available for examination. The buccopharynxes of these taxa are rather similar in most respects, and only the more obvious differences are presented here.

Prenarial arena

A strongly arcuate, anteriorly flexed ridge is present in about the centre of the arena of *T. natalensis* but absent in *T. cryptotis*.

Postnarial arena

The lateral ridge papillae are smooth and slender in *T. cryptotis*, more robust and pustulate in *T. natalensis*. The free margin of the median ridge in the latter species is more strongly serrated than in the former.

Infralabial papillae

Tomopterna cryptotis has two closely-set pairs of simple cylindrical papillae, whereas *T. natalensis* has three more widely-spaced, pustulate pairs of papillae.

Prepocket papillae

Those of *Tomopterna cryptotis* are small, almost pustulate, and more numerous (6 - 8); those of *T. natalensis* are larger, subconical, and fewer in number (3 - 6).

SPECIES ACCOUNT

Tomopterna cryptotis (Boulenger, 1907)

Rana cryptotis Boulenger, 1907, *Ann. Mag. Nat. Hist.* 20(7):109. Type locality: Mossamedes, Angola. Syntypes in the British Museum (Natural History), London.
Pyxicephalus delalandei cryptotis (Boulenger); Poynton 1964:96, fig. 49.
Pyxicephalus delalandii (non Tschudi, 1838); Van Dijk 1966:256 (part).
Tomopterna cryptotis (Boulenger); Passmore & Carruthers 1979:120, figs. Poynton & Broadley 1985b:125. Lambiris 1989a:75; 1989b:83, figs. 38 & 39, pl. 6 figs. 1a-d.

ADULT LARYNX

Material examined: SOUTH AFRICA - NATAL: AJL 2013 (m, SVL 38,6 mm), Weenen Nature Reserve. NM 7379 (m, SVL 38,8 mm), Ndumu Game Reserve. AJL 2059 (f, SVL 52,8 mm), Weenen Nature Reserve.

Advertisement call: Short clear notes, at about 3.5 kHz, and about 0.03 second long, uttered about 10 to 12 times per second (Passmore & Carruthers 1979:66), from exposed sites on mud, sand or stones at the water's edge. Calling is usually at night, but may occur on very overcast days; there is a loose choral structure.

Male larynx:

Pharyngeal mucosa: A thin layer overlying a deep submucosa, covering the dorsal surface of the arytenoid cartilage only, and clearly demarcated from the latter.

Arytenoid cartilage: The external occlusal margin is squared-off with massive superior and inferior prominentiae, which are fimbriated on their free surfaces. The internal occlusal margin is V-shaped. The arytenoid shelf is broad. Pulvinaria vocalia are well developed.

Arytenoid fossa: Elliptical; the major axis is about two-thirds the length of the medial vocal cord. The anterior border is clearly defined.

Vocal cords: The **median cord** is broad and only slightly flared at its insertions; the posterior edge has two short conical spikes demarcating the middle third of the cord. The **lateral cord** is broad, well developed and infolded longitudinally along the midline. There is a

frenulum-like transverse band overlying a slight swelling at about the mid-point.

M. hyoglossus: Originates anterior to the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX (Pl. 24, fig. 1a & b)

Identification of larvae: Lambiris 1989a; and a series from Kuiseb River, 100 km SW of Windhoek, Namibia (AJL 2786 - 2789, stages 35 - 41; 29 February 1988; collected by O. Wirminghaus), the only known member of the genus occurring in the area.

Material examined: NAMIBIA; AJL 2788; Kuiseb River, 100 km SW of Windhoek; stage 40, SVL 17,5 mm; silver impregnation.

Larval habitat: Shallow, muddy water (pools or small quiet streams) with few aquatic macrophytes.

Buccopharyngeal roof

General shape: Triangular, base about 1.3x height. General surface regularly concave; prenarial arena moderately deeply excavate.

Prenarial arena: Trapezoid, about 1.2x deeper than broad, and devoid of ornamentation.

Internal nares: Large, narrowly elliptical, set slightly obliquely. Length about 0.47 width of roof at level of nares. Internarial distance about 0.8 length of naris. Posterior margin not deeply grooved.

Narial valve: Margins shallow and smooth, with a long (about 0.6x narial length) cylindrical papilla arising at about the middle of the anterior margin.

Postnarial arena: A single smooth, weakly conical **postnarial papilla** arises near two similar, closely set **lateral ridge papillae** on either side. The **median ridge** is a strongly arcuate flap, about 0.33x the width of the roof at that level, with a pustulate free margin.

Buccal roof arena: Transversely oval. Width about 0.6x breadth of roof. Bounded laterally by a curved, posteriorly convergent, row of simple cylindrical papillae diminishing slightly in size posteriorly -- 4 subequally-spaced on the right side, 6 less regularly arranged on the

left side. Three or four feebly defined pustulations are present in the centre of the arena.

Glandular ridge: Not discernible in this specimen.

Dorsal velum: A weakly developed flap, broadly discontinuous medially, and lacking any marginal ornamentation.

Pressure cushions: Not apparent in this preparation.

Buccopharyngeal floor

General shape: Triangular, width about 1.4x height. General surface rather flat, but with a rather deep prelingual arena.

Prelingual papillae: Two large, subconical papillae on either side (one on the right side shortly bifurcate near the tip).

Lingual papillae: A pair of close-set cylindrical papillae on either side of the midline, and near the anterior border of the tongue anlage.

Buccal floor arena: Transversely oval, about 1.5x broader than deep. Demarcated by numerous subcylindrical papillae of moderate size, scattered somewhat irregularly over the whole arena. Some are terminally bifid, but there is no discernible pattern.

Buccal pockets are very indistinct in this specimen, and appear to be closed. **Prepocket papillae** are numerous, closely-set and stubby.

Ventral velum: Well developed, of subequal width throughout. The free margin bears 10 short rounded lobes, closely set on either side of the midline, with one more widely-spaced lobe laterally on either side. Supporting spicules are not obvious.

Branchial baskets: Roughly triangular; major axis transverse.

Filter plates: Curved, more or less closed. Filter rows finely folded, with narrow canals.

Tomopterna krugerensis Passmore & Carruthers, 1975

Pyxicephalus delalandei cryptotis (non Boulenger, 1907): Poynton 1864:96 (part).
Tomopterna krugerensis Passmore & Carruthers, 1975, *Koedoe*, 18:32. Type locality: Machayipan, Kruger National Park, Republic of South Africa. Holotype in the Transvaal Museum, Pretoria. Passmore & Carruthers 1979:122, figs. Poynton & Broadley 1985b:127, Lambiris 1989a:76; 1989b:86, fig. 40, pl. 6 figs 2a-c.

ADULT LARYNX (Table 4; Plate 23, fig. 2)

Material examined: SOUTH AFRICA; NATAL - AJL 2987 (m, SVL 41,0 mm), Mbazwane, Zululand. AJL 3081 (f, SVL 36,3 mm), Mantuma, Mkuzi Game Reserve.

Advertisement call: A dull knocking note at about 2.5 kHz, and about 0.02 second in duration (Passmore & Carruthers 1979:68), uttered from partly concealed positions in very short vegetation on sandy or muddy banks, or in very shallow water. There is a very loose choral structure.

Male larynx:

Pharyngeal mucosa: Thin, unfolded, overlying a shallow submucosa, and covering only the extreme dorsal portion of the arytenoid cartilage.

Arytenoid cartilage: Prominentiae are lacking. The external occlusal margin of the arytenoid cartilage is broadly U-shaped, the internal occlusal margin broadly V-shaped. The arytenoid shelf is broad and shallow. Pulvinaria vocalia are well developed.

Arytenoid fossa: Extends almost the entire length of the anterior margin of the medial vocal cord, but the anterior border is feebly defined.

Vocal cords: The medial vocal cord is rather broadly flared superiorly, less so inferiorly, and has a pair of low, rounded protruberances on the posterior margin at about mid-point. The posterior inferior margin is slightly thickened. The lateral cord is massive, infolded logitudinally along its posterior surface, and the large central swelling is bisected by a rudimentary frenulum.

M. hyoglossus: Arises below the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX

Tadpoles were not available for examination.

Tomopterna marmorata (Peters, 1854)

Pyxicephalus marmoratus Peters, 1854, *Monatsber. königl. Akad. Wiss. Berlin*: 627. Type locality: Boror, Mozambique. Holotype in the Zoologisches Museum, Berlin. Poynton 1964:99, fig. 50.

Tomopterna marmorata (Peters): Passmore & Carruthers 1979:124, figs. Poynton & Broadley 1985b:129. Lambiris 1989a:78; 1989b:87, fig. 41, pl.6 figs. 3a-c.

ADULT LARYNX (Table 4; Pl. 23, fig. 3)

Material examined: ZIMBABWE: NM 2039, 2040 (m, SVL ==), Rhino Hotel, Lundi River. SOUTH AFRICA: TRANSVAAL - NM 5531 (m, SVL 38 mm), Boulders. AJL 2980 (f, 41.6 mm), Messina.

Advertisement call: A short (about 0.3 second) note at about 1.5 and 3 kHz (Passmore & Carruthers 1979:124), uttered rapidly about 5 times per second (rate rather variable); from exposed or semi-concealed positions on mud banks, usually at night.

Male larynx:

Pharyngeal mucosa: Thin, unfolded, overlying a shallow bed of connective tissue, and covering the entire dorsal surface of the arytenoid cartilage.

Arytenoid cartilage: The outline of the external margin is squared-off by the large prominentiae, which are slightly fimbriated on their free margins. The internal occlusal margin is roughly U-shaped. The occlusal surface is rather narrow. The arytenoid shelf is shallow but very broad. Pulvinaria vocalia are very feebly developed.

Arytenoid fossa: Anterior margin moderately clearly defined, but modified by a double inward bulge.

Vocal cords: Medial vocal cord strongly flared at its insertions, and possessing a feeble midline thickening superiorly. The posterior margin has a single cusp at about mid-point, continuous with a frenulum traversing the small, simple lateral vocal cord.

M. hyoglossus: Arises anterior to the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX

Tadpoles were not available for examination.

Tomopterna natalensis (A. Smith, 1849)

Pyxicephalus natalensis A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App.: 23. Type locality: eastward of the Cape Colony. Probable type in the British Museum (Natural History), London (Poynton & Broadley 1985b:131). Poynton 1964:101.

Tomopterna natalensis (A. Smith): Van Dijk 1966:256. Passmore & Carruthers 1979:124, figs. Poynton & Broadley 1985b:131. Lambiris 1988:24, figs., pl. 3 fig. 1a-c; 1989a:78.

ADULT LARYNX (Table 4; Pl. 23, fig. 4)

Material examined: SOUTH AFRICA: AJL 2017 (m, SVL 30.7 mm), AJL 2018 (m, SVL 29.8 mm), Weenen Nature Reserve. AJL 2080 (f, SVL 38.5 mm), eGodeni, Hluhluwe Game Reserve.

Advertisement call: Loud, penetrating chirps about 0.07 second long, at about 1.5 kHz (Passmore & Carruthers 1979:126), uttered 2 - 5 times a second. Calls are made at night or on overcast days from open or partly concealed sites near the water's edge; there is a loose but definite choral structure.

Male larynx:

Pharyngeal mucosa: Thin, unfolded, overlying a fairly deep submucosa, and covering the dorsal surface of the arytenoid cartilage.

Arytenoid cartilage: The external margin is squared-off by large prominentiae, the superior prominentia being slightly fimbriated. The internal margin of the occlusal surface is rather U-shaped. The arytenoid shelf is broad and shallow, and pigmented along the mid-line. Pulvinaria vocalia are only moderately developed, the inferior pulvinarium being larger than the superior.

Arytenoid fossa: Oval, with a well-defined anterior border. The major axis is about two-thirds the length of the medial vocal cord.

Vocal cords: The medial vocal cord is broadly flared superiorly, less so inferiorly, and robust in appearance. The posterior margin has a pair of small prominences defining the middle fifth of the cord. The lateral vocal cord appears to be absent in the specimens examined. If present, it is completely concealed by the medial cord when the larynx is in a relaxed condition.

LARVAL BUCCOPHARYNX (Pl. 24, fig. 2a & b)

Identification of larvae: Lambiris 1989a, and a series from Itala Game Reserve, Natal (AJL 2544 - 2546, 2551 - 2563, stages 10/11 - 45; collected January 1986), showing the black inguinal spots diagnostic of adults from stage 43/44.

Material examined: SOUTH AFRICA; NATAL - AJL 2390; stage 34, SVL 10 mm; Hilltop, Hluhluwe Game Reserve; silver impregnation. AJL 2541, stage 35, SVL 11.5; AJL 2543, stage 38, SVL 11.5 mm (both silver impregnation); AJL 2556, stage 311/32, SVL 10.0 mm (thionine); all from 1 km NW of Craigadam, Itala Game Reserve.

Larval habitat: Shallow ponds or streams with sandy or rocky substrata, or in shallow pools on bare rock in the beds of larger rivers, with few or no aquatic macrophytes; some organic silt and small algae usually present.

Buccopharyngeal roof

General shape: Roughly triangular. Base about 1.1x height. General surface convex, prenarial arena rather deeply excavate.

Prenarial arena: Trapezoid, base about 1.3x height, with an arcuate transverse lobulated ridge across the middle.

Internal nares: Moderately large, narrowly elliptical, and slightly obliquely set. Length about 0.3x width of roof at level of nares. Internarial distance about 1.3x narial length. Margins not grooved.

Narial valve: Low, simple flaps devoid of ornamentation.

Postnarial arena: A large (about equal to length of naris) conical **postnarial papilla** with a regularly pustulose anterior margin, arises behind, and at about the midpoint of, the internal naris. It is flanked laterally on either side by two similar **lateral ridge papillae** -- one opposite the postnarial papilla, the other opposite the **median ridge**, which is a large triangular flap with a regularly denticulate free margin.

Buccal roof arena: Broadly oval, the transverse major axis about 0.4x the width of the roof. It is bounded laterally by 3 - 4 large, equally-spaced, rather robust, simple conical papillae set in single posteriorly convergent rows. 2 - 3 small pustulate papillae are present

between the last two papillae in either series. 6 - 8 small pustulations are present in the arena.

Glandular ridge: Not apparent in these preparations.

Dorsal velum: Weakly developed, broadly discontinuous in the midline, and devoid of ornamentations.

Pressure cushions: Simple, not separable into distinct medial and lateral moieties.

Buccopharyngeal floor

General shape: Triangular, base about 1.3x height. General surface irregular, with a deeply excavate prelingual arena and a shallower buccal floor divided by a broad median groove retrolingually.

Prelingual papillae: Two relatively long cylindrical papillae with pustulose anterior margins arise anteroposteriorly on either lateral wall. These are followed, linguad, by a shorter simple papilla on either side.

Lingual papillae: A pair of moderately long, simple cylindrical papillae arise from the midline just behind the anterior border of the tongue anlage. These are closely flanked posterolaterally by another one on either side.

Buccal floor arena: Transversely rectangular, the major axis about 0.7x the width of the roof. The arena is demarcated by numerous cylindrical or subconical papillae scattered irregularly over the whole arena; the central ones tend to be a little smaller than the outer ones. 20 - 30 pustulations are concentrated along the medial zone, and extend onto the velum.

Buccal pockets: Major axis about 0.25x width of floor. Deep-set and closed.

Prepocket papillae: Six simple cylindrical papillae on either side, immediately anterior to the buccal pocket.

Ventral velum: Moderately broad, of subequal width throughout, and with a slightly scalloped free margin.

Branchial baskets: Roughly triangular, major axis transverse.

Filter plates: Curved, partly closed. Filter rows short, finely folded, with narrow, rather irregular canals.

DISCUSSION

Van Dijk (*in* Branch *et al.* 1988:3) notes that Tandy & Bogert consider *Tomopterna cryptotis* to be composite, including a diploid and a tetraploid species. Confirmation, and elucidation of distributions, would have involved the examination of extensive series from the taxon's entire range -- a matter far beyond the scope of this study, and which needs to be treated as an independent investigation in its own right.

The difficulty of distinguishing between some specimens of *Tomopterna cryptotis* and *T. krugerensis* (Poynton & Broadley 1985b:127; Lambiris 1989a:77) or between *T. marmorata* and *T. krugerensis* (Poynton & Broadley 1985b:128) on the basis of external moprphological characters is very satisfactorily resolved by consistent, distinctive differences in both male (Pl. 23) and female (not illustrated) larynxes. These would eliminate the dependence on advertisement calls (not always available when most needed) for confident identification of problematic specimens.

PLATE 23
TOMOPTERNA — ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

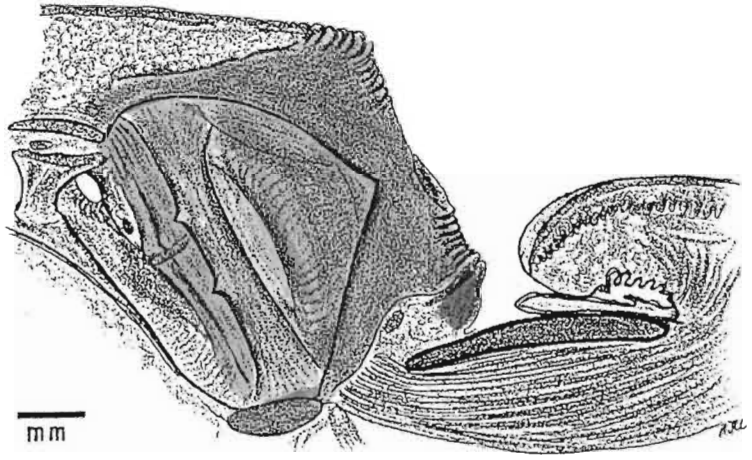


FIG. 1: *Tomopterna cryptotis* (Boulenger, 1907)
AJL 2013 (male), Weenen Nature Reserve, Natal, South Africa.

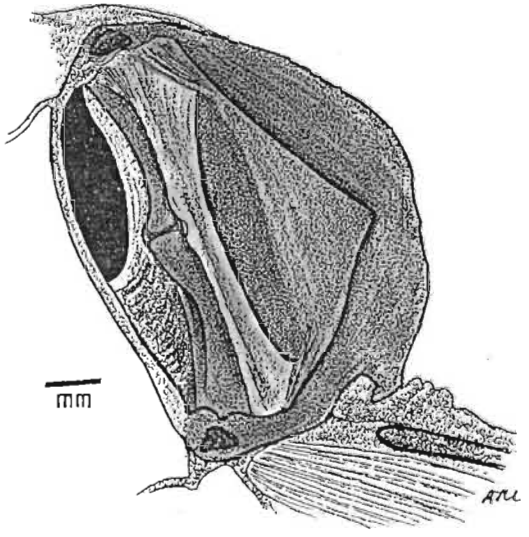


FIG. 2: *Tomopterna krugerensis* Passmore & Carruthers, 1975
AJL 2987 (male), Mbazwane, Natal, South Africa.

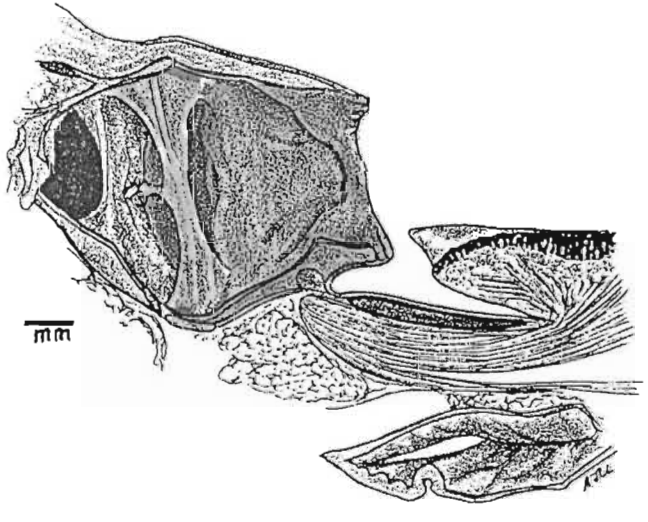


FIG. 3: *Tomopterna marmorata* Peters, 1854
NM 2039 (male), Rhino Hotel, Lundi River, Zimbabwe.

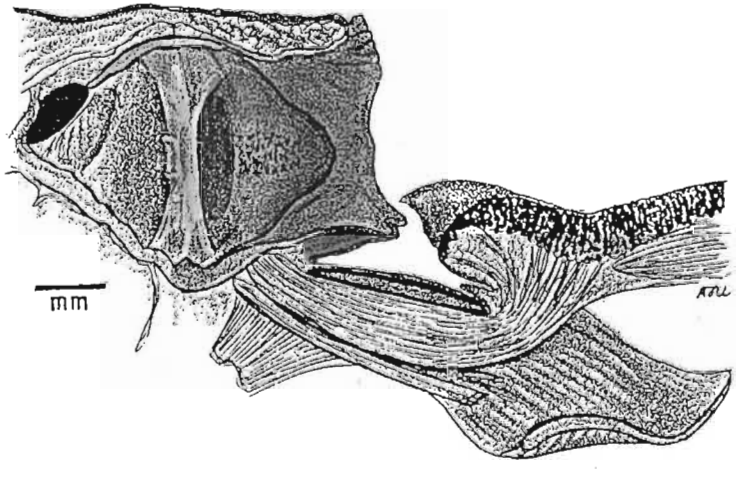


FIG. 4: *Tomopterna natalensis* (A. Smith, 1849)
AJL 2018 (male), Weenen Nature Reserve, Natal.

PLATE 24
TOMOPTERNA – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

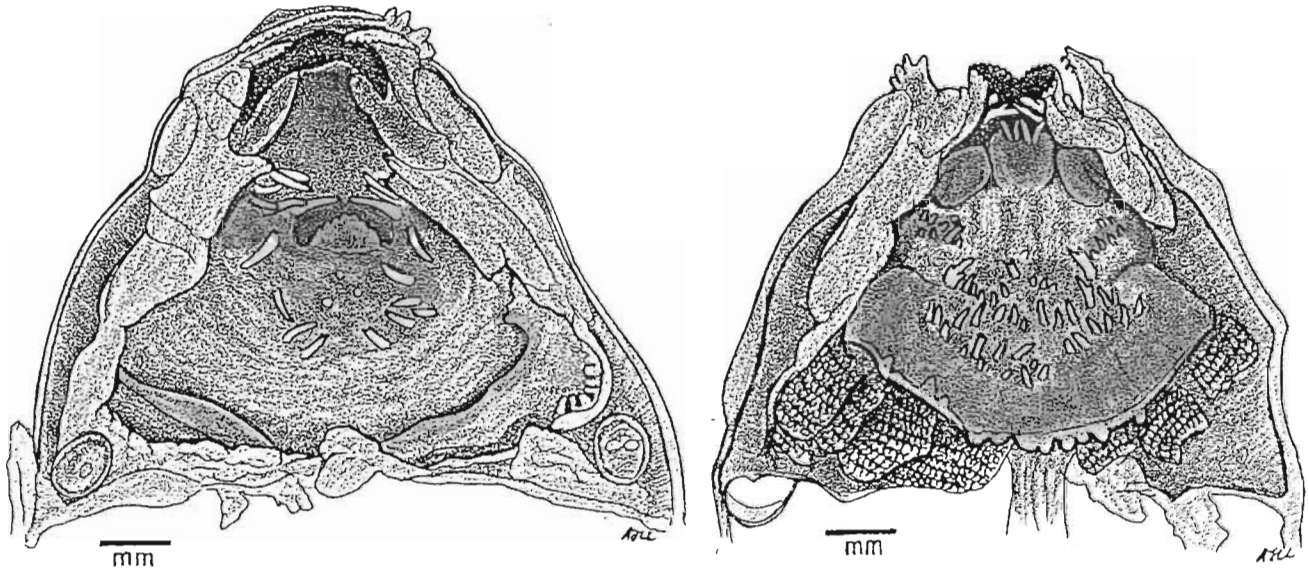


FIG. 1: *Tomopterna cryptotis* (Boulenger, 1907)
AJL 2788, Stage 38, Kuiseb River, 100 km SW of Windhoek, Namibia.

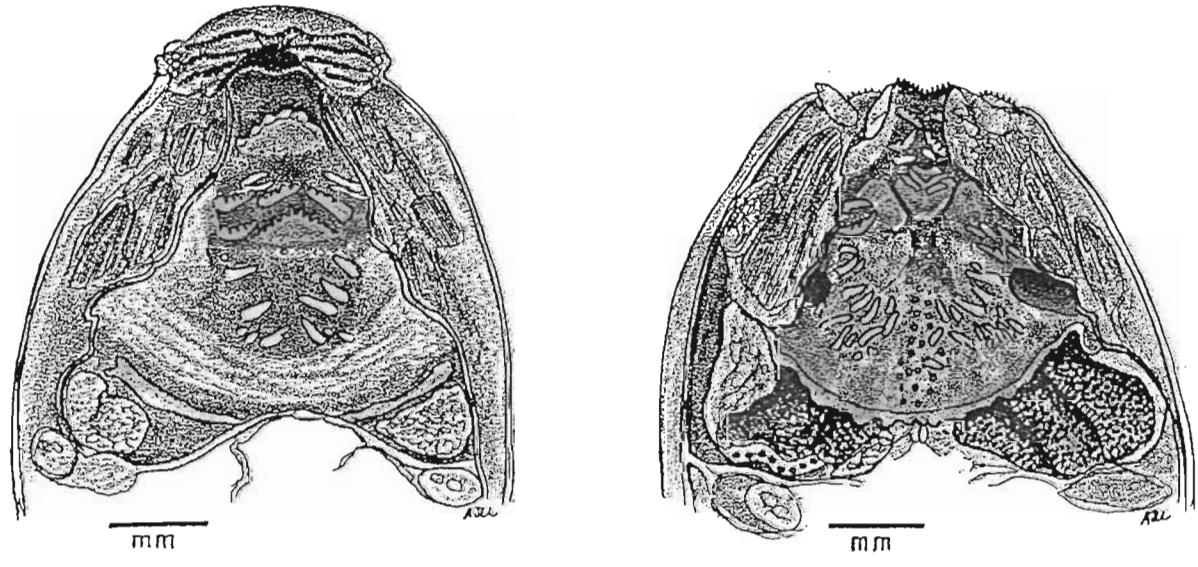


FIG. 2: *Tomopterna natalensis* (A. Smith, 1849)
AJL 2543, Stage 38, 1 km NNW of Craigadam, Itala Nature Reserve, Natal, South Africa.

Genus *Hildebrandtia* Nieden, 1907

Hildebrandtia Nieden, 1907, *Sitzber. Ges. naturf. Freunde Berlin*, 1907:229. Type species: *Pyxicephalus ornatus* Peters, 1878, by subsequent designation of Boulenger 1919.

CHARACTERS

Only one taxon is treated in this study. Characters are described in detail in the Species Account, below.

ADULT LARYNX (Pl. 25)

There is little sexual dimorphism in the adult larynx. The female is unusual, in the genera studied, in possessing a larger larynx than the male.

In both sexes the larynx is somewhat compressed anteroposteriorly. The arytenoid cartilage has large, alate prominentiae, a narrow occlusal surface lacking any obvious valve, and a shallow shelf without a definte arytenoid fossa. The medial vocal cord is a broad, simple band and the lateral cord is virtually (males) or completely (females) absent. The posterior chamber is relatively small, and the lateral wall folded (males) or smooth (females).

LARVAL BUCCOPHARYNX (Plate 26)

The larval buccopharynx possesses some remarkable features, presumably associated with the predatory, carnivorous habits of the tadpole noted by Lambiris (1989a:81, and unpublished observations). These are discussed more fully below.

The roof is simple, lacking papillae (other than a single postnarial papillae on either side, and a median ridge) and a dorsal velum. The prenarial arena is enormous, and the glandular ridge exceptionally broad.

The floor is also highly modified. Most conspicuous are the peculiar pair of rosette-like appendages on the lingual anlage and the intricate convolutions of the buccal floor arena. A second pair of pockets also appears to be present.

SPECIES ACCOUNT

Hildebrandtia ornata ornata (Peters, 1878)

Pyxicephalus ornatus Peters, 1878, *Mber. königl. Akad. Wiss. Berlin*, p. 207, pl. 2 fig. 7. Type locality: Taita [i.e. Teital, Kenya. Type in the Zoologisches Museum, Berlin.
Hildebrandtia ornata ornata (Peters): Poynton 1964:122, fig. 63. Van Dijk 1966:252, fig. Passmore & Carruthers 1979:138, figs. Lambiris 1989a:80; 1989b:102, figs 52 & 53, pl. 9 figs. 2a-c.

ADULT LARYNX (Pl. 25, figs. 1 & 2)

Material examined: ZIMBABWE: NM 2778 (m, SVL 37,4 mm), Wankie, AJL 1013 (f, SVL 50,5 mm), Kwekwe. SOUTH AFRICA: TRANSVAAL - NM 5937 (m, SVL 45,5 mm), Pafuri.

Advertisement call: A nasal quack about 0.4 second long, at about 1 kHz with strong harmonics between 2 - 3 kHz (Passmore & Carruthers 1979:148), uttered once every two or three seconds, from semiconcealed positions among short vegetation at the water's edge; usually at night, but also during overcast days.

Male larynx:

Pharyngeal mucosa: Thin, overlying a deep submucosa, which is distinct from the arytenoid cartilage.

Arytenoid cartilage: The roughly U-shaped external margin of the occlusal surface is modified by large fimbriated superior, and large smooth inferior, prominentiae. The internal occlusal margin is widely V-shaped. The occlusal surface is rather narrow. The arytenoid shelf is broad and moderately deep. Pulvinaria vocalia are feebly developed.

Arytenoid fossa: There is no distinct fossa.

Vocal cord: The medial vocal cord is moderately broad, and somewhat flared at its insertions. The posterior margin is thickened. There are no discrete supporting buttresses. The lateral vocal cord is reduced to a rudimentary fold lateral to the superior insertion of the medial cord.

Posterior chamber: Small and simple, with a somewhat folded lateral wall. The pulmonary aditus is relatively small.

M. hyoglossus: Arises below the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX (Pl. 26, fig. 1a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a, 1989b.

Material examined: SOUTH AFRICA; NATAL - AJL 2373; Makhamisa Pan, Mkuzi Game Reserve; stage 39/40, SVL 25.0 mm (silver impregnation).

Larval habitat: Pans of moderate depth, in open savannah bushveld, with silted bottoms and emergent macrophytes. Plant material does not seem to be important in the diet of at least the larger of these carnivorous tadpoles (see Discussion, below).

Buccopharyngeal roof

General shape: Roughly trapezoid, base about 1.1x height. General surface moderately concave, with a large, deeply excavate prenarial arena bounded by the massive upper beak and possessing four small pustulations medially, anterior to the nares.

Internal nares: Large, elliptical, transversely arranged. Length about 0.5x the width of the roof at the level of the nares. Internarial distance about 0.2x length of naris.

Narial valve: A simple flap on the anterior margin of the naris.

Postnarial arena: Broadly rectangular, breadth 1.8x depth. A large, simple conical **postnarial papilla** arises slightly medial to the mid-point of the posterior narial margin. **Lateral ridge papillae** are absent. The **median ridge** is a small but distinct triangular flap. There are three pustulations in the midline anterior to the median ridge, and about 6 on either side.

Buccal roof arena: There are no buccal roof arena papillae. The arena is a shallow depression between the postnarial arena and the somewhat more raised glandular ridge, over which are scattered numerous small, rather widely-spaced pustulations.

Glandular ridge: A broad zone defining the posterior limits of the buccal roof arena, and with several small, widely-spaced pustulations.

Dorsal velum: Absent.

Pressure cushions: Appear to be simple structures in this preparation.

Buccopharyngeal floor

General shape: A deep, narrow trapezoid. Base about 1.1x height. General surface elaborately sculpted with convoluted folds. Prelingual arena deeply excavate and with an irregularly-shaped floor, bounded anterolaterally by the massive lower beak.

Prelingual papillae: A palpoid papilla of moderate size below the root of the beak, on either side.

Lingual papillae: The massive, trapezoid tongue anlage is longitudinally ridged laterally, and bears a pair of large, remarkable structures (one on on either side of the posterior midline) irresistably reminiscent of a *Marchantia* archegoniophore.

Buccal floor arena: Weakly trapezoid, base about equal to height. Bounded laterally by 4 (left) or 5 (right) subconical papillae, some of which are weakly bifid terminally, and containing several small, widely scattered pustulations. The floor of the arena is elaborately convoluted by roughly bilaterally symmetrical folds.

Buccal pockets: Set far back, roughly at the level of the posterior border of the buccal floor arena. They are small and closed. A second pair of pockets is situated at about the level of the anterior border of the buccal floor arena. **Prepocket papillae** are reduced to 8 or 9 pustulations on either side.

Ventral velum: Well-developed, of subequal width throughout, and lacking both marginal ornamentation and evidence of supporting spicules.

Branchial baskets: Rather small, being only about one ninth of the total buccopharyngeal area.

Filter plates: Appear to be spongiform in this preparation.

DISCUSSION

The hyolarynx appears to show closer affinities with *Pyxicephalus* than with *Rana* or with *Ptychadena*. The larger female larynx with its broader, more robust vocal cord, is an unusual condition in the genera examined.

The tadpole displays some remarkable buccopharyngeal modifications -- again, unique among the genera examined in this study -- which appear to be related to its diet and feeding behaviour.

It may be remarked here that the tadpole of *Hildebrandtia ornata* is an actively predatory carnivore -- for example, the specimen examined ate 7 *Chiromantis* and *Kassina* tadpoles (all at about stage 38) in one night! (Unpublished observation, 21/xi/1985.) Such tadpoles are taken alive and the few remains that are found the next morning look disconcertingly like shark attack victims. I have not, unfortunately, witnessed captive tadpoles feeding.

The purpose and functions of the remarkable lingual appendages are unclear, but I hope to be able to elucidate them from histological and microanatomical studies later. Similarly, the precise purpose of the elaborate folds on the buccal floor arena remains obscure.

PLATE 25
HILDEBRANDTIA – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

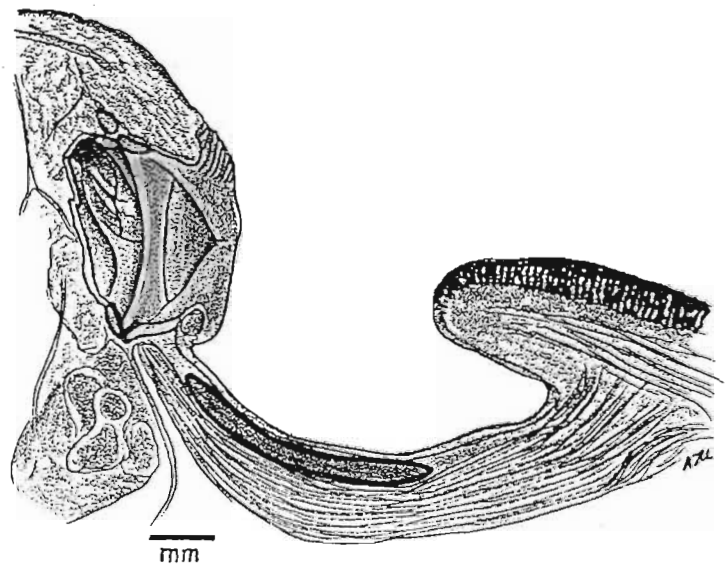


FIG. 1; *Hildebrandtia ornata ornata* (Peters, 1878)
NM 2778 (male), Wankie [= Hwange], Zimbabwe.

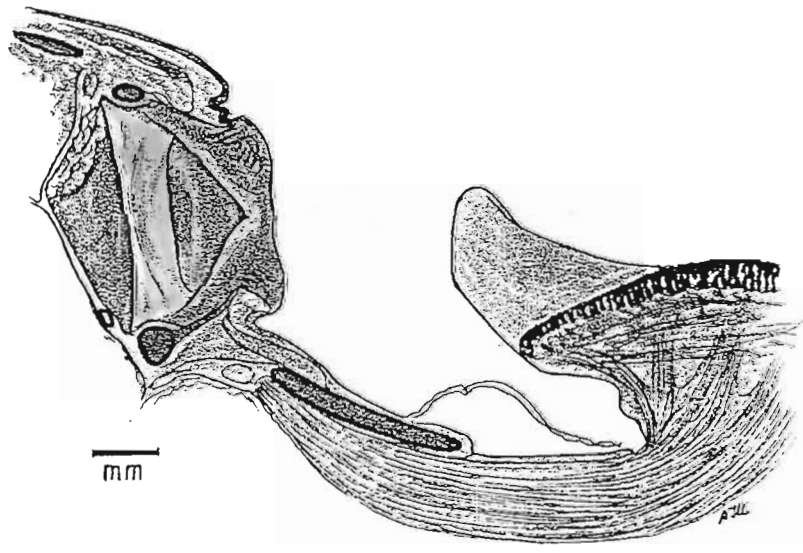


FIG. 2; *Hildebrandtia ornata ornata* (Peters, 1878)
AJL 1013 (female), Kwekwe, Zimbabwe.

PLATE 26
HILDEBRANDTIA – LARVAL BUCCOPHARYNX
Roof on left, floor on right

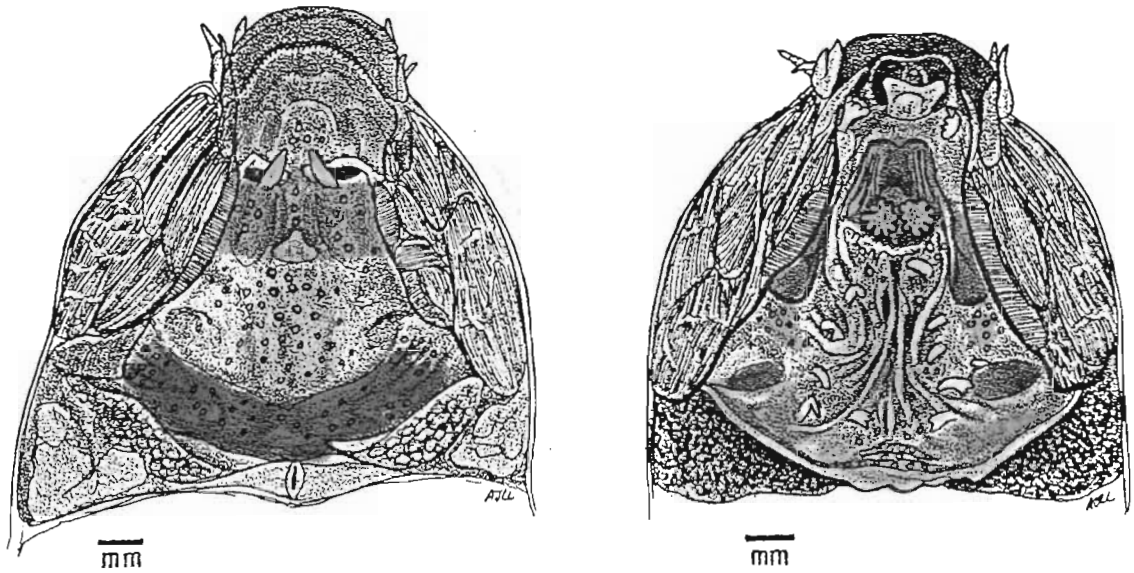


FIG. 1; *Hildebrandtia ornata ornata* (Peters, 1878)
AJL 2373, Stage 39/40, Mboneni Pan, Mkuzi Game Reserve, Natal, South Africa.

TABLE 5. Hyolaryngeal characters:
Ptychadena

0 = Unknown
1 = True
2 = Variable
3 = False
4 - Inapplicable

* = Extralimital taxon included for comparison

	ARYTENOID VALVE PRESENT ON INNER OCCLUSAL MARGIN OF CARTILAGE	ARYTENOID SHELF DOUBLE	FOVEA PRESENT ON ANTERIOR ARYTENOID SHELF	MEDIAL VOCAL CORD STRONGLY FLANGED ON ANTERIOR AND POSTERIOR MARGINS	INSERTIONS OF VOCAL CORDS FLARE INTO MASSIVE BUTTRESSES	MEDIAL VOCAL CORD DIVIDED INTO SEPARATE ANTERIOR AND POSTERIOR MOIETIES	LATERAL VOCAL CORD WELL DEVELOPED
Ptychadena oxyrhynchus	3	3	4	1	3	3	4
anchietae	3	3	4	1	3	3	1
"mascareniensis A "	3	1	3	4	1	1	4
"mascareniensis B "	1	1	1	1	1	3	3
porosissima	1	3	4	4	3	1	3
mossambica	3	3	4	3	3	3	1
"taenioscelis A"	1	3	1	1	3	3	3
"taenioscelis B"	1	3	4	3	3	3	1

Genus *Ptychadena* Boulenger, 1918

Ptychadena Boulenger, 1918, *Bull. Soc. Zool. France*, 1918:114. Type species by original designation: *Rana mascareniensis* Duméril & Bibron, 1841.

CHARACTERS

Laryngeal morphology indicates that *Ptychadena m. mascareniensis* (Duméril & Bibron, 1841) and *Ptychadena taenioscelis* Laurent, 1954, both appear to be comprised of cryptic species not separable by external characters. They are referred to as "*Ptychadena mascareniensis* A and B" and "*Ptychadena taenioscelis* A and B" here, pending clarification of nomenclatural issues.

ADULT MALE LARYNX (Table 5; Pls. 27, 28)

Shape of the arytenoid cartilage

The external occlusal margin is distinctly bilobed apically, although a definite incisura and prominentiae cannot be distinguished as such. The internal occlusal margin varies from being an almost regular arc (*Ptychadena oxyrhynchus*) to strongly V-shaped (*P. "taenioscelis* B"), with intermediate shapes in the other taxa examined. The shape of the occlusal surface does not appear to be of major diagnostic importance in the taxa examined.

The arytenoid shelf has a double step in *Ptychadena "mascareniensis* A and B" only. There is a shallow fovea in the anterior shelf in "*P. mascareniensis* B", and in the shelf of "*P. taenioscelis* A".

An arytenoid valve on the internal occlusal margin is present in *P. "mascareniensis* B", *P. porosissima* and *P. "taenioscelis* A and B". It is absent in *P. oxyrhynchus*, *P. anchietae* and *P. mossambica*.

The arytenoid fossa is narrowly elliptical and elongate. It does not show any taxonomically useful features in the species examined.

Vocal cords

The vocal cords show the most distinctive differences in the taxa examined. The presumably plesiomorphic condition of a simple, moderately broad medial cord with thickened or flanged margins, curved cross-

Table 6. Buccopharyngeal characters: *Ptychadena*

0 = Unknown
1 = True
2 = Variable
3 = False
4 = Inapplicable

	PRENARIAL ARENA RIDGE BEARS A CONTINUOUS SERIES OF LARGE, LOW PAPILLAE	ANTERIOR NARIAL MARGIN DENTICULATE	LATERAL RIDGE PAPILLAE PALPOID	FREE MARGIN OF MEDIAN RIDGE DENTICULATE	BUCCAL ROOF ARENA CLEARLY DEFINED BY REGULARLY ARRANGED LARGE PAPILLAE	BUCCAL ROOF ARENA PUSTULES NUMEROUS AND WIDELY SCATTERED	DORSAL VELUM CLEARLY DISCERNIBLE	INFRALABIAL ARENA HAS LARGE BULBOUS PAPILLAE	BUCCAL FLOOR HAS RETROLINGUAL FOLDS OR A DEPRESSION EXTENDING INTO THE ARENA	BUCCAL FLOOR ARENA DEFINED BY A ROW OF REGULARLY ARRANGED ENLARGED PAPILLAE	BUCCAL FLOOR PUSTULES NUMEROUS AND WIDELY SCATTERED	VENTRAL VELUM HAS DISTINCT SUPPORTING SPICULES	FREE MARGIN OF VENTRAL VELUM ORNAMENTED WITH LOBATE PROJECTIONS
Ptychadena oxyrhynchus	3	1	1	1	3	1	3	3	1	3	1	3	1
anchietae	1	3	3	3	1	1	3	1	1	3	1	1	1
porosissima	3	1	1	3	1	3	1	1	3	1	3	1	3

sectional profile, and lack of buttresses, frenulum and lateral cord, is shown in *Ptychadena oxyrhynchus*. In the other taxa the cords are elaborated to a greater or lesser extent.

In *Ptychadena "taenioscelis*B" the medial cord, which is flanged on the posterior margin only, bears very rudimentary buttresses. These are much more developed in *P. "taenioscelis* A." *P. anchietae* has an essentially primitive medial cord, marginal flanges are prominent and buttresses are present on the posterior margin. Elaboration of buttresses reaches its peak in those of *P. "mascareniensis* A and B".

A trend towards longitudinal splitting of the medial cord appears to be evidenced in *P. mossambica* and *P. porosissima*, culminating in that of *P. "mascareniensis* A", where division is complete.

Lateral cords are absent in *Ptychadena "mascareniensis* A". They are rudimentary in *Ptychadena "mascareniensis* B", *P. porosissima* and *P. "taenioscelis* A and B", moderately strongly developed in *P. mossambica* and most prominent in *P. anchietae*.

Pulvinaria vocalia

Pulvinaria vocalia are feebly developed in the species examined.

Posterior chamber

The rather large posterior chamber is devoid of useful features. The pulmonary aditus has a narrow cartilaginous rim in *Ptychadena "mascareniensis* A and B", *P. porosissima* and *P. mossambica*. In *P. "mascareniensis* A" and *P. mossambica* there is a thin semicircular or arcuate subadital sheet of cartilage.

LARVAL BUCCOPHARYNX (Table 6; Pls. 29, 30)

Tadpoles of only three species, *Ptychadena oxyrhynchus*, *P. anchietae* and *P. porosissima*, were examined and described in this study. Although usable for ascertaining details of the external mouthparts and oral disc, much of Wager's material (now in the Natal Museum) was poorly preserved and badly stored, and proved completely unsatisfactory for the present study. My own collection has very few *Ptychadena* tadpoles assignable with certainty to identified species.

Buccopharynxes of the taxa examined show strong overall generic similarities and only those structures showing conspicuous differences are discussed here.

Prenarial arena

An arcuate ridge of papillae is present in *Ptychadena oxyrhynchus* and *P. anchietae*. It is consists of a few small discrete pustulose papillae in *Ptychadena oxyrhynchus*; and of more numerous, larger, more or less confluent papillae in *P. anchietae*. Only small scattered pustulations are present in *P. porosissima*.

Lateral ridge papillae

Simple and conical in *P. anchietae*; pustulose and bifurcate or apically trifid in *Ptychadena oxyrhynchus* and *P. porosissima*.

Buccal roof arena

Poorly defined in *Ptychadena oxyrhynchus* by a few small, feebly developed papillae scattered randomly over the general arena surface. More definitely defined in *P. anchietae* and in *P. porosissima* by a lateral row of large conical papillae on either side.

The arena is bounded posteriorly by a narrow, continuous glandular pustulate ridge in *P. oxyrhynchus* and *P. anchietae*. The pustulations are evenly spaced but interrupted medially in *P. oxyrhynchus*; they are continuous in *P. anchietae*, but virtually in contact laterally, and more widely spaced medially. In *P. porosissima* the coarsely pustulate glandular ridge is broadly interrupted medially.

Prelingual papillae

In *Ptychadena oxyrhynchus* they are small, and the lateral papillae are terminally trifid. In *P. anchietae* and *P. porosissima* they are larger and somewhat bulbous.

Ventral velum

Supporting spicules are present in the ventral velum of *Ptychadena anchietae* and, less obviously, in *P. porosissima*, but lacking in that of *P. oxyrhynchus*.

SPECIES ACCOUNT

Ptychadena oxyrhynchus (A. Smith, 1849)

Rana oxyrhynchus A. Smith, *Ill. Zool. S. Afr., Rept.*, pl. 77, figs. 2, 2a,b,c. Type locality: "Kaffirland and the region of Port Natal" [i.e., Durban]. Lectotype in the British Museum (Natural History), London.

Ptychadena oxyrhynchus (Smith): Poynton 1964:124, fig. 64. Van Dijk 1966:258, Passmore & Carruthers 1979:152, figs. Poynton & Broadley 1985b:144. Lambiris 1989a:82; 1989b:105, figs. 54 & 55, pl. 10 figs. 1a-d.

ADULT LARYNX (Table 5; Pl. 27, fig. 1)

Material examined: ZIMBABWE: AJL 888 (m, SVL 51.0 mm), farm "Ellesmere", Saffron Walden district. AJL 737 (f, SVL 55.0 mm), 6 km west of Harare. SOUTH AFRICA: NATAL - AJL 2669 (m, SVL 47.6 mm), Doornkraal, Itala Game Reserve. AJL 2082, (m, SVL 45.7 mm), eGodeni, Hluhluwe Game Reserve.

Advertisement call: A strongly trilled call about 0.4 second long, at about 1.5 kHZ (slight frequency modulation), with clear harmonics at about 3 kHZ (Passmore & Carruthers 1979:152), uttered about once per second, from exposed sites (muddy shores, or very short grass) at the water's edge. There is a distinct choral structure.

Male larynx:

Pharyngeal mucosa: Thin, unfolded, overlying a shallow submucosa covering, and clearly differentiated from, the dorsal surface of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface rather narrow, roughly biconvex in profile, with feeble apical swellings. There is no arytenoid valve. The axial width of the arytenoid shelf is about equal to that of the occlusal surface.

Vocal cord: Only a simple, moderately broad, lorate medial cord is present. Both anterior and posterior margins are slightly flanged, and it is curved in cross-section.

Posterior chamber: Devoid of any conspicuous features.

LARVAL BUCCOPHARYNX (Table 6; Pl. 29, fig. 1a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a, and a series from Honeymoon Bend, Lake St. Lucia, Natal (AJL 3073-3076, stages 30-44; collected 27 October 1987, by S. McLean), showing the markings and webbing diagnostic of adults at Stage 44.

Material examined: SOUTH AFRICA: NATAL - AJL 3104: St. Lucia Game Park; stage 39/40, SVL 19.0 mm; silver impregnation.

Larval habitat: Shallow pools or pans, slow-flowing segments of small streams or quiet backwaters of rivers. Open water over sandy or rocky substrata, and with some emergent grasses or sedges, is preferred. Filamentous algae are abundant in the gut of the specimen examined.

Buccopharyngeal roof

General shape: Roughly triangular, the base about 1.2x the height. The general surface is regularly concave, and the prenarial arena is rather deeply excavate.

Prenarial arena: A large trapezoid, the base about 1.2x the height, and with a transverse arcuate row of 3 small, separate pustuloid papillae about one-third of the way down from the anterior margin.

Internal nares: Narrow slits, obliquely set, the medial angle directed posterad. Narial length about 0.5x the width of the roof at that level, and internarial distance about 0.4x the narial length.

Narial valve: A narrow flap on both narial margins. The anterior valve is serrated and bears a robust conical papilla (height about 0.2x narial length) near the lateral angle. The posterior flap is smooth. The posterior margin is narrowly, but deeply, incised.

Postnarial arena: A single conical **postnarial papilla** on either side, with a pustulate anterior margin, and about 0.7x the narial length, arising behind the medial third of the naris. There are two **lateral ridge papillae** -- a small simple conical superior papilla, and a large bifurcate or trifurcate inferior papilla, which is slightly pustulose. The **median ridge** is low and trapezoid, with a finely serrate free margin.

Buccal roof arena: Broad, wide and slightly curved. It is poorly defined by small, feebly developed papillae scattered somewhat randomly over the arena, interspersed with numerous small pustules.

Glandular ridge: A narrow curved zone defining the posterolateral boundary of the buccal roof arena. It bears 6 or 7 small pustules on either lateral third.

Other pustulations: A few scattered pustules are present bewtween the glandular ridge and the dorsal velum, on either side of the midline.

Dorsal velum: A feeble fold, broadly discontinuous medially.

Pressure cushions: A large medial and smaller lateral lobe.

Buccopharyngeal floor

General shape: Roughly triangular, but rather convex laterally. The floor is moderately concave, with a more deeply excavate prelingual arena, and partially divided medially by a retrolingual groove extending posterad to about the middle of the buccal floor arena.

Prelingual papillae: A small papilla, shortly trifid apically, arising from either lateral wall; and a small simple median papilla.

Lingual papillae: Four long, subequal cylindrical papillae, very closely set in a transverse row, on the posterior margin of the tongue anlage.

Buccal floor arena: Roughly rectangular, the transverse major axis about half the width of the floor, and defined by numerous long, simple, closely-spaced subconical papillae arranged in an irregular zone (no definite rows) posterolaterally. Numerous small pustulations are interspersed among the papillae; there are fewer in the central part of the arena, but they are densely concentrated in the retrolingual groove.

Buccal pockets: Transversely oval, rather deep-set, and closed. There are no pre-pocket papillae, but there are some scattered pustules anterior to the pockets.

Ventral velum: Broad, of subequal width throughout, and with a thickened free margin bearing three subequally-spaced short lobes on either side of the feebly serrated medial quarter.

Branchial baskets: Large and rather rounded.

Filter plates: Strongly curved, semi-closed. The filter rows have secondary and tertiary folds, and the channels are narrow.

Ptychadena anchietae (Bocage, 1867)

Rana anchietae Bocage, 1867, *Proc. Zool. Soc. Lond.*, 1867:843, fig. 1. Type locality: Benguella, Angola. Syntypes destroyed in the Museu Bocage, Lisbon (Frost 1985:471).

Ptychadena anchietae (Bocage): Poynton 1964:126, fig. 65. Van Dijk 1966:258. Passmore & Carruthers 1979:154, figs. Poynton & Broadley 1985b:145. Lambiris 1989a:83; 1989b:108, figs 56 & 57, pl. 10 figs 2a-d.

ADULT MALE LARYNX: (Table 5; Plate 27, fig. 2)

Material examined: ZIMBABWE: AJL 670 (m, SVL 36,3 mm), Sabi River 31,6 km NW of Sabi/Lundi confluence. SOUTH AFRICA: NATAL - AJL 2613 (m, SVL 42,0 m), Mahemane, Ndumu Game Reserve. AJL 2476 (m, SVL 39,1 mm), Shokwe area, Ndumu Game Reserve.

Advertisement call: A short trill, about 0.2 second long, at about 2 kHz and with strong harmonics showing frequency modulation at around 4 kHz (Passmore & Carruthers 1979:154), uttered at half- to one-second intervals, from exposed sites (on muddy shores or from very short grass) at the water's edge. Calling is usually at night and there is a distinct choral structure.

Pharyngeal mucosa: Thin and smooth over the dorsum of the arytenoid cartilage, somewhat folded over the anterior surface of the cartilage, which is completely covered.

Arytenoid cartilage: Occlusal surface rather narrow, with more or less regularly convex margins. The superior anterior margin is slightly ridged. The axial width of the arytenoid shelf is about 1.5 greater than that of the occlusal surface.

Vocal cords: The **median cord** is slightly flared at its insertions. The margins are thickened, especially the posterior, which also has small buttresses. the **lateral cord** is well-developed. A small medial lobe bearing a minute papilla is flanked on either side by a much larger arcuate portion.

Posterior chamber: Devoid of any conspicuous features.

LARVAL BUCCOPHARYNX (Table 6; Pl. 29, fig. 2 a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a.

Material examined: SOUTH AFRICA: NATAL - AJL 2052; Shazibe Stream, 4.4 km NW of Sodwana Bay; stage 38, SVL 13.0 mm; silver impregnation.

Larval habitat: Shallow pools and streams in grassland or open bushveld, with sandy, silted substrata.

Buccopharyngeal roof

General shape: Bluntly triangular, the base about 1.4x the height. The general surface is gently concave, but with a much deeper prenarial arena.

Prenarial arena: Roughly rectangular, about 1.6x broader than deep, and bearing a srongly arched row of large, confluent pustulations a little behind the root of the beak.

Internal nares: Narrow slits, obliquely set, the medial angle directed posterad. Narial length about 0.4x the width of the roof at that level, and internarial distance about 0.4x the narial length.

Narial valve: A smooth flap of moderate depth, on both margins. The anterior flap bears a large (0.4x narial length) conical papilla at about the mid-point. The posterior margin is fairly deeply incised.

Postnarial arena: A single large conical **postnarial papilla** on either side, about 0.7x the narial length, arising behind the medial half of the naris. There is a single **lateral ridge papilla** on the right side, similar in size and shape to the postnarial papilla (the left one possibly lost in dissection?). The **median ridge** is large and triangular, with a smooth free margin.

Buccal roof arena: Large and roughly semicircular. It is bounded laterally by a posteriorly convergent row of three large, simple, conical papillae (diminishing slightly in size posteriorly) on either side; and posterolaterally by the glandular ridge. There are numerous small pustulations within the arena, extending beyond the papillae to a lesser degree. There are three (left) and two (right) much smaller, unequal-sized extra-arenal papillae lateral to the first arenal papillae.

Dorsal velum: A feeble fold on the anterior margin of each pressure cushion.

Pressure cushions: Rather small, simple structures without any clear differentiation into lateral and medial moieties.

Buccopharyngeal floor

General shape: Roughly triangular, base about 1.2x the height. The general surface is moderately concave, with a deep prelingual arena. The buccal floor has slight retrolingual ridges, flanked by curved, posteriorly-directed folds from the paralingual cushions.

Prelingual papillae: Large and bulbous. A single median ventral papilla is flanked on either side by a similar one arising from the lateral walls of the infralabial arena.

Lingual papillae: Four cylindrical papillae, closely set in a transverse row across the middle of the tongue anlage; the middle pair slightly smaller than the outer pair.

Buccal floor arena: Roughly semicircular, the transverse major axis about 0.6x the width of the roof. Defined by two irregular rows of weakly conical papillae, varied in size but with a tendency to become smaller posteriorly. The arena contains numerous small, scattered pustulations and three small papillae posteriorly.

Buccal pockets: Narrow, transversely elongate, rather deeply set, and closed. There are two or three pustulose **prepocket papillae** on either side.

Ventral velum: Broad, of subequal width throughout, and with a thickened free margin bearing four small, indistinct lobes on either side of the small apical lobe. Two supporting spicules on either side are distinct and well-developed.

Branchial baskets: Large, more or less triangular.

Filter plates: Strongly curved, semi-closed. The filter rows have secondary and tertiary folds, and the channels are narrow.

"*Ptychadena mascareniensis* (Duméril & Bibron, 1841) : A"

[*Rana mascareniensis* Duméril & Bibron, 1841, *Erpét. Gén.*, 8:350. Type locality: "Mascareignes" and "Séchelles". Syntypes in the Museum National d'Histoire Naturelle, Paris.]

Ptychadena m. mascareniensis (Duméril & Bibron): Poynton 1964:128, fig. 62 (part, southern Mozambique and Natal material). Van Dijk 1966:258. Passmore & Carruthers 1979:156, figs. Poynton & Broadley 1985b:148 (part, southern Mozambique material). Lambiris 1989a:83; 1989b:112, fig. 60, pl. 11 figs. 1a-c (?part).

ADULT MALE LARYNX (Table 5; Pl. 27, fig. 3)

Material examined: SOUTH AFRICA: NATAL - AJL 2759 (m, SVL 21.8 mm), St. Lucia Game Park. AJL 2648 (m, SVL 38.0) and AJL 3086 (m, SVL 41.5 mm), St. Lucia Estuary. NM 5912 (m, SVL ==), Sibayi.

Advertisement call: Descriptions from Passmore & Carruthers 1979:156:

> "Two types of call are heard, usually in association with each other. One is a brief nasal bray, emitted at a rate of about two every three seconds, the other a series of clucking sounds."
>
> "Males call whilst supported on aquatic vegetation or from the bank."

The sonagram in Passmore & Carruthers (*op. cit.*) shows a rather weak band at about 0.7 kHz and a much stronger band, with some frequency modulation, between about 2.3 and 3.0 kHz.

Pharyngeal mucosa: Folded, and blending with the submucosa, behind the level of the cricoid cartilage; thin, and covering the basal half of the dorsum of the arytenoid cartilage, where it lies in a clearly defined depression.

Arytenoid cartilage: Anterior margin of occlusal surface somewhat bilobed, but not forming clearly differentiated prominentiae. There is a weak transverse axial ridge across the occlusal surface, but no distinct valve. The axial width of the anterior arytenoid shelf is about equal to that of the occlusal surface. The axial width of the posterior arytenoid shelf is about 0.4x that of the anterior shelf.

Vocal cords: The medial vocal cord is divided longitudinally into two moieties. The **anterior medial cord** is strongly flared and buttress-like at the insertions, and strongly narrowed medially. The closely-

applied posterior medial cord is similarly shaped, and its inferior insertion overlaps the posterior margin of that of the anterior cord.

There is no lateral vocal cord.

Posterior chamber: The pulmonary aditus is encircled superiorly and antero-inferiorly by a narrow rim of cartilage, which bears a small process on the superior portion.

LARVAL BUCCOPHARYNX

No reliably identified tadpoles suitable for dissection were available.

"*Ptychadena mascareniensis* (Duméril & Bibron, 1841) : B"

[*Rana mascareniensis* Duméril & Bibron, 1841, *Erpét. Gén.*, 8:350. Type locality: "Mascareignes" and "Séchelles". Syntypes in the Museum National d'Histoire Naturelle, Paris.]

Ptychadena m. mascareniensis (Duméril & Bibron): Poynton 1964:128, fig. 62 (part, Mozambique material from Beira [and futher north?]), Poynton & Broadley 1985b:148 (part, Mozambique material from Beira [and futher north?]), Lambiris 1989b:112, fig. 60, pl. 11 figs. 1a-c (?part).

ADULT MALE LARYNX (Table 5; Pl. 27, fig. 3)

Material examined: MOZAMBIQUE: NM 2889, NM 2904 (males), near Estoril, Beira.

Advertisement call: Not known.

Pharyngeal mucosa: Blending with a moderately deep submucosa; distinct from, and covering, most of the the dorsum of the arytenoid cartilage, where it lies in a clearly defined depression.

Arytenoid cartilage: Anterior margin of occlusal surface somewhat bilobed, but not forming clearly differentiated prominentiae. The antero-inferior surface is somewhat folded. There is a weak transverse axial ridge across the occlusal surface, continuous with a distinct arytenoid valve. The axial width of the anterior arytenoid shelf is about equal to that of the occlusal surface. The axial width of the posterior arytenoid shelf is about 0.7x that of the anterior shelf. The anterior shelf has a distinct medial fossa.

Vocal cords: The medial vocal cord is strongly flared at the insertions and narrower medially. The anterior margin is broadly thickened, and the posterior margin narrowly but distinctly flanged. The superior posterior buttress is elongate and tapering; the inferior posterior buttress is massive and semiluniform.

A lateral vocal cord is present, but reduced to little more than a small frenulum-like fold.

Posterior chamber: The pulmonary aditus is bordered and antero-inferiorly by a narrow rim of cartilage, which bears a conspicuous subadital discoid expansion.

LARVAL BUCCOPHARYNX

No reliably identified tadpoles were available for dissection.

Ptychadena porosissima (Steindachner, 1867)

Rana porosissima Steindachner, 1867, *Reise Novara; Amphib.*, p. 18, figs. 9-13. Holotype in the Naturhistorisches Museum, Vienna.

Ptychadena porosissima (Steindachner): Poynton 1964:129, fig. 68. Passmore & Carruthers 1979:158, figs. Poynton & Broadley 1985b:149. Lambiris 1988:40, figs., pl. 5 figs. 1a, b; 1989a:84; 1989b:114, figs 61 & 62, pl. 11 figs. 2a, b.

Ptychadena poyntoni Guibé, 1960, *Bull. Mus. Nat. Hist. Nat.*, 32:20, fig. 1. Type locality: Inhluzane, Natal, South Africa. Types in the Muséum Nationals d'Histoire Naturelle, Paris, and in the Natal Museum, Pietermaritzburg.

ADULT LARYNX (Table 5; Pl. 28, fig. 1)

Material examined: SOUTH AFRICA: NATAL - NM 2929 (m, SVL 41.0 mm), Richards Bay. NM 2921 (m, SVL 38.6 mm), Sibuluwane. NM 7483 (m, SVL 37.0 mm), Hluhluwe or Mkuzi (sic!). PARATYPES of *Ptychadena poyntoni* Guibé: SOUTH AFRICA: TRANSVAAL - NM 2918 (f, SVL 44.4 mm) Barberton. NATAL - NM 2914 (m, SVL 35.3 mm) and NM 2913 (m, SVL 37.4 mm), Ntingwe. NM 22916 (m, SVL 39.2 mm) and NM 2917 (m, SVL 37.3 mm), Cathkin Peak area. NM 2912 (f, 42.5 mm), Ntingwe.

Advertisement call: A rasping chirp about 0.2 second long, at about 2 kHz but with a strong harmonic band at about 4 kHz, both showing slight frequency modulation (Passmore & Carruthers, 1989:158), uttered about twice a second. Males call antiphonally, at night or on overcast days, concealed among emergent aquatic vegetation or from grass at the water's edge.

Male larynx:

Pharyngeal mucosa: Covers the dorsum of the arytenoid cartilage, but is not recessed therein.

Arytenoid cartilage: Margins of occlusal surface somewhat convex. The external margin is weakly bilobed. The narrow occlusal surface lacks an arytenoid valve. The axial width of the arytenoid shelf is about 2.6x that of the occlusal surface.

Vocal cords: The **medial vocal cord** is divided into a large **anterior medial cord**, strongly flared at the insertions and markedly constricted medially; and a greatly attenuated **posterior medial cord** arising from small prominences on the posteromedial surfaces of the anterior cord.

The **lateral vocal cord** largely underlies the medial cords. It is a simple fold, with a weak medial frenulum.

LARVAL BUCCOPHARYNX (Table 6; Pl. 30, fig. 1a & b)

Identification of larvae: Lambiris 1989a, 1989b.

Material examined: SOUTH AFRICA; NATAL - AJL 3091; Stage 32, SVL 12 mm; St. Lucia Estuary; silver impregnation.

Larval habitat: Shallow pans or pools in open grassy wetlands, with silted sandy substrata. The gut of the specimen examined contained silt and filamentous algae.

Buccopharyngeal roof

General shape: A deep trapezoid, the base equal to the height. The general surface is shallowly excavate, with a deeper prenarial arena.

Prenarial arena: Trapezoid, the base about 1.4x the height. 9 small pustules are scattered over the surface.

Internal nares: Narrow slits, obliquely set, the medial angle directed posterad. Narial length about 0.5x the width of the roof at that level, and internarial distance about 0.5x narial length.

Narial valve: Narrow flaps on the anterior and posterior margins. The anterior flap is crenate and bears a large papilla (about 0.4x narial length) a little lateral to the mid-point. The posterior margin is not deeply incised.

Postnarial arena: A single large, conical **postnarial papilla** arising behind either naris, about midway between the lateral limits of the medial ridge and the posterior border of the naris. The **lateral ridge papilla** is large, slightly pustulate, and with a short-armed bifurcation near the base. The **median ridge** is a low transverse flap with a slightly undulant free margin.

Buccal roof arena: A small rectangle (transverse major axis about 0.4x width of roof), bounded laterally by three large, simple, conical papillae on either side; a small papilla is set just anterior to the middle papilla on either side. There are 9 rather symmetrically-arranged pustules in the arena.

Additional pustulations: A pair of large pustules is set on either side of the midline, halfway between the dorsal velum and the glandular ridge.

Glandular ridge: A lobulate ridge on either side, set close to the buccal roof arena, with a medial gap about 1.4x greater than the length of either ridge.

Dorsal velum: A feeble discontinuous flap closely applied to the anterior margins of the pressure cushions.

Pressure cushions: Large, triangular and flattened, with a peculiar roseate-like protruberance behind the anterior margins.

Buccopharyngeal floor

General shape: Somewhat hastate, the branchial baskets being prolonged posteolaterally. The infralabial arena is similarly hastate, and rather deeply excavate. The buccal floor proper is rather flat.

Infralabial papillae: A large, robust palp arises from the lateral wall on either side, below the root of the beak. A median ventral papilla is somewhat lorate.

Lingual papillae: Four closely-set simple subconical papillae arranged in a slightly curved transverse row arise from the anterodorsal margin of the tongue anlage.

Buccal floor arena: Roughly rectangular, the transverse major axis about 0.5x the width of the floor. It is defined laterally and posteriorly by a row of 9 approximately equally spaced, simple conical papillae of moderate size (4 on the left side, 5 on the right), with 2 (left) and 1 (right) further papillae between the the arena papillae and the dorsal velum. The centre of the arena contains 10 small pustules.

Buccal pockets: Broadly oval, rather deep-set, and closed. There are 4 **prepocket pustulations** on either side.

Ventral velum: Broad, of subequal width throughout, and with a faintly lobulated free margin. There are four supporting spicules, two on either side of the midline.

Branchial basket: Elongately triangular, the base (left side) about 0.7x the height), and the major axis directed posterolaterally.

Filter plates: Arched and partially closed. The filter rows are narrow, as the are channels between them.

Ptychadena mossambica (Peters, 1854)

Rana mossambica; Peters, 1854, *Monatsber. Preuss. Akad. Wiss. Berlin*, 1854:626. Type locality: Tete, Mozambique. Type in the Zoologisches Museum, Universität Humboldt, Berlin.

Ptychadena vernayi (FitzSimons); Poynton 1964:135, fig. 72. Van Dijk 1966:258.

Ptychadena mossambica (Peters); Passmore & Carruthers 1979:160, figs. Poynton & Broadley 1989b:155. Lambiris 1989a:86; 1989b:120, fig. 65, pl. 12 figs. 2a-c.

ADULT LARYNX (Table 5; Text-fig. 32a; Pl. 28, fig. 2)

Material examined: ZAMBIA: AJL 1362 (m, SVL 35.0 mm) and AJL 1363 (f, SVL 42.5 mm), 16 km W. of Chisamba. ZIMBABWE - AJL 741 (m, SVL 39.0 mm), farm "Audley End", Darwendale district. SOUTH AFRICA: NATAL - AJL 2459 (m, SVL 41.3 mm), Makhamisa Pan, Umfolozi Game Reserve.

Advertisement call: A harsh quack about 0.1 second long, with a fundamental band at about 0.7 kHz and a strong harmonic band, showing marked frequency modulation, between 2 and 3 kHz (Passmore & Carruthers 1979:160); uttered repeatedly, about twice a second, usually at night, from grass in or at the water's edge, with no definite choral pattern.

Male larynx:

Pharyngeal mucosa: A thin layer covering the anterodorsal surface of the arytenoid cartilage, which is somewhat recessed to receive it.

Arytenoid cartilage: Anteroposteriorly compressed. The external margin of the narrow occlusal surface is bilobed, and the internal margin sinuously curved. The axial width of the arytenoid shelf is equal to that of the occlusal margin. The arytenoid fossa is poorly defined.

Vocal cords: The **medial cord** is broad, with somewhat flared insertions; the buttresses are rather inconspicuous. There is a curved longitudinal medial ridge, and the posterior margin is strongly flanged. The **lateral cord** is a simple fold.

Posterior chamber: The anteroventral margin of the pulmonary aditus has a narrow cartilaginous rim with a subadital expansion.

LARVAL BUCCOPHARYNX

Reliably identified tadpoles were not available for examination.

"*Ptychadena taenioscelis* Laurent, 1954" : A

Ptychadena taenioscelis Laurent, 1954, *Ann, Mus, Roy, Congo Belge*, 34:25, pl. 4 fig. 6, pl. 5 fig. 1. Type locality: Lukula, eastern Congo. Holotype in the Musée Royal d'Afrique Centrale, Tervuren. Poynton 1964:132, fig. 70. Van Dijk 1966:258. Passmore & Carruthers 1979:162, figs. Poynton & Broadley 1985b:153. Lambiris 1989a:85.

Ptychadena smithi Guibé, 1960, *Bull, Mus, Hist, Nat, Hist.*, 32:202, fig. 2. Type locality: Mseleni, Zululand. Syntypes and paratypes in the Natal Museum, Pietermaritzburg.

ADULT MALE LARYNX (Table 5; Pl. 28, fig. 3)

Material examined: SOUTH AFRICA: NATAL - NM 2938 (m, SVL 32.0 mm), Sibuluwane. PARATYPES of *P. smithi*: NM 225a-c (males, SVL 30.6; 27.8; 26.8 mm), Mseleni.

Advertisement call: Descriptions from Passmore & Carruthers 1979: 162.

"A nasal bleat, repeated at a rate of about one call per second."

"Males call from the muddy water margins."

The sonagram in Passmore & Carruthers (*op. cit.*) shows a broad fundamental band between 1 and 2 kHz, and a strong harmonic band at about 3 kHz, both showing some frequency modulation.

Pharyngeal mucosa: Thin, over a deeper submucosa distinct from the underlying arytenoid cartilage.

Arytenoid cartilage: Occlusal surface moderately broad, the external margin bilobed, the internal margin arcuate. There is a well-defined arytenoid valve on the internal occlusal margin. The arytenoid shelf has a shallow but distinct anteromedian fovea. The axial width of the shelf is about 0.8x that of the occlusal surface

Vocal cords: The **medial cord** is rather broadly flared at the insertions. The strongly flanged posterior margin has narrow but large, distinct buttresses.

The **lateral cord** is reduced; only a medial posterior prominence projects beyond the posterior margin of the medial cord..

Posterior chamber: The pulmonary aditus is encircled anteroventrally by a narrow cartilaginous rim.

LARVAL BUCCOPHARYNX

Reliably identified material does not appear to be available.

"*Ptychadena taenioscelis* Laurent, 1954" : B

[*Ptychadena taenioscelis* Laurent, 1954, *Ann. Mus. Roy. Congo Belge*, 34:25, pl. 4 fig. 6, pl. 5 fig. 1. Type locality: Lukula, eastern Congo. Holotype in the Musée Royal d'Afrique Centrale, Tervuren.] Poynton 1964:132, fig. 70 (part). Van Dijk 1966:258 (part?). Passmore & Carruthers 1979:162, figs. (part). Lambiris 1989a:85 (part).

ADULT MALE LARYNX (Table 5; Pl. 28, fig. 4)

Material examined: SOUTH AFRICA: NATAL - NM 5903a (m, SVL 32.0 mm), NM 5903b (m, 25.0 mm), NM 5903c (m, SVL 25.3 mm), all from Sibayi,15.

Advertisement call: Not known.

Pharyngeal mucosa: Blends with the submucosa, forming a relatively deep layer covering the anterodorsal surface of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface narrow, the external margin bluntly V-shaped, the internal margin acutely so. The axial width of the arytenoid shelf is about 2.3x that of the occlusal surface.

Vocal cords: The **medial cord** is broad and simple. The strongly flanged posterior margin has small but distinct buttresses.

The **lateral cord** is a simple fold.

Posterior chamber: Has no features of taxonomic value.

LARVAL BUCCOPHARYNX

The tadpole does not appear to be known.

DISCUSSION

Adult laryngeal morphology and, to a much lesser extent (because of the limited material available), larval buccopharyngeal morphology, tends to support the taxonomic conclusions of Poynton 1964, Poynton & Broadley 1985b, and of Lambiris 1989a. However, these character suites indicate that the taxonomy of at least some of the species considered here needs to be re-examined.

Ptychadena m. mascareniensis

Adult laryngeal morphology (Pl. 27, figs. 3 & 4) indicates that south-east African populations of the taxon currently called *Ptychadena m. mascareniensis* (Duméril & Bibron, 1841) consists of two species indistinguishable, at present, by means of the diagnostic characters generally used in the genus. These are called "*Ptychadena mascareniensis* A" and "*P. mascareniensis* B" in the present study.

"*Ptychadena mascareniensis* A" appears to extend northwards from Zululand into southern Mozambique -- Professor Neville Passmore informs me (in discussion) that frogs in this area all have the same calls.

"*P. mascareniensis* B" appears to be centred on Beira, Mozambique. The advertisement call of this population does not appear to be known. The range of this population has not been established, since such an investigation would have extended beyond the scope of the present study.

Material from the type localities has not been examined and it is not yet clear which (if either) of these populations is referable to *Ptychadena m. mascareniensis* **sensu strictu**. Populations in south-east Africa are widely disjunct (locality data in Poynton & Broadley 1985b: 148) and a comprehensive examination of larynxes, sonagrams and other characters from populations through the species' entire range is clearly necessary.

Ptychadena porosissima

Poynton's relegation of *Ptychadena poyntoni* Guibé, 1960 to the synonymy of *Ptychadena porosissima* was confirmed by Lambiris (1989a:85), who, however, noted that the available material (from Natal) showed a considerable range of variation. Examination of hyolarynxes, including

those of the paratypes of *Ptychadena poyntoni* held in the Natal Museum, shows no differences in larynxes from the two taxa, thus tending to confirm that they are conspecific.

The *Ptychadena taenioscelis* complex

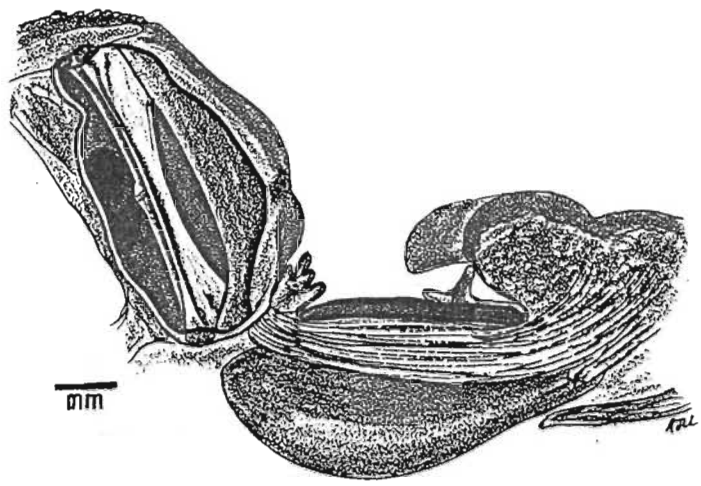
Ptychadena smithi Guibé, 1960 was referred by Poynton (1964:247) to the synonymy of *Ptychadena taenioscelis*, an action supported by Lambiris (1989a:86) with some reservations. Comparison of male paratype *P. smithi* larynxes with those of male *P. taenioscelis* from Sibuluwane (the population most remote from the type localities of *P. smithi*) shows that they are identical, and that *Ptychadena smithi* is indeed a synonym of *Ptychadena taenioscelis*.

Three males from Sibayi, though otherwise indistinguishable from *P. taenioscelis*, possess larynxes that differ remarkably from the latter species -- indeed, they somewhat approach the female type of larynx.

Snout-vent lengths of the Sibayi males (vocal sacs are present) range from 25.0 - 32.0 mm, as compared with the range for *P. smithi* paratypes of 26.8 - 30.6 mm, and 32.0 mm for the Sibuluwane specimen. This would appear to preclude possible differences due to age (such differences are not, in fact, particularly conspicuous in males of other genera studied).

There seems to be *prima facie* evidence to postulate that, in Natal, *Ptychadena taenioscelis* Laurent (of which *P. smithi* Guibé is a synonym) occurs in central and northern Zululand and that there is an undescribed sibling species in southern Zululand. Further fieldwork will be needed to elucidate differences in advertisement calls and in tadpoles, and to determine the ranges of the two taxa.

The populations variously called *Ptychadena pumilio* and *P. taenioscelis* pose complex taxonomic problems (Frost 1985:475; Poynton & Broadley 1895b:153; Lambiris 1989a:86) which morphological characters currently considered of diagnostic value do not seem likely to resolve. The use of adult laryngeal and larval buccopharyngeal characters may prove useful in this respect, but is clearly beyond the scope and aims of the present investigation.



(a) *Ptychadena mossambica* (Peters); AJL 2459 (male), Makhamisa Pan, Umfolozi Game Reserve, Natal, South Africa.

(b) *Ptychadena* cf. *frontalis* Laurent; AJL 1362 (male), 16 km west of Chisamba, Zambia.

TEXT-FIG. 32: HYOLARYNXES OF (A) *PTYCHADENA MOSSAMBICA* (PETERS) AND (B) *PTYCHADENA* cf. *FRONTALIS* LAURENT

The *Ptychadena mossambica / frontalis / floweri* group

Poynton & Broadley (1985b: 155) noted that this species

> "shows an east-west cline, most notably in size and degree of webbing. ... The webbing specified in the Diagnosis does not apply to all Zambian material, particularly to the western Marshi series ... Intermediate conditions between the eastern and western extremes are nevertheless shown; in two AJL specimens from near Chisamba, Zambia, for example, virtually only two phalanges of the fourth toe are free of the main webbing in one specimen ... [this specimen], a 41,5 mm female, keys out as *frontalis* Laurent in both Schmidt & Inger's (1959) and Poynton's (1970) key. Neither of the Chisamba specimens shows a light dorsal band and there seems no very clear way of separating extensively webbed specimens from *frontalis* if they lack a band. The situation needs investigating.

The second specimen, a male, is similar but has less extensive webbing on one foot, almost three phalanges of the first toe being free (compared with two phalanges on the other foot, and on both feet of the female).

The larynx of the male was compared with that of South African material (Text-fig. 32). It is apparent that while there are close similarities, there are also marked differences. These specimens manifestly are not *Ptychadena mossambica* as currently recognised, but I have not been able to examine specimens of *P. frontalis* and their identity must remain uncertain for the moment.

The m. hyoglossus is relaxed in the specimen of *Ptychadena mossambica* illustrated but contracted in that of *Ptychadena ?frontalis*. Nevertheless, the larynxes of both seem to be in a similar state of relaxation (both were killed with an injection of barbiturate). The main differences may be summarised thus:

Mucosa and submucosa deeper in *P. ?frontalis* than in *P. mossambica*.

Occlusal surface of arytenoid cartilage narrower in *P. ?frontalis*, and possessing a strong arytenoid valve, which is lacking in *P. mossambica*.

Medial vocal cord in *P. ?frontalis* more slender, with less strongly flared and less robust insertions than those of *P. mossambica*, and lacking the median longitudinal ridge present in the latter species.

Lateral vocal cord possesses a frenulum in *P. ?frontalis*, but not in *P. mossambica*.

Vocal sac much larger in *P. ?frontalis* than in *P. mossambica*. (The size and disposition of vocal sacs in this genus appears to be a useful character.

Lambiris (1989a) could not distinguish between tadpoles of *Ptychadena mossambica* and *P. mascareniensis* as there recognised. The matter still needs to be resolved, but this will be possible only when positively identified tadpoles of all the taxa within these complexes are available for study.

PLATE 27
PTYCHADENA – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

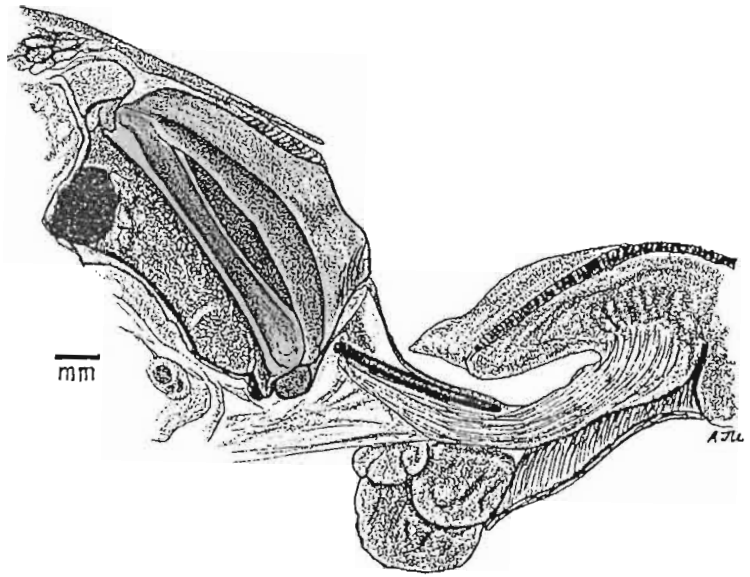


FIG. 1; *Ptychadena oxyrhynchus* (A. Smith, 1849)
AJL 888 (male), Atlantica Ecological Research Station, 23 km W. of Harare, Zimbabwe.

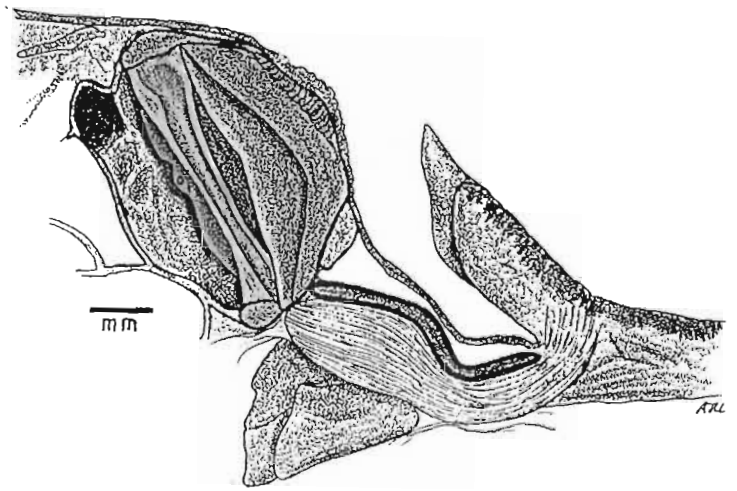


FIG. 2; *Ptychadena anchietae* (Bocage, 1867)
AJL 2613 (male), Mahemane, Ndumu Game Reserve, Natal, South Africa.

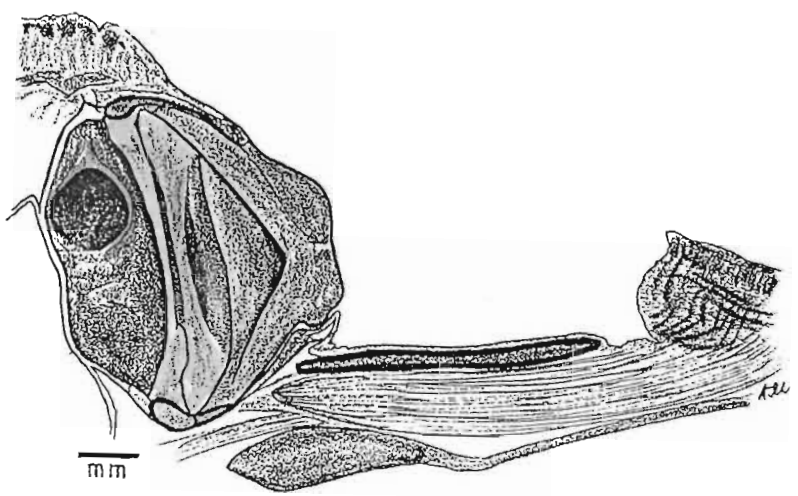


FIG. 3; "*Ptychadena mascareniensis* A"
NM 5912 (male), Sibayi, Natal, South Africa.

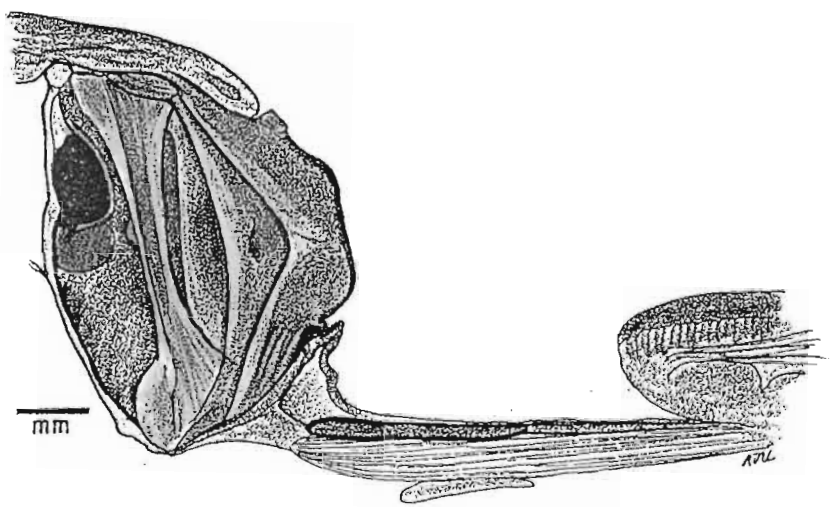


FIG. 4; "*Ptychadena mascareniensis* B"
NM 2889 (male), Beira - swamp north of Estoril, Mozambique.

PLATE 28
PTYCHADENA – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

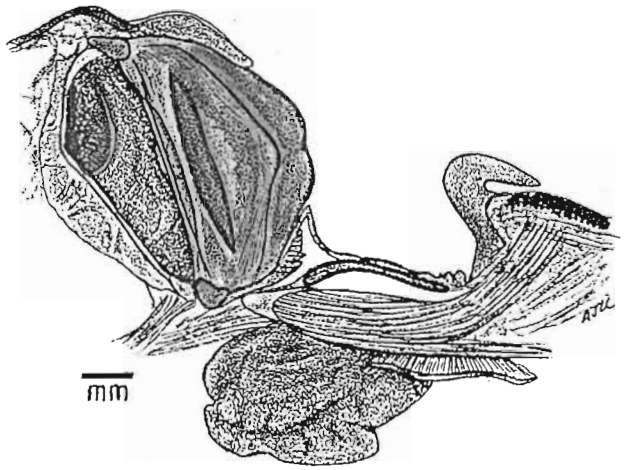


FIG. 1; *Ptychadena porosissima* (Steindachner, 1867)
NM 2914 (male), Ntingwe, Natal, South Africa,
[Paratype of *Ptychadena poyntoni* Guibé, 1960.]

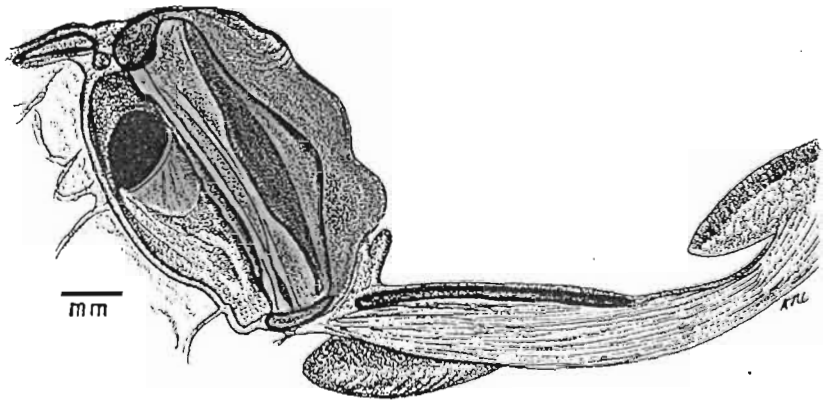


FIG. 2; *Ptychadena mossambica* (Peters, 1854)
AJL 2459 (male), Makhamisa Pan, Umfolosi Game Reserve, Natal, South Africa.

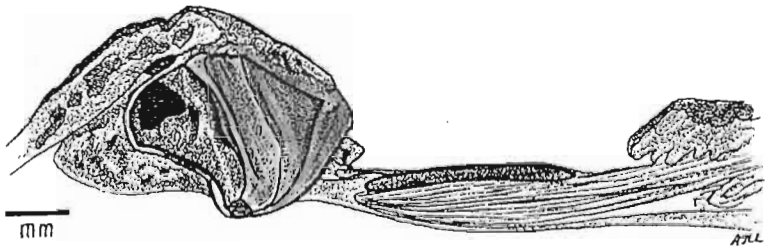


FIG. 3; *Ptychadena taenioscelis* Laurent, 1954
NM 5903a (male), Sibayi, Natal, South Africa.

PLATE 29
PTYCHADENA – LARVAL BUCCOPHARYNXES

Roof on left, floor on right.

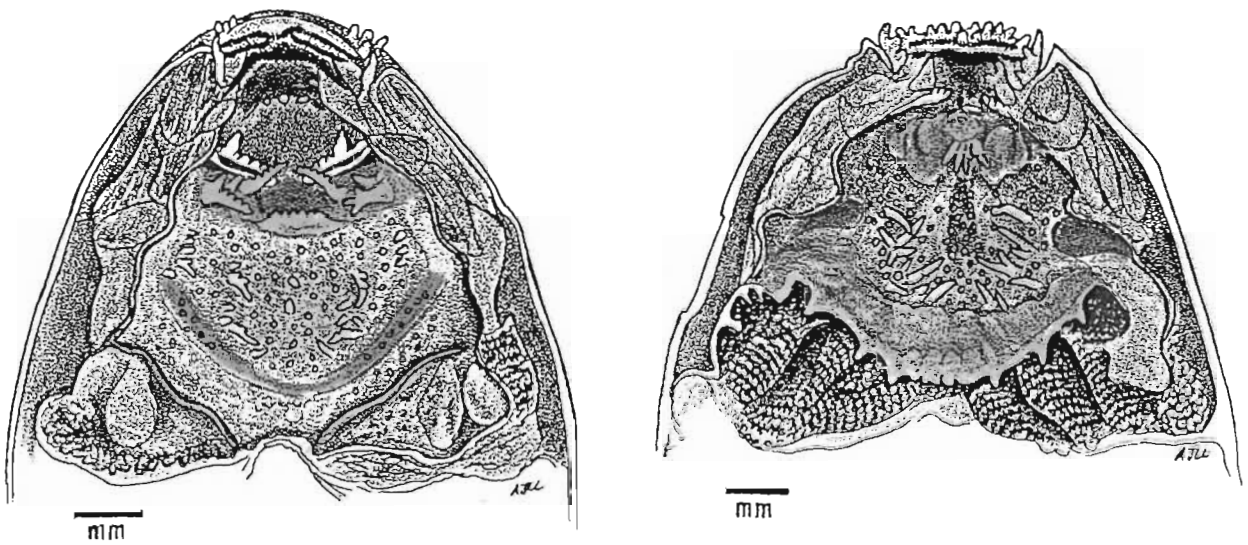


FIG. 1: *Ptychadena oxyrhynchus* (A. Smith, 1848)
AJL 3104, Stage 39/40, St. Lucia Game Park, Lake St. Lucia, Natal, South Africa.

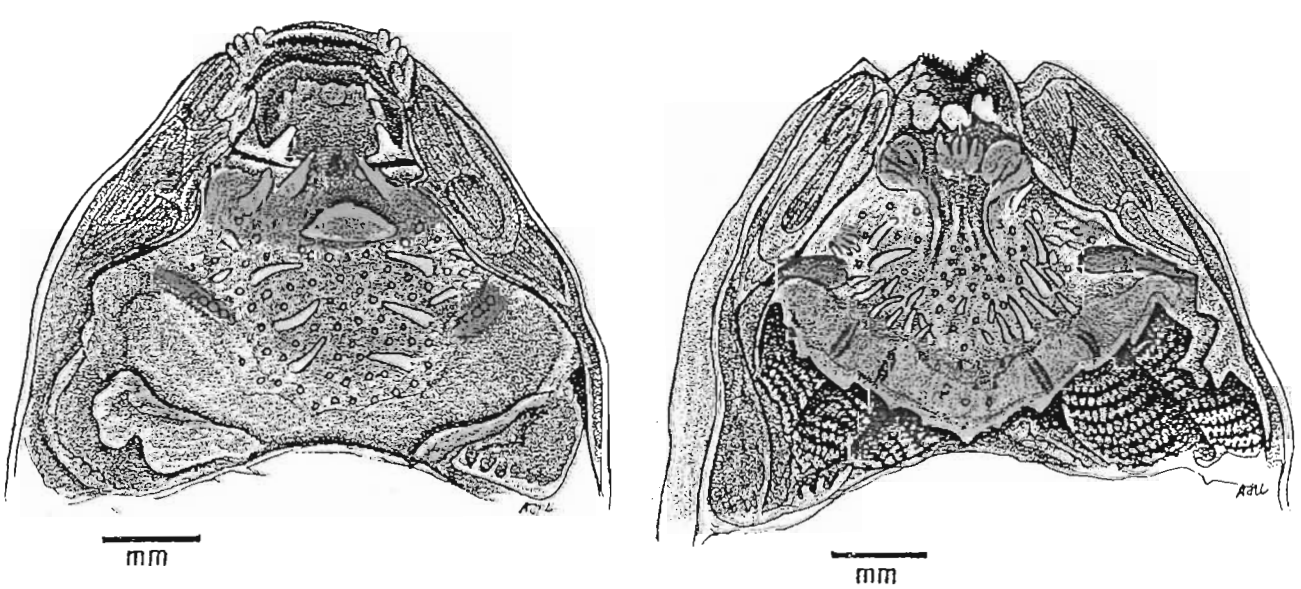


FIG. 2: *Ptychadena anchietae* (Bocage, 1867)
AJL 2052, Stage 38, Shazibe Stream, 4.4 km NNW of Sodwana Bay, Natal, South Africa.

PLATE 30
PTYCHADENA – LARVAL BUCCOPHARYNX
Roof on left, floor on right

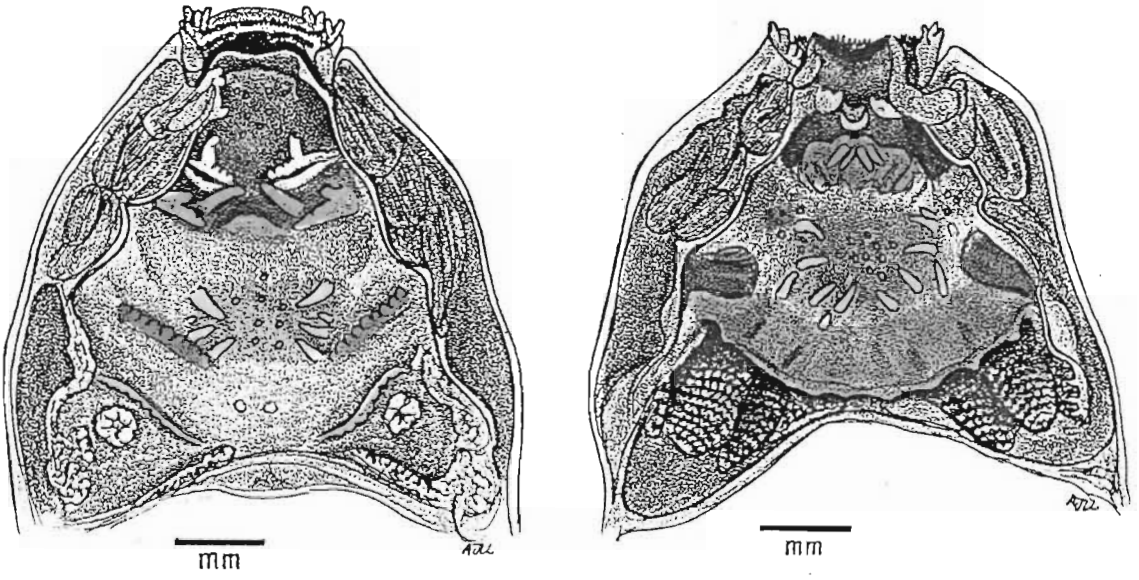


FIG. 1: *Ptychadena porosissima* (Steindachner, 1867)
AJL 3901, Stage 32, St. Lucia Estuary, Natal, South Africa.

TABLE 7. Laryngeal characters:
Rana

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	EXTERNAL MARGIN OF ARYTENOID CARTILAGE FIMBRIATED	INTERNAL MARGIN OF ARYTENOID CARTILAGE V-SHAPED	OCCLUSAL SURFACE OF ARYTENOID CARTILAGE STRONGLY RIDGED NEAR PULVINARIA VOCALIA	ARYTENOID VALVE PRESENT	ANTERIOR MARGIN OF ARYTENOID FOSSA CLEARLY DEMARCATED	MEDIAL VOCAL CORD FLANGED ON AT LEAST ONE MARGIN	SUPERIOR CARTILAGINOUS BUTTRESS PRESENT
Rana angolensis	3	1	3	1	1	1	3
dracomontana	3	3	3	1	3	3	3
fuscigula	1	3	3	3	1	3	1
umbraculata	1	3	3	1	3	3	3
sp. A	1	1	1	3	3	3	3

Genus *Rana* Linnaeus, 1758

Rana Linnaeus, 1758, *Syst. Nat.*, ed. 10, p. 210. Type species by subsequent designation of Fitzinger, 1843: *Rana temporaria* Linnaeus, 1758.

CHARACTERS

Laryngeal and buccopharyngeal characters, and larval morphology, indicate that *Rana vertebralis* Hewitt, 1927 as currently recognised (Lambiris 1989a:94) is a complex of three cryptic species in which the adults otherwise appear to be morphologically indistinguishable. These are here called *Rana vertebralis* Hewitt, 1927, *Rana umbraculata* Bush, 1954, and *Rana* sp. A.

ADULT LARYNX (Table 7; Pls. 31 & 32)

Discussion is restricted to the male larynx only. Sexual dimorphism is marked -- the larynx of female *Rana fuscigula* is illustrated as an example (Pl. 31, fig. 4). Adults of Species A are not known. Larynxes of male *R. vertebralis* were not available for study.

Shape of the arytenoid cartilage

The occlusal surface is narrow superiorly and inferiorly, but expanded mesially to a greater or lesser extent by aliform prominentiae apicales. There is no discernible incisura in any of the taxa examined.

The prominentiae show considerable interspecific variation with regard to size, shape and the degree of marginal sculpturing.

The internal margin of the occlusal surface varies from arcuate (*Rana fuscugula*, *R. dracomontana* and *R. umbraculata*) to obtusely (*R. angolensis*) or more acutely (*R. vertebralis*) V-shaped.

The arytenoid valve is rather narrow, but well-defined, in *Rana angolensis*. It is broader and less well-defined in *R. dracomontana* and *R. umbraculata*, and virtually absent in *R. fuscigula* and *R. vertebralis*.

The arytenoid shelf is rather broad. Melanocytes are present in *Rana dracomontana* and *R. fuscigula*, but not in the other taxa examined.

The arytenoid fossa is a narrow oval. The posterolateral margin is clearly defined by the anterior border of the medial vocal cord. The

TABLE 8. Buccopharyngeal characters:
Rana

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	PRENARIAL PAPILLAE SET IN A SEMICIRCULAR ROW	POSTNARIAL PAPILLAE PUSTULATE	LATERAL RIDGE PAPILLAE PALPOID	MEDIAN RIDGE LESS THAN HALF THE WIDTH OF THE POSTNARIAL ARENA	MEDIAN RIDGE WITH A PAIR OF LARGE APICAL PAPILLAE	BUCCAL ROOF ARENA BORDERED BY TWO OR MORE ROWS OF PAPILLAE	BUCCAL ROOF ARENA DENSELY PUSTULATE	INFRALABIAL ARENA HAS THREE OR MORE PAIRS OF SIMPLE PAPILLAE	LINGUAL PAPILLAE SIMPLE AND NUMEROUS	PREPOCKET PAPILLAE NUMEROUS	AT LEAST HALF OF BUCCAL FLOOR ARENA DENSELY PAPILLATE	VENTRAL VELUM MUCH NARROWER MEDIALLY THAN LATERALLY
Rana angolensis	1	3	1	3	3	1	1	3	1	1	1	3
dracomontana	1	3	1	3	3	1	3	3	3	4	1	1
fuscigula	3	1	3	3	3	1	1	1	1	1	1	3
vertebralis	3	3	1	1	1	3	3	3	1	3	3	1
sp. A	1	1	3	1	3	1	1	3	1	4	1	3

anterior margin is moderately distinct in *Rana angolensis* and *R. fuscigula* but poorly defined in the other taxa examined, the arytenoid shelf curving gently down without forming a clear lip.

Vocal cords

The **medial vocal cord** is broad, with somewhat flared insertions. The anterior margin is generally short and concave, defining the posterolateral border of the arytenoid fossa. This form is least obvious in *Rana angolensis*.

Both margins are slightly flanged in *Rana angolensis*, the posterior margin only in *R. dracomontana*, and neither in the other taxa examined.

A styliform superior posterior buttress is present in *Rana fuscigula*; in *R. vertebralis* and *R. umbraculata* the posterior margins are merely thickened superiorly and inferiorly.

The lateral vocal cord is a large, somewhat undulant fold in all taxa examined.

Pulvinaria vocalia

Most developed in *Rana angolensis*, least in *R. dracomontana*.

Posterior chamber

Does not appear to possess any features of taxonomic value.

LARVAL BUCCOPHARYNX (Table 8; Pls. 33 - 35)

Topotypical tadpoles of *Rana umbraculata* do not appear to be available. Most of Wager's *Rana vertebralis* (**sensu lato**) material in the Natal Museum was poorly preserved and is not suitable for dissection. By external morphological and geographical criteria it all appears to be referable to *Rana vertebralis* as here recognised.

Prenarial arena

Large and deep, bearing an arcuate row of short pustulate papillae, the number and disposition of which show consistent interspecific differences. They are fewest and least arcuate in *Rana vertebralis* and *R. fuscigula*, and most elaborate in *R. dracomontana*.

Narial valve

The anterior flap bears a large papilla only in *Rana fuscigula*; in the other species examined it is variously sculpted, ranging from being finely serrate in Sp. A, to pectinate in *Rana dracomontana*.

Postnarial papillae

Tall conical papillae, finely pustulose on the anterior surface in *Rana fuscigula* and Sp. A, but smooth in the other taxa examined. Multiple (2 - 4 on either side) in all the taxa examined except for *Rana vertebralis*. Most of the specimens examined show slight lateral asymmetry, the number of papillae on one side being one more or less than on the other.

Lateral ridge papillae

There are two sets on either side -- a large, palpoid papilla with a fleshy base bearing 3 or 4 digitations; and, immediately behind, one (two in *R. fuscigula*) simple cylindrical or subconical papilla (with a few tiny papillae around its base in *Rana vertebralis*).

(NB: In the specimens of *Rana fuscigula* and Sp. A illustrated, the line of dissection was inadvertently so placed that the palpoid papillae appear on the floor portions of these preparations.)

Median ridge

The shape of the median ridge (small and triangular in *Rana vertebralis* and Sp. A, low and wide in the other species) and the degree of elaboration of the free surface, appear to show useful interspecific features. In *Rana dracomontana, R. fuscigula* and Sp. A there is a single small median protruberance. In all the other taxa examined, there is a pair of paramedian lobes -- papilliform in *Rana vertebralis*, papillate in *R. angolensis*.

Dorsal velum

Reduced, with a wide medial break, in all of the species examined. It is best developed, with papillate margins, in *Rana angolensis* and *R. dracomontana*.

Buccal floor arena

Large in all of the species examined, and bounded lateroposteriorly by a single or roughly double (verging on triple) border of papillae. Pustulations are widespread in all but *Rana vertebralis*, where they are confined to the anterior portion of the arena.

Prelingual papillae

Large and palpoid in all of the species examined. There are no conspicuous interpecific differences.

Lingual papillae

Numerous and elaborately arranged. The interspecific differences (best seen by examining the illustrations) appear to be consistent in the material examined.

Buccal floor arena

Massive, and occupying much of the buccal floor. It is bounded by multiple rows of papillae posteriorly, and one or two anterolaterally. The arrangement and overall number of papillae appear to be consistently distinctive. Arena pustulations are absent in *Rana angolensis* and *R. fuscigula*, reduced in Sp. A, and extensive in *R. dracomontana* and *R. fuscigula*.

Buccal pockets

There appear to be few, if any, diagnostically useful features. In *Rana vertebralis*, however, they are small and virtually concealed by the lateral expansions of the ventral velum. Prepocket papillae are fairly numerous in all species examined except *Rana dracomontana* and Sp. A.

Ventral velum

There are clear interspecific differences, particularly in the midline width (strongly narrowed in *Rana dracomontana* and *R. vertebralis*, of subequal width in the other taxa examined) and in the elaborate appendages of the free margin. These are, however, better described visually than verbally, and the plates should be consulted directly.

Rana angolensis Bocage, 1866

Rana angolensis Bocage, 1866, *J. Sci. Math. Phys. Nat., Lisboa*, 1:73. Type locality: Duque du Bragança, Angola. Holotype formerly in the Museu Bocage, but destroyed in 1978 by fire. Poynton 1964:103, fig. 53. Van Dijk 1966:259. Channing 1979:797, figs. Passmore & Carruthers 1979:130, figs. Lambiris 1988:26, figs., pl. 3 figs. 2a-c; 1989a: 88; 1989b:90, figs. 43 & 44, pl. 7 figs. 1a-h.

ADULT LARYNX (Table 7; Pl. 31, fig. 1)

Material examined: SOUTH AFRICA: NATAL - AJL 2031 (m, SVL 72.0 mm), Kamberg Nature Reserve. AJL 2060 (f, SVL 811.7 mm), Weenen Nature Reserve. EASTERN CAPE - AJL 327 (m, SVL 60.0 mm), Grahamstown.

Advertisement call: A croak about 0.1 second long, between about 0.5 and 2.0 kHz (Passmore & Carruthers 1979:130), often preceded by a short rattle. Calls are made both by day and at night, from the banks or from aquatic vegetation. There is a loose choral structure.

Male larynx:

Orientation: The anteroposterior axis is directed upwards at an angle of about 65° from the horizontal.

Pharyngeal mucosa: Thick and deeply folded, covering the anterodorsal surface of the arytenoid cartilage. The submucosa is clearly distinguishable from the cartilage.

Arytenoid cartilage: Prominentiae relatively small; the inferior prominentia a little larger and more conspicuous than the superior. The internal margin of the occlusal surface is broadly V-shaped, and bears a narrow but distinct arytenoid valve. The arytenoid shelf is broad and shallow. The major axis of the narrowly elliptical arytenoid fossa is about 0.4x the length of the posterior margin of the medial vocal cord. Pulvinaria vocalia (especially the inferior) are massively developed.

Vocal cords: The **medial vocal cord** is broad, slightly flared at the insertions, and moderately flanged on both margins. Distinct buttresses are lacking. There is no frenulum. The **lateral vocal cord** is broad and prominent, but lacking obvious features.

Posterior chamber: Narrow, and lacking obvious features.

LARVAL BUCCOPHARYNX (Table 8; Pl. 33, figs. 1a & b)

Identification of larvae: Lambiris 1989a, 1989b.

Material examined: MALAWI; AJL 3308a; Tributary of Lunzi river, 24 km N. of Blantyre; stage 33, SVL 17,7 mm; thionine stain. SOUTH AFRICA; NATAL - AJL 2344, stage 37, SVL 20,0 mm; and AJL 2345, stage 41, SVL 23,0 mm; Main gate, Giant's Castle Game Reserve; thionine stain. AJL 3511; Nembe Stream, Kwa Dlozi Bridge, Pietermaritzburg district; stage 37/38, SVL 23,0 mm; silver impregnation.

Larval habitat: Most water bodies, such as pools, pans, streams and rivers. Substratum type varies from silt and sands of various grades, to stony or rocky. Aquatic macrophytes of various types are usually present, as are the algae on which they avidly feed.

Buccopharyngeal roof

General shape: Narrowly triangular, the base about 0.9x the height. The general surface is regularly concave, with a more deeply excavate prenarial arena.

Prenarial arena: A large trapezoid. Six short, pustulose papillae, grouped in pairs, are arranged in an anterolateral arc. Another pair is present close to the anterior medial narial margin.

Internal nares: Narrowly elliptical, transversely set. Narial length about 0.38x the width of the roof at that level.

Narial valve: Anterior margin strongly pectinate. Posterior margin simple, and not deeply incised.

Postnarial arena: 2 - 4 postnarial papillae, about 0.6x narial length, are set transversely behind each naris. There are two lateral ridge papillae on either side -- a large, more anteroventral palpoid papilla and a smaller, more posterodorsal simple subconical papilla. The median ridge is broad (about 0.5x the width of the roof at that level) and low, with a pustulate free margin bearing two short, round, closely-set paramedial lobes.

Buccal roof arena: Large, about 0.7x the width of the roof. Bounded laterally and posteriorly by a double row of conical papillae, tending to diminish slightly in size posteriorly. The arena is densely and evenly pustulate.

Glandular ridge: A narrow ridge with a small medial gap.

Dorsal velum: Narrow, with a small medial gap, and closely applied to the anterior border of the pressure cushions. The free edge bears rather long papillae.

Pressure cushions: Rather small. The lateral lobe is bulbous but smaller than the flatter medial lobe.

Buccopharyngeal floor

General shape: Triangular, the base about equal to the height. The concave floor is slightly deepened retrolingually; the floor of the rather deep prelingual arena is slightly raised centrally.

Prelingual papillae: Two or three pairs of small conical paramedial papillae are set in an anteriorly convergent wedge on the arena floor. A larger palpoid papilla (3 - 4 lobes on a fleshy base) arises from about the middle of the ventrolateral junction.

Lingual papillae: 7 subequal cylindrical or subconical papillae, about equal in size to those of the buccal floor arena and arranged in a broad posterorly-directed wedge, arise from the anterodorsal margin of the tongue anlage.

Buccal floor arena: Massive, covering most of the floor between the lingual arena and the ventral velum. It is bounded laterally by a short double row of subconical, subequal papillae, and by five rather regular rows posterolaterally. There are no pustulations.

Buccal pockets: Broadly oval, closed. There are 6 - 10 prepocket papillae on either side, similar to those of the buccal floor arena.

Ventral velum: Broad, of subequal width throughout. The free margin is thickened, and bears about 5 papillae (usually long, but some rather short) on the outer thirds; the middle third bears 5 or 6 more regularly sized, closely set papillae, flanked by a double papilla on either side.

Branchial baskets: Arcuate.

Filter plates: Curved, semi-closed. The complexly folded filter rows have short intercalary partial rows and narrow channels.

Rana dracomontana Channing, 1978

Rana angolensis (non Bocage, 1866): Poynton 1964:103 (part), Van Dijk 1966:259 (part?), Passmore & Carruthers 1979:130 (part).

Rana dracomontana Channing, 1978, *Ann. Natal Mus.*, 23:361. Type locality: "top of Sani Pass (29°35's, 29°17'E), 2872", Lesotho (holotype) and "in the vicinity of the Manaung river and its tributaries (29°33's, 29°13'E)" (paratypes). Types in the Natal Museum, Pietermaritzburg. Lambiris 1988:28, figs, pl. 3 figs. 3a & b; 1989a:91.

ADULT MALE LARYNX (Table 7; Pl. 31, fig. 2)

Material examined: LESOTHO: AJL 2814 (♂, SVL 70.0 mm), Sehlabathebe National Park.

Advertisement call: (Summarised from Channing, 1978:363) Biphasic, a slowly pulsed phase about 1 second long at about 1.8 kH followed by a short (143 - 603 ms) rapidly pulsed croak at about 1 kHz. Calls are uttered "some distance from the water, or at the water's edge" (Channing 1979:819).

Orientation: The anteroposterior axis is directed upwards at an angle of about 45° from the horizontal.

Pharyngeal mucosa: Rather thin, overlying a deeper submucosa and covering the dorsum of the arytenoid cartilage only. The submucosa blends into the arytenoid cartilage anterodorsally.

Arytenoid cartilage: External margin of the occlusal surface bi-convex, the border of the inferior prominentia sharply angled. The arytenoid valve is distinct, but not sharply defined. The posterior occlusal margin is arcuate. The axial width of the arytenoid shelf is about 1.3x that of the occlusal surface, and the shelf is pigmented. It curves gently into a rather weakly defined elliptical arytenoid fossa, the major axis of which is about 0.4x the length of the posterior margin of the medial vocal cord.

Vocal cord: The **medial cord** is moderately broad, and flared at the insertions. The posterior margin is strongly flanged; buttresses are virtually absent. There is no frenulum. The **lateral cord** is large and prominent, with an undulant posterior margin.

Posterior chamber: Shows no features of diagnostic value.

LARVAL BUCCOPHARYNX (Table 8; Pl. 33, fig. 2a & b)

Identification of larvae: Based on a series from the Sehonghong/Makhapung River and the Sani/Mangaun River confluences, Lesotho (AJL 2961 - 2965, stages 25 - 42), showing webbing diagnostic of the adults at Stage 42; collected by Dr. P. Skelton, September 1988.

Material examined: LESOTHO: AJL 2965; Sehonghong/Makhapung River confluence; stage 38, SVL 27.7 mm; silver impregnation.

Larval habitat: Cold, stony-bottomed alpine streams with clear water and few aquatic macrophytes (Skelton).

Buccopharyngeal roof

General shape: Outline highly arched; base about 0.9x height. The prenarial arena is deeply excavate, the buccal roof shallowly concave.

Prenarial arena: Deeply arcuate, and bearing 9 short, pustulate papillae on the periphery of a large raised semicircular prominence in the centre of the arena.

Internal nares: Broadly elliptical, and set transversely. Width of naris about 0.4x width of roof at that level; internarial distance about 0.44x narial width.

Narial valve: Anterior margin strongly pectinate laterally, shortly lobulate medially. Posterior margin shallow, simple; not deeply incised.

Postnarial arena: Three conical **postnarial papillae** behind either naris, the medial one largest, the lateral one much smaller (about 0.3x the length of the medial one). Two **lateral ridge papillae**, a large palpoid anteroventral one and a smaller posterodorsal subconical one, on either side. The **median ridge** is broad (about 0.4x the width of the roof at that level) and low; the pustulate free margin has a triangular apical papilla.

Buccal roof arena: Large, about 0.6x the width of the roof. Bounded laterally by a single row of medium-height subconical papillae, and posteriorly by a double row of similar papillae. The arena is covered with a moderately dense scattering of tiny pustules.

Glandular ridge: A narrow ridge adjacent to the posterior border of the buccal floor arena.

Additional papillae are present on the left side of this preparation, opposite the anterior lateral border of the buccal floor arena. **Additional pustulations** occur between the glandular ridge and the velar hiatus.

Dorsal velum: Short but well-developed, with a pectinate free border, and interrupted medially.

Buccopharyngeal floor

General shape: Bluntly triangular; base about 1.2x height. Prelingual arena deeply excavate; buccal floor shallowly concvave, and with a pair of posteriorly-diverging ridges retrolingually.

Prelingual papillae: A tall conical medial papilla arises from the floor of the arena. It is flanked on the left side by a large palp arising from the posterior lateroventral portion of the arena wall; that of the right side is smaller and set still further back.

Lingual papillae: A tall cylindrical medial papilla is closely flanked on either side by a papilla of equal height but much broader, and terminally trifid. The posterodorsal surface of the tongue anlage bears a transverse row of three closely set pustulate papillae mesially.

Buccal floor arena: Massive, occupying nearly the entire space between the lingual arena and the dorsal velum. It is flanked anterolaterally by a double (staggered single?) row of tall conical papillae; the posterior half of the arena is largely filled with similar papillae. Pustulations are scattered densely and evenly between the papillae, and between the retrolingual ridges; there are fewer between the ridges and the anterolateral papillae.

Buccal pockets: Relatively small, oval, closed. Four **prepocket papillae**, a little smaller than those of the buccal floor arena, are discernible on the right side.

Ventral velum: Strongly narrowed medially. The posterior margin is somewhat thickened and bears 6 (left) or 5 (right) rather irregularly spaced and uneven-sized lobulate projections (tending to diminish in size laterally), with a small, symmetrical pair of lobes paramedially.

Branchial baskets: Large and arcuate.

Filter plates: Large, open, with narrow rows bearing secondary and tertiary folds. The channels are narrow.

Rana fuscigula Duméril & Bibron, 1841

Rana fuscigula Duméril & Bibron, 1841, *Erpét. Gén.*, 8:386. Type locality: "environs du Cap de Bonne-Espérance". Trewavas 1933:486, figs. 66 & 67. Poynton 1964:108, fig. 54. Van Dijk 1966:259. Channing 1979:797. Passmore & Carruthers 1979:132, figs. Lambiris 1988:30, figs., pl. 3 figs. 4a-c; 1989a:93.

ADULT LARYNX (Table 7; Pl. 31, figs. 3 & 4)

Material examined: SOUTH AFRICA: NATAL - AJL 2010 (m, SVL 78,6 mm), Lourie's Dam, Coleford Nature Reserve. NM 6218 (m, SVL 79,2 mm) Trout Hatchery, Underberg. NM 6390 (m, SVL 82,0), Impendhle. AJL 6228 (f, SVL 103,5 mm), Sani Pass Hotel.

Advertisement call: A long series of short taps, spaced about 0.1 second apart, at about 1.5 kHz; interspersed with a short grunt about 0.3 second long, at 1 kHz, with a strong harmonic showing frequency modulation at about 1.5 - 2 kHz (Passmore & Carruthers 1979:132). Calls are usually uttered during the day, among floating or emergent vegetation in deep water or, less often, from the water's edge.

Male larynx:

Orientation: The anteroposterior axis is directed upwards at about 30° from the horizontal.

Pharyngeal mucosa: Thin, over a shallow submucosa, and clearly demarcated from the underlying anterodorsal surface of the arytenoid cartilage.

Arytenoid cartilage: Prominentiae massively lobulate; the inferior one somewhat crenate on the anteroventral flexure. The occlusal surface lacks an arytenoid valve, and the internal margin is arcuate. The very broad arytenoid shelf (axial width twice that of the occlusal surface) has numerous large melanocytes scattered over the surface. The arytenoid fossa is elliptical; its major axis is about 0.44x the posterior length of the medial vocal cord.

Vocal cords: The **medial cord** is broadly flared at the insertions, and the anterior margin is strongly concave. The posterior margin is not flanged, but bears styliform superior and inferior buttresses. There is no frenulum. The **lateral cord** is prominent, with an undulent posterior border.

Posterior chamber: Large and rather thin-walled, with a few small scattered melanocytes. The posterodorsal margin of the pulmonary aditus is crenulate; the anteroventral margin is supported by a narrow cartilaginous rim.

LARVAL BUCCOPHARYNX (Table 8; Pl. 34, fig. 1a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 2351; Emerald Stream, 4,5 km NW of Cobham Forestry Station; stage 39, SVL 28,0 mm); silver impregnation. AJL 3498a; Jouberts Vlei se Loop River, 16 km NE of Mooi River; stage 38, SVL 32,0 mm; silver impregnation.

Like *Rana angolensis*, rather eurytopic but possibly preferring somewhat deeper waters than the former species. Fine details of habitat and biological requirements need further study.

Buccopharyngeal roof

General shape: Narrowly triangular, the base equal to the height. The general surface is regularly concave; the prenarial arena is deeply excavate.

Prenarial arena: A large trapezoid. A double ridge of coarse pustulations traverses the arena about one-third of the way down; behind this are three small pustules arranged in an inverted triangle.

Internal nares: Narrowly elliptical; obliquely set, the medial angle directed posterad. Narial length about 0.48x the width of the roof at that level.

Narial valve: Anterior margin strongly pustulose; a verrucose prenarial papilla (length about 0.5x that of naris) arises above the lateral angle. Posterior margin simple, and not deeply incised.

Postnarial arena: Three **postnarial papillae**, about 0.8 - 1.0x narial length, are set obliquely behind each naris. There is a large palpoid **lateral ridge papillae** on either side. The **median ridge** is broad (about 0.5x the width of the roof at that level) and low, with a pustulate free margin bearing a slightly larger apical pustule.

Buccal roof arena: Large, about 0.7x the width of the roof. Bounded laterally and posteriorly by an irregular double (triple?) row of

conical papillae, tending to diminish slightly in size posteriorly. The arena is moderately densely and evenly pustulate.

Glandular ridge: A narrow continuous ridge close behind the arena.

Dorsal velum: Narrow, weak, with a small medial gap, and closely applied to the anterior border of the pressure cushions. The free edge bears short irregular papillae.

Pressure cushions: Rather small. The lateral lobe is bulbous but smaller than the flatter medial lobe.

Buccopharyngeal floor

General shape: Triangular, the base about 0.8x the height. The concave floor is slightly deepened retrolingually; the floor of the prelingual arena is more deeply excavate.

Prelingual papillae: Two or three pairs of small conical paramedial papillae are set in a posteriorly convergent wedge on the arena floor. A larger palpoid papilla (3 - 4 lobes on a fleshy base) arises from about the middle of the ventrolateral junction.

Lingual papillae: 4 subequal cylindrical papillae, about equal in size to those of the buccal floor arena and arranged transversely,, arise anterodorsally on either side of a bifurcate median papilla.

Buccal floor arena: Massive, covering the entire the floor between the lingual arena and the ventral velum. It is bounded anterolaterally by a short double row of subconical, subequal papillae; the posterior half of the arena is covered with numerous irregularly scattered papillae. Pustulations cover the entire arena.

Buccal pockets: Oval, closed. There are 2 - 4 prepocket papillae on either side, similar to those of the buccal floor arena.

Ventral velum: Moderately broad, of subequal width throughout. The free margin is slightly thickened, and bears 5 long papillae, widely spaced laterally but closer together mesially, and flanking a short, robust, closely-set paramedian pair.

Branchial baskets: Arcuate.

Filter plates: Curved, semi-closed. The filter rows, with secondary and tertiary folds, have short intercalary partial rows and narrow channels.

Rana vertebralis Hewitt, 1927

Rana vertebralis Hewitt, 1927, *Rec. Albany Mus.*, 3:404, text-fig. 2, pl. 24 fig. 2. Type locality: Summit of Mont-aux-Sources. Holotype in the Port Elizabeth Museum, Port Elizabeth. Poynton 1964:109, fig. 55. Van Dijk 1966:259. Channing 1979:797, figs. Passmore & Carruthers 1979:134, figs. Lambiris 1988:31, figs., pl. 4 figs. 1 a & b); 1989a:94.

Rana ?umbraculata Bush: Van Dijk 1966:259 (part?).

ADULT LARYNX (Pl. 32, fig. 1)

Adult male larynxes were not available for study. In the *Rana vertebralis / Rana umbraculata* complex, the female larynx shows less dimorphism than is true of the other species examined. The larynx of male *R. vertebralis* probably resembles that of the female quite closely, but differing in possessing a distinct lateral vocal cord.

LARVAL BUCCOPHARYNX (Table 8; Pl. 33, fig. 2a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 2252; Tugela River, 700 metres NE of Crow's Nest Peak, nr. Mont-aux-Sources; stage 31; SVL 19.6 mm; silver impregnation.

Larval habitat: Cold (frequently ice-covered), stony- or rocky-bottomed alpine streams with clear, briskly-flowing water and few, if any, aquatic macrophytes. The diet appears to consist principally of unicellular and small multicellular algae.

Buccopharyngeal roof

General shape: Deeply trapezoid, base 1.1x the height. The prenarial arena is more deeply excavate than the shallowly concave buccal roof.

Prenarial arena: A large trapezoid. A large, somewhat conical pustulose median papilla, set close behind the root of the beak, is flanked on either side by a smaller, more rounded papilla; and, more laterally, by still smaller pustules arranged in a broad curve.

Internal nares: Narrowly elliptical, and set transversely. Width of naris about 0.35x the width of the roof at that level; internarial distance about 0.6x narial width.

Narial valve: Anterior margin serrated. Posterior margin smooth, with a small papilla closely associated with it.

Postnarial arena: A long (about 0.6x narial width) cylindrical postnarial papilla, arising behind the middle of the narial margin, is flanked by the lateral ridge papillae. These consist of a large palpoid anterior papilla and a long, smooth subconical posterior one which has two small pustulose papillae at its base. The median ridge is narrow (about 0.2x width of roof at that level) and low; the pustulose free margin is surmounted by a pair of long paramedian papillae.

Buccal roof arena: Large, about 0.6x the width of the roof. Bounded laterally and posteriorly by a row of long subconical papillae diminishing slightly in size posteriorly; some on the left side show, in varying degrees, a tendency to bifurcate. There is a single median papilla in the posterior half of the arena. About 20 small pustules are spread in a transverse band over the anterior quarter of the arena.

Glandular ridge: A short pustulate ridge flanking the lateral boundaries of the buccal roof arena.

Dorsal velum: Feeble, bipartite, and closely applied to the pressure cushions.

Pressure cushions: Rather small, but distinctly divided into medial and lateral lobes.

Buccopharyngeal floor

General shape: Triangular, the base about 1.2x the height. The prelingual arena is deeply excavate. The buccal floor is moderately deeply concave, with a pair of short, posteriorly divergent retrolingual ridges extending into the anterior quarter of the buccal floor arena.

Prelingual papillae: A tiny median papilla in the centre of the arena floor, with a pair of paramedial papillae immediately anterior to the tongue anlage. There is a tiny subconical lateral papilla present on either side, at the root of the beak, followed by a larger conical, then by a still larger bifid (left) or trifid (right) papilla, all set along the ventrolateral flexure.

Lingual papillae: 8 long, subequal, closely-set subconical papillae, are arranged in an arch along the anterodorsal margin of the tongue anlage, four on either side of the midline.

Buccal floor arena: Massive, occupying almost the entire space between the labial arena and the ventral velum. Bounded laterally by numerous closely-spaced simple subconical papillae, increasing in size posteriorly, where they form an irregular double row. There is a slight tendency to doubling or bifurcation. About 9 papillae occupy the posteromedian portion of the arena. There are no pustulations in the arena.

Buccal pockets: Not visible in this preparation. 5 simple cylindrical **prepocket papillae** (?) are present on the right side of this preparation.

Ventral velum: Moderately broad, but distinctly constricted mesially. The free margin is thickened and bears 5 (left) or 6 (right) blunt papillate lobes on either side of the short, stout paramedian pair. These are smaller and more widely-spaced laterally, but those on either side of the paramedian pair are smaller and more closely-set.

Branchial baskets: Damaged in this specimen.

Filter plates: Strongly arched, and semi-closed. The finely-folded filter rows have a few rather irregularly intercalated partial rows. The channels are narrow.

Rana umbraculata Bush, 1952

Rana umbraculata Bush, 1952, *Ann. Natal Mus.*, 12:153, pls. 3-6, text-figs. 1, 2. Type locality: Umzimkulu River, Drakensberg Gardens, Natal. Holotype in the Port Elizabeth Museum, Port Elizabeth; paratypes in the Natal Museum, Pietermaritzburg.

Rana vertebralis (non Hewitt, 1927): Poynton 1964:109 (part), Channing 1979:797 (part), Passmore & Carruthers 1979:134 (part), Lambiris 1988:31 (part); 1989a:94 (part).

ADULT LARYNX (Table 7; Pl. 34, fig. 2)

Material examined: SOUTH AFRICA: NATAL - NM 981 (m, 94,5 mm) and NM 982 (f, SVL 103,0 mm), Drakensberg Gardens (PARATYPES), NM 2609 (m, SVL 76,0 mm), Drakensberg Gardens.

Advertisement call: See "Species A", *infra*, and the Discussion.

Male larynx:

Orientation: The anteroposterior axis is directed upwards at about 35° from the horizontal.

Pharyngeal mucosa: Thin and folded, over a deep submucosa distinct from the underlying anterodorsal portion of the arytenoid cartilage.

Arytenoid cartilage: Prominentiae apicales moderately expanded; the anterior border of the superior prominentia crenate, that of the inferior prominentia smooth. The internal margin of the occlusal surface is broadly arcuate. The arytenoid valve is not strongly defined. The arytenoid shelf is shallow and moderately broad (axial width equal to that of the occlusal margin). The major axis of the elliptical arytenoid fossa is about 0.4x the posterior length of the medial vocal cord; the anterior margin is weakly defined.

Vocal cords: The **medial cord** is broad, widely flared at the margins, and bears large superior and inferior buttresses. There is no frenulum. The anterior margin is strongly concave. The **lateral cord** is large but simple, with a slightly undulant posterior margin.

Posterior chamber: Lacks and features of taxonomic value.

LARVAL BUCCOPHARYNX

No topotypic material suitable for dissection was available.

Rana sp. A

Rana vertebralis (non Hewitt, 1927): Poynton 1964:109 (part), Channing 1979:797 (part), Passmore & Carruthers 1979:134 (part), Lambiris 1989a:94 (part).

ADULT LARYNX (Table 7; Pl. 32, fig. 3)

Material examined: LESOTHO: AJL 2779 (m, SVL 67,2 mm), and AJL 2780 (m, SVL 80,0 mm), Top of Sani Pass, AJL 3509 (f, SVL 120,0 mm), Sani Road Bridge, Sehonghong River.

Advertisement call: The call described by Passmore & Carruthers (1979:134) under the name *Rana vertebralis* appears to be referable to "Sp. A" as here recognised (see Discussion, *infra*). It is quoted here:

> "Two different calls are commonly heard. One is a low-pitched stuttering groan. The other is several seconds of hollow knocking, at a rate of about seven per second.

Male larynx:

Orientation: The anteroposterior axis is directed upwards at an angle of about 30° from the horizontal.

Pharyngeal mucosa: Thin, over a deep submucosa covering the dorsum of the arytenoid cartilage.

Arytenoid cartilage: Prominentiae apicales greatly expanded, the anterior margins of both strongly ridged. The internal margin of the occlusal surface is V-shaped. There is no distinct arytenoid valve. The arytenoid shelf is shallow and moderately broad (axial width equal to that of the occlusal surface). The arytenoid fossa is oval; its major axis is about 0.36x the posterior length of the medial vocal cord.

Vocal cords: The **medial vocal cord** is broad, and widely flared at its insertions. The anterior margin is strongly concave. The posterior margin bears short, stout, but not strongly developed, buttresses. The well-developed **lateral cord** has a weak frenulum mesially.

Posterior chamber: Has no features of taxonomic value.

LARVAL BUCCOPHARYNX (Table 8; Pl. 35, fig. 1a & b)

Identification of larvae: Based on a series from the Sani, Sehonghong and Sanquebuthu Rivers (AJL 2966 - 2974, stages 38 - 43), differing markedly in habitus (Text-fig. 17) and in external mouthparts from *Rana vertebralis* and *R. umbraculata* tadpoles, although transformates at Stage 43 are indistinguishable from those of the latter two species at the same stage. Collected by Dr. Paul Skelton, 21 - 25 September 1989.

Material examined: LESOTHO: AJL 2966: Sani Road Bridge, Sehonghong River; stage 36, SVL 28,5 mm; silver impregnation. AJL 2969: Mahonghong/Makhapung River confluence; stage 38, SVL 28,0 mm; silver impregnation; AJL 2973: Mahonghong/Makhapung River confluence; thionine stain.

Larval habitat: Cold, clear, rocky- or stony-bottomed alpine streams with few aquatic macrophytes (Skelton). Small multicellular algae were found in the guts of the specimens examined.

Buccopharyngeal roof

General shape: Triangular, base about 1.2x height. Prenarial arena deeply excavate, with a slightly raised large central platform; buccal roof rather narrow, and only slightly concave.

Prenarial arena: A deep trapezoid. A pair of pustules flank the medial third of the beak, immediately below its base. The anterior and lateral borders of the central platform bear a series of large pustules -- a medial close-set group of three flanked on either side by a single one and, on the lateral margins, by another pair.

Internal nares: Narrowly elliptical and set slightly obliquely, the medial angle directed posterad. Width of naris about 0.38x the width of the roof at that level; internarial distance about 0.75x narial width.

Narial valve: Anterior margin strongly crenate. Posterior margin smooth, moderately deeply incised.

Postnarial arena: Three closely-spaced postnarial papillae pustulose on their anterior margins, are set transversely behind either naris. The medial one is largest (length equal to narial width), the lateral one shortest (about 0.66x narial width). There is a small median

pustule between the two sets. The **lateral ridge papillae** are large and palpoid, with slightly pustulose digits, and tending to divide basally into two groups on either side. The **median ridge** is moderately broad (about 0.7x the width of the roof at that level) and somewhat curved; the free margin is bluntly serrate.

Buccal roof arena: About 0.5x the width of the roof. Roughly semicircular, bordered laterally and posteriorly by an irregular (more or less double) row of closely-spaced, smooth, subconical papillae of moderate height. The arena is covered with regularly scattered pustules, which extend forward to the postnarial arena.

Additional papillae: 4 - 6 are present lateral to the buccal roof arena (on the left side only in AJL 2973).

Glandular ridge: A short non-pustulate ridge close to the posterolateral margin of the arena, on either side.

Dorsal velum: Feebly developed.

Pressure cushions: Coarsely lobulated, but not clearly separable into medial and lateral moieties.

Buccopharyngeal floor

General shape: Triangular, base about 1.5x the height. Prelingual arena deeply excavate medially; buccal floor regularly concave, but with a recessed chiasma anteromedially.

Prelingual papillae: A pair of small, cylindrical paramedian papillae on the floor, at a level slightly anterior to the bases of the larger triple group arising at the extreme posterior ventrolateral flexure of the arena, on either side.

Lingual papillae: A pair of large cylindrical paramedian papillae are flanked on either side by 2 - 3 close-set smaller papillae, arranged transversely on the anterodorsal margin of the tongue anlage.

Buccal floor arena: Large, occupying about 0.7 of the area between the labial arena and the ventral velum. It is bounded laterally by a roughly double, row of large, smooth, closely-spaced subconical papillae showing some tendency to bifurcate near their bases; and posteriorly by three or four rows of similar, but slightly smaller, papillae, which tend to encroach the anterior margin of the ventral velum. Pustules occur

between the papillae and on the triangle between the posterior arms of the chiasma.

Buccal pockets: Large, oval, closed. Prepocket papillae are lacking.

Branchial baskets: Large and rounded.

Filter plates: Medial plate very small; lateral plate very large, curved and semi-closed. The filter rows are finely-folded, and the channels are narrow.

DISCUSSION

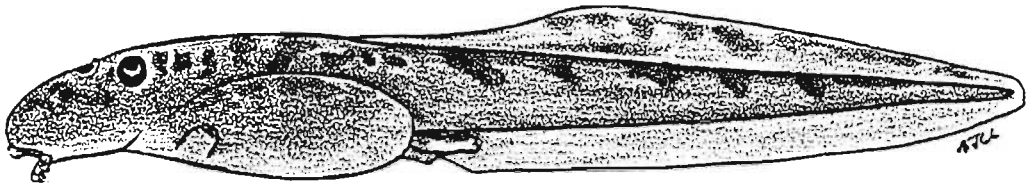
South African *Rana* species have often proved difficult to distinguish by means of external morphology, in both adult and larval stages (Lambiris 1989a:88 ff). Channing (1978:365) has remarked that a number of sibling species may occur in southern Africa. This genus therefore provides a useful test case for both assessing the taxonomic value of adult laryngeal and larval buccopharyngeal characters, and for testing taxonomic conclusions reached previously (Poynton 1964; Channing 1979; Passmore & Carruthers 1979; Lambiris 1989a).

The *Rana angolensis* group

The present taxonomic concept of the *Rana angolensis* group, within the designated study area, is confirmed. However, a peculiar tadpole from Ondangwa, Namibia, presently identified as that of *Rana fuscigula* (not dissected for the present study) suggests that a more widely-based investigation of the genus would be desirable.

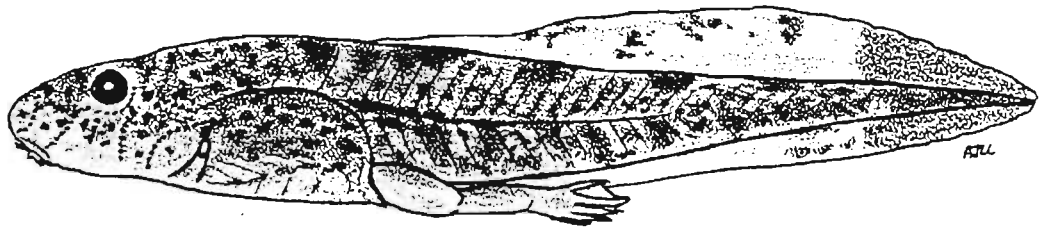
Three morphologically similar species are currently recognised in South Africa: *Rana angolensis* Bocage, *R. dracomontana* Channing, and *R. fuscigula* Duméril & Bibron, which are sometimes distinguishable only with difficulty. Adult laryngeal morphology has proved invaluable for separating specimens of *Rana angolensis* and *R. fuscigula* where head width/tibia length ratios (the most reliable character in general use) are borderline. *Rana dracomontana* is also easily separable from the externally almost identical *R. angolensis* by laryngeal characters. Lambiris's doubts (1989a:91 ff) about the validity of *Rana dracomontana* prove to be groundless, as the present study "utilising morphological characters that can be applied to museum specimens", as there called for, has now convincingly demonstrated.

Tadpoles of *Rana angolensis* and *R. fuscigula* are not always separable with confidence, most of the characters used in the keys of Van Dijk (1966:259) and Lambiris (1989a:38) showing a measure of overlap in some populations or individuals. Tadpoles of both species were used extensively in developing dissecting and silver impregnation techniques,



cm

(a) *Rana vertebralis* Hewitt: AJL 2235, Stage 31, Tugela River, 700 m NE of Crow's Nest Peak, Drakensberg Mts., Natal, South Africa.



cm

(b) *Rana* sp. A: AJL 2967, Stage 40, Sani Road Bridge, Sehonghong River, Lesotho.

TEXT-FIG. 33: TADPOLES OF (A) *RANA VERTEBRALIS* HEWITT AND (B) *RANA* SP. A, LEFT LATERAL VIEW.

and the differences described above (based on much shorter series from collections) are consistent throughout, irrespective of the condition of such features as shape of dorsal fin, pigmentation of tail (both notoriously variable) or infra-angular tooth rows (less variable, but still not completely reliable).

The tadpole of *Rana dracomontana*, previously unknown, is readily distinguished from that of *R. angolensis* and *R. fusigula* not only buccopharyngeally, but also on the basis of external characters. Descriptions of southern African *Rana* tadpoles are in preparation.

The *Rana vertebralis* group

Rana vertebralis as previously recognised (e.g. Poynton 1964, passmore & Carruthers 1979. Lambiris 1989a) proves to be a group of three species indistinguishable as adults on the basis of external and pectoral girdle characters (Lambiris 1989a:95 for *R. vertebralis* and *R. umbraculata*), but readily separated by means of laryngeal and buccopharyngeal morphology. Tadpoles also differ in habitus and in details of external mouthparts. Channing's suggestion concerning sibling species among southern African *Rana* appears to be well founded. The taxa here recognised may be summarised as follows:

Rana vertebralis Hewitt, 1927 (Text-fig. 33a)

A high-altitude (above 2800 metres) species. The tadpole reaches a total length of about 50 mm at stages 38 - 40; it is strongly compressed dorsoventrally, and has a large suckerlike oral disc and a tooth-row formula of II : [3+3 - 5+5] / IV. It is restricted to the northern Natal/ Lesotho Drakensberg range, in the vicinity of Mont-aux-Sources.

Rana umbraculata Bush, 1952

A lower-altitude (below about 2500 metres) species. The few poorly-preserved tadpoles available have a tooth row formula of II : [6+6 - 8+8] / IV. The general habitus appears to resemble that of *Rana vertebralis*. The species is retricted to the central Natal Drakensberg range.

Rana sp. A (Text-fig. 33b)

A high-altitude (above 2900 metres species. The tadpole reaches a total length of 75 - 80 mm at stages 38 - 40; it is less compressed and more rounded than that of *R. vertebralis*, and the oral disc is smaller and not sucker-like. The tooth row formula is I : 4+4 / 1+1 : II. The species appears to be restricted to the Lesotho plateau above the central and southern Natal/Lesotho Drakensberg range.

The call described and illustrated with a sonagram, under the name *Rana vertebralis* Hewitt in Passmore & Carruthers (1979:134) be referable to *Rana* sp. A as here recognised, since the call was recorded from "Sani Pass, Lesotho". A sonagraphic analysis of calls from the three areas indicated above would, when available, be of great value.

Complete representation of laryngeal and buccopharyngeal character suites for all three taxa was not possible in this study.

Males are much less well represented in collections than are females, probably because of their much smaller size. The few males that were available for dissection were poorly fixed and preserved and, because of excessive softness of the tissues, too compressed from crowded storage to be used in this study. (This is surely an example *par excellence* of the need for formalin fixation, irrespective of what preservative is subsequently used.)

Male larynxes of only *Rana umbraculata* and *Rana* sp. A were examined, none from the Mont-aux-Sources area being available.

Female larynxes of all three taxa were examined but proved to be of no value taxonomically, being virtually identical to one another.

Similarly, tadpoles only of *Rana vertebralis* and *Rana* sp. A were in a dissectable condition, and fresh material of *R. umbraculata* needs to be collected.

Nevertheless, the combination of laryngeal and buccopharyngeal characters examined, and their apparent geographical separation, afford *prima facie* evidence of the existence of three separate taxa. More extensive fieldwork and collection of better-preserved material is needed, however, before the conclusions reached here can be definitely confirmed.

PLATE 31
RANA — ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

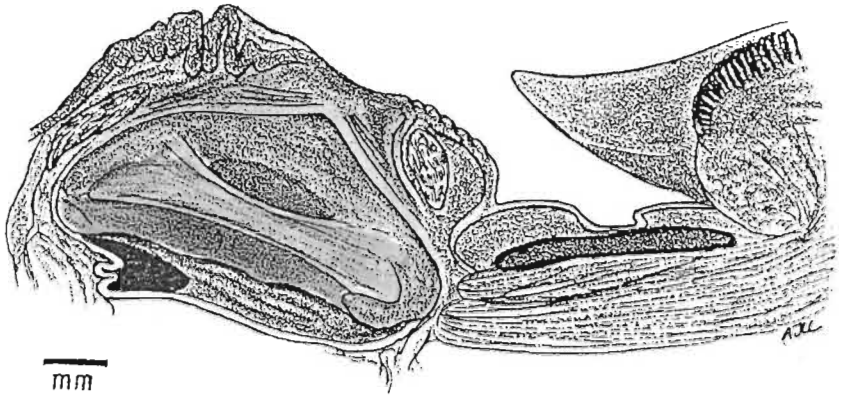


FIG. 1; *Rana angolensis* Bocage, 1866
AJL 327 (male), Grahamstown, Eastern Cape, South Africa.

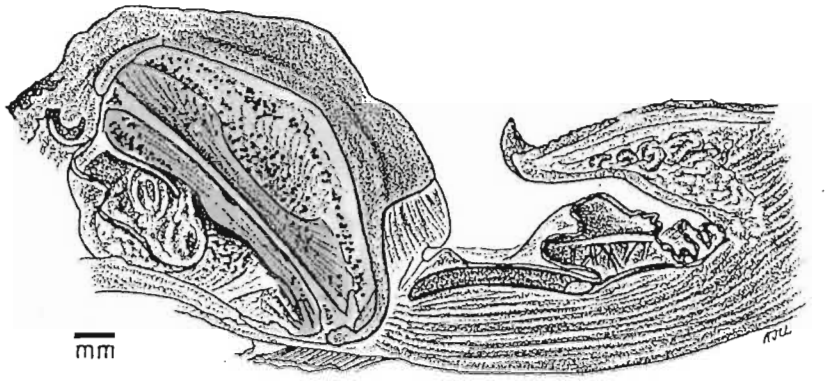


FIG. 2; *Rana dracomontana* Channing, 1978
AJL 2814 (male), Sehlabathebe National Park, Lesotho.

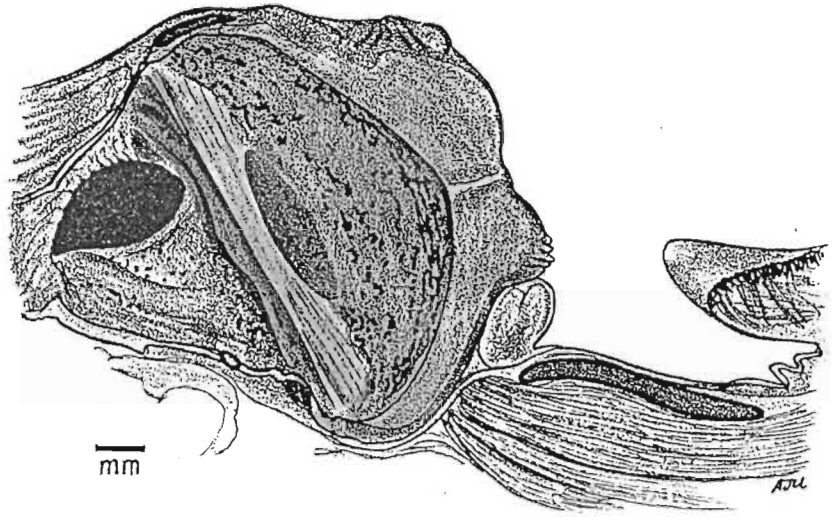


FIG. 3; *Rana fuscigula* Duméril & Bibron, 1841
NM 6214 (male), Underberg, Natal, South Africa.

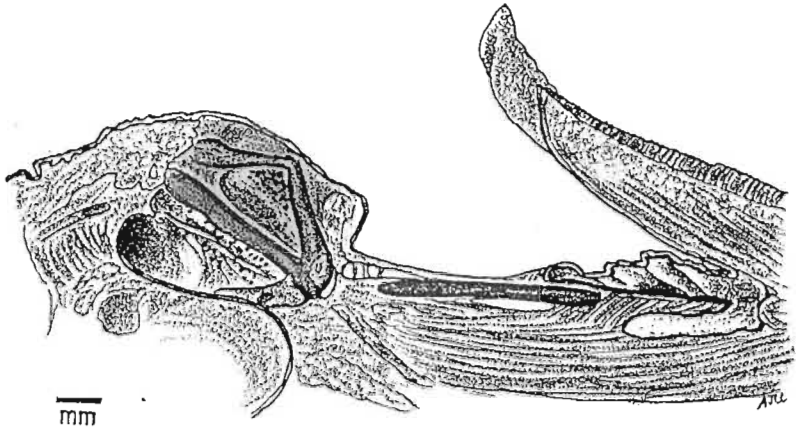


FIG. 4; *Rana fuscigula* Duméril & Bibron, 1841
AJL 2010 (female), Coleford Nature Reserve, Natal, South Africa.

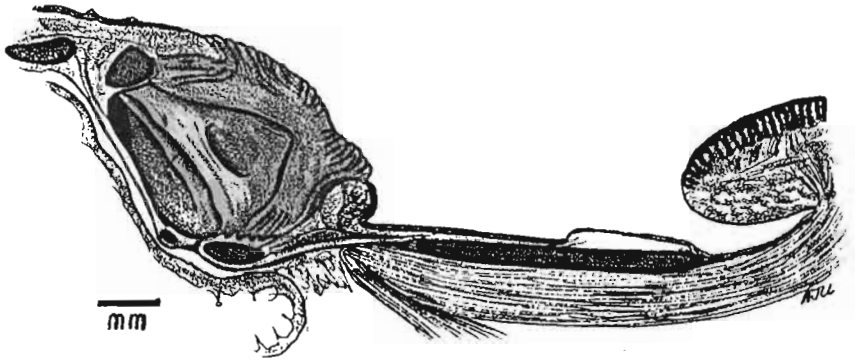


FIG. 1; *Rana vertebralis* Hewitt, 1927
NM 973 (female), Cathedral Peak, Drakensberg Mts., Natal, South Africa.

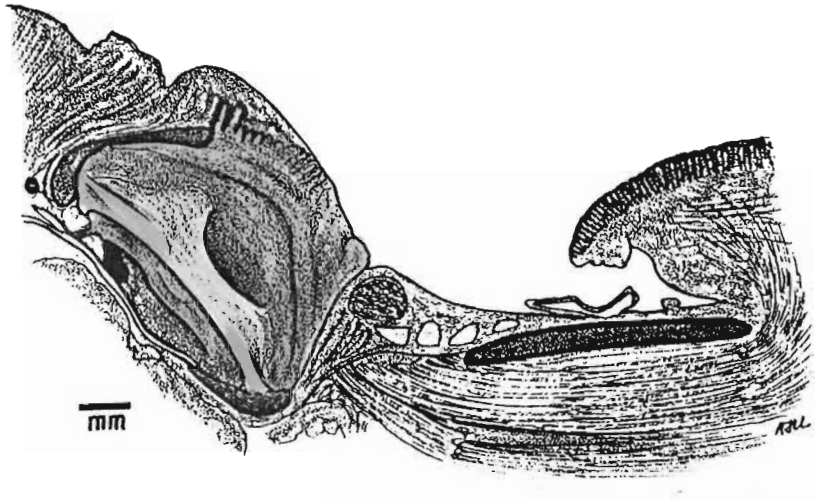


FIG. 2; *Rana umbraculata* Bush, 1952
NM 981 (male), Drakensberg Gardens, Natal, South Africa. PARATYPE.

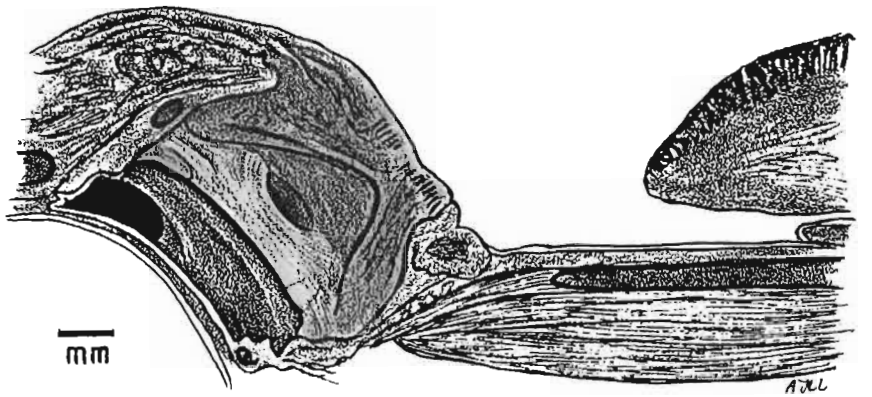


FIG. 3; *Rana* sp. A
AJL 2779 (male), Top of Sani Pass, Lesotho.

PLATE 32
RANA — ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

PLATE 33
RANA – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

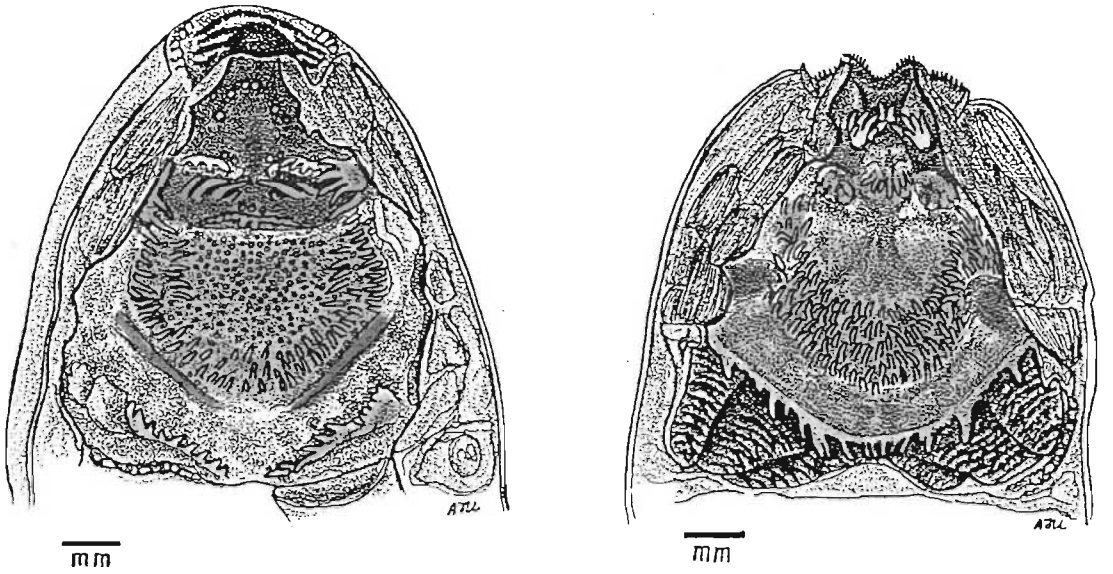


FIG. 1: *Rana angolensis* Bocage, 1866
AJL 3511, Stage 37/38, Nembe Stream; Kwa Dlozi bridge, above Henley Dam, Pietermaritzburg dist., Natal, South Africa.

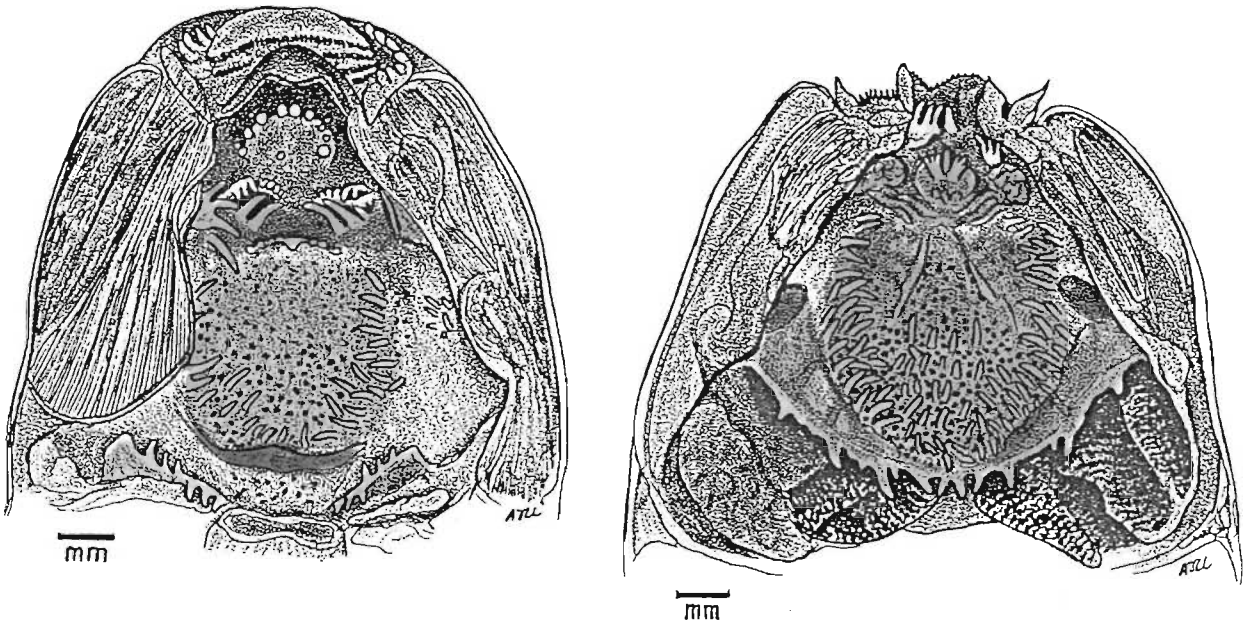


FIG. 2: *Rana dracomontana* Channing, 1978
AJL 2965, Stage 38, Sehonghong / Makhapung River confluence, Lesotho.

PLATE 34
RANA – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

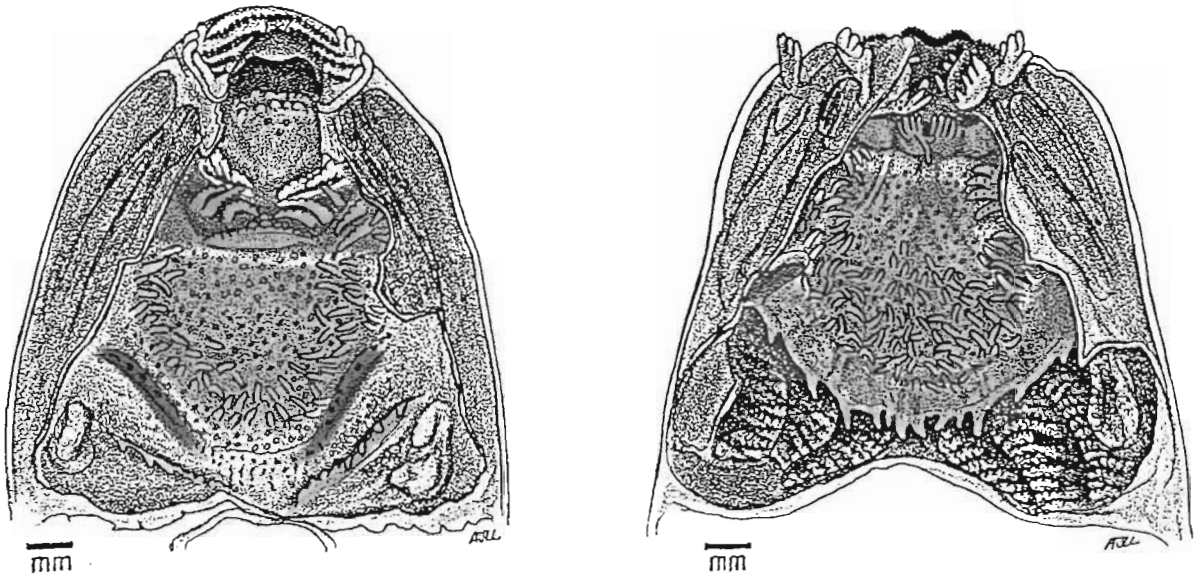


FIG. 1: *Rana fuscigula* Duméril & Bibron, 1841
AJL 3498a, Stage 38, Jouberts Vlei se Loop River, 16 km NE of Mooi River, Natal, South Africa.

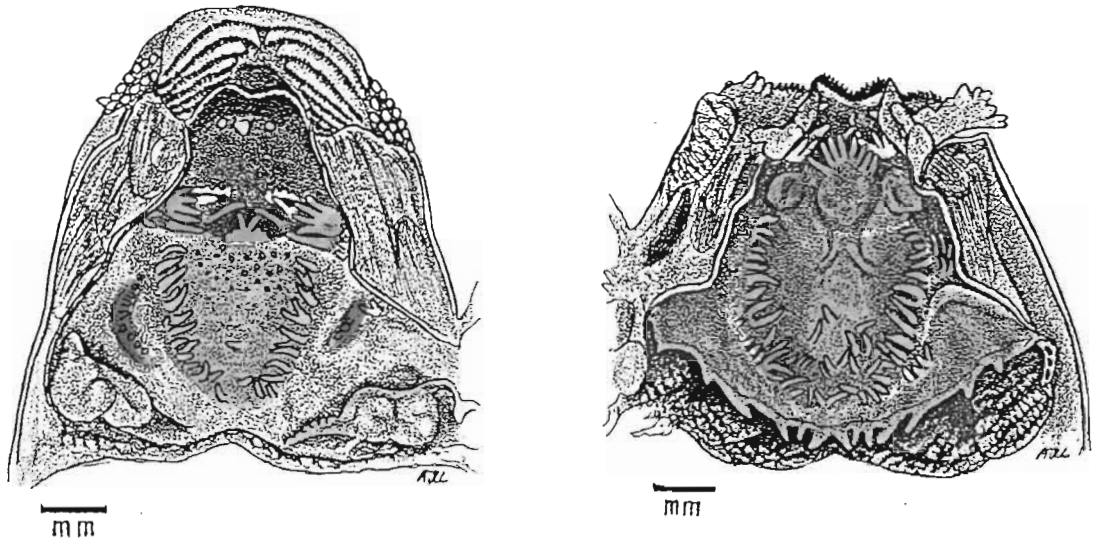


FIG. 2: *Rana vertebralis* Hewitt, 1927
AJL 2252, Stage 31, Tugela River, 700 m NE of Crow's Nest Peak, Drakensberg Mountains, Natal, South Africa.

PLATE 35
RANA – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

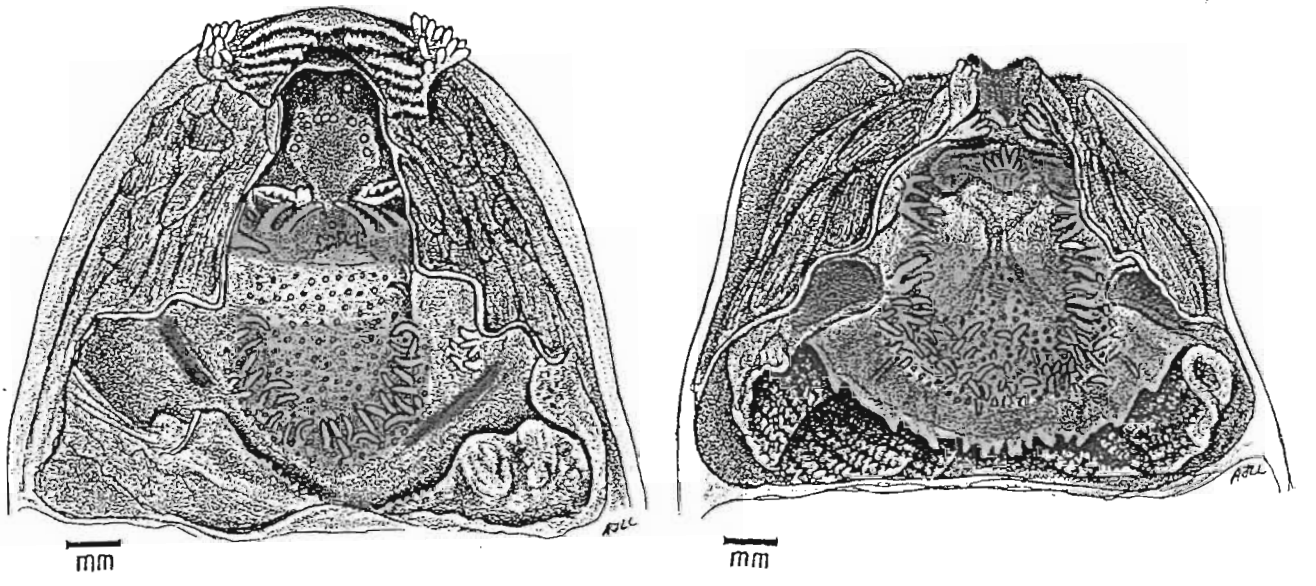


FIG. 1: *Rana* sp. A
AJL 2973, Stage 37, Mahonghong / Makhapung River confluence, Lesotho.

TABLE 9. Laryngeal characters: *Strongylopus*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	INTERNAL MARGIN OF ARYTENOID CARTILAGE V-SHAPED	EXTERNAL MARGIN OF ARYTENOID OCCLUSAL SURFACE STRIATED	INTERNAL MARGIN OF ARYTENOID OCCLUSAL SURFACE STRIATED	PART OF ARYTENOID SHELF STRIATED	ARYTENOID FOSSA WIDE	MIDDLE PORTION OF MEDIAL VOCAL CORD NARROW	INSERTIONS OF VOCAL CORDS HAVE FINE LIGAMENTOUS INCLUSIONS	LATERAL VOCAL CORD PRESENT	MASSIVE FRENULUM FROM VOCAL CORD TO LATERAL WALL OF POSTERIOR CHAMBER
Strongylopus hymenopus	3	3	0	3	1	3	3	1	3
wageri	1	3	3	3	1	3	3	3	1
grayii grayii	1	3	3	1	1	1	1	1	3
fasciatus fasciatus	3	1	1	3	3	1	1	1	3

Genus *Strongylopus* Tschudi, 1838

Rana Linnaeus, 1758, *Syst. Nat.*, ed. 10, p. 210. Type species by subsequent designation of Fitzinger, 1843: *Rana temporaria* Linnaeus, 1758.

Strongylopus Tschudi, 1838:38. Type species yet to be designated (Dubois 1981:250).

CHARACTERS

ADULT LARYNX (Table 9; Pls. 36 & 37)

Discussion is restricted to the male larynx only. Sexual dimorphism is not marked, being expressed principally in the absence of the lateral vocal cord and of the frenulum in females (cf. *Strongylopus wageri* male and female larynxes, Pl. 36, figs. 2 & 3). The adult of Sp. A (Lambiris 1987, 1989a) is unknown.

Shape of the arytenoid cartilage

The external margin of the occlusal surface is bilobed to a greater or lesser extent, according to the size of the prominentiae apicales. They are smallest in *Strongylopus wageri* and *S. hymenopus*; intermediate in *S. g. grayii*; and largest in *S. f. fasciatus*, where they are strongly ridged.

The internal occlusal margin is V-shaped in *Strongylopus hymenopus* only. It is striated inferiorly in *S. hymenopus* and in *S. f. fasciatus*.

The arytenoid shelf is slightly striated near the inferior insertion of the medial vocal cord in *S. g. grayii*, and elaborately striated superiorly and inferiorly in *S. f. fasciatus*.

The arytenoid fossa is narrow in *S. f. fasciatus*, broadly oval in the other taxa examined.

Vocal cords

The **medial vocal cord** is robust. It is relatively narrow medially only in *Strongylopus g. grayii* and *S. f. fasciatus*, in which two species weak buttresses are also discernible.

The **lateral vocal cord** is massively developed in *S. g. grayii* and *S. f. fasciatus*, less so in *S. hymenopus*, and reduced to a broad

TABLE 10. Buccopharyngeal characters: *Strongylopus*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

* = extralimital taxon included for comparison

	PRENARIAL ARENA HAS NUMEROUS LARGE PUSTULATIONS SYMMETRICALLY ARRANGED	ANTERIOR SURFACE OF PRENARIAL PAPILLAE PUSTULOSE	HEIGHT OF MEDIAN RIDGE EQUAL TO, OR GREATER THAN, LENGTH OF BASE	MEDIAN RIDGE HAS TWO APICAL PROJECTIONS	A ROW OF PUSTULATIONS ON, OR CLOSE TO, BASE OF MEDIAN RIDGE	GLANDULAR RIDGE A BROAD CONTINUOUS BAND	INFRALABIAL ARENA HAS MASSIVE PALPOID LATERAL PAPILLAE	MORE THAN ONE PAIR OF LINGUAL PAPILLAE PRESENT	BUCCAL FLOOR ARENA PAPILLAE DO NOT IRREGULARLY ENCROACH UPON THE ARENA	PUSTULATIONS COVER THE BUCCAL FLOOR ARENA	BUCCAL FLOOR ARENA COVERS HALF OR MORE OF THE AREA BETWEEN THE LINGUAL ZONE AND THE VENTRAL VELUM	VENTRAL VELUM SLIGHTLY CONSTRICTED MESIALLY	APPENDAGES OF VENTRAL VELUM SHORT AND STUBBY
Strongylopus hymenopus	1	3	1	1	3	3	1	3	1	2	1	3	1
wageri	3	3	3	3	3	3	1	3	1	1	3	1	1
grayii grayii	3	1	1	3	3	3	3	1	3	1	1	3	3
fasciatus fasciatus	1	3	3	3	1	1	1	3	3	3	1	1	3
sp. A*	3	1	3	1	1	3	3	3	1	3	1	1	1

frenulum confluent with the lateral wall of the posterior chamber, in *S. wageri*.

Pulvinaria vocalia

These are well developed in all species examined, but do not appear to show features of diagnostic value.

Posterior chamber

Does not appear to possess features of diagnostic value.

M. hyoglossus

The m. hyoglossus originates anterior to the inferior pulvinarium vocale in all the taxa examined. It does not appear to show any diagnostically useful features.

LARVAL BUCCOPHARYNX (Table 10; Pls. 38 - 40)

Prenarial arena

Large and deep, with no (*Strongylopus g. grayii*), a few (*S. wageri*, Sp. A) or numerous large pustules (*S. hymenopus, S. f. fasciatus*). In Sp. A there is a median fossa just anterior to the internarial space.

Narial valve

The slight differences in narial valve structure appear to be of limited diagnostic value. All but Sp. A have a short conical medial papilla on the anterior valve.

Postnarial papillae

Smooth and subconical in *Strongylolpus hymenopus, S. wageri* and *S. f. fasciatus*, more robust and serrated on the anterior surface in *S. g. grayii* and Sp. A.

Lateral ridge papillae

Massive palpoid structures, with two or three digitations arising from a broad fleshy base. In *Stronglylopus f. fasciatus* and in Sp. A they are pustulate on the anterior surfaces; in *fasciatus* they tend to bifurcate down to, or almost down to, the base.

Median ridge

There is considerable interspecific variation in the median ridge. It is merely two confluent short, rounded papillae in *Strongylopus wageri*; a small low triangular ridge with two paramedian papillae in Sp. A; somewhat taller and with two or three apical papillae in *S. hymenopus* and *S. f. fasciatus* respectively, and largest in *S. g. grayii*. There appears to be a loose correlation between an increase in the size of the median ridge with an increase in number of buccal roof arena papillae.

Dorsal velum

Only in *Strongylopus g. grayii* and *S. f. fasciatus* is the dorsal velum at all well developed and ornamented with distinct papillae on the free margin. There appear to be no other useful diagnostic characters.

Prelingual papillae

In most of the species examined there is a pair of massive, palpoid papillae rising from the lateral walls. In Sp. A they are considerably diminished in size, and in *Strongylopus g. grayii* they are reduced to two or three small conical papillae on either side.

Lingual papillae

There is a single pair of lingual papillae in most of the taxa examined; in *Strongylopus g. grayii* there are six, arranged in a close-set transverse row.

Buccal floor arena

The arena is large, covering more than two-thirds of the floor, in *Strongylopus hymenopus* and Sp. A; in the other taxa it covers only half to two-thirds of the floor. The arena papillae are moderately tall, smooth, subconical papillae arranged in rather irregular rows; there are no clear-cut interspecific differences in their arrangement. Pustulations are generally numerous and wide-spread, but are few and localised in *S. f. fasciatus* and in Sp. A.

Buccal pockets

The pockets are large and closed. They do not appear to show any distinctive features of diagnostic value. Prepocket papillae are present only in *Strongylopus hymenopus* and *S. f. fasciatus*.

Ventral velum

There are distinct interpsecific differences in velum morphology, particularly pertaining to the shape and disposition of the supporting spicules and the marginal appendages. These differences cannot be concisely described, and are best appreciated by consulting the plates directly.

SPECIES ACCOUNT

Strongylopus hymenopus (Boulenger, 1920)

Rana hymenopus Boulenger, 1920, *Ann, Mag, Nat, Hist,*, 9:106. Type locality: South Africa. Holotype in the British Museum (Natural History), London. Poynton 1964:118, fig. 60, Passmore & Carruthers 1979:144, figs.

Strongylopus hymenopus (Boulenger); Van Dijk 1966:259, Channing 1979:797, figs. Lambiris 1987:455, figs. 1-9; 1988:38, figs., pl. 4 figs. 5a & b; 1989a:96.

ADULT LARYNX (Pl. 36, fig. 1)

Material examined: SOUTH AFRICA: NATAL - NM 6001 (m, SVL 50,0 mm), Royal Natal National Park. NM 651 (m, SVL 47,9 mm), Cathkin Peak (5800 ft.). NM 6227 (m, SVL 51,0 mm), Sani Pass, 7400 ft. NM 271 (f, SVL 46,5 mm), Royal Natal National Park.

Advertisement call: Description from Passmore & Carruthers, 1979:144:

"A rapid chattering of eight or nine notes interspersed with long pauses."

The sonagram figured by Passmore & Carruthers (op. cit.) shows part of a call, with two notes at about 1 kHz, approximately 0.1 second apart, over a very low (below 0.3 kHz) continuous, somewhat trilled, tone.

Male larynx:

Pharyngeal mucosa: The mucosa and submucosa form a deep layer over the dorsum of the arytenoid cartilage, blending into it anterodorsally.

Arytenoid cartilage: Prominentiae apicales rather small. The inferior half of the occlusal surface is longitudinally striated. The internal occlusal margin is V-shaped. The arytenoid shelf is broad (axial width twice that of occlusal surface) and moderately shallow. The arytenoid fossa is a broad oval, the minor axis equal to the width of the arytenoid shelf.

Vocal cords: The **medial cord** is broad, slightly flared at the insertions, and devoid of marginal flanges or buttresses. The **lateral cord** is well developed, somewhat arched apically, and is linked to the medial cord by a narrow frenulum.

LARVAL BUCCOPHARYNX (Table 10; Pl. 38, fig. 1a & b)

Identification of larvae: Lambiris 1987, and a series (AJL 2331 - 2340, stages 36 - 46) showing the diagnostic markings and webbing of adults; from the Tugela River, 700 m NE of Crow's Nest Peak, Natal Drakensberg Mts.; collected 14 June 1985.

Material examined: SOUTH AFRICA; NATAL - AJL 2332; loc. cit. supra; stage 39, SVL 19,2 mm; silver impregnation.

Larval habitat: Shallow rocky or stony-bottomed streams, devoid of aquatic macrophytes, in alpine grassland; under ice about 12 - 15 mm thick. The gut contains small filamentous algae.

Buccopharyngeal roof

General shape: Roughly trapezoid, the base about 1.2x the height. The prenarial arena is deeply excavate, and the buccal roof is regularly concave.

Prenarial arena: Large rounded pustules or short stubby papillae, more or less confluent, form an irregular arch across the middle of the arena.

Internal nares: Narrow transverse ellipses, about 0.33x the width of the roof at that level. Internarial distance equal to narial width.

Narial valve: A flap of moderate height on either narial border. The anterior flap bears a short conical medial papilla. The posterior margin is somewhat incised.

Postnarial arena: A simple subconical **postnarial papilla** (height subequal to narial width) rises from immediately behind the medial half of either naris. The **lateral ridge papilla** is a massive bilobed palp. The **median ridge** is a moderately high triangle (height about 0.6x width of base), surmounted by a pair of short paramedian papillae; its free margin is otherwise regular.

Buccal roof arena: Width about 0.5x that of the roof. It is demarcated laterally by a single row of 4 (left) or 3 (right) equally-spaced smooth, subconical papillae slightly shorter than the postnarial papillae. There are about 18 small pustulations evenly scattered over the arena.

Additional papillae: Present on the extreme lateral limits of the roof, opposite the arena. A few pustulose papillae are also present on the extreme lateral limits of the glandular ridge.

Glandular ridge: A more or less continuous, rather poorly defined, ridge about midway between the buccal roof arena and the dorsal velum.

Dorsal velum: A barely distinguishable fold on the anterior border of each pressure cushion.

Pressure cushions: Somewhat damaged in this preparation.

Buccopharyngeal floor

General shape: Bluntly triangular; base about 1.2x height. Prelingual arena moderately excavate; buccal floor regularly concave.

Prelingual papillae: A massive palp arising from the posterolateral wall on either side.

Lingual papillae: A pair of close-set tall, smooth subconical papillae arising from about the mid-dorsal surface of the tongue anlage.

Buccal floor arena: Massive, covering about four-fifths of the buccal floor, and bounded by smooth subconical papillae set in an irregular double (left) or single (right) row laterally, and in about three rows posteriorly. The papillae are irregular in size, tending to be smaller anteriorly. The arena is covered with numerous evenly-scattered minute pustulations.

Buccal pockets: Large, broadly oval and closed, but with deeply incised anterior borders. Five rather stubby prepocket papillae are flanked medially by two much taller ones.

Other pustulations: A triangular group of about 10 pustules on the midline of the ventral velum.

Ventral velum: Broad, subequal in width throughout; with a thickened posterior margin bearing short papillate projections, rather irregular in size, shape and disposition. 2 (left) and 3 (right) supporting spicules are present.

Branchial baskets: Rather rounded; about one-quarter the total buccopharyngeal area.

Filter plates: Details are not clearly discernible in this preparation. They are partly closed, with narrow channels.

Strongylopus wageri (Wager, 1961)

Rana wageri Wager, 1961, *Afr. Wild Life*, 15:151, figs. No type locality or type specimen designated. Poynton 1963:329. Type locality by subsequent designation of Poynton: "Weza Forest Reserve, southern border of Natal, at about 5500 ft (1680 m)". Holotype and five paratypes, by subsequent designation of Poynton 1963:329, in the Natal Museum, Pietermaritzburg. Poynton 1964:112, fig. 56. Channing 1979:797. Passmore & Carruthers 1979:136, figs. Lambiris 1987:457; 1988:33, figs., pl. 4 figs. 2a-c; 1989a:97.

ADULT LARYNX (Table 9; Pl. 36, figs. 2 & 3)

Material examined: SOUTH AFRICA: NATAL - NM 5968 (m, SVL 38,9 mm), Weza Forest, NM 6410 (m, SVL 38,5 mm), Lundy's Hill, NM 2672 (f, SVL ==), NM 6408 (f, SVL 38,2 mm), NM 7348 (f, SVL 48,5 mm), NM 7352 (f, SVL 53,0 mm), Entumeni Nature Reserve.

Advertisement call: Four or five rapidly repeated tapping notes between about 1 and 2.2 kHz, uttered over about 0.5 second (Passmore & Carruthers 1979:136); at irregular intervals, from semi-concealed positions at the edges of streams, or even when partly submerged. There is a loose choral structure.

Male larynx:

Pharyngeal mucosa: Thin and smooth, with a deeper submucosa overlying the dorsum of the arytenoid cartilage, and tending to blend with it.

Arytenoid cartilage: Occlusal surface rather broad; the profile of the external border is rather squared-off by the somewhat triangular prominentiae. The arytenoid shelf is broad (axial width 1.5x that of occlusal surface) and shallow. The arytenoid fossa is broadly oval, as wide as the arytenoid shelf.

Vocal cords: The **medial cord** is very broad; the anterior margins of the insertions are widely flared. Neither margin is flanged, and there are no supporting buttresses. The frenulum is massive, extending posterad and confluent with the lateral wall of the posterior chamber. The **lateral cord** is absent.

LARVAL BUCCOPHARYNX (Table 10; Pl. 38, fig. 2a & b)

Identification of larvae: Lambiris 1987, and a series (AJL 2319 - 2329, stages 25 - 42/43) showing markings and webbing diagnostic of

post-metamorphics from stage 42; from the Bushmans River, alt. 1700 m, Giant's Castle Game Reserve, Natal; collected June 1985.

Material examined: SOUTH AFRICA: NATAL - AJL 2321, stage 37, SVL 13,1 mm, and AJL 2322, stage 38, SVL 13,3 mm; loc. cit. supra; silver impregnation.

Larval habitat: Cool to cold narrow, gently-flowing channels and small streams, or quiet, shallow backwaters of larger rivers; with sandy or stony beds and little silt. Aquatic macrophytes absent or minimal, but small algae (generally non-filamentous) algae are present.

Buccopharyngeal roof

General shape: Bluntly triangular; base about 1.1x height. General surface concave medially, but flattening out posterolaterally; prenarial arena rather deep.

Prenarial arena: Trapezoid, base about 2.3x height. One or two pustules present in the middle of the arena.

Internal nares: Narrowly elliptical; transverse to slightly oblique anteromedially. Width of naris about 0.3x width of roof at that level; internarial distance equal to narial width.

Narial valve: A well-developed flap on both margins. The anterior flap bear a small triangular medial projection.

Postnarial arena: A large (0.6 - 1.0x narial width), smooth, subconical **postnarial papilla** arises behind the medial half of either naris; there is a much shorter (almost pustulose) papilla at its base, set lateral to it. The **lateral ridge papilla** is a massive, trifurcate palp. The **median ridge** is reduced to two large, confluent pustules.

Buccal roof arena: Demarcated on either side by a row (converging posteriorly) of 3 - 5 regularly-spaced smooth cylindrical papillae, diminishing markedly in size posteriorly (where they are about half the height of the anteriormost papilla). The arena contans about 10 tiny pustules scattered evenly over the surface.

Additional papillae are present on the lateral walls of the buccal roof.

Glandular ridge: Weakly developed, broadly interrupted medially, and with a row of pustules along either ridge.

Dorsal velum: A barely distinguishable fold on the anterior border of each pressure cushion.

Pressure cushions: Broad, triangular, and with a coarse ridge along the major axis.

Buccopharyngeal floor

General shape: Roughly triangular; base about 1.3x the height. Surface regularly concave, with a deep prelingual arena.

Prelingual papillae: A robust, rather large cylindrical papilla arising from either mid-lateral wall, immediately anterior to a large pustulate quadrifid palp.

Lingual papillae: A pair of long, cylindrical paramedian papillae arising on the anterodorsal surface of the tongue anlage.

Buccal floor arena: Wide, extending laterally to the buccal pockets; but not deep, occupying only the posterior half of the buccal roof. It is bordered posterolaterally by 3 irregular rows of close-set subequal, cylindrical papillae (some slightly clavate terminally). A few tiny pustules are scattered over the arena floor and beyond it, towards the lingual arena; a few anterior to the buccal pockets are larger.

Additional pustulations are present on the anteromedial border of the ventral velum.

Ventral velum: Moderately broad, but narrowed latarally and slightly constricted medially. The slightly thickened free margin bears four broad, stubby projections (increasing in size medially) on either side of a close-set group composed of a short, broad paramedial pair of lobes flanked on either side by one or two smaller, more triangular projections. There are three equally-spaced supporting spicules on either side of the midline.

Branchial baskets: Large, about 0.4 of the buccopharyngeal area.

Filter plates: Strongly arched, almost closed. The filter rows bear secondary and tertiary folds, and the channels are narrow.

Strongylopus grayii grayii (A. Smith, 1849)

Rana grayii A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, pl. 78 fig. 2, 2a-c. Type locality: "western districts of the Cape Colony". Holotype in the British Museum (Natural History), London.

Rana grayi grayi Smith: Poynton 1964:113, fig. 57.

Strongylopus grayi (Smith): Van Dijk 1966:259.

Rana grayii Smith: Passmore & Carruthers 1979:138, figs.

Strongylopus grayii grayii (Smith): Channing 1979:797. Lambiris 1987:457; 1988:35, figs., pl. 4 figs. 3a-c; 1989a:99.

ADULT LARYNX (Table 9; Pl. 37, fig. 1)

Material examined: SOUTH AFRICA: NATAL - NM 2645 (m, SVL 36 mm), World's View, Pietermaritzburg. NM 6203 (m, SVL 38,0 mm), Solitude, nr. Loskop, Drakensberg. NM 986 (f, SVL 40 mm), Qudeni Forest. EASTERN CAPE - AJL 576 (m, SVL 33,5 mm), Hogsback Forest. LESOTHO: AJL 2817 (f, SVL 40,0 mm), Sehlabathebe National Park.

Advertisement call: A dull, regular tapping about 0.01 second long, at about 2 kHz (Passmore & Carruthers 1979:138), uttered about once a second (the actual rate varying with the number of males calling), while concealed in vegetation at the water's edge (sometimes exposed). Calling is at night or on overcast days. There is a strong choral structure.

Male larynx:

Pharyngeal mucosa: Thin, covering only the posterior portion of the dorsum of the arytenoid cartilage.

Arytenoid cartilage: Superior pulvinarium vocale a triangular lobe; inferior pulvinarium more prominent, more rounded, and with a strongly fimbriated anterior margin. The arytenoid shelf is broad (axial width about 1.8x that of the occlusal surface), and striated on the inferior apex. The arytenoid fossa is broadly elliptical, about 0.6x the width of the arytenoid shelf.

Vocal cords: The moderately broad **medial cord** is widely flared at the insertions, which have rather weak, styliform buttresses a little anterior to the posterior margins. There is no frenulum. The **lateral cord** is massive, somewhat convoluted superiorly, and has a vertical ridge on the medial surface.

LARVAL BUCCOPHARYNX (Table 10; Pl. 39, fig. 1a & b)

Identification of larvae: Lambiris 1987. Series reared from eggs laid by identified adults.

Material examined: SOUTH AFRICA: NATAL - AJL 3510a, stage 36, SVL 15,7 mm; AJL 3510b, stage 36, SVL 15,0 mm; AJL 3510c, stage 36, SVL 16,1 mm; all from 2,7 km ESE of Hilton; silver impregnation.

Larval habitat: Any quiet, shallow body of water with gently sloping wet banks covered with vegetation.

Buccopharyngeal roof

General shape: Bluntly triangular; base about equal to height. Roof convex medially, with inflected walls laterally. Prenarial arena broad and deeply excavate.

Prenarial arena: Paraboloid. Devoid of papillae, pustules or other ornamentation.

Internal nares: Narrowly elliptical, set transversely. Width of naris about 0.4x width of roof at that level; internarial distance about 0.7x narial width.

Narial valve: A well-developed flap on both margins. The anterior flap bears a small median papilla; in AJL 3510a (Pl. 39, fig. 1a) there is a posterior medial papilla on the right naris.

Postnarial arena: A massive (about 1.3x narial length) postnarial papilla, pustulate on the anterior surface, arises well behind each naris, at the level of (but dorsal to) the lateral ridge papillae; these latter are large, smooth, trifid palps. The median ridge is tall and triangular (base equal to height and to narial width), slightly serrated apically.

Buccal roof arena: Demarcated on either side by a row of 4 - 6 tall, smooth, subconical papillae, largest anteriorly, and somewhat convergent posteriorly; interpersed irregularly with short stubby papillae. The arena has about 20 small pustules evenly scattered over its surface.

Additional papillae: A pair of short cylindrical papillae on the dorsolateral walls of the buccal roof, level with the anterior boundary of the buccal roof arena.

Glandular ridge: A short pustulate ridge between each half of the dorsal velum and the buccal roof arena.

Dorsal velum: Well developed, but interrupted medially, and with 3 - 6 fleshy projections on the medial half of each velum.

Pressure cushions: Large, flat structures with several large folds on the ventral surface.

Buccopharyngeal floor

General shape: Bluntly triangular; height about 1.2x height. Surface concave, with a small, deeply excavate prelingual arena.

Prelingual papillae: Two or three small cylindrical or subconical papillae arising from the posterolateral wall of the arena. There is a tiny shallow median fossa on the floor of the arena.

Lingual papillae: Four very close-set paramedian cylindrical papillae are flanked on either side by a more robust conical papilla, all arising from the anterodorsal surface of the tongue anlage.

Buccal floor arena: Roughly semicircular, occupying about 0.6 of the buccal floor. Bounded laterally and posteriorly by smooth, subequal, subconical papillae set in two or three irregular rows. Pustules are scattered over the arena floor, and anteriorly to the lingual arena.

Additional pustulations: A single row of evenly spaced pusulations are arranged along the anterior border of the ventral velum, and 3 - 4 along its mid-line. A few pustules also occur in the prepocket area.

Buccal pockets: Narrowly oval, rather deep-set, and deeply incised anteriorly. There are no prepocket papillae.

Ventral velum: Rather broad, and slightly deeper medially than laterally. The thickened posterior margin bears three large fleshy papillae (the inner two more closely-spaced), flanking 5 - 6 smaller fleshy lobes on the middle third of the velum.

Branchial chambers: Roughly triangular, and occupying about one quarter of the buccopharyngeal area.

Filter plates: Arched, semi-closed. Filter rows with secondary and tertiary folds, and narrow channels.

Strongylopus fasciatus fasciatus (A. Smith, 1849)

Rana fasciata A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, pl. 78 fig. 1a-c. Type locality: "Africa" [i.e. southern Africa, probably the southern Cape -- Lambiris 1989a:101].

Rana fasciata fasciata Smith: Poynton 1964:115, fig. 58.

Strongylopus fasciatus (Smith): Van Dijk 1966:259, Channing 1979:797.

Strongylopus fasciatus fasciatus (Smith): Poynton & Broadley 1985b: 137, Lambiris 1987:456; 1988:36, figs., pl 4 figs. 4a, b; 1989a:100; 1989b:98, figs. 49 & 50, pl. 8 figs. 2a-c.

ADULT LARYNX (Table 9; Pl. 37, fig. 2)

Material examined: SOUTH AFRICA; NATAL - NM 6444 (m, SVL 36,5 mm), Cathkin Peak Forest Reserve, NM 6466 (m, SVL 33,5 mm), Vernon Crookes Nature Reserve, EASTERN CAPE - AJL 353 (m, SVL 35,2 mm), and AJL 354 (f, SVL 42,0 mm), Port Alfred.

Advertisement call: Three or four sharp chirps about 0.03 second long, at about 3 kHz, uttered in rapid succession, with short pauses between each series; from thick grass at, or just in, the water's edge. Calls are made both at night and by day.

Male larynx

Pharyngeal mucosa: Thin, but slightly rugose, over a deeper submucosa covering the dorsum of the arytenoid cartilage.

Arytenoid cartilage: Prominentiae apicales rounded and boldly flared, the superior prominentia much larger than the inferior, and both strongly ridged. The internal occlusal margin is slightly flexed apically, and bears strongly striated posterior expansions on both the superior and the inferior apices. The arytenoid shelf is broad (axial width about twice that of the occlusal surface). The arytenoid fossa is a rather constricted ellipse about 0.2x the width of the arytenoid shelf.

Vocal cords: The moderately broad **medial vocal cord** is widely flared at the insertions. The superior insertion has a weak styliform premarginal posterior buttress; the inferior insertion has a weak marginal posterior and more robust postmarginal anterior buttress. The posterior margin of the cord is slightly thickened. There is no frenulum. The **lateral cord** is well developed, but only about 0.75x the length of the lateral cord, and has a thickened posterior margin.

LARVAL BUCCOPHARYNX (Table 10; Pl. 39, fig. 2a & b)

Identification of larvae: Lambiris 1987.

Material examined: ZIMBABWE: AJL 1793, stage 34, SVL 14.1 mm, Rhodes Dam, Nyanga National Park; silver impregnation.

Larval habitat: Shallow streams, pans or dams with emergent grasses, and lightly silted rock, sand or clay substrata.

Buccopharyngeal roof

General shape: Bluntly triangular; base about 1.2x height. Prenarial arena rather deeply excavate; buccal roof concave medially.

Prenarial arena: Slightly trapezoid; base about equal to height. A posteriorly-curved ridge immediately behind the root of the beak is followed by two rather irregular rows, each interrupted medially, of large confluent pustules.

Internal nares: Narrow oblique slits, directed slightly posteriorly medially. Width of naris about 0.35x the width of the roof at that level; internarial distance about 0.85x the narial width.

Narial valve: A low flap on either margin, the anterior flap bearing a small cylindrical median papilla.

Postnarial arena: A long (about equal to narial width), smooth, subconical postnarial papilla arises behind the medial margin of either naris. It is flanked laterally and slightly posterad by a large, bifurcate palpoid lateral ridge papilla, with pustulations on the anterior surfaces of each lobe (completely separate, with an intercalary papilla, on the right side). The median ridge is a triangular flap (base about 1.25x narial width) with three pustules on an apical pedicel, and a row of five equally-spaced pustules along the base.

Buccal roof arena: A small oval bounded laterally by four subequally spaced papillae of unequal height (two supernumary papillae just outside the arena on the left side). The numerous tiny arena pustules spread anteriorly towards the median ridge, and posteriorly to the anteromedian border of the velum.

Additional papillae: A pair of small papillae is present on the lateral walls of the buccal roof, opposite the arena, on either side.

Glandular ridge: A broad continuous pustulate band following the anterior margin of the dorsal velum.

Dorsal velum: Low and shortly interrupted medially, but well-developed and bearing four rather long papillae on each medial half of the velum.

Pressure cushions: Large, and bearing a pair of pulvinate folds on the ventral surface.

Buccopharyngeal floor

General shape: Triangular, the base about 1.3x the height. The prelingual arena is deeply excavate. The buccal floor is concave, with a shallow triangular retrolingual fossa.

Prelingual papillae: A large palp with five lobes carried on a fleshy base, arising posterolaterally.

Lingual papillae: A pair of tall, smooth cylindrical paramedian papillae arising from the anterodorsal surface of the tongue anlage.

Buccal floor arena: Semicircular, occupying about 0.6 of the buccal floor. It is bounded laterally and posteriorly by 27 irregularly-disposed smooth, sub-cylindrical papillae, which are largest anteriorly. About 12 small pustules are set in a group posteromedially.

Buccal pockets: Broadly oval, closed. 4 (left) or 3 (right) small prepocket papillae are present, interspersed with a few pustules.

Ventral velum: Rather broad, but constricted medially. The thickened posterior margin bears 5 (left) or 7 (right) papilliform lobes, smallest laterally, on either side of a similar pair of paramedian lobes. There are six supporting spicules, the outer one on either side on the posterior border of the buccal pocket.

Branchial chambers: Large and rather rounded.

Filter plates: Strongly arched and semi-closed. The filter rows and the channels are narrow.

Strongylopus sp. A

Rana hymenopus (non Boulenger, 1920): Wager 1986:170, fig. (part).
Strongylopus sp. A: Lambiris 1989a:101, figs. 16 & 17.

ADULT LARYNX

The adult is unknown.

LARVAL BUCCOPHARYNX (Table 10; Pl. 40, figs. 1a & b)

Identification of larvae: Lambiris 1989.

Material examined: LESOTHO : NM 6005, stage 36, SVL 15,6 mm, "Basutoland," [= Lesotho - no precise locality recorded,] Silver impregnation.

Buccopharyngeal roof

General shape: Bluntly triangular. Base about equal to height. Prenarial arena deeply excavate; roof gently concave.

Prenarial arena: A pair of paramedian pustules in the anterior quarter of the roof. A small pustulate papilla arises from the midlateral wall on either side. There is a relatively large fossa just anterior to the internarial space.

Internal nares: Narrow oblique slits, directed slightly posteriorly medially. Width of naris about 0.33x width of roof at that level; internarial distance equal to narial width.

Narial valve: A well-developed flap on both borders. The anterior flap bears three pustules on the medial half.

Postnarial arena: A large (height equal to narial width) conical **postnarial papilla**, pustulate on the anterior surface, arises a short distance behind the middle of each naris; it has a much smaller (less than half its height) smooth conical papilla at (right) or lateral to (left) its base. The **lateral ridge papilla** is a moderately large bifid palp, each lobe slightly pustulate on the anterior surface. A small conical papilla lies anteroventral to its base. The **median ridge** is a low flap (base 1.66x narial width), with a pair of small paramedian papillae apically.

Buccal roof arena: Small, ovoid, and bounded posterolaterally by a row of three widely-spaced cylindrical papillae, slightly smaller

posteriorly, between or just outside which are two or three smaller papillae on either side. The arena is covered with numerous evenly-scattered papillae which extend just beyond the boundaries of the arena.

Additional papillae: Four (left) or two (right) pustulose papillae on the lateral walls of the roof, opposite the buccal roof arena.

Glandular ridge: Feebly developed, extending transversely just behind the buccal roof arena.

Dorsal velum: Moderately well developed, with a short medial interruption. Three tiny lobes are present on the extreme medial portion of each half of the velum.

Pressure cushions: Large, but lacking obvious features.

Buccopharyngeal floor

General shape: Triangular, the base about 1.2x the height. The prelingual arena is narrow and deep. The buccal floor is gently concave, with a short retrolingual ridge not extending into the buccal floor arena.

Prelingual papillae: A small pustulate cylindrical papilla arises from the midlateral wall on either side. Immediately behind it is a relatively small pustulate palpoid papilla.

Lingual papillae: A pair of small cylindrical paramedian papillae arise from the anterodorsal border of the tongue anlage.

Buccal floor arena: Massive, occupying almost the whole area between the lingual arena and the ventral velum. It is bounded laterally by a zone of irregularly-disposed subconical papillae of unequal height (tending to be smaller anteriorly). Pustules are restricted to a circular patch on the posteromedial border of the arena; a few encroach upon the velum medially.

Buccal pockets: Relatively small, oval, closed; the anterior border is deeply incised.

Ventral velum: Rather broad, of subequal width throughout. The base is irregularly thickened, with broad, posteriorly-directed ridges. The posterior margin has eight papillate projections arranged asymmetrically (3 + 5) about the laterally divergent paramedian pair.

Branchial baskets: Rather rounded.

Filter plates: Details are not very clear in this preparation.

DISCUSSION

Adult laryngeal and larval buccopharyngeal characters of the taxa examined accord well with the species currently recognised in this genus.

Small differences in the calls of grassland and forest populations of *Strongylopus g. grayii* have been noted (Poynton, cited in Passmore & Carruthers 1979:138; and personal observations in Natal and the Eastern Cape), and the various colour morphs also require clarification (Jacobsen, *in* Branch *et al.* 1988:3).

No significant differences could be found in larynxes of either sex from specimens taken in forest (Qudeni Forest, Hogsback) or in grassland (World's View, Sehlabathebe, Loskop), in the present investigation. However, a much more extensive study involving larger series from both habitat types, and representing all colour morphs, is required before the significance of the slight differences in calls can be assessed properly. Such an undertaking was considered to be beyond the scope and aims of the present study.

The tadpoles identified by Wager (1965, 1986) as *Strongylopus hymenopus* were shown by Lambiris (1987, 1989a) to be taxonomically composite. Some were indeed tadpoles of *S. hymenopus*, but others (Sp. A) did not appear to be referable to any known southern African member of the genus. Most of the tadpoles are in poor condition and unsuitable for dissection, but buccopharyngeal morphology of one of the few specimens in reasonable condition tends to confirm the suggestion that they represent an undescribed species. There are, unfortunately, no accurate locality records for these specimens and so far no live tadpoles have been found for rearing through to adults.

PLATE 36

STRONGYLOPUS — ADULT HYOLARYNXES

Median sagittal section. View into left half. Anterior to right.

FIG. 1: *Strongylopus hymenopus* (Boulenger, 1920)
NM 6001 (male), Royal Natal National Park, Natal, South Africa.

FIG. 2: *Strongylopus wageri* (Wager, 1961).
NM 5968 (male), Weza Forest, Natal, South Africa.

FIG. 3: *Strongylopus wageri* (Wager, 1961).
NM 7352 (female), Entumeni Nature Reserve, Natal, South Africa.

PLATE 37
STRONGYLOPUS – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right,

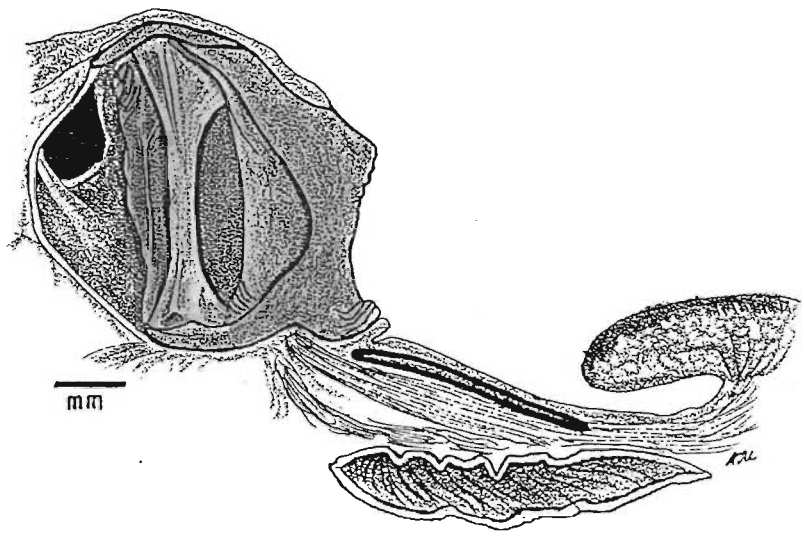


FIG. 1: *Strongylopus grayii grayii* (A. Smith, 1849)
AJL 567 (male), Hogsback Forest, Eastern Cape, South Africa.

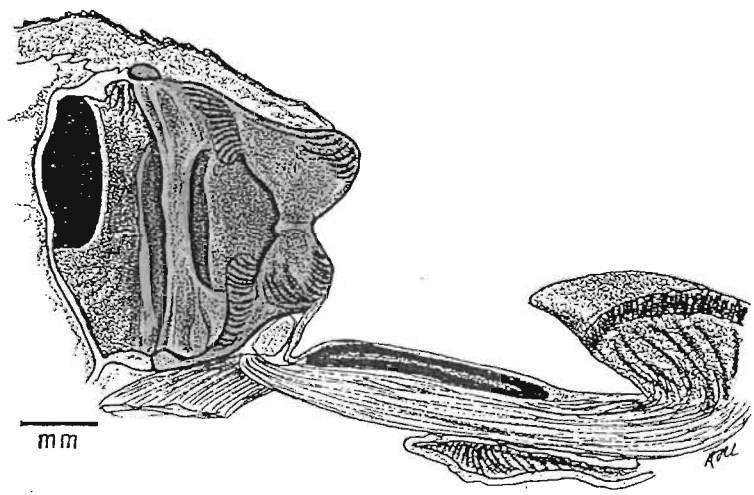


FIG. 2: *Strongylopus fasciatus fasciatus* (A. Smith, 1849)
AJL 353 (male), Port Alfred, Eastern Cape, South Africa.

PLATE 38
STRONGYLOPUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

FIG. 1: *Strongylopus hymenopus* (Boulenger, 1920)
AJL 2332, Stage 39, Tugela River, 700 m NE of Crow's Nest, Drakensberg Mountains, Natal, South Africa.

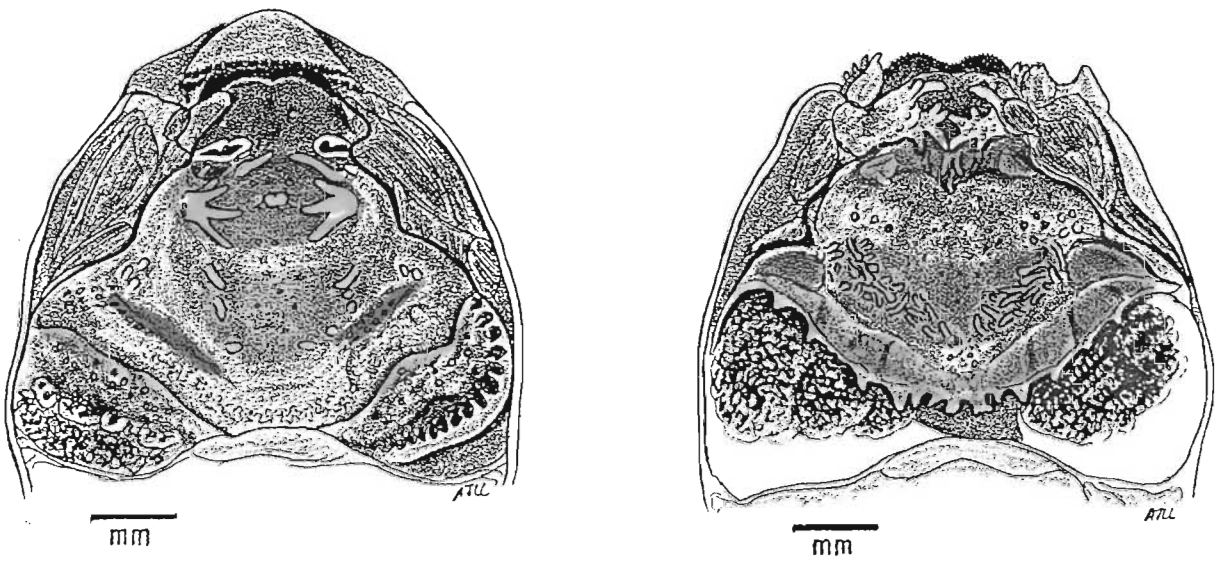


FIG. 2: *Strongylopus wageri* (Wager, 1961)
AJL 2321, Stage 37, Giant's Castle Game Reserve, Natal, South Africa.

PLATE 39
STRONGYLOPUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

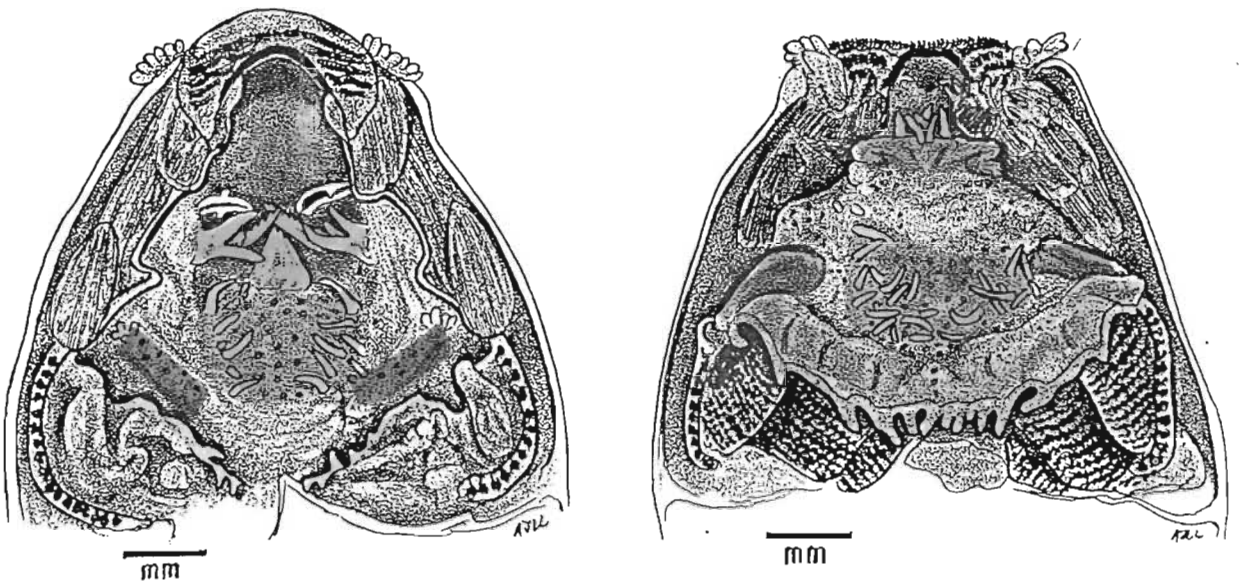


FIG. 1: *Strongylopus grayii grayii* (A. Smith, 1846)
AJL 3510a, Stage 36, 2,7 km ESE of Hilton, Natal, South Africa.

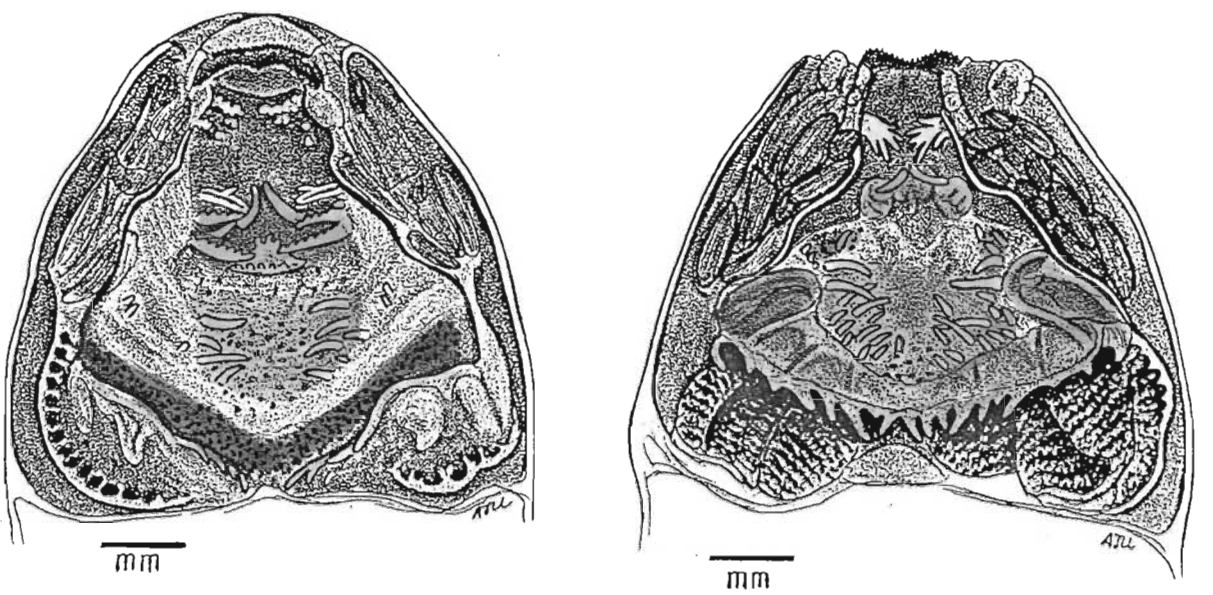


FIG. 2: *Strongylopus fasciatus fasciatus* (A. Smith, 1849)
AJL 1793, Stage 34, Inyanga, Zimbabwe.

PLATE 40
STRONGYLOPUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

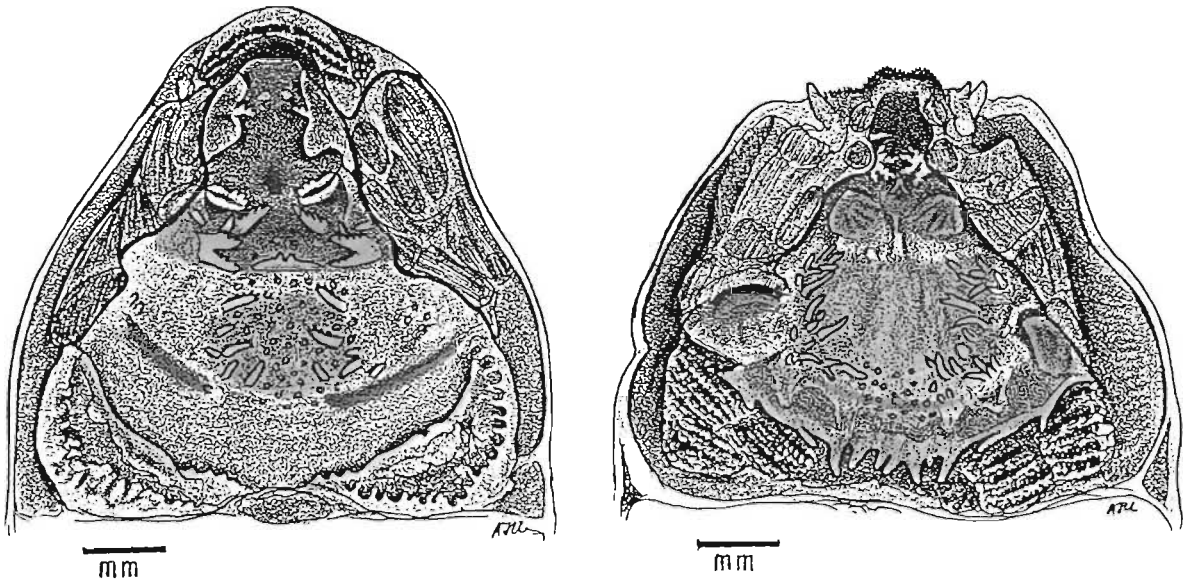


FIG. 1: *Strongylopus* sp. A
NM 6005, Stage 36, "Basutoland" [= Lesotho].

TABLE 11. Laryngeal characters:
Phrynobatrachus

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	SUPERIOR EXTERNAL MARGIN OF ARYTENOID CARTILAGE RUGOSE	INTERNAL MARGIN OF ARYTENOID CARTILAGE V-SHAPED	MAJOR AXIS OF ARYTENOID FOSSA EQUAL TO LENGTH OF ANTERIOR BORDER OF VOCAL CORD	BOTH BORDERS OF MEDIAL VOCAL CORD DISTINCTLY FLANGED	VOCAL CORD FLANGES ROBUST	A WELL-DEVELOPED FRENULUM PRESENT	A DISTINCT LATERAL VOCAL CORD PRESENT	POSTERIOR CHAMBER HAS CARTILAGINOUS SUPPORTS IN THE POSTERIOR WALL
Phrynobatrachus natalensis	3	3	3	3	4	1	1	3
acridoides	1	1	3	1	3	1	1	3
mababiensis	3	3	1	1	1	3	3	1

Subfamily PHRYNOBATRACHINAE Laurent, 1940

A new genus is provisionally recognised. It is treated after the genus *Cacosternum*, to which it appears to be closely allied.

Genus *Phrynobatrachus* Günther, 1862

Stenorhynchus A. Smith (non Hemprich), 1849, *Illus. Zool. S. Afr., Rept.*, App., p. 23. Type species by monotypy: *Stenorhynchus natalensis* A. Smith, 1849.

Phrynobatrachus Günther, 1862, *Proc. Zool. Soc. Lond.*, 1862:190. Type species by monotypy: *Phrynobatrachus natalensis* Günther, 1862.

CHARACTERS

ADULT LARYNX (Tables 11 & 13; Pl. 41)

The larynxes of *Phrynobatrachus natalensis* and *P. acridoides* show strong similarities; that of *P. mababiensis* differs notably from the other two species examined, in lacking a distinct lateral vocal cord.

Arytenoid cartilage

Interspecific differences are few. The principal ones are seen in the occlusal surface, particularly in the shape of the internal margin (more or less arcuate in *Phrynobatrachus natalensis* and *P. mababiensis*, V-shaped in *P. acridoides*); and in the rugosity of the external margin in *P. acridoides*. In *P. mababiensis* the major axis of the arytenoid fossa is equal to the length of the anterior margin of the vocal cord, but less in *P. natalensis* and *P. acridoides*. In none of the species examined is there an arytenoid valve.

Vocal cords

The **medial vocal cord** in *Phrynobatrachus natalensis* and *P. acridoides* is long and slender, and barely (*P. natalensis*) or distinctly but very narrowly (*P. acridoides*) flanged; in *P. mababiensis* the cord is much broader and both margins are strongly flanged. Discrete buttresses are discernible only in *P. acridoides*.

The lateral cord in both *P. natalensis* and *P. acridoides* is well developed and possesses a median cartilaginous projection, which shows consistent interspecific differences. It is shorter and contained in a fold of the lateral cord in *P. natalensis*, longer and not so contained in *P. acridoides*.

Posterior chamber

Phrynobatrachus natalensis seems to have a smaller pulmonary aditus than the other two species examined. The chamber itself is essentially featureless, but in *P. acridoides* cartilaginous supports are discernible around the aditus and across the ventral floor of the chamber.

M. hyoglosssus

This muscle does not seem to show any features of diagnostic value.

LARVAL BUCCOPHARYNX (Pl. 42)

Only larvae of *Phrynobatrachus natalensis* and *P. mababiensis* are described. Reliably identified tadpoles of *P. acridoides* were not available for study.

Prenarial arena

Large lateral wall palps were seen only in *Phrynobatrachus natalensis*.

Postnarial arena

Postnarial papillae are small and set well back from the internal nares in *Phrynobatrachus natalensis*, massive and strongly conical in *P. mababiensis*. Lateral ridge papillae are massive palps in *P. natalensis*, and conical flaps in *P. mababiensis*.

Buccal roof arena

In *Phrynobatrachus natalensis* the arena is bounded on either side by a row of four subconical papilla, convergent posteriorly. In *P. mababiensis* there are but two such papillae on either side, not posteriorly convergent.

Lingual papillae

There are four conical papillae in *P. natalensis*, and a single anteromedian pustule in *P. mababiensis*.

Buccal floor arena

Delimited by numerous cylindrical or subconical papillae of unequal height in *P. natalensis*, a few showing some degree of bifurcation. In *P. mababiensis* they are fewer (2 - 3 on either side) and rather bizarrely shaped.

Prepocket papillae

Small, pustulate papillae are present only in *Phrynobatrachus natalensis*.

Ventral velum

Broad in both species, but with a few small, stubby, rather irregular projections on the posterior margin only in *Phrynobatrachus natalensis*.

SPECIES ACCOUNT

Phrynobatrachus natalensis (A. Smith, 1849)

Stenorhynchus natalensis A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App., p. 23. Type locality: "the country around Natal" [i.e. Durban]. Holotype in the British Museum (Natural History), London.

Phrynobatrachus natalensis Günther, 1862, *Proc. Zool. Soc. Lond.*, 1862:190. Type locality: Port Natal [i.e., Durban].

Phrynobatrachus ranoides Boulenger, 1894, *Proc. Zool. Soc. Lond.*, 1894:644, pl. 39 fig. 2. Type locality: "near Pietermaritzburg". Holotype in the British Museum (Natural History), London.

Phrynobatrachus natalensis (A. Smith): Poynton 1964:137, fig. 74. Van Dijk 1966:272. Passmore & Carruthers 1979:167, figs. Poynton & Broadley 1985:160. Lambiris 1988:42, figs., pl. 5 figs. 2a-e; 1989a:105; 1989b:122, figs. 66 & 67, pl. 13 figs. 1a-j.

ADULT LARYNX (Table 11; Pl. 41, fig. 1)

Material examined: ZIMBABWE: AJL 1033 (f, SVL 27,5 mm), 30 km east of Chegutu. AJL 1281 (f, SVL 28,0 mm), Mgwalaati Farm, 22 km ENE of Mrewa. AJL 1205 (f, SVL 25,0 mm), 6 km NE of Gweru. SOUTH AFRICA: NATAL - AJL 2084 (m, SVL 29,0 mm), Entrance gate, Umfolozi Game Reserve. AJL 2287 (m, SVL 27,4 mm), Mazuwi, Umfolozi Game Reserve.

Advertisement call: A trilled snore about 0.5 second long, at about 2 kHz (Passmore & Carruthers, 1979:166), uttered every half-second or so, from partly concealed positions in emergent vegetation in shallow water. Calling is both at night and during the day in overcast weather. There is a well-structured choral pattern.

Male larynx:

Pharyngeal mucosa: Does not extend onto the surface of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface very broadly U-shaped on both margins, and rather narrowed apically. The superior and inferior apices of the arytenoid fossa are acuminate.

Vocal cords: The **medial vocal cord** is rather narrow, lorate, and slightly flared on the superior insertion only. The margins are not flanged. The **lateral vocal cord** is similar in shape to the medial cord, by which it is largely covered. The long, fusiform frenulum is enclosed in a narrow triangular fold of the lateral cord.

Posterior chamber: The greatest diameter of the pulmonary aditus is less than half the major axis of the posterior chamber.

LARVAL BUCCOPHARYNX (Pl. 42, fig. 1a & b)

Identification of larvae: Lambiris 1989a.

Material examined: ZIMBABWE; AJL 1882a, 1882b, both stage 30, SVL 7,5 mm; Monavale, Harare; silver impregnation.

Larval habitat: Shallow silt-bottomed ephemeral pools and pans, with short emergent grasses and sedges growing rather densely marginally and less densely centrally.

Buccopharyngeal roof

General shape: Triangular, base about 11.1x height. General surface rather regularly concave; prenarial arena trapezoid, deeply excavate.

Prenarial arena: A large median pustule in the posterior half of the arena, a little anterior to the internal nares. It is flanked on either side by a large palpoid papilla arising from the lateral walls.

Internal nares: Moderately narrow oblique slits, directed anteromedially. Width of naris about 0.65x width of roof at mid-narial level; internarial distance about 0.3x narial width.

Narial valve: A well-developed flap on both margins, but lacking ornamentation. The posterior margin is not deeply grooved.

Postnarial arena: Two conical **postnarial papillae** present on either side -- a medial one about 0.33x narial width, and a slightly smaller lateral one. There is a small median pustule between the nares and the postnarial papillae. The **lateral ridge papilla** is a massive palp with 3 - 4 digitations. The **median ridge** is a rather large equilateral triangle, the base about 0.2x the width of the roof at that level, and has somewhat lobulated margins.

Buccal roof arena: An inverted trapezoid, bounded by a row of equally spaced conical papillae, tending to increase very slightly posteriorly. The arena contains 15 - 18 regularly-arranged pustules, largest anteriorly.

Glandular ridge: A well-defined band, continuous across the roof, lying against the base of the dorsal velum.

Dorsal velum: Narrow but well-developed, with three or four short, bluntly lobulate projections on the medial quarter. The velum is narrowly interrupted medially.

Pressure cushions: Divided by an obliquely transverse ciliary groove into anterior and posterior portions.

Buccopharyngeal floor

General shape: Broadly triangular, the base about 1.3x the height. General surface moderately concave, but with a small ridged retrolingual chiasma more deeply grooved between the arms. The lingual arena is flanged by a curved ridge on either side. The prelingual arena is square and deeply excavate, with a deeper median groove.

Prelingual papillae: A long narrow cylindrical papilla arises on either side from the posterolateral wall, the length being about 0.5x the width of the arena at that level.

Lingual papillae: Four equal-sized, regularly spaced cylindrical papillae about the length of the prelingual papillae, arranged in a slightly curved transverse row.

Buccal floor arena: Roughly semicircular, bounded laterally and posteriorly by a single (but irregularly staggered) row of papillae; they are essentially tall conical, but show some tendency to bifurcate and are rather irregular in size, tending to be smaller posteriorly. The arena has 6 - 8 irregularly scattered pustules, of approximately equal size.

Buccal pockets: Rather narrow, pyriform, closed, and shallowly set. There are three small, pustulate **prepocket papillae** on either side.

Ventral velum: Rather broad, of subequal width throughout. The thickened free margin bears 7 - 8 very closely-set stubby scallops on the median third; the lateral portions bear two widely-spaced blunt papillate projections. Supporting spicules are present, but are not conspicuous.

Branchial baskets: Large and rather rounded.

Filter plates: Open. Filter rows appear to have secondary and tertiary folds, and the channels are rather narrow.

Phrynobatrachus acridoides (Cope, 1867)

Staurois acridoides Cope, 1867, *J. Acad. Nat. Sci. Philadelphia*, 6:198. Type locality: Zanzibar Island. Syntypes in the Academy of Natural Sciences, Philadelphia.

Phrynobatrachus acridoides (Cope): Poynton 1964:140, fig. 75. Passmore & Carruthers 1979:168, figs. Poynton & Broadley 1985b:158. Lambiris 1989a:106; 1989b:125, fig. 68, pl. 14 figs. 1a-c.

ADULT LARYNX (Tables 11 & 13; Pl. 42, fig. 2)

Material examined: ZANZIBAR - NM 3231 (m, SVL 24,3 mm), and NM 3232 (f, SVL 25,3 mm) - topotypes. SOUTH AFRICA: NATAL - NM 3236 (m, SVL 24,6 mm, and NM 3235 (f, SVL 23,2 mm), both from Kosi Bay, Zululand.

Advertisement call: A harsh snore (about 50 pulses per second), about 1 second long, at about 2 kHz, with weaker harmonics at about 3 kHz (Passmore & Carruthers 1979:168). Calls are uttered from among emergent grassy vegetation in shallow water, in chorus both during the day and at night.

Male larynx:

Pharyngeal mucosa: Reduced to an extremely thin layer not visible at low magnification, over the arytenoid cartilage.

Arytenoid cartilage: External margin of occlusal surface broadly U-shaped, internal margin V-shaped. The arytenoid fossa is broadly elliptical.

Vocal cords: The **medial vocal cord** is rather narrow, lorate, and slightly flanged on both margins. The posterior margin is slightly swollen (weak buttresses?) superiorly and inferiorly. The **lateral vocal cord** is rather narrow, obscured superiorly by the medial cord, and traversed at about the mid-point by a long fusiform frenulum (not contained in a fold of the lateral cord) that projects well beyond its posterior margin.

Posterior chamber: The greatest diameter of the pulmonary aditus is about half the major axis of the posterior chamber.

LARVAL BUCCOPHARYNX

The tadpole appears to be unknown.

Phrynobatrachus mababiensis FitzSimons, 1932

Phrynobatrachus mababiensis FitzSimons, 1932, *Ann. Transvaal Mus.*, 15:40; Type locality: Tsotsoroga Pan, Mababe Flats. Holotype in the Transvaal Museum, Pretoria. Passmore & Carruthers 1979:170, figs. Poynton & Broadley 1985b:165. Lambiris 1989a:107; 1989b:128, figs. 70 & 71, pl. 14 figs. 2a-d.

Phrynobatrachus vanrooyeni Hoffman, 1940, *Soöl. Navors. Nas. Mus. Bloemfontein*, 1:90, fig. 2b. Type locality: Broedershoek, nr. Greytown, Natal. Holotype in the National Museum, Bloemfontein.

Phrynobatrachus broomi FitzSimons, 1948, *Robert Broom Commem. Vol.* (Roy. Soc. S. Afr.), p. 239, figs. 3,4,7. Type locality: Mount Edgecombe, nr. Durban, Natal. Types in the Transvaal Museum, Pretoria.

Phrynobatrachus ukingensis mababiensis FitzSimons; Poynton 1964:141, fig. 76. Van Dijk 1966:272.

ADULT MALE LARYNX (Tables 11 & 13; Pl. 41, fig. 3)

Material examined: SOUTH AFRICA; NATAL - AJL 2085 (m, SVL 18.6 mm), Hluhluwe Game Reserve. AJL 3067 (m, SVL 13.6 mm) St. Lucia Estuary.

Advertisement call: A sustained buzz at about 4 kHz (Passmore & Carruthers 1979:170), up to 2 seconds long, often followed by a series of short clicks. Calls are uttered at night in close chorus and on overcast days from concealed positions in grassy wetlands and shallow puddles.

Pharyngeal mucosa: Reduced to an extremely thin layer, not distinguishable at low magnification, over the arytenoid cartilage.

Arytenoid cartilage: Both margins of the occlusal surface arcuate, the inner margin somewhat irregular. The arytenoid shelf is subequal in width to the occlusal surface. The arytenoid fossa is elliptical; its posterior margin extends along the entire anterior border of the medial vocal cord.

Vocal cords: Only the medial cord is present. It is broad and flat, with strongly flanged margins.

Posterior chamber: The maximum diameter of the pulmonary aditus is greater than half the major axis of the posterior chamber.

LARVAL BUCCOPHARYNX (Pl. 42, fig. 2a & b)

Identification of larvae: Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 3069, stage 38, SVL 5,3 mm; Honeymoon Bend, Lake St. Lucia; silver impregnation.

Larval habitat: Grassy marshes or shallow standing water with emergent grass clumps, on clayey or silted substrata. The diet appears to consist largely of microscopic algae.

Buccopharyngeal roof

General shape: Triangular, base about 1.4x height. General surface regularly concave, the prenarial arena moderately excavate.

Prenarial arena: A narrow transverse rectangle, with a paramedial pair of low, large pustules immediately behind the root of the beak.

Internal nares: Narrow slits, set transversely. Width of naris about 0.4x width of roof at that level; internarial distance about 0.6x narial width.

Narial valve: A simple, well-developed flap on both margins. The posterior margin is not deeply grooved.

Postnarial arena: A massive conical **postnarial papilla**, somewhat flattened, arises immediately behind the medial portion of either naris. A smaller, clavate postnarial papilla arises behind the lateral angle of either naris. The **lateral ridge papilla** is large, broad and triangular, with a finely scalloped anterior margin. The **median ridge** is triangular, with smooth margins and an acuminate apex.

Buccal roof arena: Small and rather square, bounded by two tall conical papillae on either side, and containing 12 - 14 regularly scattered pustules.

Glandular ridge: A well-defined band, continuous across the roof, lying against the base of the dorsal velum.

Dorsal velum: Narrow, rather weakly developed, and lacking ornamentation on the free border. The medial gap is about 0.5x the length of either velum.

Pressure cushions: Rather large, triangular, with a somewhat pustulose surface. There is no clearly discernible ciliary groove.

Buccopharyngeal floor

General shape: Broadly triangular, base about 1.8x height. General surface shallowly concave, with a deeper prelingual arena.

Prelingual papillae: A single subconical papilla, the length about half the width of the prelingual arena at that level, arises from either posterolateral margin.

Lingual papillae: A small pustulose papilla on the anteromedial margin of the tongue anlage.

Buccal floor arena: A broad inverted trapezoid, bounded laterally on either side by two or three large papillae of rather bizarre form, with a tendency to bifurcate or to bear numerous short projections. The arena is devoid of pustules, but there are 8 - 10 small pustules scattered about the midline between the arena and the ventral velum.

Buccal pockets: Oval to pyriform, closed, shallowly set, and deeply grooved anteriorly. Prepocket papillae are absent.

Ventral velum: Rather broad, of subequal width throughout. The free margin lacks ornamentation, but is divided into thirds by a pair of distinct notches. There are no distinct supporting spicules.

Branchial baskets: Damaged in these specimens.

Filter plates: Details are not clearly discernible. The filter rows are broad, and appear to have secondary and tertiary rows; the channels are rather narrow.

DISCUSSION

Poynton & Broadley (1985b:157) have commented on the considerable geographic and intrapopulation variation, complicated by the slight morphological differences between species, that occurs in this genus. This is particularly true of *Phrynobatrachus mababiensis* and the closely related (and frustratingly similar) species *P. minutus* and *P. parvulus*.

It soon became apparent, in considering this genus, that any treatment restricted to those taxa occurring in Natal would be grossly inadequate. The several species included in the synonymy of the taxa currently recognised (e.g. Poynton 1964; Passmore & Carruthers 1979; Poynton & Broadley 1985b; Lambiris 1989a) need to be examined more carefully, but this should only be done in the context of a review of the whole genus. Such a review would extend far beyond the scope of the present study and although the superficial approach adopted here is open to criticism, I have considered it better to give an incomplete account than to omit the genus altogether.

It should be noted that male and female larynxes from topotypical *Phrynobatrachus acridoides* were quite indistinguishable from those of specimens from Natal, in contrast with the marked geographical variation (over a smaller area) found in *Ptychadena m. mascareniensis*.

PLATE 41

PHRYNOBATRACHUS – ADULT HYOLARYNXES

Median sagittal section, View into left half, Anterior to right.

FIG. 1: *Phrynobatrachus natalensis* (A. Smith, 1849)
AJL 2287 (male), Mazuwi, Umfolozi Game Reserve, Natal, South Africa.

FIG. 2: *Phrynobatrachus acridoides* (Cope, 1867)
NM 3236b (male), Kosi Bay, Natal, South Africa.

FIG. 3: *Phrynobatrachus mababiensis* FitzSimons, 1932
AJL 2085 (male), Hluhluwe Game Reserve, Natal, South Africa.

PLATE 42
PHRYNOBATRACHUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

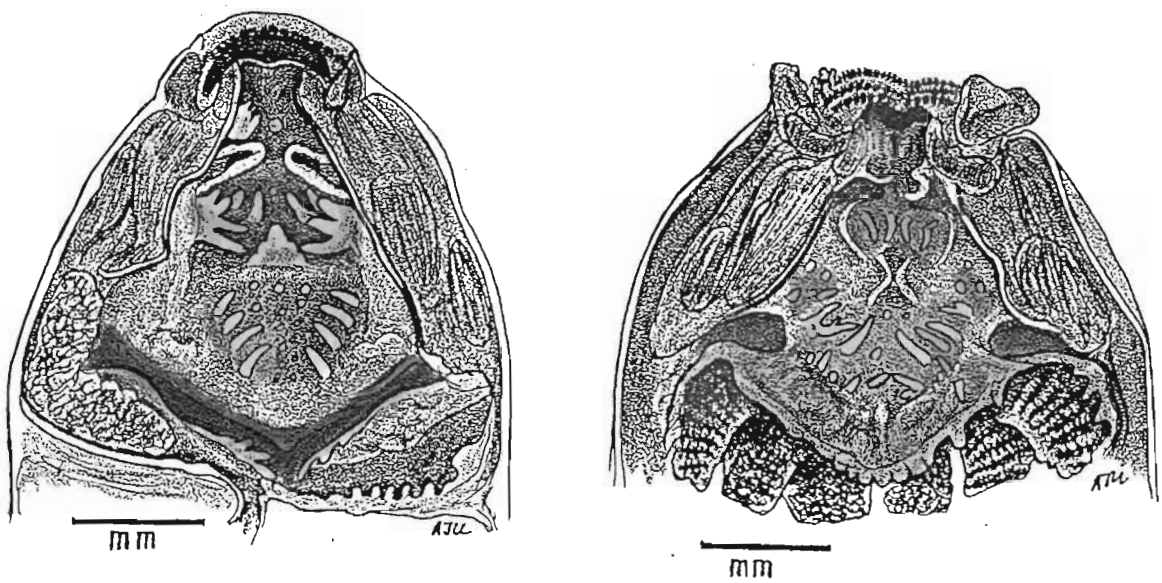


FIG. 1; *Phrynobatrachus natalensis* (A. Smith, 1849)
AJL 1882b, Stage 30, Harare, Zimbabwe.

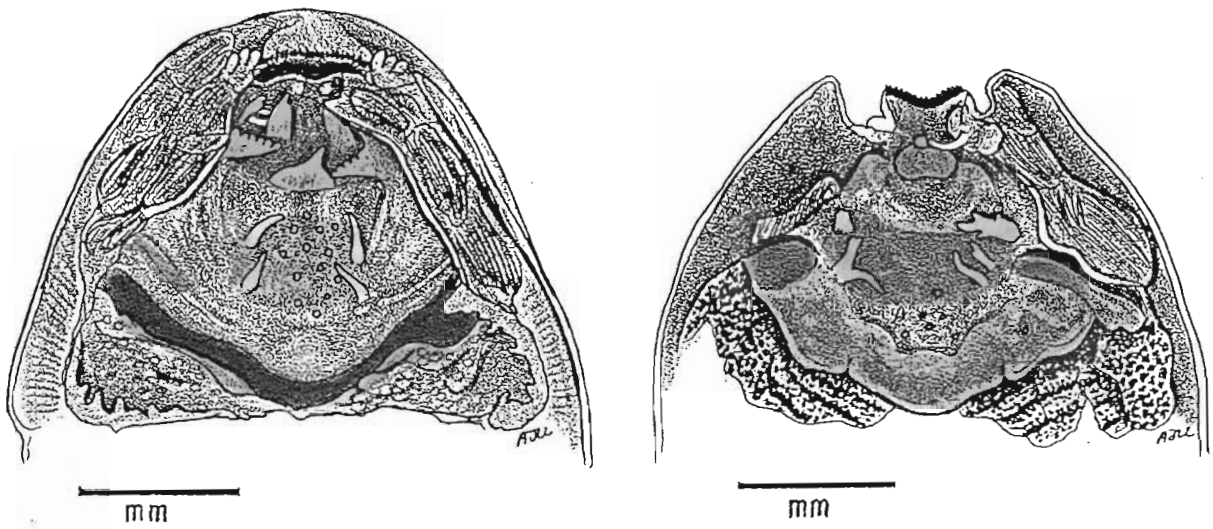


FIG. 2; *Phrynobatrachus mababiensis* FitzSimons, 1932
AJL 3069, Stage 38, Honeymoon Bend, Lake St. Lucia, Natal, South Africa.

Genus *Natalobatrachus* Hewitt & Methuen, 1913

Natalobatrachus Hewitt & Methuen, 1913, *Trans. Roy. Soc. S. Afr.*, 3:107. Type species by monotypy: *Natalobatrachus bonebergi* Hewitt & Methuen, 1913.

CHARACTERS

The characters of the adult larynx and the larval buccopharynx are described in the species account, below. Those of the larynx are differentiated from other Phrynobatrachine genera in Table 13.

The female larynx differs from that of the male principally in its much smaller size and in lacking a distinct lateral vocal cord (Pl. 13).

SPECIES ACCOUNT

Natalobatrachus bonebergi Hewitt & Methuen, 1913

Natalobatrachus bonebergi Hewitt & Methuen, 1913, *Trans. Roy. Soc. S. Afr.*, 3:107, pl. 7, figs. 1-4. Type locality: Mariannhill, Natal. Holotype in the Port Elizabeth Museum. Cotypes in the Transvaal Museum, Pretoria. Poynton 1966:144, fig. 77. Van Dijk 1966:272, fig. Passmore & Carruthers 1979:174, figs. Lambiris 1989a:108.

ADULT LARYNX (Table 13; Pl. 43, figs. 1 & 2)

Material examined: SOUTH AFRICA: TRANSKEI - NM 5857 (m, SVL 28,0 mm), Port St. Johns. NATAL - AJL 2589 (f, SVL 34,3 mm), Vernon Crookes Nature Reserve. NM 6905 (f, SVL 34,5 mm), Umtamvuna Nature Reserve.

Advertisement call: A soft, very short click at about 3.6 kHz (Passmore & Carruthers 1979:174) repeated irregularly. Calls are uttered from exposed positions at or near the water's edge, or from within rock crevices near water. Calls are uttered at night and on overcast days; I have not noted any definite choral sequence.

Male larynx:

Pharyngeal mucosa: A deep mucosa and submucosa overlies and blends with the dorsum of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface asymmetrical, there being a large inferior prominentia only. The internal occlusal margin is slightly notched at the apex. The arytenoid shelf is broad, the width in the midline being about twice that of the occlusal surface. The arytenoid fossa is narrowly elliptical, the major axis extending the whole length of the medial vocal cord.

Vocal cords: The **medial cord** is narrow, and widely flared at the insertions. It lacks marginal flanges and cartilaginous buttresses. The **lateral cord** is broad, with a convex posterior margin, and is traversed by a well-defined frenulum.

Posterior chamber: Moderately large, with a buttress-like pillar between the anterior margin of the large pulmonary aditus and the posterior margin of the lateral vocal cord.

LARVAL BUCCOPHARYNX (Pl. 44, fig. 1a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a.

Material examined: SOUTH AFRICA: TRANSKEI - AJL 3363a, stage 38, SVL 11,5 mm; Umzimvubu River Mouth, Port St. Johns; silver impregnation.

Larval habitat: Dark, thickly forested ravine streams with shallow, gently flowing water over stony or rocky beds. The diet appears to consist of small algae.

Buccopharyngeal roof

General shape: Triangular, base about 1.2x height. General surface shallowly concave, with a slight ridge behind the buccal roof arena, and with a rather deep prenarial arena.

Prenarial arena: Devoid of papillae or pustules.

Internal nares: Narrow, transversely set. Width about 0.4x width of roof at that level; internarial distance about 0.34x narial width.

Narial valve: A well-developed flap on both margins. The anterior valve bears a triangular projection at about mid-point.

Postnarial arena: The **postnarial papillae** are moderately tall (slightly less than narial width), conical (left) or cylindrical (right), arising at about, or a little internal to, the midpoint of the posterior narial margin. There are two small palpoid **lateral ridge papillae** on either side, arranged anteroposteriorly. The anterior papilla is a little smaller than the posterior one. The **median ridge** is roughly trapezoid, with a small peak apically. The base is about 0.25x the width of the floor at that level, and is set between the anterior pair of lateral ridge papillae.

Buccal roof arena: Outline planoconvex, extending almost the whole width of the buccal roof. It is bounded by a closely spaced row of regular short conical papillae on the right side, and by less regularly shaped, more widely spaced, papillae on the left side. Both rows converge posteriorly, with only a narrow median break.

Glandular ridge: A broad, well-defined ridge on either side, abutting the dorsal velum.

Dorsal velum: Moderately deep and well developed, but lacking ornaments on the free margin. The median gap is about 0.25x the length of either velum.

Pressure cushions: Details are not clearly discernible in this preparation.

Buccopharyngeal floor

General shape: Rather cardioid. Base subequal to height. General surface shallowly concave, with a deep, narrow prelingual arena.

Prelingual papillae: A pair of large, short, broad palps, with 5 (left) or 6 (right) short digitations, arising from the posterior half of the arena floor, immediately before the tongue anlage.

Lingual papillae: A pair of close-set cylindrical papillae of moderate length, arising from the anterodorsal border of the tongue anlage.

Buccal floor arena: A large semicircular area bounded laterally and posteriorly by a closely-spaced row of irregular papillae -- larger, more robust, and generally bifurcate anteriorly; smaller, and more conical or cylindrical posteriorly. There are about 10 tiny pustules in the arena.

Buccal pockets: Transversely elliptical, shallow, closed; anterior margin rather deeply grooved. Four small **prepocket papillae** are present on the left side.

Ventral velum: Broad, slightly deeper medially than laterally. The free margin is slightly thickened, and bears about 4 separated villiform projections laterally, and three short, close-set papillate projections on either side of the small, rounded paramedian lobes. (The right side of the velum was damaged in dissection.)

Branchial baskets: Large, deeply arched, not completely filled by the filter plates. The major axes diverge posterolaterally.

Filter plates: Large, arched, semiclosed. The filter rows are short and coarsely folded, and the channels are moderately narrow.

PLATE 43
NATALOBATRACHUS – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right,

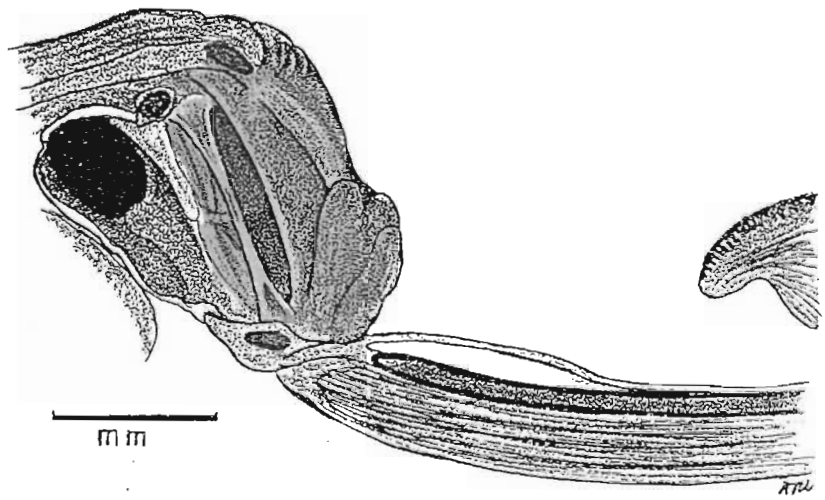


FIG. 1: *Natalobatrachus bonebergi* Hewitt & Methuen, 1913
NM 5857 (male), Port St. Johns, Transkei, South Africa,

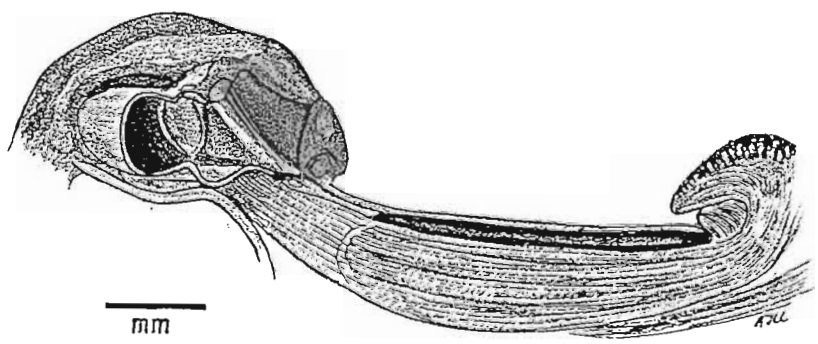


FIG. 2: *Natalobatrachus bonebergi* Hewitt & Methuen, 1913
AJL 2589 (female), Vernon Crookes Nature Reserve, Natal, South Africa,

PLATE 44
NATALOBATRACHUS – LARVAL BUCCOPHARYNXES

Roof on left, floor on right.

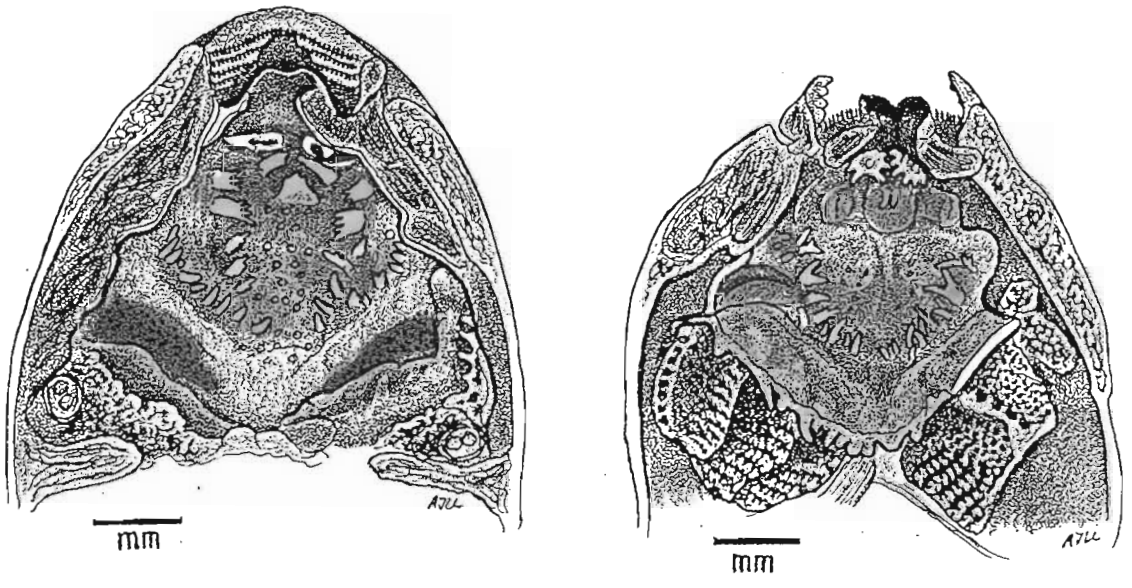


FIG. I: *Natalobatrachus bonebergi* Hewitt & Methuen, 1913
AJL 3363a, Stage 38, Umzimvubu River Mouth, Port St. Johns, Transkei, South Africa.

TABLE 12. Laryngeal characters: *Cacosternum*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

* = extralimital taxa included for comparison

	EXTERNAL SURFACE OF ARYTENOID CARTILAGE ONLY PARTIALLY COVERED BY DISCRETE MUCOSA	SUPERIOR AND INFERIOR PROMINENTIAE APICALES PRESENT	PROMINENTIAE APICALES RUGOSE	MIDDLE PORTION OF MEDIAL VOCAL CORD LESS THAN TWO-THIRDS WIDTH OF SUPERIOR INSERTION	ANTERIOR MARGIN OF MEDIAL VOCAL CORD STRONGLY ARCUATE	POSTERIOR MARGIN OF MEDIAL VOCAL CORD STRONGLY FLANGED	LATERAL VOCAL CORD PRESENT	LATERAL VOCAL CORD WELL DEVELOPED	LATERAL VOCAL CORD SEPARATE FROM MEDIAL VOCAL CORD
Cacosternum boettgeri	1	3	4	3	1	1	1	1	3
nanum	3	3	4	1	1	1	1	1	1
parvum	3	3	4	3	1	1	3	4	4
striatum	1	3	4	3	3	3	1	3	3
*namaquense**	1	1	3	3	3	3	3	4	4
*capense**	1	1	1	1	3	1	3	4	4

Genus *Cacosternum* Boulenger, 1887

Cacosternum Boulenger, 1887, *Ann. Mag. Nat. Hist.*, 20:51. Type species by monotypy: *Cacosternum nanum* Boulenger, 1887.

CHARACTERS

ADULT LARYNX (Tables 12 & 13; Pls. 45 - 48)

Cacosternum has proved the most intractable of the genera examined in this study. Although both generic and specific characters can be readily perceived by inspection, the unusually protean form of the larynx in this genus makes them extraordinarily difficult to express verbally. The character matrix presented here (Table 12) depends as much for diagnosis on negative as on positive attributes.

One species, *Cacosternum poyntoni*, is known only from the female holotype. Illustrations of larynxes from females of all species examined are therefore included for diagnosis of this species, but their characters are not discussed in the species accounts. Important features of the female larynx are discussed under the relevant subheadings below.

Arytenoid cartilage

The arytenoid cartilage shows distinct interspecific differences in shape, but most of these cannot be described concisely in words and are accordingly not discussed further. The plates should be consulted directly for relevant details.

Distinct prominentiae apicales, in males, are present only in *Cacosternum namaquense* (where they are not clearly defined) and in *C. capense*, where they are distinct but small, and rugose. Prominentiae are present in the females of *Cacosternum boettgeri* (large and fairly clearly defined). *C. parvum* (fairly large, and clearly defined); and *C. namaquense* (a large, distinct superior lobe only).

The occlusal surface is smooth and lacks an arytenoid valve in all species examined.

One or both pulvinaria vocalia are massive in *Cacosternum boettgeri, nanum, striatum* and *namaquense*.

Vocal cords

The lateral vocal cord is present in the males of *Cacosternum boettgeri*, *C. nanum* and *C. striatum* only, and in the females of *C. boettgeri*, *C. nanum*, *C. parvum* and *C. striatum* only.

Both cords show useful interspecific differences, but fall into two principal types: (a) Narrow medially, flared at the insertions, and flanged on the posterior margin to various degrees; and (b) A simple, slightly curved band of more or less uniform width, closely applied to the arytenoid shelf, and not flared or flanged.

When a type (a) medial cord is present, there is also a discrete arytenoid fossa; with the type (b) medial cord, this is necessarily absent.

In males, type (a) vocal cords are present in *Cacosternum boettgeri*, *C. nanum*, *C. striatum*, *C. parvum* and *C. capense*. (In the last two taxa there is no lateral cord, and in *C. striatum* the lateral cord is more like that of the type (b) group.)

Type (b) cords are present in the male of *C. namaquense* and in the females of the other taxa examined. (The single male *C. namaquense* dissected had a distinct vocal sac and was definitely not a female.)

Type (b) cords are probably plesiomorphic and type (a) cords apomorphic. The vocal cords of *Cacosternum namaquense*, *C. capense* and *C. parvum* seem to form a bridge between the type (b) and type (a) patterns. Among type (a) cords, that of *Cacosternum striatum* is probably the least advanced, and that of *C. nanum* the most highly derived.

Posterior chamber

No taxonomically useful characters could be discerned in the posterior chamber or the pulmonary aditus.

M. hyoglossus

The m. hyoglossus arises in different positions, as can be seen by inspecting the plates, but no clear pattern could be discerned.

LARVAL BUCCOPHARYNX (Pl. 49)

Positively identified tadpoles of only two species, *Cacosternum boettgeri* and *C. nanum* were available for dissection. Tadpoles of *C.*

capense, preserved in alcohol, proved unsuitable for dissection and study. Larval buccopharyngeal characters appear to be somewhat more amenable to comparative studies than the adult larynxes, at least in the taxa available.

Prenarial arena

Large (*C. boettgeri*) to moderately large (*C. nanum*) and deep, with (*C. boettgeri*) or without (*C. nanum*) lateral palps. In both taxa there is a large arcuate ridge across the roof of the arena, more elaborate in *C. boettgeri* than in *C. nanum*. This could prove to be a taxonomically useful feature in other species as well.

Internal nares and narial valves

The internal nares are large and slightly posteromedially directed in *C. boettgeri*, smaller and more obliquely set in *C. nanum*. The anterior narial margin in *C. boettgeri* is slightly denticulate medially, but unadorned in *C. nanum*. The posterior flap has a distinct triangular prominence in *C. nanum*, which is greatly reduced in *C. boettgeri*.

Postnarial arena papillae

The postnarial and lateral ridge papillae of *C. boettgeri* are distinctly pustulate or serrate, whereas in *C. nanum* they are only slightly so.

Median ridge

High, with a denticulate free margin in *C. boettgeri*, and lower, with a smooth free margin in *C. nanum*.

Buccal roof arena

Few differences are apparent here. The buccal roof arena papillae of *C. nanum* appear to be larger than those of *C. boettgeri*. Extra-arenal pustules in both species seem to have an essentially similar pattern of distribution, but those of *C. boettgeri* are concentrated on a more clearly defined posterolateral ridge than is present in *C. nanum*.

Glandular ridge

That of *C. boettgeri* is broad, clearly defined, and continuous across the buccal roof; that of *C. nanum* is narrow, less clearly defined, and interrupted medially.

Prelingual papillae

Prelingual papillae appear to be lacking in both species.

Lingual papillae

A pair of close-set papillae arise from the mid-dorsum of the tongue anlage in both species. In *C. boettgeri* they are short and cylindrical; in *C. nanum* they are mere pustules.

Buccal floor arena

In both species the buccal floor arena is a deep semicircle bounded posteriorly and laterally by tall conical papillae, and containing scattered pustules. There are few clear differences between them.

Buccal pockets and prepocket papillae

The buccal pockets are large, oval or pyriform, and closed in *C. boettgeri*; they are deep, narrow, transverse slits in *C. nanum*. **Prepocket papillae** are short, pustulate structures in *C. boettgeri*, and little more than strongly verrucose patches in *C. nanum*.

Ventral velum

The ventral velum is broad and supported by spicules in both species. The free margin bears relatively long papillate lobes on either side of the shorter median group in *C. boettgeri*, whilst in *C. nanum* they are much shorter and less clearly defined.

Filter plates

C. nanum has partial filter rows intercalated beween the complete rows, a feature not shown in the *C. boettgeri* material examined.

SPECIES ACCOUNT

Cacosternum boettgeri (Boulenger, 1882

Arthroleptis boettgeri Boulenger, 1882, *Cat. Batr. Sal. Brit. Mus.*, p. 118, pl. 11, fig. 6. Type locality: Kaffraria [i.e., Eastern Cape Province]. Holotype in the British Museum (Natural History), London.

Cacosternum boettgeri (Boulenger); Poynton 1964:146, fig. 79. Van Dijk 1966:256, fig. Passmore & Carruthers 1979:182, figs. Poynton & Broadley 1985b:174. Lambiris 1988:44, figs., pl. 5 figs. 3a-c; 1989a:110; 1989b:131, figs. 72 & 73, pl. 15 figs. 1a-g.

ADULT LARYNX (Tables 12 & 13; Pl. 45, figs. 1 & 2)

Material examined: SOUTH AFRICA: NATAL - AJL 2469 (m, SVL 19.3 mm), Makhamisa Pan, Umfolozi Game Reserve. EASTERN CAPE - AJL 595 (m, SVL 17.5 mm), Gquamhashe Reserve. ZIMBABWE - AJL 1107 (f, SVL 20.0 mm), 4 km NE of Kadoma.

Advertisement call: About eight explosive ticks, about 0.8 second apart, at about 5 kHz (Passmore & Carruthers 1979:182), making a short rapid rasp; uttered in (or, less commonly, near) very shallow water, among emergent grassy vegetation. Calls are uttered both at night and during cloudy days, in close chorus.

Male larynx:

Pharyngeal mucosa: A deep mucosa and submucosa overlies the dorsum of the arytenoid cartilage, which is slightly recessed.

Arytenoid cartilage: Occlusal surface vertically elongate, rather narrow and slightly swollen, but not possessing definite prominentiae. The internal occlusal margin is somewhat notched below the mid-point. The superior pulvinarium vocale is massive. An elliptical arytenoid fossa is present.

Vocal cords: The **medial cord** is narrow medially, broadly flared at the insertions, and strongly flanged on the posterior margin. The **medial cord** is also narrow medially, strongly flared at the insertions, and has a small shallowly mammillate posteromedian prominence. It is largely covered by the medial cord.

LARVAL BUCCOPHARYNX (Pl. 49, fig. 1a & b)

Identification of larvae: Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 2419a; stage 41, SVL 9.0 mm; Mboneni Pan, Mkuzi Game Reserve; silver impregnation.

Larval habitat: Very shallow standing water (usually temporary water bodies) with emergent grassy vegetation, on lightly silted sands, loams or clays. Small algae form an important part of the diet.

Buccopharyngeal roof

General shape: Bluntly triangular, base about equal to height. General surface shallowly concave, with a curved ridge behind the buccal roof arena. The prenarial arena is rectangular anteroposteriorly, and deeply excavate.

Prenarial arena: 3 - 4 cylindrical or weakly branched papillae arise from the middle of the lateral walls. A large arcuate ridge traverses the roof of the arena; the posterior margin is smooth, the anterior margin bears a broad serrate band.

Internal nares: Narrow slits, posteromedially oblique. Width about 0.4x the width of the roof at that level. Internarial distance about 0.5x narial width.

Narial valve: A deep flap on both margins. The anterior flap bears three (two on one side in AJL 2419a) small triangular projections medially; the posterior flap bears a single, slightly larger one almost at the medial angle. The posterior margin is deeply grooved.

Postnarial arena: The conical **postnarial papillae** are serrate or denticulate on the anterior margin, and arise slightly internal to the narial mid-point, a little behind the postnarial groove. Their length is about 0.5x the narial width. There are two slightly larger **lateral ridge papillae** on either side, with rather irregular profiles; their bases are almost confluent, with a smaller (about half the height) intercalated cylindrical papilla with a bifid apex. The **median ridge** is roughly semicircular, the base about 0.4x the width of the roof at that level, and the free margin is serrate.

Buccal roof arena: Square, about 0.3x the width of the roof, and bounded laterally by three (two on one side in AJL 2419a) equally-spaced conical papillae, slightly smaller posteriorly. The arena contains about 30 fairly regularly arranged pustules.

Additional pustules: The arena is bounded posteriorly by a broad curved ridge traversing the buccal roof, bearing pustules arranged in a double row medially and a single row laterally.

Glandular ridge: Broad, traversing the buccal roof without a break, immediately anterior to the dorsal velum. It is finely verrucose.

Dorsal velum: Rather weakly developed, with a small median gap, and with feebly pustulate margins.

Buccopharyngeal floor

Somewhat triangular, but with distinctly convex sides; base about 1.3x height. General surface shallowly concave, with a small, deep prelingual arena.

Prelingual papillae: Apparently lacking. Those described above as prenarial papillae lie at about the middle of the lateral walls and their association with either arena is ambiguous.

Lingual papillae: A pair of short, close-set cylindrical papillae arise from the mid-dorsum of the tongue anlage.

Buccal floor arena: Large, semicircular, occupying most of the floor between the lingual arena and the ventral velum. It is bounded laterally and posteriorly by moderately tall simple conical papillae, arranged irregularly in a roughly double row. About 10 or 12 small pustules are present in the arena.

Buccal pockets: Large, pyriform, shallow, closed. There are 5 - 8 **prepocket pustules** on either side.

Ventral velum: Broad, slightly wider laterally than medially, with six regularly-spaced supporting spicules clearly visible. The thickened free margin bears three regularly-spaced fleshy projections on either side of 5 or 6 smaller, close-set medial papillate lobes.

Branchial baskets: Large and rounded; the major axes diverge posterolaterally.

Filter plates: Large, curved, open. The filter rows bear secondary and tertiary folds, and the channels are narrow.

Cacosternum nanum Boulenger, 1887

Cacosternum nanum Boulenger, 1887, *Ann. Mag. Nat. Hist.*, 20:52. Type locality: Kaffraria [i.e., Eastern Cape Province]. Holotype in the British Museum (Natural History), London. Van Dijk 1966:256.

Cacosternum boettgeri albiventer Hewitt, 1926, *Ann. Natal Mus.*, 5:438, fig. 1b. Type locality: Mariannhill, Natal. Holotype in the Natal Museum, Pietermaritzburg.

Cacosternum magnaglandiferus Inger, 1959, *South African Animal Life*, 6:523, fig. 3. Type locality: Storms River Mouth, Eastern Cape. Holotype in the University of Lund, Sweden.

Cacosternum nanum nanum Boulenger: Poynton 1964:147, fig. 80. Passmore & Carruthers 1979:184, figs. Poynton & Broadley 1985b:174. Lambiris 1988:46, figs., pl. 5 figs. 4a-c; 1989a:112

ADULT LARYNX (Tables 12 & 13; Pl. 45, figs. 3 & 4)

Material examined: SOUTH AFRICA: NATAL - AJL 1897 (m, SVL 18,8 mm), Umpambinyoni River, Scottburgh. AJL 2600 (m, SVL 18,1 mm), Itala Nature Reserve. EASTERN CAPE - AJL 2997 (m, SVL 17,6 mm), and AJL 2998 (f, SVL 23,5 mm), Katberg.

Advertisement call: A creaking chirp about 0.03 second long, at about 3.2 kHz (Passmore & Carruthers 1979:184), repeated three or four times a second for several seconds. Calls are uttered at night or during cloudy days, in chorus, from grassy vegetation in very shallow standing water.

Male larynx:

Pharyngeal mucosa: A relatively deep, folded mucosa covers the whole surface of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface vertically elongate, narrow, and not possessing prominentiae. The internal occlusal margin is somewhat notched a little below the mid-point. The superior pulvinarium vocale is massive. An elliptical arytenoid fossa is present.

Vocal cords: The **medial cord** is very narrow medially, broadly flared at the insertions, and strongly flanged on the posterior margin. The medial cord is similar in appearance, and lies well posterior to the median cord. It has a tiny acuminate projection at about the middle of the posterior margin.

LARVAL BUCCOPHARYNX (Pl. 49, fig. 2a & b)

Identification of larvae: Separated from *Cacosternum boettgeri* by the key in Lambiris 1989a, but identification as *C. nanum* is circumstantial, being based on material outside the known range of *Cacosternum parvum*.

Material examined: SOUTH AFRICA; NATAL - NM 5831; stage 40, SVL 8.5 mm; Charters Creek, Lake St. Lucia; silver impregnation.

Larval habitat: Very shallow standing water (usually temporary water bodies) with emergent grassy vegetation, on lightly silted sands, loams or clays. Small algae form an important part of the diet.

Buccopharyngeal roof

General shape: Somewhat trapezoid, the apex very narrow; base about 1.4x height. General surface shallowly concave, with a slightly deeper central portion, and a deep, transversely rectangular prenarial arena.

Prenarial arena: Lateral wall papillae lacking. A prominent arcuate ridge traverses the roof of the arena; it lacks any ornamentation.

Internal nares: Moderately narrow, transversely set. Width about 0.37x width of roof at that level; internarial distance about 0.75x narial width.

Narial valve: A moderately deep flap on both margins. The posterior flap bears a moderately large triangular projection medially; the anterior flap is unadorned. The posterior margin is not deeply grooved.

Postnarial arena: A single conical **postnarial papilla** on either side arises well behind the middle of the naris (the distance between naris and papilla a is little less than the internarial distance). The anterior margin of the papilla is faintly verrucose. There are two close-set conical **lateral ridge papillae** on either side, the anterior one about half the height of the posterior papilla; the latter has a sligly verrucose anterior margin. The **median ridge** is a low curved flap, the base about 0.3x the width of the roof at that level. The middle third of the free margin is demarcated by slight notches on either side.

Buccal roof arena: An inverted trapezoid, bounded by two tall conical papillae on either side, and enclosing about 20 small pustules.

Additional pustules are scattered fairly densely over the depression in the buccal roof surrounding the arena.

Glandular ridge: A narrow band immediately anterior to each half of the dorsal velum, with a rather broad median gap.

Dorsal velum: A weakly defined flap closely associated with the small, featureless pressure cushions.

Buccopharyngeal floor

General shape: Roughly triangular; base about 1.3x height. General surface shallowly concave, with deep grooves on either side of the lingual arena, and a shallow elongately trapezoid depression down the middle of the buccal floor. The prelingual arena is deeply excavate.

Prelingual papillae: Absent.

Lingual papillae; A pair of small, close-set pustules on the mid-dorsum of the tongue anlage.

Buccal floor arena: Large, semicircular, occupying most of the floor between the lingual arena and the ventral velum. It is bounded laterally and posteriorly by rather tall simple subconical papillae, somewhat irregularly spaced, and set in a single row. About 10 small pustules occur in the depression in the centre of the arena.

Buccal pockets: Narrow, deep, more or less transverse curved slits, with dense prepocket verrucosities.

Ventral velum: Broad, of subequal width throughout, and possessing four prominent supporting spicules on either side of the midline. The thickened free margin bears three very short projections on either side of the median group of three pairs of somewhat larger, better-defined lobes.

Branchial baskets: Damaged in this preparation, but apparently large and rather rounded.

Filter plates: Details are not clear in this preparation. The rather broad filter rows have secondary and tertiary folds, and partial rows are intercalated between the whole rows. The channels are narrow.

Cacosternum parvum Poynton, 1963

Cacosternum nanum parvum Poynton, 1963, *Ann. Natal Mus.*, 15:323. Type locality: Mooi River, Natal. Holotype in the Natal Museum, Pietermaritzburg. Poynton 1964:149, fig. 81. Passmore & Carruthers 1979:184, fig. Lambiris 1988:47, pl. 5 figs. 5a & b; 1989a:113.

ADULT LARYNX (Tables 12 & 13; Pl. 46, figs. 1 & 2)

Material examined: SOUTH AFRICA: NATAL - NM 6424a (m, SVL 15,4 mm), and NM 6424b (m, SVL 16,5 mm), Cathkin Peak Forest Reserve. TRANSVAAL - NM 3384 (f, SVL 15,1 mm), Sabie.

Advertisement call: A short chirp at about 3 kHz, repeated three or four times a second, from among emergent grassy vegetation in very shallow standing water. Calls are uttered in chorus at night and during cloudy days.

Male larynx:

Pharyngeal mucosa: A rather deep, folded mucosa covers the whole surface of the arytenoid cartilage.

Arytenoid cartilage: The occlusal surface is narrow and more or less U-shaped; the internal occlusal margin is slightly notched apically. The mid-line width of the arytenoid shelf is about twice that of the occlusal surface. The arytenoid fossa is rather broadly elliptical.

Vocal cord: Only the **medial cord** is present. It is rather broad medially, and flared at the insertions. The posterior margin is strongly flanged.

LARVAL BUCCOPHARYNX

No reliably attributable tadpoles were available for study.

Cacosternum poyntoni Lambiris, 1988

Cacosternum poyntoni Lambiris, 1988, *S. Afr. J. Zool.*, 32:63-66, figs. 1-5. Type locality: Town Bush Valley, Pietermaritzburg. Holotype in the Natal Museum, Pietermaritzburg. Lambiris 1989a:113.

ADULT FEMALE LARYNX (Pl. 46, fig. 3)

Material examined: SOUTH AFRICA: NATAL - NM 1063 (f, SVL 15,0 mm), Town Bush Valley, Pietermaritzburg. Holotype.

Advertisement call: Not known.

Pharyngeal mucosa: A deep layer covering the entire surface of the arytenoid cartilage.

Arytenoid cartilage: The anterodorsal portion of the narrow occlusal surface is slightly concave, the anteroventral portion slightly convex. The internal occlusal margin is apically acuminate. There are no prominentiae. The pulvinaria vocalia are only moderately enlarged. The arytenoid shelf below the midline is broad. There is no arytenoid fossa.

Vocal cord: Rather narrow, slightly curved, lorate, and lacking flanged borders or buttresses.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

Cacosternum striatum FitzSimons, 1947

Cacosternum striatus FitzSimons, 1947, *Ann. Natal Mus.*, 11:130, fig. 6. Type locality: Country Club Golf Course, Durban. Types in the Transvaal Museum, Pretoria. Lambiris 1989a:111 (part).

Cacosternum boettgeri (non Boulenger, 1882): Poynton 1964:146 (part). Passmore & Carruthers 1979:182 (part).

ADULT LARYNX (Tables 12 & 13; Pl. 47, figs. 1 & 2)

Material examined: SOUTH AFRICA: NATAL - TM 21445 (m, SVL 13,8 mm), TM 21446 (m, SVL 113,5), and TM 21448 (f, SVL 12,0 mm), Country Club Golf Course, Durban. Paratypes.

Advertisement call: Unknown.

Male larynx:

Pharyngeal mucosa: Extends over the dorsum of the arytenoid cartilage.

Arytenpoid cartilage: The occlusal surface is moderately narow and rather elongate vertically. The superior prominentia is elongate and a little less broad than the occlusal surface proper. The internal occlusal margin is broadly arcuate. The pulvinaria vocalia are only moderately enlarged. The arytenoid shelf is about as wide as the occlusal surface inferiorly, tapering superiorly. The arytenoid fossa is elliptical, the major axis almost equal to the length of the anterior margin of the medial vocal cord.

Vocal cords: The **medial vocal cord** is moderately broad medially, and flared at the insertions. The posterior margin is weakly flanged at the insertions. The **lateral cord** is a simple fold, partly covered by the medial cord.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

DISCUSSION

Despite the difficulty of verbally describing certain features of larynxes in this genus, the several species of *Cacosternum* currently recognised can easily be separated on laryngeal characters. These characters are particularly useful in the case of *Cacosternum nanum* and *C. parvum*, in which the external features generally used for diagnosis (the degree of development of the metacarpal and palmar tubercles; and the eyelid/interorbital width ratio) are often extremely difficult to interpret satisfactorily.

Cacosternum boettgeri

Cacosternum boettgeri shows "particularly complex deme structure" in Natal (Poynton 1964:147), and field studies indicate that the species as currently recognised may comprise several sibling species. A more detailed study of Natal populations than was possible in this survey is needed. The type locality of *C. boettgeri*, "Kaffraria" -- the Eastern Cape Province -- is too vague to be of any value, but the Gquamhashe Reserve specimens examined agree exactly with the Umfolozi specimen from Natal. The status of *Cacosternum striatum*, referred to the synonymy of *C. boettgeri* by Poynton (1964) is discussed below.

The *Cacosternum nanum* group

Two subspecies of *Cacosternum nanum*, namely *Cacosternum nanum nanum* Boulenger, 1887, and *Cacosternum nanum parvum* Poynton, 1963 are generally recognised (e.g. Poynton 1964; Passmore & Carruthers 1979; Lambiris 1989a). The two forms are externally very similar, but may be separated in the field by differences in call and by habitat preferences (*C. nanum* occurring below, and *C. parvum* above, about 1200 metres). They may easily be separated by the considerable differences in laryngeal morphology (Pl. 45, figs, 3 & 4; Pl. 46, figs. 1 & 2 respectively). The larval buccopharynx of *Cacosternum parvum* has yet to be described, otherwise the situation is exactly parallelled by *Rana angolensis* Bocage and *Rana dracomontana* Channing. It seems inconsistent, bearing in mind the similarities between the two cases, to treat treat one pair as

subspecies and the other pair as species, particularly as there seems to be no evidence of introgression between *Cacosternum nanum* and *C. parvum*. These two forms are therefore treated here as full species.

The status of *Cacosternum magnaglandiferus* Inger, 1959 from the Eastern Cape (referred to the synonymy of *C. nanum* [Poynton 1964:149]) requires further investigation, but this is beyond the scope and aims of the present study. Tadpoles from the Storms River Mouth do not seem to be available at present.

Cacosternum poyntoni

This species is known only from the female holotype. The larynx of the holotype was compared with female larynxes from all known species of *Cacosternum* occurring in southern Africa (Plates 45 - 48). It most closely resembles that of *Cacosternum striatum*, but differs therefrom in having a narrower arytenoid occlusal surface (which also differs distinctly in shape) and a more slender vocal cord; the pulvinariae vocaliae are small in *Cacosternum poyntoni*, massive in *C. striatum*. Female larynxes of the other taxa differ more markedly, as inspection of the plates will show.

Cacosternum striatum

Examination of the larynxes of the three paratypes of *Cacosternum striatum* (Plate 47) confirms the validity of this species. (TM 21445 and 21448 are males, not females as indicated by FitzSimons, and TM 21446 is a subadult female.)

FitzSimons' original form of the species name, *striatus*, must be amended to *striatum* to agree in gender with the generic name, in conformity with Article 31(b) of the International Code of Zoological Nomenclature (3rd edition). The Greek *sternon* (assimilated into Latin as *sternum*) is neuter and *striatum*, the nominative singular of *striatus*, is the correct form in this combination.

In resurrecting *Cacosternum striatum* from the synonymy of *C. boettgeri*, to which it had been referred by Poynton (1964:147), Lambiris

(1989a:111) included in his discussion some recently collected specimens from Boston, Natal, and Sehlabathebe, Lesotho. These specimens agreed closely in most respects with FitzSimons' description of *C. striatum*, although differing in having a light heel-to-heel line along the posterior surface of the hind limbs, and were believed to be referable to that species.

Closer comparison of the Boston and Sehlabathebe specimens with the paratypes of *Cacosternum striatum*, including comparison of male larynxes, shows that they are not conspecific, and that laryngeal differences (Table 13) are sufficient to indicate removal from this genus. The generic status of these specimens is discussed in the account directly following.

At present, *Cacosternum striatum* must be considered to be known only from the type specimens.

Additional material examined

Male and female larynxes of two extralimital taxa (the remaining southern African species in the genus) were examined for comparison with *Cacosternum poyntoni* and *C. striatum*. They were also required in considering the status of the Sehlabathebe and Boston specimens formerly included in *Cacosternum striatum*, discussed below.

Cacosternum namaquense Werner, 1910
(Table 12; Pl. 48, figs. 1 & 2) MATERIAL EXAMINED: NM 3395 (m, SVL 20,4 mm), and NM 3396 (f, SVL 23,5 mm), both ex South African Museum, no locality.

Cacosternum capense Hewitt, 1910
(Table 12; Pl. 48, figs. 3 & 4) MATERIAL EXAMINED: NM 3397 (m, SVL 27,4 mm), between Hopesfield and Malmesbury, Western Cape. NM 3403 (f, SVL 21,2 mm), Faure, Western Cape.

PLATE 45

CACOSTERNUM – ADULT HYOLARYNXES

Median sagittal section. View into left half. Anterior to right.

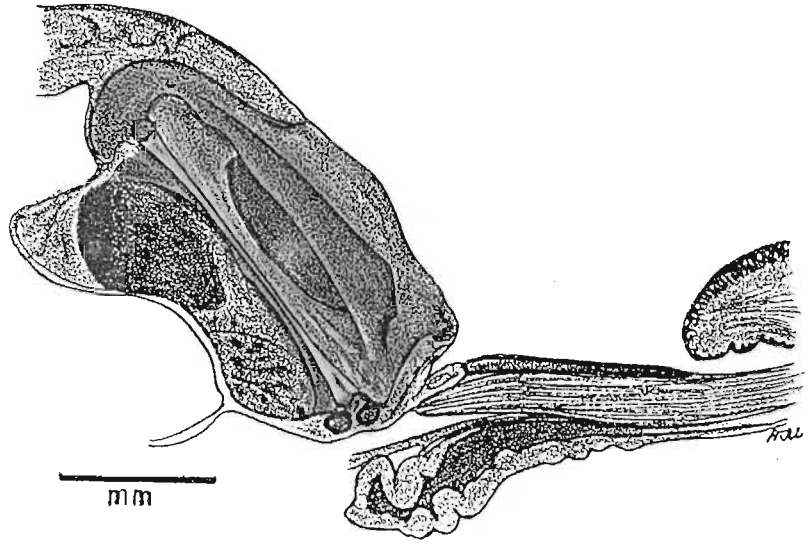


FIG. 1: *Cacosternum boettgeri* (Boulenger, 1882)
AJL 406 (male), Strydenberg, Northern Cape, South Africa.

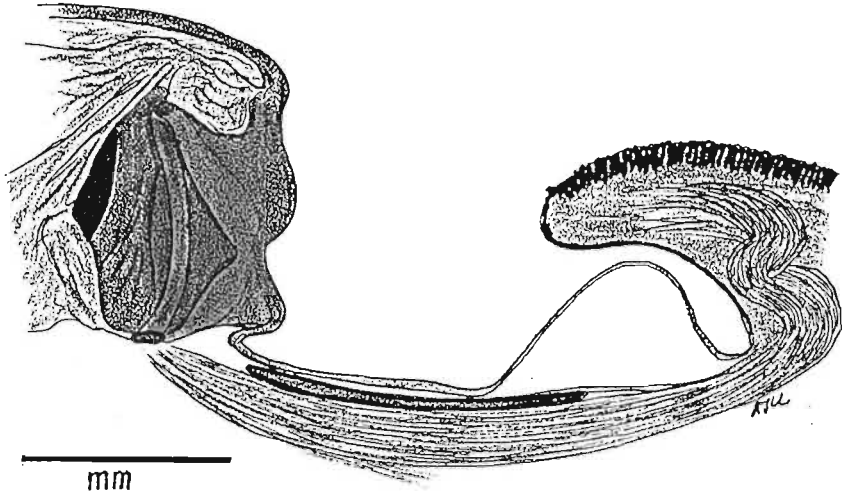


FIG. 2: *Cacosternum boettgeri* (Boulenger, 1882)
AJL 1243 (female), Kwekwe, Zimbabwe.

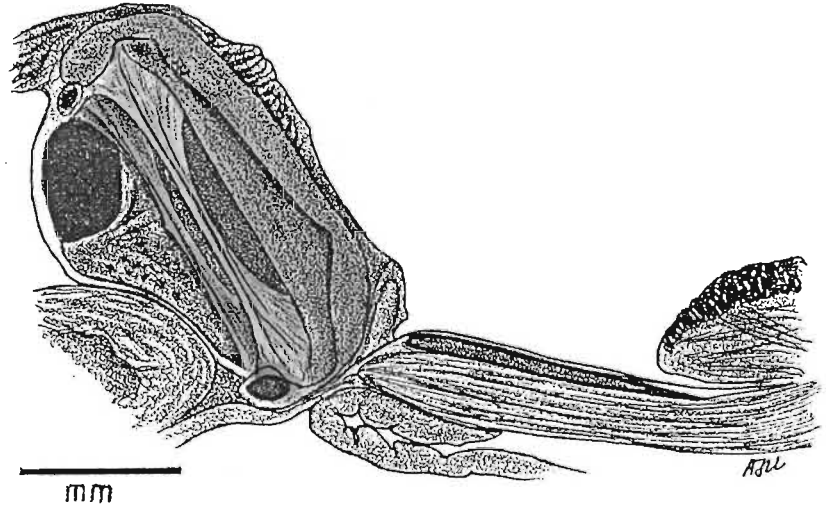


FIG. 3: *Cacosternum nanum* Boulenger, 1887
AJL 2997 (male), Katberg, Eastern Cape, South Africa.

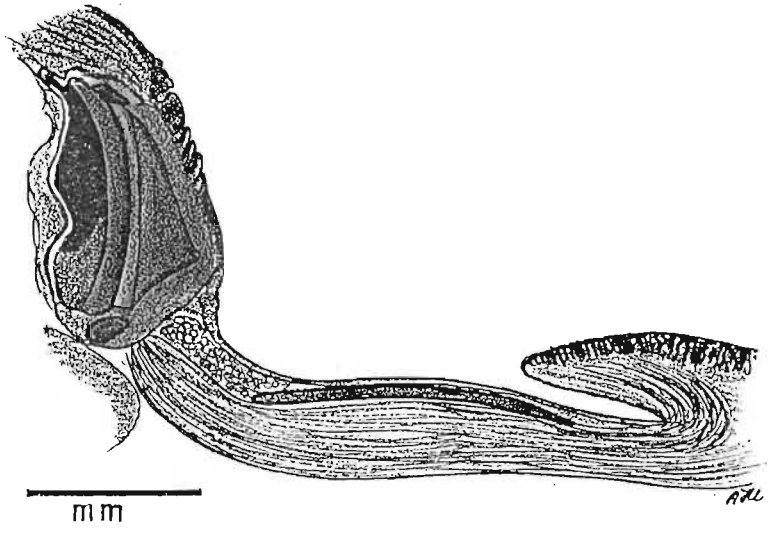


FIG. 4: *Cacosternum nanum* Boulenger, 1887
AJL 2998 (female), Katberg, Eastern Cape, South Africa.

PLATE 46
CACOSTERNUM — ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

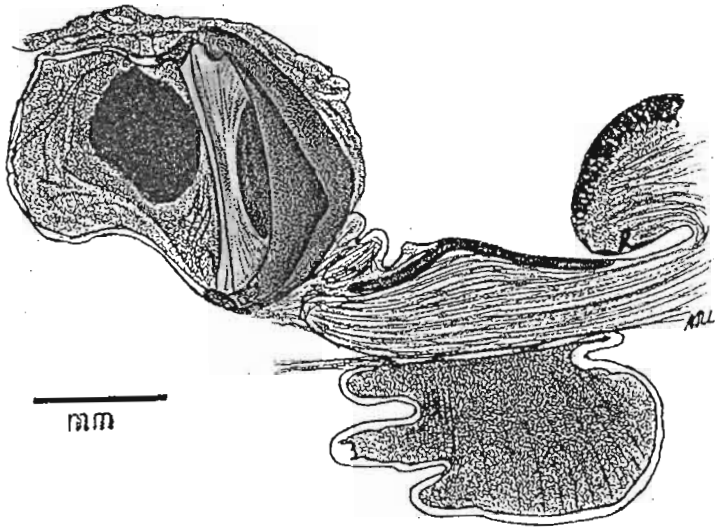


FIG. 1: *Cacosternum parvum* Poynton, 1963
NM 6424b (male), Cathkin Peak Forest Reserve, Natal, South Africa.

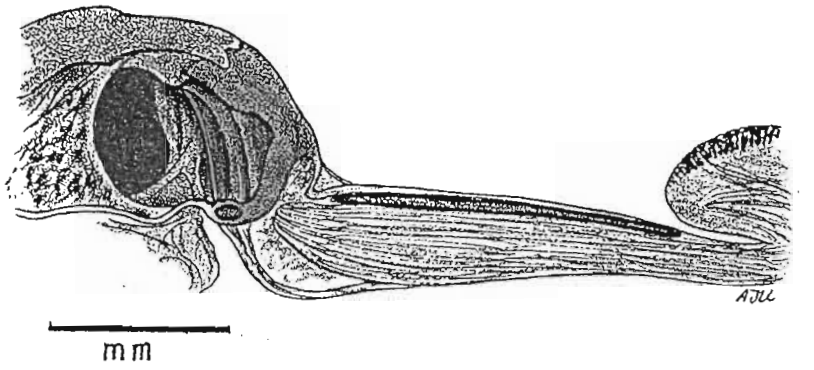


FIG. 2: *Cacosternum parvum* Poynton, 1963
NM 3384 (female), Sabie, Eastern Transvaal, South Africa.

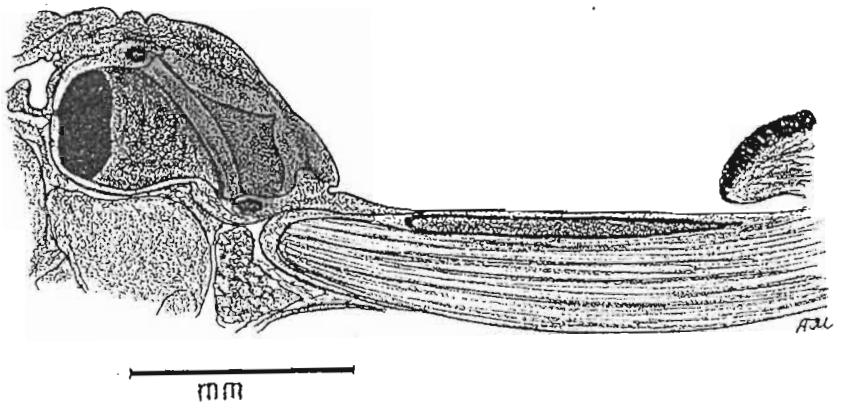


FIG. 3: *Cacosternum poyntoni* Lambiris, 1988
NM 1063 (female), Town Bush Valley, Pietermaritzburg,
Natal, South Africa. HOLOTYPE

PLATE 47
CACOSTERNUM – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

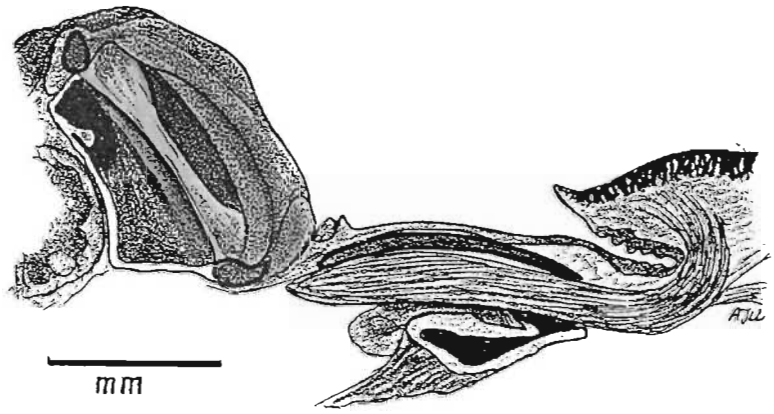


FIG. 1: *Cacosternum striatum* FitzSimons, 1947
TM 21445 (male), Country Club Golf Course, Durban, Natal, South Africa. PARATYPE

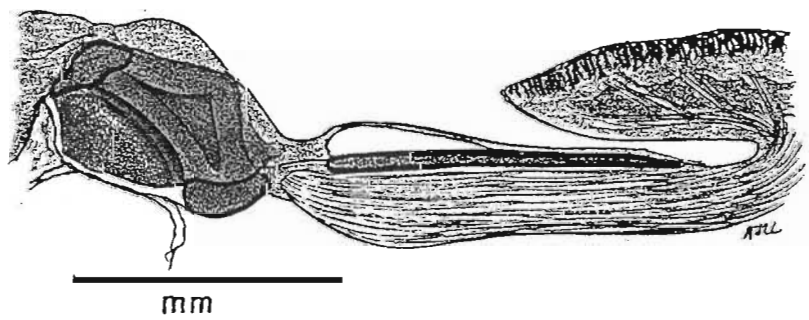


FIG. 2: *Cacosternum striatum* FitzSimons, 1947
TM 21446 (female), Country Club Golf Course, Durban, Natal, South Africa. PARATYPE

PLATE 48
CACOSTERNUM – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

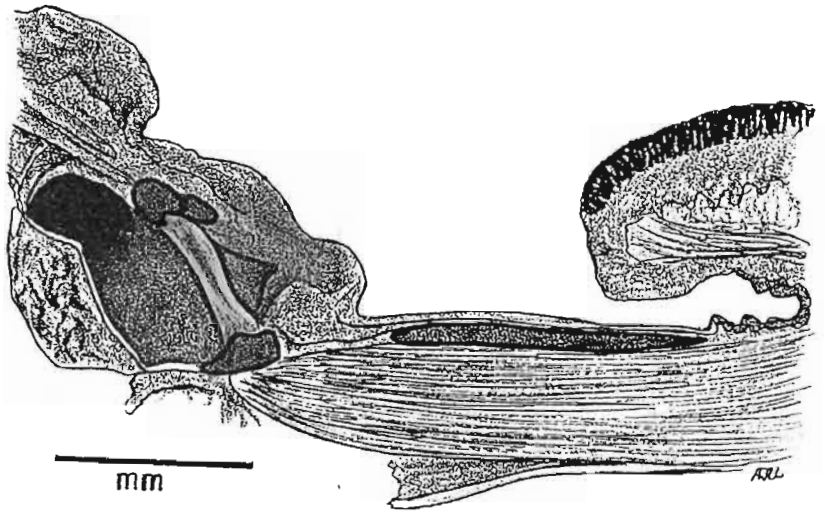


FIG. 1: *Cacosternum namaquense* Werner, 1910
NM 3395 (male). No locality.

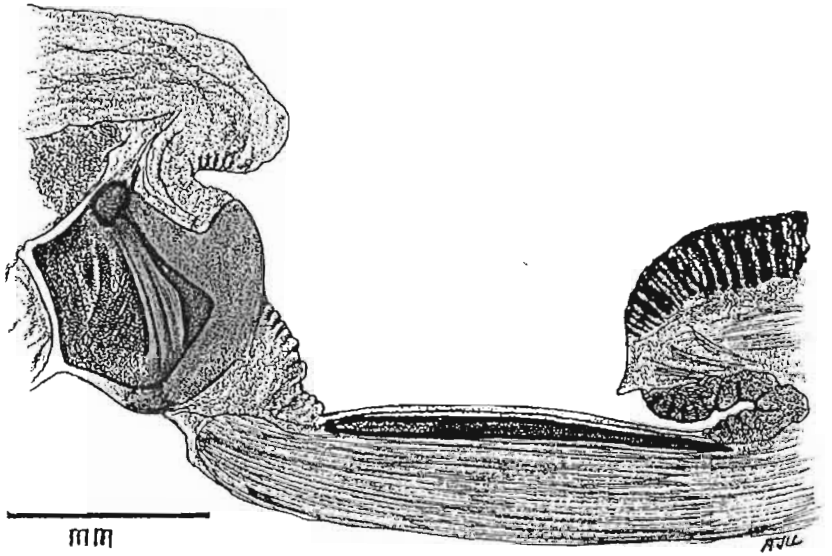


FIG. 2: *Cacosternum namaquense* Werner, 1910
NM 3396 (female). No locality.

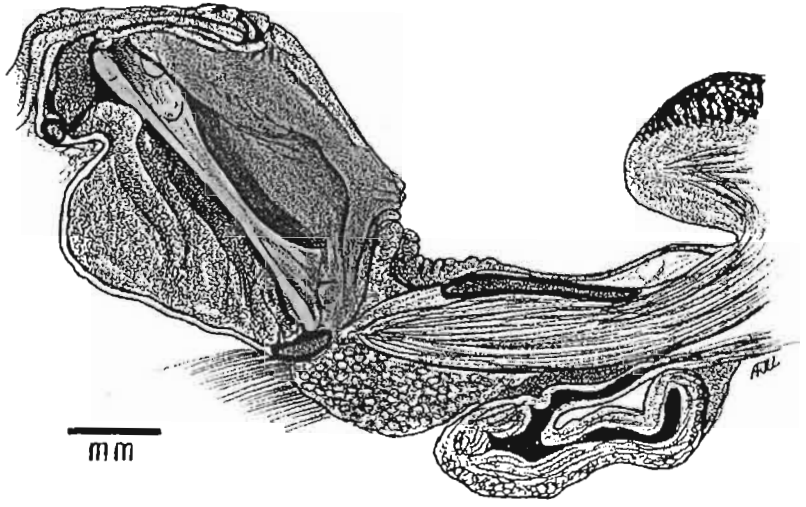


FIG. 3: *Cacosternum capense* Hewitt, 1925
NM 3397 (male). Between Hopefield and Malmesbury, Western Cape, South Africa.

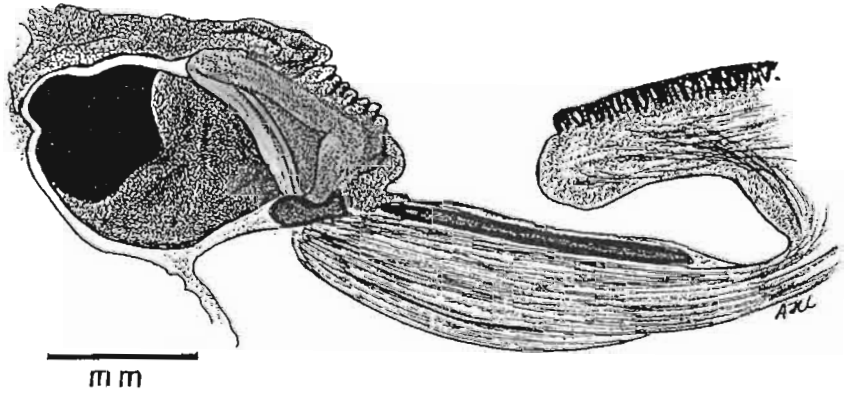


FIG. 4: *Cacosternum capense* Hewitt, 1925
NM 3403 (female). Between Hopefield and Malmesbury, Western Cape, South Africa.

PLATE 49
CACOSTERNUM – LARVAL BUCCOPHARYNXES
Roof on left, floor on right

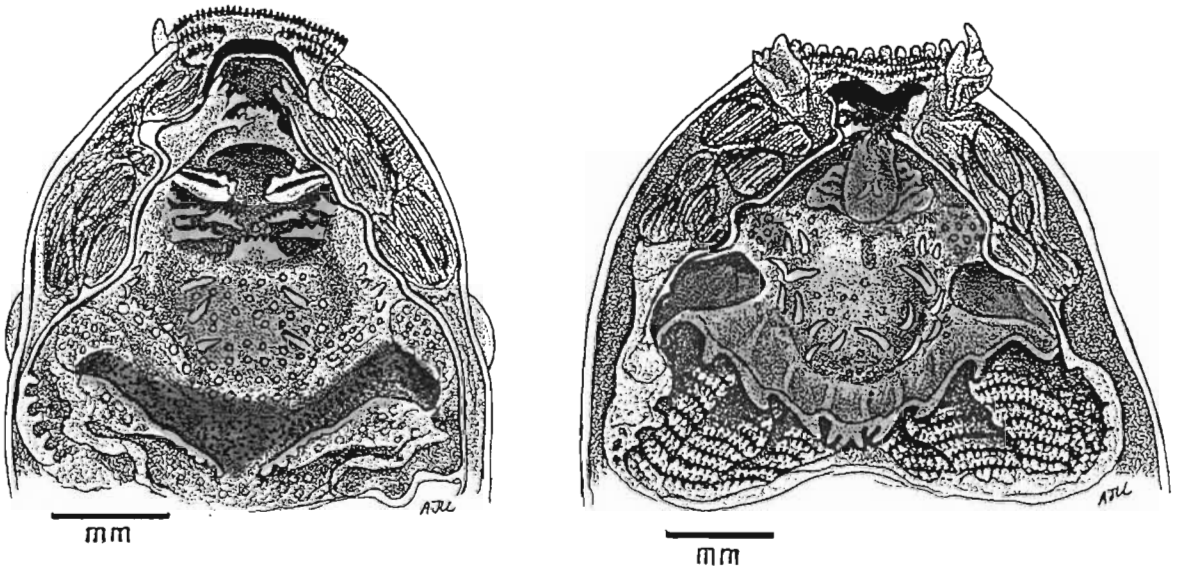


FIG. 1: *Cacosternum boettgeri* (Boulenger, 1882)
AJL 2419a, Stage 41, Mboneni Pan, Mkuzi Game Reserve, Natal, South Africa.

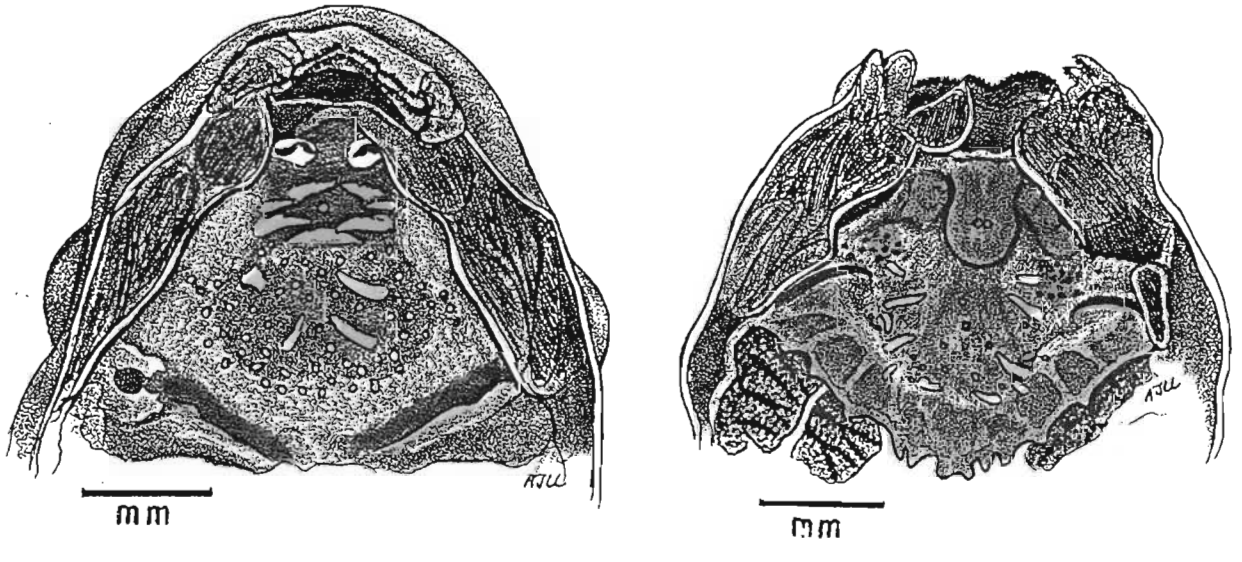


FIG. 2: *Cacosternum nanum* Boulenger, 1887
NM 5831a, Stage 40, Charters Creek, Natal, South Africa.

TABLE 13. Laryngeal characters: South African Phrynobatrachine genera

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	INCISURA AND APICAL CARTILAGE PRESENT	POSTERIOR MARGIN OF ARYTENOID OCCLUSAL SURFACE STRAIGHT	ARYTENOID SHELF PRESENT	INFERIOR INSERTION OF MEDIAL VOCAL CORD FLARED	LARGE TRIANGULAR CARTILAGINOUS BUTTRESSES ON MEDIAL VOCAL CORD	LATERAL VOCAL CORD PRESENT	LATERAL VOCAL CORD NARROW, CLOSELY APPLIED TO POSTERIOR MARGIN OF MEDIAL VOCAL CORD	POSTERIOR BORDER OF LATERAL VOCAL CORD STRONGLY FLANGED	FRENULUM PRESENT	FRENULUM PROJECTS WELL BEYOND POSTERIOR MARGIN OF LATERAL VOCAL CORD
Lygobatrachus gen. nov.	1	1	3	1	3	1	3	3	3	4
Phrynobatrachus	3	3	1	3	3	2	3	3	2	1
Natalobatrachus	3	3	1	1	3	1	3	3	1	3
Cacosternum	3	3	1	1	3	2	3	3	3	4
Microbatrachella	3	3	1	1	1	1	3	1	3	4
Anhydrophryne	3	3	1	3	3	1	1	3	3	4
Arthroleptella	3	3	1	1	3	1	3	3	1	3

Genus *Lygobatrachus*, gen. nov.

A new genus is provisionally recognised here for small frogs from Sehlabathebe National Park, Lesotho, and from Boston, Natal, previously considered by Lambiris (1989a:1111) to be referable to *Cacosternum striatum* FitzSimons, 1947. Comparison with the types of *C. striatum* shows that they are not conspecific. These frogs do not appear to be referable to any Phrynobatrachine genus currently recognised. A detailed characterisation of this taxon (including external and skeletal features) is in preparation and only laryngeal morphology is discussed here.

NOTE: The manuscript name "*Lygobatrachus orestheus*" used in this thesis is a manuscript name of no nomenclatural standing [International Commission for Zoological Nomenclature, 3rd Edition, Articles 8a, b and Article 9 (11)], and is used here purely for convenience in discussion.

CHARACTERS

ADULT LARYNX (Table 13; Pl. 50, fig. 1)

The larynx of male *Lygobatrachus* has been compared with those of all other Phrynobatrachine species known to occur in South Africa, and differs from all in possessing an apical cartilage set in a well-defined incisura; in having a straight posterior arytenoid occlusal margin; and in lacking an arytenoid shelf (Table 13).

A detailed description of the larynx is presented in the species account, below.

Lygobatrachus orestheus, sp. nov.

Cacosternum striatus (non FitzSimons, 1947); Lambiris 1989a:111 (part, Boston and Sehlabathebe specimens).

ADULT MALE LARYNX (Table 13; Pl. 50, fig. 1)

Material examined: LESOTHO - AJL 2815 (m, SVL 12.3 mm), and AJL 2816 (m, SVL 13.1 mm), Sehlabathebe National Park.

Advertisement call: A quick, double, cricket-like chirp at about 5 kHz, uttered at short intervals, from concealed positions in grass tussocks just above water level, in wetlands. Calls are uttered both at night and during the day, in cloudy weather.

Pharyngeal mucosa: A fairly thick layer of smooth mucosa and submucosa overlies the whole surface of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface vertically elongate, considerably narrowed superiorly and inferiorly, broad medially. The anterior margin of the occlusal surface is somewhat curved with a conspicuous U-shaped incisura apicalis and small prominentiae apicales enclosing a small but well developed triangular cartilago apicalis. The occlusal surface is smooth and lacks any trace of an arytenoid valve. The posterior occlusal margin between the anterior insertions of the medial vocal cord, is straight. There is no arytenoid shelf. The planoconvex arytenoid fossa extends the length of the anterior margin of the medial vocal cord. The pulvinaria vocalia are large and well developed, the superior pulvinarium more so than the inferior.

Vocal cords: The **medial cord** is broad, flared at the insertions (slightly more so superiorly than inferiorly), flattened in section, and lacks marginal flanges. Long, rather narrow, triangular buttresses are present but are not especially conspicuous. There is no frenulum. The **lateral cord** is narrow and gently curved, slightly concave posteriorly, with a small papilla at about the middle of the posterior margin.

Posterior chamber: Of moderate size. The diameter of the pulmonary aditus is about 0.4x the major diameter of the chamber. The aditus has a slight thickening on the anteroventral margin. The lateral wall of the

chamber is supported by a transverse cartilaginous process below the aditus.

M. hyoglossus: The m. hyoglossus arises below the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX

Tadpoles reared from eggs laid by the Boston specimens (M. Burdon) appear to have been lost. Additional material has not yet been obtained.

DISCUSSION

Although these tiny frogs are superficially similar to *Cacosternum striatum*, the laryngeal morphology differs so much from those of southern African *Cacosternum* species that they are here not considered congeneric.

The larynx of male *Lygobatrachus* has been compared with those of all other Phrynobatrachine species known to occur in South Africa -- *Phrynobatrachus natalensis*, *acridoides*, *mababiensis* (Pl. 41), *Natalobatrachus bonebergi* (Pl. 43), *Cacosternum boettgeri*, *nanum*, *parvum*, *poyntoni*, *striatum*, *namaquense*, *capense* (Pl. 45 - 48), *Microbatrachella capensis* (Pl. 51), *Anhydrophryne rattrayi* (Pl. 52), *Arthroleptella hewitti*, *lightfooti*, and *Arthroleptella* sp. nov. (Pl. 54).

The larynx differs so markedly from those of other Phrynobatrachine taxa examined (Table 13), particularly in the possession of an incisura apicalis and cartilago apicalis, in having a straight interior occlusal margin, and in lacking an arytenoid shelf, that a new genus is provisionally recognised here to accomodate this undescribed species.

A more detailed characterisation, including comparisons with the central and northern African genera *Arthroleptides* Nieden, 1910, *Dimorphognathus* Boulenger, 1906, *Nothophryne* Poynton, 1963, *Petropedetes* Reichenow, 1874, and *Phrynodon* Parker, 1935, is in preparation.

Larynxes from specimens of the following extralimital taxa were examined for consideration of the taxonomic status of these frogs:

Microbatrachella capensis (Boulenger, 1910)
(Table 13; Pl. 51, figs. 2 & 3) MATERIAL EXAMINED: NM 3300 (m, SVL 15,0 mm), NM 3301 (m, SVL 14,0 mm), and NM 3299 (f, SVL 17,0 mm); Landsdowne, Ottery, nr. Cape Town, Western Cape, South Africa.

Anhydrophryne rattrayi Hewitt, 1919
(Table 13; Pl. 52, figs. 1 & 2) MATERIAL EXAMINED: AJL 272 (m, SVL 21,0 mm), and AJL 268 (f, SVL 20,5 mm); Hogsback, Eastern Cape, South Africa.

PLATE 50
LYGOBATRACHUS – ADULT HYOLARYNX
Median sagittal section. View into left half. Anterior to right.

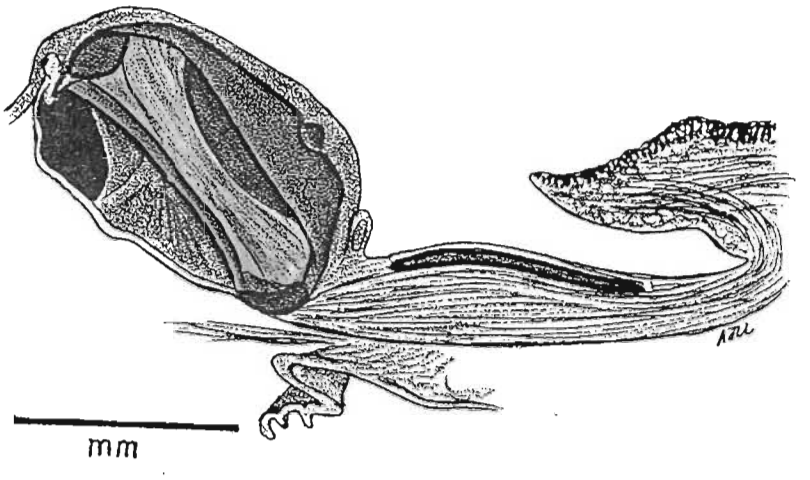


FIG. 1: *Lygobatrachus orestheus* Gen. et sp. nov.
AJL 2815 (male), Sehlabathebe National Park, Lesotho.

PLATE 51
MICROBATRACHELLA – ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

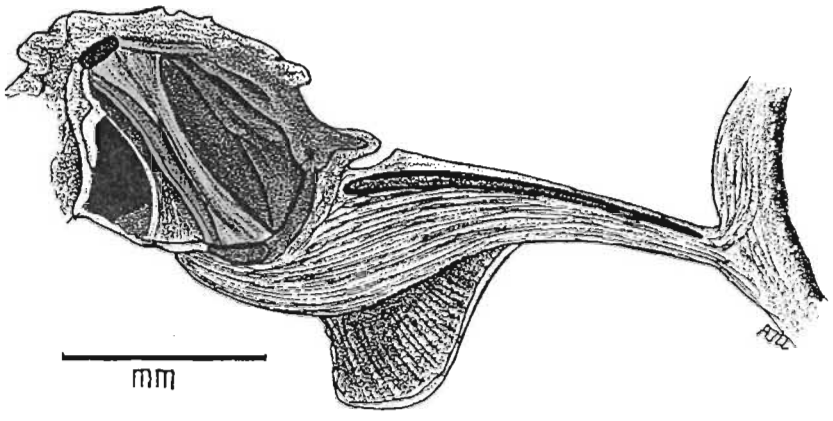


FIG. 1; *Microbatrachella capensis* (Boulenger, 1910)
NM 3301 (male), Landsdown, near Ottery, Cape Town, Western Cape, South Africa.

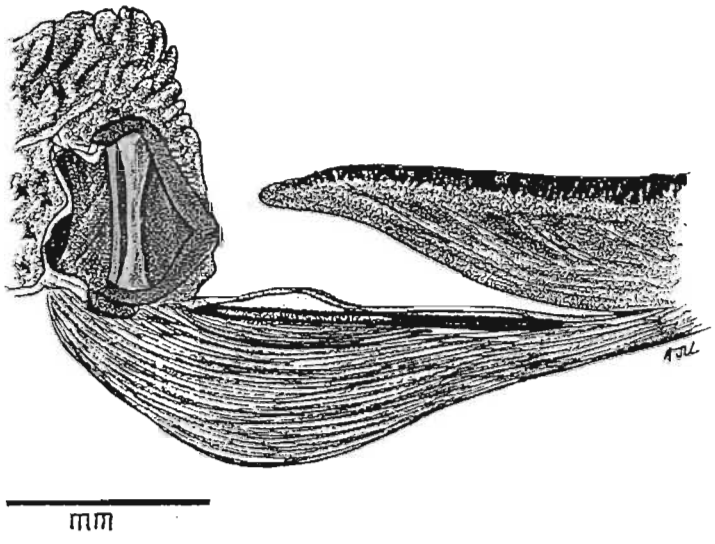


FIG. 2; *Microbatrachella capensis* (Boulenger, 1910)
NM 3299 (female), Landsdown, near Ottery, Cape Town, Western Cape, South Africa.

PLATE 52
ANHYDROPHRYNE – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

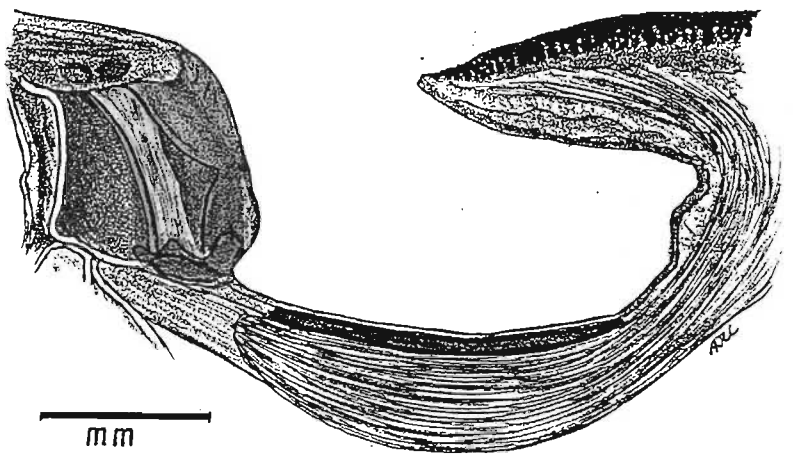


FIG. 1: *Anhydrophryne rattrayi* Hewitt, 1919
AJL 272 (male). Hogsback Forest, Eastern Cape, South Africa.

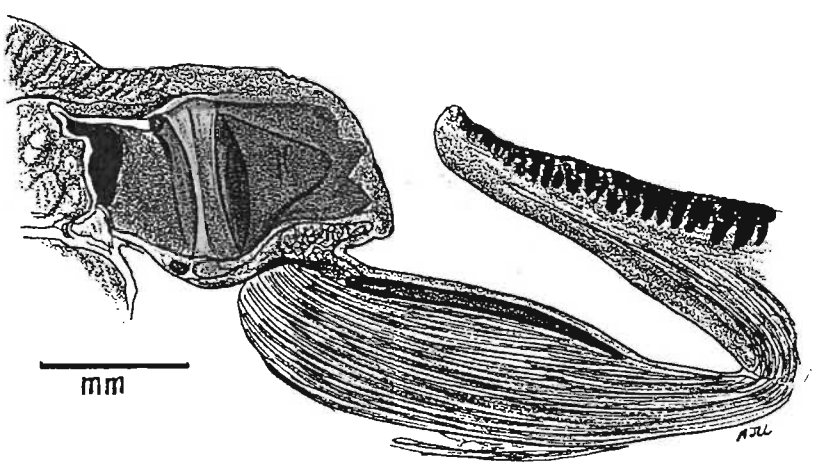


FIG. 2: *Anhydrophryne rattrayi* Hewitt, 1919
AJL 268 (female). Hogsback Forest, Eastern Cape, South Africa.

PLATE 53
ANHYDROPHRYNE – LARVAL BUCCOPHARYNX
Roof on left, floor on right

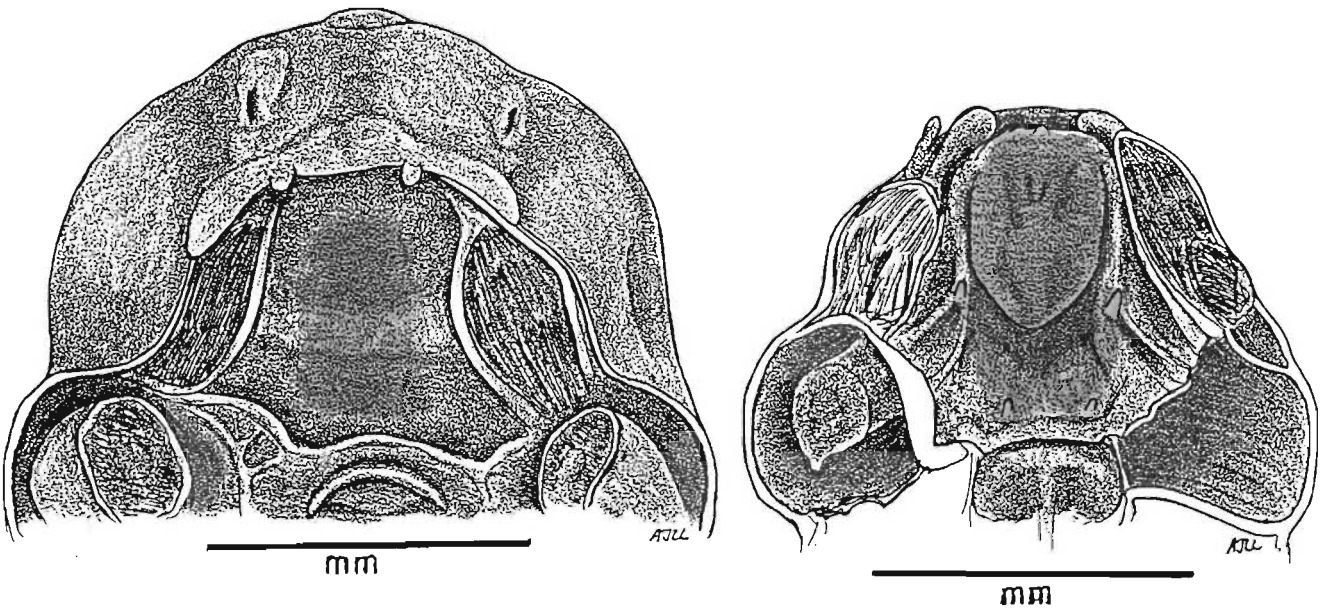


FIG. 1: *Anhydrophryne rattrayi* Hewitt, 1919
AJL 3394a, Stage 41, Hogsback Forest, Eastern Cape, South Africa.

TABLE 14. Laryngeal characters: *Arthroleptella*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

* = extralimital taxon included for comparison

	INFERIOR PROMINENTIA VOCALIA LARGE AND DISTINCT	SUPERIOR PROMINENTIA APICALIS RIDGED	INTERNAL MARGIN OF ARYTENOID OCCLUSAL SURFACE V-SHAPED	MEDIAL VOCAL CORD BROAD AND RATHER FLAT	MEDIAL VOCAL CORD FLANGED ON BOTH MARGINS	FRENULUM A SINGLE MEDIAL STRUCTURE	POSTERIOR MARGIN OF LATERAL VOCAL CORD STRONGLY ARCHED	POSTERIOR MARGIN OF LATERAL VOCAL CORD THICKENED
Arthroleptella hewitti	3	3	1	1	1	1	1	3
sp. nov. [Bishop, in prep.]	1	3	1	1	3	1	3	3
*lightfooti**	1	1	3	3	3	3	3	1

Genus *Arthroleptella* Hewitt, 1926

Arthroleptella Hewitt, 1926, *Ann. S. Afr. Mus.*, 20:426. Type species by original designation: *Arthroleptis lightfooti Boulenger*, 1910.

CHARACTERS

ADULT LARYNX (Tables 13 & 14; Pl. 54)

The larynx of the extralimital *Arthroleptella lightfooti* Boulenger, 1910, is included for comparison and for complete cover of the genus. A new species from Natal (Bishop, in prep.) has not yet been formally described and is here called "*Arthroleptella* sp. nov."

Pharyngeal mucosa

The pharyngeal mucosa covers the dorsum of the arytenoid cartilage in all three species but differs markedly in sectional profile. In *Arthroleptella lightfooti* it is smooth; in *A. hewitti* there are two or three conical protruberances anteriorly; and in *Arthroleptella* sp. nov. the anterior portion is thrown into deep, conspicuous plications.

Arytenoid cartilage

Superior and inferior prominentiae are feebly developed in *A. hewitti*, but are well developed in *A. lighfooti*. In *Arthroleptella* sp. nov. there is but a single massive inferior prominentia.

The occlusal surface is essentially broadly U-shaped in *Arthroleptella hewitti* and in *Arthroleptella* sp. nov., and distinctly squared-off in *A. lighfooti*.

Only in *A. lighfooti* is the anterosuperior portion of the occlusal surface adorned with a series of four or five short horizontal ridges.

The internal occlusal margin is U-shaped in *A. hewitti* and in *Arthroleptella* sp. nov., and strongly notched superiorly and apically in *A. lightfooti*.

Vocal cords

The medial vocal cord is flat and rather broad (more so inferiorly than superiorly) in *Arthroleptella hewitti* and in *Arthroleptella* sp. nov. It is narrower and more cylindrical in *Arthroleptella lightfooti*.

The lateral vocal cord shows considerable interspecific variation. In *A. hewitti* it is broad, strongly arched posterad, and traversed by a large, well defined frenulum that is broadly flared basally. In *Arthroleptella* sp. nov. it is much narrower, barely convex posteriorly, and is traversed by a much weaker, smaller frenulum. In *A. lightfooti* it is broad, with a thickened posterior margin, and the frenulum is arcuate.

Posterior chamber

The posterior chamber is relatively large in all three taxa. In *Arthroleptella hewitti* the wall anterior to the pulmonary aditus is thrown into vertical, somewhat chevron-like folds; it is irregularly folded in *Arthroleptella* sp. nov., and virtually smooth in *A. lightfooti*.

M. hyoglossus

In *Arthroleptella hewitti* and *Arthroleptella* sp. nov. the m. hyoglossus arises anterior to the inferior arytenoid symphysis and the inferior portion of the cricoid cartilage. In *A. lightfooti* it arises posterior to the cricoid cartilage.

LARVAL BUCCOPHARYNX (Pl. 55)

The buccopharynx of *Arthroleptella lightfooti* has been dissected and included for comparison with other direct-development taxa discussed in this survey; tadpoles of Natal taxa suitable for dissection were not available.

Buccal roof

A transverse ridge, with a slight median cusp, lies immediately behind the superior labium. The buccal roof is devoid of any other ornamentation.

Buccal floor

A pair of massive prelingual papillae (one on either side) lie transversely immediately anterior to the tongue anlage.

The buccal floor arena is flanked by a single large conical papilla on either side, but lacks any other structures.

There is no evidence of buccal pockets.

A large, broad, ventral velum is present.

No identifiable gill elements could be discerned in the single specimens dissected.

SPECIES ACCOUNT

Arthroleptella hewitti FitzSimons, 1947

Arthroleptella hewitti FitzSimons, 1947, *Ann. Natal Mus.*, 11:125, figs. 4a, b. Type locality: Cathedral Peak area, Drakensberg. Holotype in the Transvaal Museum, Pretoria. Poynton 1964:153, fig. 85. Van Dijk 1966:273. Passmore & Carruthers 1979:182, figs. Lambiris 1988:48, figs., pl. 5 figs. 1a & b; 1989a:114.

Arthroleptella hewitti minor FitzSimons, 1947, *Ann. Natal Mus.*, 11:128, fig. 5. Type locality: Bulwer, Natal. Holotype in the Transvaal Museum, Pretoria.

Arthroleptis lawrencei Loveridge, 1954, *Ann. Natal Mus.*, 13:97. Type locality: Town Bush, Pietermaritzburg. Holotype in the Natal Museum, Pietermaritzburg.

ADULT LARYNX (Tables 13 & 14; Pl. 54, fig. 1.)

Material examined: SOUTH AFRICA: NATAL - NM 1246 (m, SVL 19,9 mm), Lundies Hill, Umkomaas River. NM 634 (m, SVL 23,9 mm), Nkandla Forest. NM 3491 (f, SVL 24,0 mm), Karkloof. Topotypes of *Arthroleptis lawrencei* - NM 1108a (m, SVL 19,2 mm), NM 1108b (m, SVL 20,7 mm), NM 1108c (m, SVL 22,6 mm), Bat's Cave, Town Bush, Pietermaritzburg.

Advertisement call: A short (about 0.3 second long) chirp at about 2.2 kHz (Passmore & Carruthers 1979:194), uttered in short bursts five or six times a second, from concealed positions in moss or very short grass in wet areas. Calls are uttered both at night and on cloudy days.

Male larynx:

Pharyngeal mucosa: Smooth, overlying a rather deep submucosa sharply separated from the arytenoid cartilage. It is thrown into two or three conical protruberances anteriorly.

Arytenoid cartilage: The occlusal surface is broadly U-shaped, with very feebly developed expansions on the external margin. The arytenoid shelf is very broad, about 2.2x the apical width of the occlusal surface, and bears a single ridge parallel to the border of the large, elliptical arytenoid fossa.

Vocal cords: The **medial cord** is broad and flat, with flanged margins. It is only slightly flared superiorly, and more so inferiorly. There are no cartilaginous buttresses. The frenulum is large and well developed, rather triangular with considerably extended apices. The base (lateral and posterior to the anterior margin of the medial cord) extends almost across the length of the medial cord. The posterior

prolongation traverses the **lateral cord**, which is broad and has a strongly arcuate posterior margin.

Posterior chamber: Rather large, horizontally elongate. The lateral wall between the pulmonary aditus and the posterior margin of the lateral cord is thrown into six or seven vertical, somewhat chevron-like folds.

M. hyoglossus: Arises anterior to the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX

No tadpoles suitable for dissection were available.

Arthroleptella sp. nov. [Bishop, in prep.]

Arthroleptella sp. nov.: Bishop, 1985, *S. Afr. J. Sci.*, 81:209.

ADULT MALE LARYNX (Tables 13 & 14; Pl. 54, fig. 2)

Material examined: SOUTH AFRICA: NATAL - PB 13 (m, SVL 17,0 mm), and PB 19 (m, SVL 16,0 mm), about 15 km NE. of Ixopo. PARATYPES.

Advertisement call: Bishop (1985:209) has described the call as:

> "... a trilled cricket-like mating call with 10 pulses, repeated three or four times with an interval of a second between calls. The duration of the call is 55 ms and the midpoint of the frequency range is at 5,5 kHz. Males produce vocalisations throughout the day and night, on misty days, from concealed positions at the base of grass tussocks."

Pharyngeal mucosa: Thin, over a deep submucosa that is sharply demarcated from the dorsum of the arytenoid cartilage, and thrown into a number of deep, conspicuous plications anteriorly.

Arytenoid cartilage: The occlusal surface is of moderate width, broadly U-shaped, and bears a massive mammillate inferior prominentia vocalia, the base of which extends across most of the anteroinferior external margin. The arytenoid shelf is very broad, about twice the width of the occlusal surface above the level of the prominentia, and has a slight lentiform depression behind the occlusal margin. The fossa extends almost fully the length of the medial vocal cord.

Vocal cords: The **medial vocal cord** is broad and flat. It is slightly flared superiorly, and more so inferiorly. Only the posterior margin is flanged. There are no cartilaginous buttresses. The frenulum is a narrow band traversing the **lateral cord**, which is moderately broad and with a barely curved posterior margin.

Posterior chamber: Rather large, posterodorsally elongate. The lateral wall is thrown into a few irregular folds.

M. hyoglossus: Arises anterior to the inferior pulvinaria vocalia.

LARVAL BUCCOPHARYNX

Tadpoles of this species were not dissected for examination.

Arthroleptella lightfooti (Boulenger, 1910)

Arthroleptis lightfooti Boulenger, 1910, *Ann. S. Afr. Mus.*, 5:538. Type locality: Newlands, near Cape Town. Type apparently lost (Poynton 1964:152).
Arthroleptella lightfooti (Boulenger): Poynton 1964:152, fig. 84. Passmore & Carruthers 1979:192, figs.

ADULT MALE LARYNX (Tables 13 & 14; Pl. 54, fig. 3)

Material examined: SOUTH AFRICA: WESTERN CAPE - NM 5273 (m, SVL 16,4 mm), and NM 5798 (m, SVL 17,3 mm), Cape Town.

Advertisement call: Passmore & Carruthers (1979:192) describe the call as:

> "A rapidly pulsed insect-like chirp produced at irregular intervals."
>
> "Wet mossy areas associated with mountain streams and hillside seepages ... Calling males remain well concealed in cavities in the mud or moss."

The sonagram figured by Passmore & Carruthers shows a chirp about 0.8 second long at about 4 kHz.

Pharyngeal mucosa: Thin and smooth, overlying a deeper submucosa sharply separated from the arytenoid cartilage, and lacking folds.

Arytenoid cartilage: Superior and inferior prominentiae are moderately well developed. The superior prominentia bears four or five short horizontal ridges on the occlusal surface. The internal margin of the arytenoid occlusal surface is distinctly notched superiorly and apically. The arytenoid shelf is slightly wider than the occlusal surface at the apical notch, and has neither a posterior ridge nor a shallow depression.

Vocal cords: The **medial cord** is narrow, somewhat cylindrical, and flared superiorly and inferiorly. It lacks marginal flanges and buttresses. The **lateral cord** continues insensibly from the posterolateral aspect of the medial cord. It is broad, with a thickened posterior margin, and doubly traversed by an arcuate frenulum.

Posterior chamber: Rather large, elongate posterodorsally, and lacking distinct folds.

M. hyoglossus: Arises behind the inferior portion of the cricoid cartilage.

LARVAL BUCCOPHARYNX (Pl. 55, figs. 1a & b)

Identification of larvae: Van Dijk 1966.

Material examined: SOUTH AFRICA; WESTERN CAPE - AJL 3390a; Cape Town; stage 21, SVL 3,25 mm; silver impregnation.

Larval habitat: Encapsular; eggs laid under vegetational debris in mossy areas on wet ground and seepage areas.

Buccopharyngeal roof

General shape: Roughly trapezoid, base about 1.1x height. The roof is shallowly concave, and apart from a transverse fold (slightly cusped medially) behind the superior labium, lacks any of the structures found in free-living larvae. The buccal roof is flanked by enormous muscle masses on either side.

Buccopharyngeal floor

General shape: Roughly square. The floor is shallowly concave, with a pair of large but low eminences flanking the tongue anlage.

Prelingual papillae: A massive conical papilla arises on either side of the prelingual arena, the apices directed medially.

Lingual papillae: The tongue anlage bears no papillae, at least at this stage of development.

Buccal floor arena: A wide, short arena is defined by a single large, robust conical papilla on either side. There are no pustulations.

Buccal pockets: Absent.

Ventral velum: Broad, with a median notch in the anterior margin. The slightly thickened posterior margin lacks appendages.

Branchial baskets: Neither branchial baskets nor gill elements are discernible in this preparation.

DISCUSSION

Adult larynx

Larynxes from males of the two Natal species of *Arthroleptella* have much in common, the principal differences being the degree of folding of the pharyngeal mucosa and submucosa, and the massively enlarged inferior prominentia vocalia in *Arthroleptella* sp. nov.

The male larynx of *Arthroleptella lightfooti*, on the other hand, differs markedly from the two Natal forms, notably in the smooth mucosa, the completely different shape of the arytenoid occlusal surface, the striated superior prominentia vocalia, and especially in the general structure of the vocal cords. The narrow cylindrical medial cord of *Arthroleptella lightfooti* is totally at variance with the broad, flat cord of the two Natal species; as is also the lateral cord, with its thickened posterior margin, arcuate frenulum, and more elaborate confluence with the medial cord.

These differences between the larynxes of *Arthroleptella lightfooti* and of the two Natal species are so pronounced that one cannot but wonder if they do not indicate a generic difference. The pectoral girdle is very similar to that of the other two taxa, however, and the question must, for the moment, remain open.

Larval buccopharynx

Of the direct development larvae examined (*Breviceps*, *Anhydrophryne* and *Arthroleptella*), the buccopharynx of *Arthroleptella lightfooti* approaches most nearly the condition obtaining in free-living larvae. In *Arthroleptella lightfooti* (Pl. 55) the buccal floor arena is smaller than that of *Anhydrophryne*, but there is a large, well developed ventral velum. In *Anhydrophryne rattrayi* (Pl. 53) there is a large buccal floor arena demarcated by four small papillae, but no ventral velum. The buccopharynx of *Breviceps pentheri* (Pl. 20) lacks all structures apart from the tongue, and is probably the most highly specialised. These features correlate well with the progressively drier oviposition sites utilised in these genera.

PLATE 54
ARTHROLEPTELLA – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

FIG. 1: *Arthroleptella hewitti* FitzSimons, 1947
NM 1108a (male), Bats Cave, Town Bush, Pietermaritzburg, Natal, South Africa. (Topotype of *A. lawrencei* Loveridge.)

FIG. 2: *Arthroleptella* sp. nov. (Bishop, in prep.)
PB.013 (male). About 15 km NW of Ixopo, Natal, South Africa.
PARATYPE

FIG. 3: *Arthroleptella lightfooti* (Boulenger, 1910)
NM 5273 (male). Cape Town, Western Cape, South Africa.

PLATE 55
ARTHROLEPTELLA – LARVAL BUCCOPHARYNX
Roof on left, floor on right

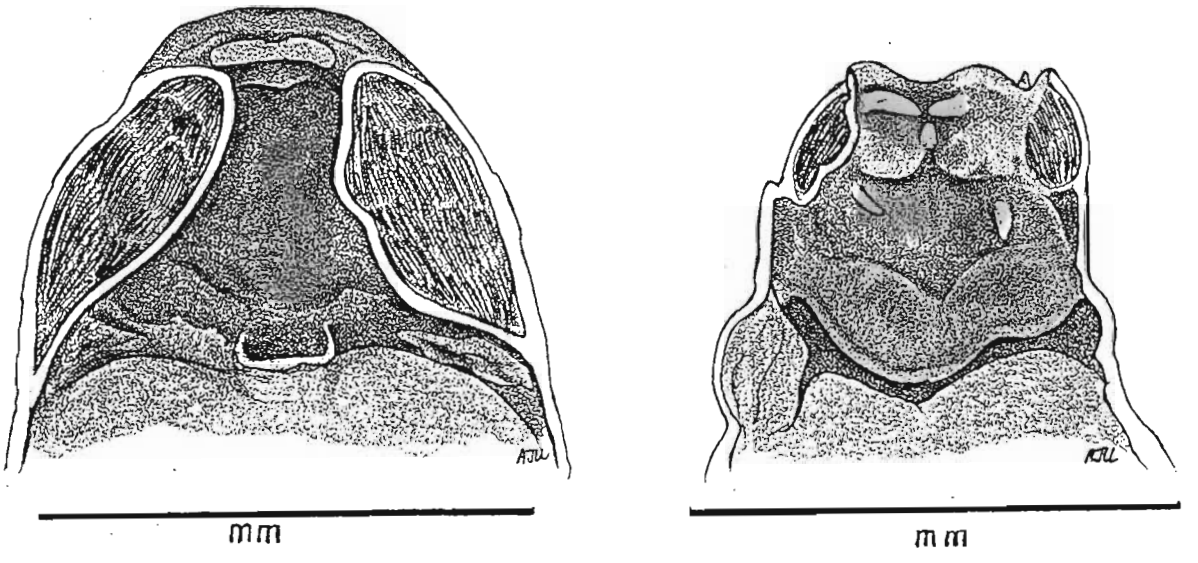


FIG. 1: *Arthroleptella lightfooti* (Boulenger, 1910)
AJL 3390a; Stage 21, Cape Town, Western Cape, South Africa.

Subfamily ARTHROLEPTINAE Mivart, 1869

Genus *Arthroleptis* A. Smith, 1849

Arthroleptis A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App., p. 24. Type species by monotypy: *Arthroleptis wahlbergii* A. Smith, 1849.

Schoutedenella de Witte, 1921, *Rev. Zool. Afr.*, 9:18. Type species by monotypy: *Schoutedenella globosa* de Witte, 1921.

Coracodichus Laurent, 1940, *Rev. Zool. Bot. Afr.*, 34:85. Type species by original designation: *Arthroleptis whytii* Boulenger, 1897.

CHARACTERS

ADULT LARYNX (Plate 56)

The larynxes of the two taxa examined, *Arthroleptis wahlbergii* and *A. stenodactylus*, have a fairly close general resemblance to those of the Phrynobatrachinae, and differ quite considerably from those of the Hyperoliidae (which generally tend to have more complex arytenoid cartilage / arytenoid fossa / vocal cord structures and relationships), as can easily be seen by inspecting the plates.

Arytenoid cartilage

The arytenoid cartilage is large and deep. Prominentiae apicales are absent.

The occlusal surface is rather weakly defined, but variously ridged or corrugated in the two species examined. Only in *Arthroleptis wahlbergii* is there any clear indication of an arytenoid valve. The internal margin is U-shaped in *Arthroleptis wahlbergii*, cusped in *A. stenodactylus*.

The arytenoid shelf is broad (*Arthroleptis stenodactylus*) to very broad (*A. wahlbergii* and the arytenoid fossa is rather small, with a rather rounded anterior margin.

Pulvinaria vocalia are feebly developed in both species.

Vocal cords

The medial cord is flat and broad (*Arthroleptis stenodactylus*) or very broad (*A. wahlbergii*). It lacks marginal flanges and cartilaginous buttresses.

A lateral cord is discernible only in *Arthroleptis stenodactylus*. It is small and mostly obscured by the medial cord. A fusiform frenulum protrudes beyond the posterior margin of the lateral cord, as is the case in *Phrynobatrachus*.

Posterior chamber

No taxonomically useful characters could be found.

M. hyoglossus

The m. hyoglossus arises approximately below the level of the inferior insertion of the medial vocal cord.

LARVAL BUCCOPHARYNX

No tadpoles suitable for dissection were available for study.

SPECIES ACCOUNT

Arthroleptis wahlbergii A. Smith, 1849

Arthroleptis wahlbergii A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App., p. 24. Type locality: "interior of South Africa". Holotype in the British Museum (Natural History), London.

Arthroleptis wageri FitzSimons, 1930, *Ann. Natal Mus.*, 14:42. Type locality: Port St. Johns, Transkei. Holotype in the Transvaal Museum, Pretoria.

Arthroleptis dalenei Hoffman, 1940, *Soöl. Navors. Nas. Mus. Bloemfontein*, 1:97. Type locality: Mazongwaan Forest, Greytown, and the Bluff, Durban. Holotype in the National Museum, Bloemfontein.

Arthroleptis lawrencei Loveridge, 1954, *Ann. Natal Mus.*, 13:97. Type locality: "Town Bush, Pietermaritzburg, Natal". Holotype in the Natal Museum, Pietermaritzburg.

Arthroleptis wahlbergi A Smith: Poynton 1964:160, fig. 89. Passmore & Carruthers 1979:206, figs.

Arthroleptis wahlbergii A. Smith: Poynton & Broadley 1985a:536. Lambiris 1989a:116.

ADULT MALE LARYNX (Pl. 56, fig. 1)

Material examined: SOUTH AFRICA: NATAL - AJL 1896 (m, SVL 23,0 mm), Scottburgh. AJL 1975 (m, SVL 23,0 mm), Monteseel.

Advertisement call: A thin, plaintive "weep!" about 0.2 second long, at 4 kHz (Passmore & Carruthers 1979:206), uttered in chorus about once a second, from concealed positions in dense grass or bush in or near water. Calling is both at night and on overcast days.

Pharyngeal mucosa: Thin and smooth, over a deeper submucosa covering the dorsum of the arytenoid cartilage. The anterior surface of the cartilage is covered by mucosa only.

Arytenoid cartilage: Broad and deep. The external margin of the occlusal surface is a rather square U-shape. The occlusal surface is feebly defined by the folds of the arytenoid valve; there is no sharp step to the shallow, broad arytenoid shelf. The major diameter of the arytenoid fossa is about 0.75x the length of the medial vocal cord.

Vocal cord: Only the medial cord is visible. It is very broad (medial width about 0.25x length) and flat, flared more widely superiorly than inferiorly, slightly thickened along the posterior margin, and lacks buttresses.

Posterior chamber: The pulmonary aditus is rather small (about 0.25x the diameter of the posterior chamber). The lateral wall anterior to the aditus is rather folded.

LARVAL BUCCOPHARYNX

No tadpoles suitable for dissection were available for study.

Arthroleptis stenodactylus Pfeffer, 1893

Arthroleptis stenodactylus Pfeffer, 1893, *Jrb. Hamburg. Wiss. Anst.*, 10:93, pl. 1, fig. 11. Type locality: Kihengo, Tanganyika. Holotype destroyed. Poynton 1964:163, fig. 92, Passmore & Carruthers 1979:208, figs. Poynton & Broadley 1985a:536. Lambiris 1989a:117; 1989b:134, fig. 74, pl. 16 figs. 1a-c.

Arthroleptis whytii Boulenger, 1897, *Proc. Zool. Soc. Lond.*, 1897:802. Type locality: Kondowe to Karonga; Nyika Plateau; Misuku Mountains, Nyasaland [restricted to Misuku Mountains by Loveridge, 1953].

ADULT LARYNX (Pl. 56, fig. 2)

Material examined: SOUTH AFRICA: NATAL - NM 5802 (m, SVL 31.3 mm), and NM 5804 (m, SVL 26.0 mm), Eastern Shores, Lake St. Lucia. MALAWI: AJL 3204 (f, SVL 22.0 mm), Nkhata Bay, Lake Malawi.

Advertisement call: A short (about 0.05 second) chirp at about 2.3 kHz (Passmore & Carruthers 1979:208) uttered, in chorus, about twice a second, from the cover of vegetational debris near water.

Male larynx:

Pharyngeal mucosa: Fairly thick and smooth, over a deeper submucosa covering the dorsum of the arytenoid cartilage only.

Arytenoid cartilage: Broad and deep. The external margin of the broad occlusal surface is U-shaped, and somewhat corrugated on the anterosuperior margin. The internal occlusal margin is quite clearly defined. Its shape is irregular, with a pronounced cusp dividing the arytenoid shelf into two parts -- a narrow superior portion, about as wide as the vocal cord; and a broadly ovate inferior portion about twice the width of the vocal cord. The major diameter of the weakly defined arytenoid fossa is about 0.3x the length of the medial vocal cord.

Vocal cords: The **medial cord** is moderately broad (medial width about 0.15x length) and flat. It is slightly but distinctly flared superiorly and inferiorly. The margins are not flanged, and there are no buttresses. The **lateral cord** is small and covered, for the most part, by the lateral cord. A short fusiform frenulum extends beyond the posterior margin at about the mid-point.

LARVAL BUCCOPHARYNX

The tadpole appears to be unknown.

DISCUSSION

Adult larynx

Arthroleptis wahlbergii, as currently recognised, includes in the synonymy (e.g. Poynton 1964; Lambiris 1989a) three forms -- *A. wageri* FitzSimons, 1930; *A. dalenei* Hoffman, 1940; and *A. lawrencei* Loveridge, 1954 -- that are poorly, if at all, separable on external morphological and on pectoral girdle characters. Specimens from the Transkei and from Zululand are, however, larger and more robust than those from other parts of the species' range, approaching *Arthroleptis stenodactylus* in general habitus.

Smith's type locality ("Inhabits the interior of South Africa") is meaningless and makes the collection of topotypes (in any useful sense) impossible. The type material was not available for study, and the attribution of the larynx described and illustrated here to *Arthroleptis wahlbergii* **sensu stricto** is, at present, purely conjectural.

A detailed study of laryngeal morphology throughout the species' range, correlated with analysis of advertisement calls, size and other morphological features, is needed to ascertain the status of the forms currently relegated to the synonymy of *Arthroleptis wahlbergii*. Such a major investigation could not be undertaken as part of this general survey, as extending far beyond its scope and time available.

It is possible that laryngeal morphology could shed light on the status of *Coracodichus* and *Schoutedenella*, but again this would involve the examination of far more extralimital material than would be justified in the present study.

The status of the family Arthroleptidae (*sensu* Frost 1985) has been a matter of some disagreement (Lambiris 1989a:69). Lynch (*in* Frost 1985:14) remarks that "The recognition of this family [Arthroleptidae] is premature given that no phylogenetic justification or diagosis has been presented." Although it is not the aim of the present study to address issues of classification above the species level, it may be

remarked that the larynxes of the two taxa examined have an overall similarity to those of the Phrynobatrachine genera studied, particularly with respect to the the fusiform frenulum found in both *Phrynobatrachus* and *Arthroleptis*. A study of larynxes drawn from all Phrynobatrachine and Arthroleptine genera may be useful in resolving this issue.

Larval buccopharynx

The only tadpole specimens available were too damaged by alcohol preservation to be dissectable. Comparison with other direct-development larvae would be interesting, in view of the trends shown in *Breviceps*, *Anhydrophryne* and *Arthroleptella*.

PLATE 56
ARTHROLEPTIS – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

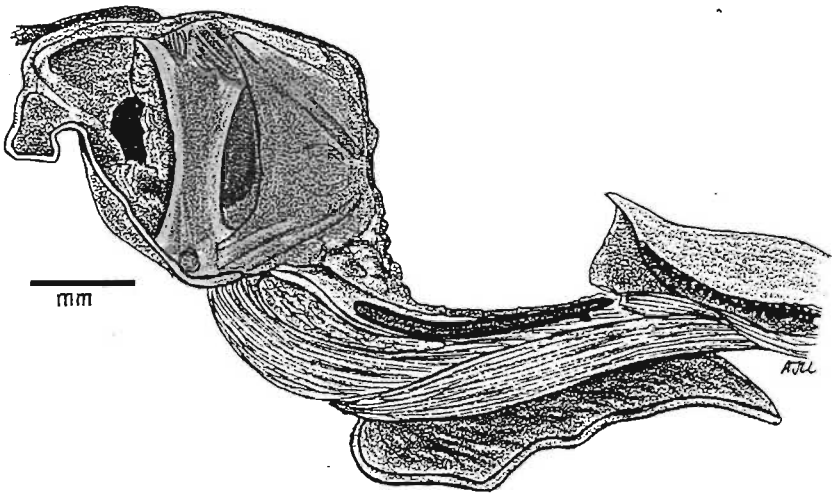


FIG. 1: *Arthroleptis wahlbergii* A. Smith, 1849
AJL 1896 (male), Scottburgh, Natal, South Africa.

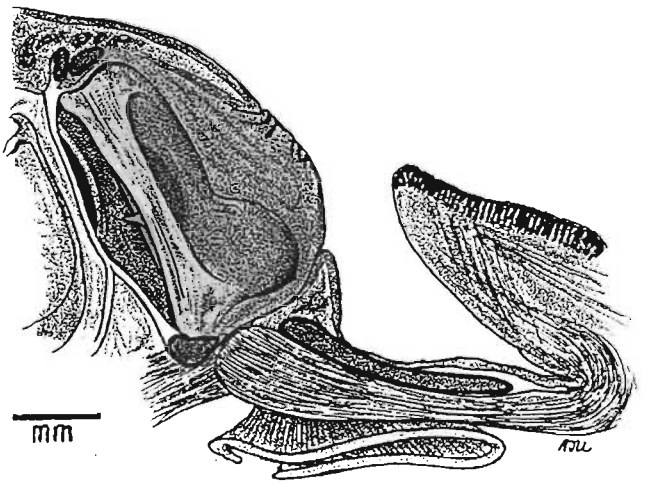


FIG. 2: *Arthroleptis stenodactylus* Pfeffer, 1893
NM 5804 (male), Lake St. Lucia, E. shore, Natal, South Africa.

Family RHACOPHORIDAE Hoffman, 1932 (1859)

Genus *Chiromantis* Peters, 1854

Chiromantis Peters, 1854, Mber. Königl. Akad. Wiss. Berlin, 1854:626. Type species by monotypy; *Chiromantis xerampelina* Peters, 1854.

CHARACTERS

ADULT LARYNX (Pl. 57)

The characteristics of the single species treated are described in detail in the species acount, below.

Sexual dimorphism is not marked. The female larynx is slightly smaller than that of the male, and resembles it in most respects. It differs in having a narrower occlusal surface and in lacking a clearly defined arytenoid shelf.

LARVAL BUCCOPHARYNX (Pl. 58)

The characters of the single species treated are described in detail in the species account, below. Only the buccopharynx of a free-swimming larva has been examined and described; those of early stages still developing within the nest have not been studied in this survey.

SPECIES ACCOUNT

Chiromantis xerampelina Peters, 1854

Chiromantis xerampelina Peters, 1854, *Mber. Königl. Akad. Wiss. Berlin*, 1854:626. Type locality: Tete and Sena, Mozambique. Syntypes in the Zoologisches Museum, Berlin. Poynton 1964:157, fig. 88. Van Dijk 1966:273. Passmore & Carruthers 1979:202, figs. Poynton & Broadley 1987:165. Lambiris 1989a:119; 1989b:39, figs. 77 & 78, pl. 15 figs. 2a-c.

Chiromantis umbelluzianus Ferreira, 1921, *J. Sci. Math. Phys. Nat. Lisboa*, 2:205, pls. i, ii. Type locality: Umbelluzi Bridge, 50 km from coast, Lourenço Marques [= Maputo] district. Holotype destroyed.

Chiromantis microglossus Ahl, 1929, *Zool. Anz.*, 80:34. Type locality: Damara. Holotype in the Zoologisches Museum, Berlin.

ADULT LARYNX (Pl. 57, figs. 1 & 2)

Material examined: SOUTH AFRICA: TRANSVAAL - AJL 2931 (m, SVL 65,0 mm), Karino. ZIMBABWE: AJL 1441 (f, SVL 56,5 mm), Sanyati River Mouth, Lake Kariba.

Advertisement call: Subdued trilled chirps and croaks, 0.1 - 0.2 second long, between 1 - 2 kHz (Passmore & Carruthers 1979:202), uttered at night, individually or in loose chorus, from branches overhanging water.

Male larynx:

Pharyngeal mucosa: Thick, deeply folded, blending into the submucosa, and covering the anterodorsal portion of the arytenoid cartilage.

Arytenoid cartilage: Somewhat anteroposteriorly compressed. The occlusal surface is widely V-shaped, rather narrow but well defined, and bears a large, convoluted inferior prominentia only. There is no arytenoid valve. The arytenoid shelf is relatively broad (axial width about 2.5x occlusal surface width), tapering superiorly and inferiorly. The arytenoid fossa is narrowly elliptical and extends the full width of the anterior margin of the medial vocal cord. The pulvinaria vocalia are weakly developed.

Vocal cords: The medial vocal cord is flat, broad and robust. The anterior margin is thickened, particularly towards the insertions. The posterior margin has a large rectangular superior cartilaginous buttress

and an inferior marginal thickening. The **lateral cord** is well developed, and somewhat triangular in shape. There is no obvious frenulum.

Posterior chamber: Slightly smaller than the anterior chamber. The small pulmonary aditus is bordered by a cartilaginous rim anteriorly.

M. hyoglossus: Arises below the inferior insertion of the medial vocal cord.

LARVAL BUCCOPHARYNX (Pl. 58, fig. 1a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 2431; Mboneni Pan, Mkuzi Game Reserve; stage 35/36, SVL 15.2 mm; silver impregnation.

Larval habitat: Up to about stage 26, development is within the foam nest created by the parents, and nourishment is provided by a large internal yolk sac. Subsequent development is in water, generally a seasonal but long-lasting pool, or a stream with minimal flow, over a fine sandy or silted substratum. Aquatic macrophytes tend to be few and not very large. The diet of the free-swimming larva seems to consist principally of small algae.

Buccopharyngeal roof

General shape: Triangular, but with very rounded apices. Base about 1.3x height. General surface concave, with a broad, paraboloid, deep prenarial arena and a large but shallow fossa in the buccal roof bounded posterolaterally by a somewhat raised rim.

Prenarial arena: A median papilla is flanked by a shallow oval eminence on either side. There are no pustulations.

Internal nares: Narrow slits, very slightly angled posteromedially. The narial width is about 0.42x the width of the roof at that level. The internarial distance is about 0.4x the narial width.

Narial valve: Well-developed flaps on the anterior and posterior margins. The anterior flap bears a subconical papilla (height equal to internarial distance) at about the mid-point. The posterior margin is rather deeply grooved.

Postnarial arena: Wide but very narrow. A cylindrical **postnarial papilla** (height about 0.5x the narial width) arises shortly behind the medial third of the internal naris. It has a small pustulate papilla set laterally near its base. The **lateral ridge papilla** is minute, arising immediately behind the lateral angle of the internal naris. The **median ridge** is a semicircular flap set just behind the postnarial papillae; the base is only a little less than the interpapillary distance. The free margin of the median ridge is pustulose.

Buccal roof arena: Somewhat rectangular, about 0.5x the width of the buccal fossa, and bounded laterally by 2 (right) or 3 (left) very short cylindrical papillae. The arena contains numerous densely scattered pustules which extend slightly beyond the arena, but not outside the fossa.

Glandular ridge: A broad, well-defined band traversing the width of the buccal roof posteriorly.

Dorsal velum: Apparently lacking.

Pressure cushions: Large and well developed. The medial cushion is transversely ovate, the lateral cushion longitudinally narrowed.

Buccopharyngeal floor

General shape: Triangular, but with very rounded apices. Base about 1.4x height. General surface concave, with a deep prelingual arena and a shallow retrolingual chiasma extending into the anterior half of the buccal floor arena.

Prelingual arena: A small conical papilla arises, on either side, from the middle of the ventrolateral junction. A pair of large papillae (a smooth papilla set directly dorsal to a pustulose one) arises from the posterolateral wall of the arena.

Lingual papillae: A group of three close-set stubby, conical papillae arise from the mid-dorsum of the tongue anlage, the posterior margin of which also bears a close-set row of five large pustules.

Buccal floor arena: Large, semicircular, occupying most of the buccal floor between the lingual arena and the ventral velum. It is bordered laterally and posteriorly by numrous pustulate or stubbily cylindrical papillae (two of which, on the left side in this specimen,

are terminally bifid), set in a rather irregular row. The posterior half of the arena contains about 7 similar papillae, irregularly arranged.

Buccal pockets: Narrowly elliptical, shallow, closed, and not deeply grooved marginally. There are no prepocket papillae.

Ventral velum: Broad, of subequal width throughout, and with a thickened free margin bearing papillate appendages. The middle third of the velum bears a group of three (right) or four (left) close-set lobes on either side of a median lobe; these are flanked laterally, after a short space, by a pair of close-set lobes, and finally by a single, more lateral lobe. Supporting spicules are present, but only the paramedian pair are at all distinct.

Branchial baskets: Large, hemispherical, about 0.3 of the buccopharyngeal area. The major axis is directed posterolaterally.

Filter plates: Broad, open, with complete rows only. The filter rows have secondary and tertiary folds, and the channels are narrow.

PLATE 57
CHIROMANTIS – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

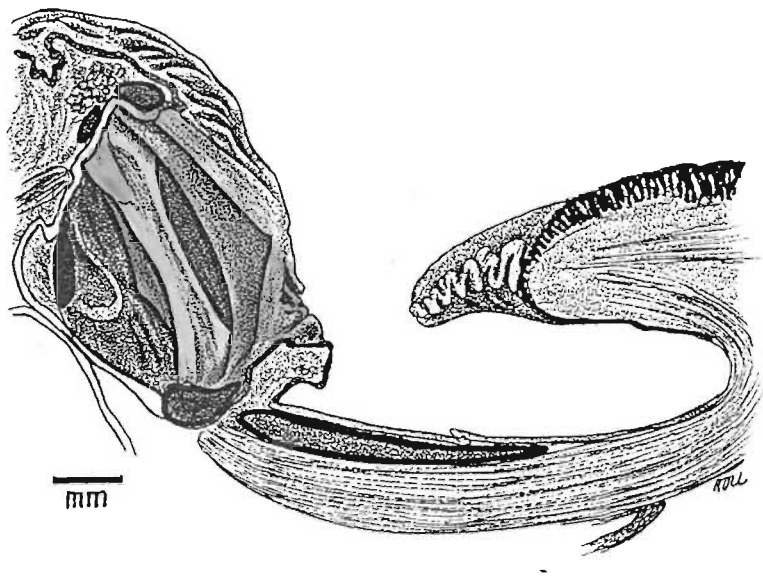


FIG. 1: *Chiromantis xerampelina* Peters, 1854
AJL 2931 (male), Karino, Nelspruit district, Transvaal, South Africa.

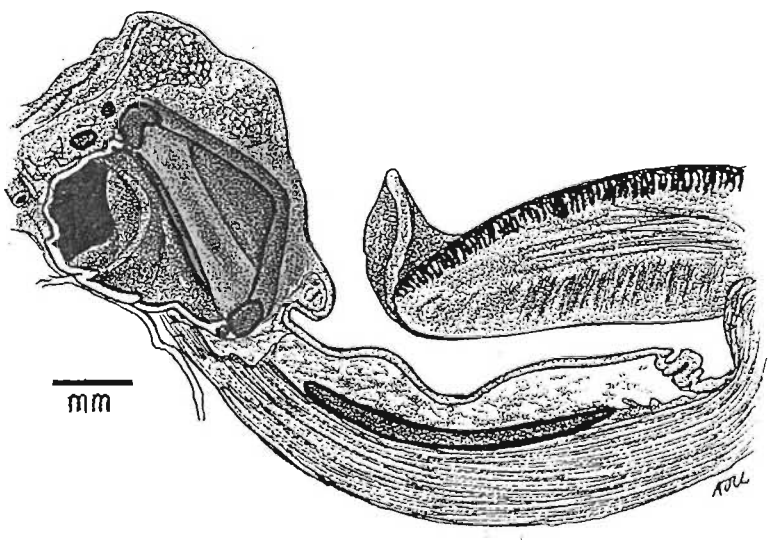


FIG. 2: *Chiromantis xerampelina* Peters, 1854.
AJL 1441 (female), Sanyati River Mouth, Lake Kariba, Zimbabwe.

PLATE 58
CHIROMANTIS – LARVAL BUCCOPHARYNX
Roof on left, floor on right.

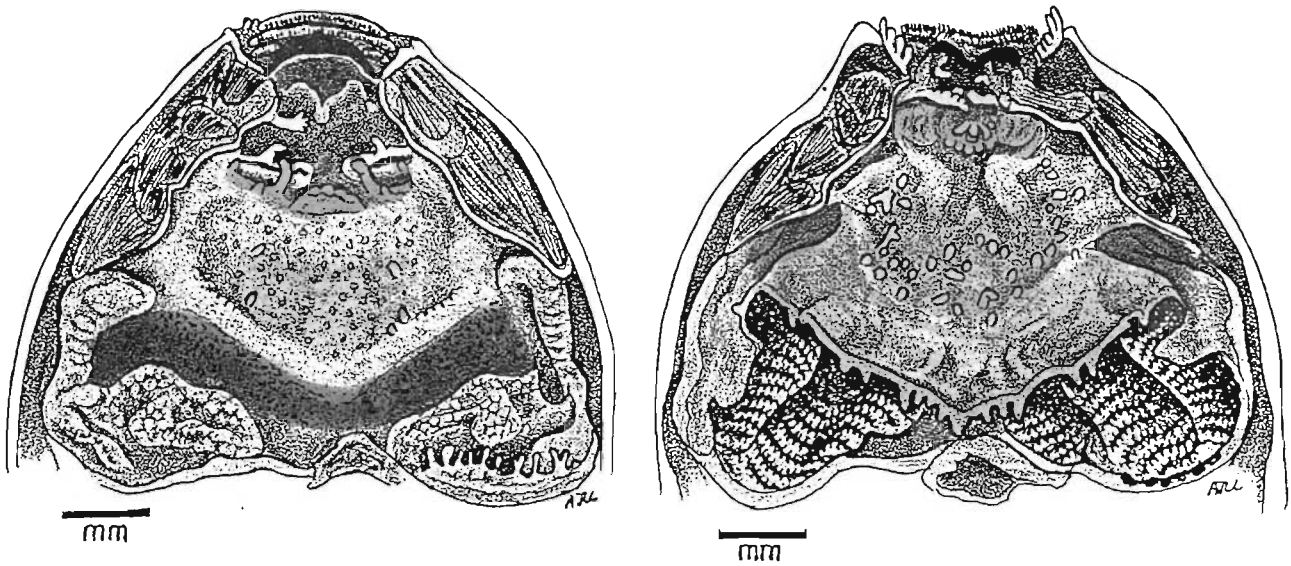


FIG. 1: *Chiromantis xerampelina* Peters, 1854
AJL 2431, Stage 35/36, Mboneni Pan, Mkuzi Game Reserve, Natal, South Africa.

TABLE 15. Laryngeal characters: *Leptopelis*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	MUCOSA COVERS THE WHOLE EXTERNAL SURFACE OF THE ARYTENOID CARTILAGE	OCCLUSAL SURFACE BROAD	ARYTENOID VALVE PRESENT	MEDIAN POSTERIOR MARGIN OF ARYTENOID SHELF ENTERS ARYTENOID FOSSA	BUTTRESSES OF MEDIAL VOCAL CORD LARGE AND CONSPICUOUS	BUTTRESSES OF MEDIAL VOCAL CORD FLANGED	FRENULUM BROAD
Leptopelis natalensis	3	1	3	1	1	3	3
mossambicus	1	3	1	3	1	1	1
xenodactylus	3	1	3	1	3	1	1

Family HYPEROLIIDAE Laurent, 1943

Subfamily LEPTOPELINAE Laurent, 1972

Genus *Leptopelis* Günther, 1859 "1858"

Leptopelis Günther, 1859 "1858", *Cat. Batr. Sal. Brit. Mus.*, p. 89. Type species by monotypy: *Hyla aubryi* Dumeril, 1856.

CHARACTERS

ADULT LARYNX (Table 15; Pl. 59)

Interspecific differences in male larynxes of the taxa examined are summarised in Table 15. The large hemiscyphiform arytenoid cartilage, tiny arytenoid fossa and rather convoluted medial vocal cord appear to be common generic features.

Sexual dimorphism (*Leptopelis natalensis*, Pl. 59, figs 3 & 4) is marked, the larynx of the female being much simpler than that of the male.

Arytenoid cartilage

The occlusal surface is semicircular, and of roughly subequal width throughout. There are no prominentiae. Only in *Leptopelis mossambicus* is there an arytenoid valve. The apical width of the occlusal surface is about half the axial width of the arytenoid shelf in *Leptopelis natalensis* and *L. xenodactylus*, and about one quarter of the axial width of the shelf in *L. mossambicus*.

The arytenoid shelf is clearly defined in all three taxa. It is traversed by a slightly raised triangular segment, the apex of which enters the arytenoid fossa in *Leptopelis natalensis* and *L. xenodactylus*.

The arytenoid fossa is circular, very small (0.11 - 0.12x the length of the medial vocal cord) but deep, and contained in the arytenoid shelf, close to its posterior border. The anterior border of the medial vocal cord does not enter margin of the fossa.

Pulvinaria vocalia are large to massive. In *Leptopelis natalensis* the inferior pulvinarium is much larger than the superior, whereas in *L. mossambicus* the reverse is true. In *L. xenodactylus* the superior and inferior pulvinaria are equally large.

Vocal cords

Medial and lateral vocal cords are present and well developed.

The **medial cord** is basically lorate, but is somewhat twisted, arcuate, delicately membranous, and distinctly (*Leptopelis mossambicus* and *L. xenodactylus*) or barely (*L. natalensis*) flanged on the posterior margin. The cord is tapered at the insertions in *L. natalensis* and *L. mossambicus*, which have single large superior and inferior cartilaginous buttresses. In *L. xenodactylus* the cord is less tapered, and the buttresses are smaller expansions of the posterior flange.

The **lateral cord** is distinctly arcuate in *Leptopelis natalensis* and *L. xenodactylus*, much less so in *L. mossambicus*. The posterior margin is thickened by a distinct rim. The cord is traversed by a distinct frenulum in *L. mossambicus*, and a progressively poorly defined one in *L. xenodactylus* and *L. natalensis*.

Posterior chamber

The posterior chamber lacks distinctive features. The pulmonary aditus is of moderate size in *Leptopelis natalensis* and *L. mossambicus*, and large in *L. xenodactylus*. In all three species it is more or less encircled by a rim of cartilage.

M. hyoglossus

The m. hyoglossus arises from a distinct aponeurosis well anterior to the inferior pulvinaria vocalia in all three species.

LARVAL BUCCOPHARYNX (Pl. 60)

Only the tadpole of *Leptopelis natalensis* was available for dissection. A single tadpole of *L. mossambicus* (AJL 2680), still to be described, was not dissected for this study; that of *L. xenodactylus* is still unknown.

SPECIES ACCOUNT

Leptopelis natalensis (A. Smith, 1849)

Polypedates natalensis A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App., p. 25. Type locality: "a small river to the westward of Port Natal [i.e., Durban]. Holotype in the British Museum (Natural History), London.

Leptopelis natalensis (A. Smith); Poynton 1964:168, fig. 95. Van Dijk 1966:257, Passmore & Carruthers 1979:218, figs. Lambiris 1989a:121.

ADULT LARYNX (Table 15; Pl. 59, fig. 1)

Material examined: SOUTH AFRICA: NATAL - AJL 2004 (m, SVL 43.8 mm) and 2005 (m, SVL 45.0 mm), Krantzkloof Nature Reserve. AJL 2881 (m, SVL 37.7 mm), Ngoye Forest, Eshowe district. AJL 1960 (f, SVL 53.2 mm), Waterfall.

Advertisement call: A loud quack about 0.3 second long, at about 2 kHz (Passmore & Carruthers 1979:218) often uttered in closely-spaced pairs at long to very long intervals; and sometimes preceded by a soft buzzing at the same pitch. Calls are uttered from leafy branches or from broad leaves near, or overhanging, water. Calls are usually uttered at night.

Male larynx:

Pharyngeal mucosa: Thin, blending with a thicker submucosa covering the dorsum and anterior surfaces of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface semicircular, more or less subequal in width throughout, and lacking an arytenoid valve. It is about half the axial width of the broad arytenoid shelf. The apex of the arytenoid triangle enters the anterior margin of the fossa. The diameter of the arytenoid fossa is about 0.11x the length of the medial vocal cord. The inferior pulivinarium vocale is massive.

Vocal cords: The **medial cord** is basically lorate, but tapered towards the insertions, and somewhat twisted. The posterior margin is not, or barely, flanged. There are single large, triangular superior and inferior cartilaginous buttresses. The **lateral cord** is large, strongly arcuate, and has a thick posterior rim. The frenulum is very feebly developed.

Posterior chamber: The pulmonary aditus is bordered anteroventrally by a stout cartilaginous rim.

LARVAL BUCCOPHARYNX (Pl. 60, fig. 1a & b)

Identification of larvae: Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 2891; Hluhluwe Game Reserve; stage 39/40, SVL 15,0 mm); silver impregnation. TRANSKEI - AJL 3361a, stage 38, SVL 14,4 mm, and AJL 3362a, stage 40, SVL 20,0 mm; Umzimvubu River Mouth, Port St. Johns; silver impregnation.

Larval habitat: Pools and pans with rather dense marginal emergent grassy vegetation, on silted substrata. The diet consists of fragments from soft parts of macrophytes, and of algae.

Buccopharyngeal roof

General shape: Roughly triangular, base about 1.2x height. The general surface is concave, with a slightly deeper fossa containing the buccal roof arena. The prenarial arena is large, trapezoid and deep, with a medially cusped ridge behind the beak.

Prenarial arena: There are four pustules -- one immediately behind the apex of the median cusp, and three set in a transverse row immediately behind it, across the middle third of the arena.

Internal nares: Broad, pyriform, the apices directed medially. The major axis is set slightly anteromedially. The narial width is about 0.43x the width of the roof at that level, and the internarial distance is about 0.25x the narial width. There is a small cylindrical **prenarial papilla** arising from the anterior margin, immediately lateral to the anterior narial valve.

Narial valve: Consists of three flaps. The **anterior valve** is deeper laterally than medially. It occupies the middle portion of the anterior margin and is about 0.6x the narial width. The free margin is ctenate. The **posterior valve** is of equal width throughout. It extends over the medial portion of the margin, and is about 0.4x the narial width. The free margin is serrate or ctenate. The medial angle has a simple **medial valve**. The lateral border of the naris is emarginate.

Postnarial arena: Postnarial papillae appear to be absent, the large to massive conical structures present all appearing to be **lateral ridge papillae**. There are 3 - 4 on either side, set dorsoventrally, and diminishing in size ventrally. The anterior margin of each is pustulate. The largest one on each side is pustulose over the whole surface, and in two instances is slightly bifid terminally on one side. The **median ridge** is a broad arcuate flap as wide as the buccal roof arena. The slightly thickened free margin bears four irregular papillate projections, two of which are paramedial. There are 6 - 8 small pustules along the base of the ridge.

Buccal roof arena: Outline U-shaped; about 0.4x the width of the buccal roof. The arena is bordered posterolaterally by 8 - 10 tall, narrow cylindrical papillae (diminishing slightly in size posteriorly) on either side, interspersed with a number of smaller papillae. There are about 30 - 35 pustules rather densely scattered over the arena.

Additional papillae: The prominences of the buccal roof flanking the arena have 5 - 8 smaller papillae on either side.

Dorsal velum: There appears to be no dorsal velum.

Pressure cushions: Rather small, slightly convoluted, and only feebly divided into lobes.

Buccopharyngeal floor

General shape: Triangular, the base about 11.1x the height. General surface more or less regularly concave. The trapezoid prelingual arena is deeply excavate.

Prelingual arena: A small bifid papilla arises from the lower part of the lateral wall on either side, the apex directed medially. A similar median papilla arises from the floor immediately anterior to the tongue anlage. The walls of the arena each bear a horizontal **lateral ridge**, the medial margin of which is finely lobulate (3 - 4 lobules on each), and which is prolonged posteriorly into a J-shaped papilla with a bluntly trifid tip. The flexure of the papilla reaches the middle of the tongue anlage on each side.

Lingual papillae: The tongue anlage bears five close-set papillae on the anterodorsal surface, set in two transverse rows. The anterior row consists of three tall conical papillae, the posterior row of two

slightly shorter ones. The tongue anlage has three large, close-set pustules on the middle of the posterior margin.

Buccal floor arena: Large, semicircular, occupying the full width of the floor between the buccal pockets. It is bounded laterally and posteriorly by conical papillae, tallest and more robust anteriorly, becoming shorter and more gracile posteriorly. The largest ones tend to have a pair of short protruberances at about mid-point, and to have confluent, or almost confluent, bases. The smaller papillae are more distinctly separated. The arena contains about 20 - 25 scattered pustules. The apex of the arena is capped by a much denser group of about 15 small pustules lying immediately before the anterior margin of the ventral velum.

Buccal pockets: Large, pyriform to oval, closed, shallow, and with narrowly but deeply grooved anterior margins. There are 3 - 5 small **prepocket papillae** on either side.

Ventral velum: Broad and well developed, slightly narrower medially. The thickened free margin bears three rather long, robust, equally-spaced papillae on either side of a shorter pair of paramedian lobes. There are three prominent supporting spicules on either side, the velum having a pair of calyculate depressions between the spicules, on either side of the medial quarter.

Branchial baskets: Large, rounded, the major axis directed rather posterolaterally.

Filter plates: Large, strongly imbricate, with broad rows that have secondary and tertiary folds. The channels are rather narrow.

Leptopelis mossambicus Poynton, 1985

Leptopelis concolor (non Ahl, 1929); Poynton 1964:169, fig. 97, Van Dijk 1966:257, *Leptopelis* sp.; Passmore & Carruthers 1979:220, figs.

Leptopelis mossambicus Poynton, 1985c, *S. Afr. J. Sci.*, 81:467, fig. 1. Type locality: Maputo, Mozambique. Holotype in the Natal Museum, Pietermaritzburg. Lambiris 1989a:122; 1989b, figs. 81-83.

ADULT MALE LARYNX (Table 15; Pl. 59, fig. 2)

Material examined: SOUTH AFRICA: NATAL - AJL 2285 (m, SVL 52.3 mm), Mazuwi, Umfolozi Game Reserve, AJL 2457 (m, SVL 54.8 mm), Makhamisa Pan, Umfolozi Game Reserve.

Advertisement call: A loud di-syllabic quack at about 2 kHz, very similar to that of *Leptopelis natalensis*, and uttered from leafy branches near or at the water's edge, at night. There does not appear to be any choral structure.

Pharyngeal mucosa: Moderately thick, covering the entire surface of the arytenoid cartilage, and slightly corrugated anterodorsally.

Arytenoid cartilage: The occlusal surface is semicircular, subequal in width throughout, and narrow (about 0.25x the axial width of the arytenoid shelf). It has a prominent arytenoid valve. The apical shelf is broad, with a wide, slightly cusped step the apex of which does not enter the arytenoid fossa. The diameter of the arytenoid fossa is about 0.10x the length of the medial vocal cord. The superior pulvinarium vocale is massive.

Vocal cords: The **medial cord** is basically lorate, but tapered towards the insertions, and somewhat twisted. The posterior margin is strongly flanged. There are single large, triangular cartilaginous buttresses, the apices of which are continuous with the posterior flange. The **lateral cord** is of moderate size and traversed by a well-developed frenulum. The posterior margin, which is strongly thickened, is slightly peaked medially.

Posterior chamber: The pulmonary aditus is bordered anteroventrally by a cartilaginous rim.

LARVAL BUCCOPHARYNX

The single specimen available was not dissected for this study.

Leptopelis xenodactylus Poynton, 1963

Leptopelis xenodactylus Poynton, 1963, *Ann. Natal Mus.*, 15:328. Type locality: Underberg, Natal. Holotype in the Natal Museum, Pietermaritzburg. Poynton 1964:171, fig. 98. Van Dijk 1966:257, 277. Passmore & Carruthers 1979:222, figs. Lambiris 1988:50, figs., pl. 6 fig. 2a, b; 1989z:123.

ADULT LARYNX (Table 15; Pl. 59, figs. 3 & 4).

Material examined: SOUTH AFRICA; NATAL - LR 2235 (m, SVL 43,8 mm), Weza Forest. NM 1147 (f, SVL 53,5 mm), Underberg (HOLOTYPE). NM 7244 (f, SVL 32,5 mm), Injasuti Outpost, Giant's Castle Game Reserve.

Advertisement call: Passmore & Carruthers (1979:222) describe the call as:

> "One or two deep, brief croaks, separated by long intervals. Sometimes preceded by a very soft buzzing."
> "Males call from well concealed locations at the base of grass tussocks and from burrows in the marsh."

The sonagram figured by Passmore & Carruthers depicts a vibrant call about 0.1 second long, at about 3.2 kHz.

Male larynx:

Pharyngeal mucosa: Thin, overlying the anterodorsal portion of the arytenoid cartilage only.

Arytenoid cartilage: The occlusal surface is semicircular, with a small prominence inferiorly, and about half the width of the arytenoid shelf. There is no arytenoid valve. The apex of the arytenoid shelf triangle enters the arytenoid fossa, the diameter of which is about 0.1x the length of the medial vocal cord. The pulvinaria vocalia are massive.

Vocal cords: The **medial cord** is lorate, and not markedly tapered towards the insertions, nor markedly twisted. The distinct flange on the posterior margin of the cord is continuous with the rather small buttresses. The **lateral cord** has a strongly thickened posterior margin, and is slightly peaked medially. The frenulum is feebly developed.

LARVAL BUCCOPHARYNX

The tadpole is unknown.

DISCUSSION

Adult laryngeal characters

Poynton & Broadley (1987:167) remarked that

> "... the systematics of the genus is still inadequate. Differential characters in the genus are exceptionally difficult to discern, and field studies especially in Malawi, Zambia and Angola will have to be well advanced before the present situation can show much improvement."

Although only three species in this large genus have been examined, laryngeal characters seem sufficiently distinctive to suggest that thay may prove useful in other parts of the genus' range.

The larynx of the holotype of *Leptopelis xenodactylus* was damaged at the time of preservation, the collector having thrust a pin (which subsequently rusted) through the tongue and larynx! The larynxes of a juvenile and an adult female of this species showed no allometric variation.

Larval buccopharyngeal characters

The single specimen of what appears to be *Leptopelis mossambicus* presently available (inner metatarsal tubercle about as long as first toe) was not dissected for this study, as it has still to be measured and examined in detail.

The tadpole of *Leptopelis xenodactylus* is unknown, and Van Dijk's key (1966:257) in which "*xenodactylus* and (?=) *bocagei*" is separated from *concolor* [= *mossambicus*] on the basis of "Discs on toes not visible in five-toed stages" is presumably conjectural, since he later (p. 277) specifically states of the tadpole of *L. xenodactylus*, "Undescribed (unless it is a subspecies of *L. bocagei*)" (sic!).

An examination of buccopharynxes of tadpoles from species in other parts of the genus' range should prove to be an interesting exercise, and may help clarify some of the problems in this troublesome genus.

PLATE 59

LEPTOPELIS – ADULT HYOLARYNXES

Median sagittal section. View into left half. Anterior to right.

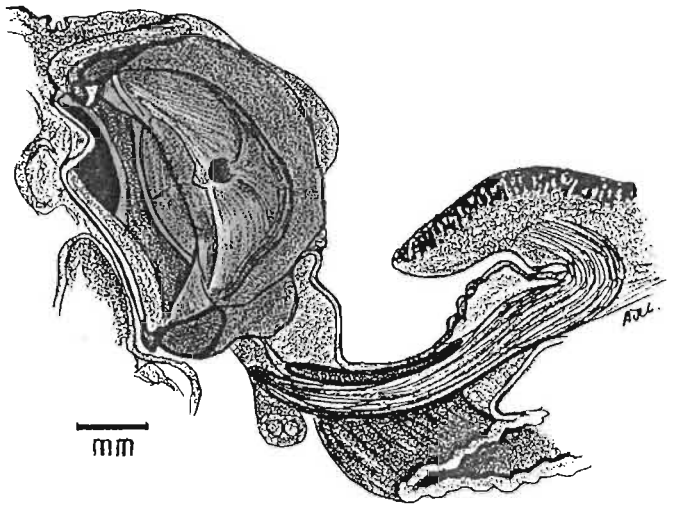


FIG. 1: *Leptopelis natalensis* (A. Smith, 1849)
AJL 2004 (male), Krantzkloof Nature Reserve, Natal, South Africa.

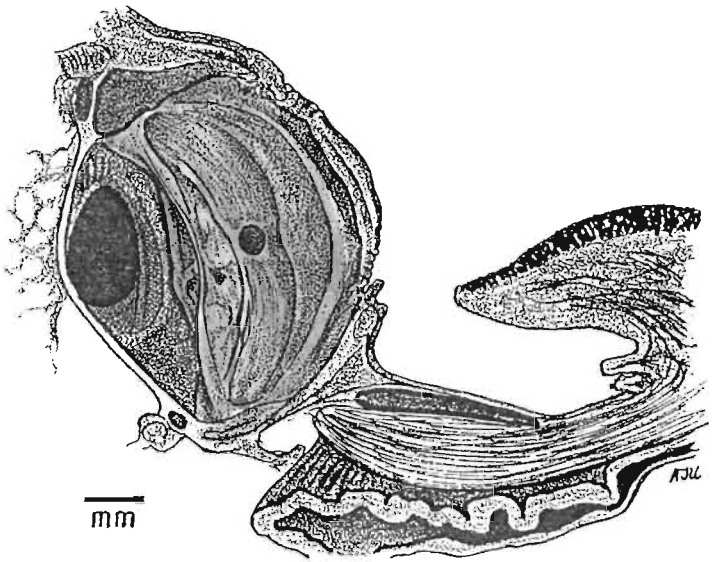


FIG. 2: *Leptopelis mossambicus* Poynton, 1985
AJL 2285 (male), Mazuwi, Umfolozi Game Reserve, Natal.

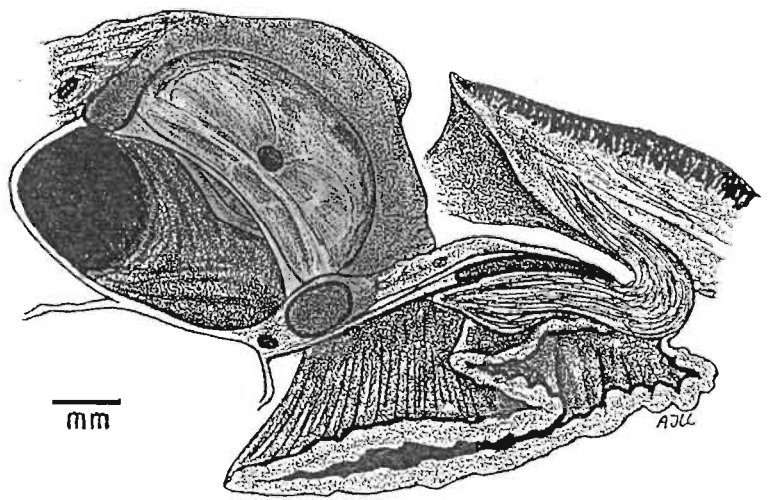


FIG. 3: *Leptopelis xenodactylus* Poynton, 1963
LR 2235 (male), Weza Forest, Natal, South Africa.

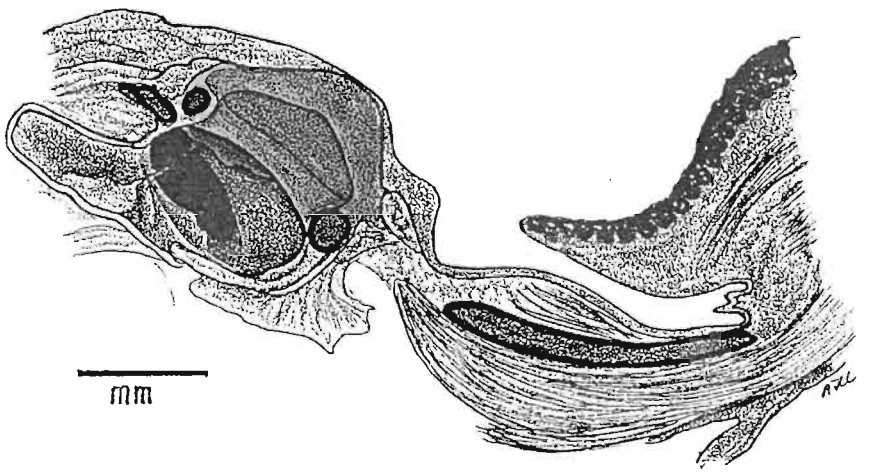


FIG.4: *Leptopelis xenodactylus* Poynton, 1963
NM 7244 (female), Injasuti Outpost, Giant's Castle Game Reserve, Natal, South Africa.

PLATE 60
LEPTOPELIS – LARVAL BUCCOPHARYNX
Roof on left, floor on right.

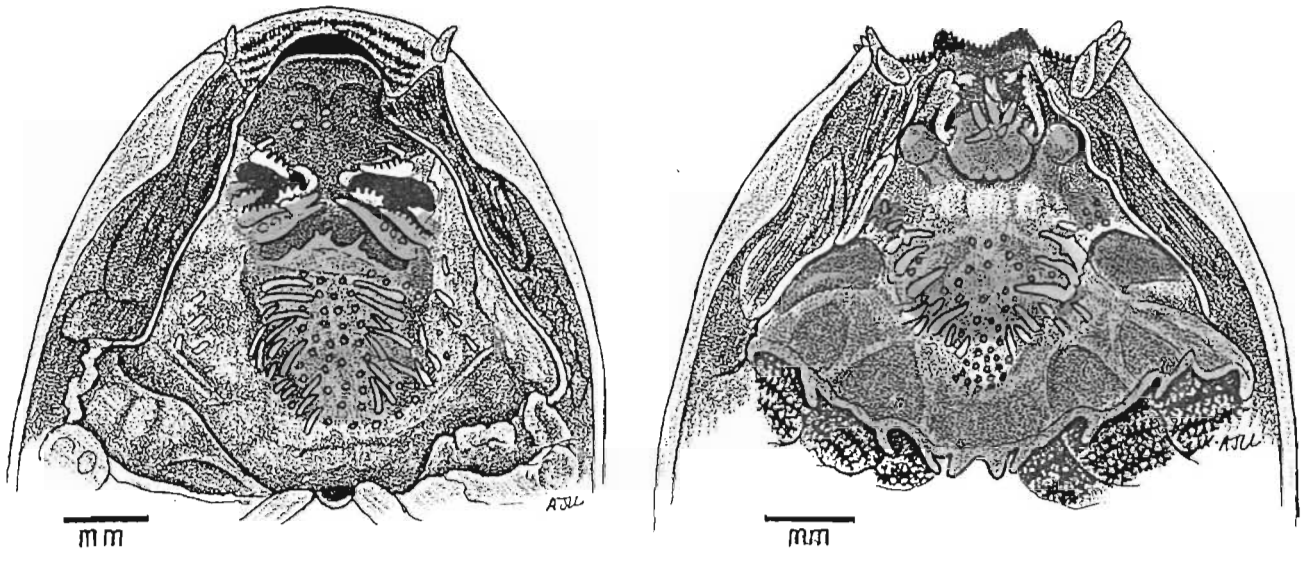


FIG. 1: *Leptopelis natalensis* (A. Smith, 1849)
AJL 3362a, Stage 40, Umzimvubu River Mouth, Port St. Johns, Transkei, South Africa.

TABLE 16. Laryngeal characters:
Kassina and *Semnodactylus*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	EXTERNAL MARGIN OF ARYTENOID OCCLUSAL SURFACE BLUNTLY V-SHAPED	ARYTENOID VALVE NARROW	ANTERIOR MARGIN OF MEDIAL VOCAL CORD DISTINCTLY ARCUATE	ANTERIOR MARGIN OF MEDIAL VOCAL CORD HAS AT LEAST AN INFERIOR BUTTRESS OR THICKENING	ANTERIOR MARGIN OF MEDIAL VOCAL CORD FLANGED	POSTERIOR MARGIN OF MEDIAL VOCAL CORD FLANGED	LATERAL VOCAL CORD MASSIVE
Kassina maculata	3	1	1	1	1	3	1
senegalensis	1	3	1	3	3	1	3
Semnodactylus wealii	3	1	3	1	1	3	3

Subfamily KASSININAE Laurent, 1972

CHARACTERS

The genera *Kassina* and *Semnodactylus* are considered jointly in this section, and in the Discussion (after *Semnodactylus*), in view of the close similarities in both adult laryngeal and in larval buccopharyngeal characters. In discussing *Kassina senegalensis* I have used the terms "Form 1", "Form 3" and "*angeli*" as defined by Poynton & Broadley (1987:181) to indicate patterns of dorsal marking.

ADULT LARYNX (Table 16; Pls. 61, 63)

Character variation in the species examined is summarised in Table 16. Analysis is restricted to the male larynx only. There is marked sexual dimorphism. The female larynx is smaller than that of the male, there is no distinct arytenoid shelf, the lateral vocal cord is absent, and the medial vocal cord is smaller and simpler in structure.

Shape of the arytenoid cartilage

The arytenoid cartilage is anteroposteriorly compressed in *Kassina maculata* and *Semnodactylus wealii*, and more cardioid in *K. senegalensis*.

The occlusal surface is smooth in all three taxa. There is a narrow arytenoid valve on the posterior margin of the occlusal surface, dorsal to the posterior occlusal notch, in *Kassina maculata* and *Semnodactylus wealii*, and a much more strongly developed one (very broad medially) in *K. senegalensis*.

The arytenoid shelf is only a little less broad than the axial width of the occlusal surface in all three taxa. The posterior margin is coarsely granular in *Kassina maculata* and *K. senegalensis*.

The arytenoid fossa is rather narrowly elliptical, and smaller in *Kassina senegalensis* and *Semnodactylus wealii* (0.30 - 0.46x length of medial vocal cord) than in *K. maculata* (0.48x length of medial vocal cord).

The pulvinaria vocalia are large and well developed in all three species.

TABLE 17. Buccopharyngeal characters: *Kassina* and *Semmodactylus*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	POSTERIOR LATERAL PALP OF PRENARIAL ARENA DISTINCTLY SEPARATE FROM ANTERIOR LATERAL PALP	PRENARIAL ARENA WITH A PAIR OF PARAMEDIAN PUSTULES	ANTERIOR NARIAL VALVE WITH PUSTULATE OR DENTICULATE PAPILLAE	FREE MARGIN OF MEDIAL RIDGE SERRATE OR PUSTULATE	BUCCAL ROOF ARENA EXTENDS MORE THAN THREE QUARTERS OF BUCCAL ROOF LENGTH	DORSAL VELUM WELL DEVELOPED, ANTERIOR TO GLANDULAR RIDGE	MEDIAN INFRALABIAL PAPILLA LANCEOLATE	BUCCAL FLOOR ARENA PUSTULATE	BUCCAL FLOOR ARENA PUSTULES NUMEROUS AND CLOSELY SPACED
Kassina maculata	3	3	3	3	1	1	1	1	1
senegalensis	3	1	1	1	3	1	1	3	4
Semnodactylus wealii	1	3	1	1	3	3	3	1	3

Vocal cords

Medial and lateral vocal cords are present in all three species.

The **medial cord** in all three species is lorate and only moderately flared at the insertions.

The anterior margin is flanged in *Kassina maculata* and *S. wealii*; the posterior margin is flanged in *K. senegalensis*.

Buttresses are present in all three species. In *Kassina maculata* only the posterior superior, but both the anterior and posterior inferior buttresses, are present. In *K. senegalensis* only the posterior superior and inferior buttresses are present, and in *Semnodactylus wealii* all four buttresses are present.

A frenulum is present in all three species.

The **lateral cord** is massive, about the same size as the medial cord, in *Kassina maculata*; it is much smaller, and partly obscured by the medial cord, in *K. senegalensis* and *Semnodactylus wealii*.

Posterior chamber

The posterior chamber is about the same size as the anterior chamber in *Kassina maculata* and *K. senegalensis*, slightly larger in *Semnodactylus wealii*. The lateral wall is thrown into folds, but these do not appear to be sufficiently constant to be of diagnostic value.

The pulmonary aditus is small in *Kassina senegalensis* and in *Semnodactylus wealii*, rather larger in *K. maculata*.

LARVAL BUCCOPHARYNX (Table 17; Pls. 62, 64)

Character variation in the three species is summarised in Table 17.

The large papillae arising from the lateral walls common to the prenarial and prelingual arenas are so placed that association with one or the other is dependent on the exact line of dissection in any given specimen. Examination of larvae divided in the median sagittal plane shows that these appendages tend to have epaxial origins and are therefore treated as belonging to the prenarial arena even when, in some dissections, they appear associated on one or both sides with the prelingual arena.

Prenarial arena

A deep inverted U-shape in all three species, with a pair of pustules posterolaterally on either side in *Kassina maculata*, a pair medially and a single one posteromedially in *K. senegalensis*, and none in *Semnodactylus wealii*.

The lateral wall papillae are large (*Kassina maculata* and *K. senegalensis*) to massive (*Semnodactylus wealii*) palps, the shape of which shows differences at the species level (see Plates).

Internal nares and valves

The internal nares are massive, oval or almost rounded, with more or less elaborate narial valves. The posterior flap is simple in all three species. The anterior flap bears a large elaborate palpoid papilla arising from the middle portion in *Kassina maculata* and *K. senegalensis*, and a pustulose papilla arising from the anterolateral margin in *Semnodactylus wealii*.

Postnarial arena

The postnarial arena presents a very similar facies in all three species, with three large conical papillae (a postnarial and two lateral ridge papillae) on either side flanking a broad but low median ridge that is smooth (*Kassina maculata* or somewhat denticulate (*K. senegalensis, Semnodactylus wealii*) on the free margin.

Buccal roof arena

Rather small in all three species, and bounded laterally by few short, conical papillae (3 on either side in *Kassina maculata* and *K. senegalensis*, 2 in *Semnodactylus wealii*). The arena, and the buccal roof beyond it, are covered with scattered pustules in all three species; they are least widely spread in *Semnodactylus wealii*.

Glandular ridge

Present in all three species as a rather narrow zone closely associated with the dorsal velum, and with a broad medial gap. It lies posterior to the velum in *Kassina maculata* and *K. senegalensis*, anteriorly in *Semnodactylus wealii*.

Dorsal velum

Well developed in *Kassina maculata* and *K. senegalensis*, but reduced to a feeble fold in *Semnodactylus wealii*. In all three species there is a broad medial gap, and the free margin lacks adornments.

Pressure cushions

Moderately large, and transversely elongate, in all three species. The surface is coarsely convoluted in *Kassina maculata*, less so in *K. senegalensis*, and pustulose in *Semnodactylus wealii*.

Infralabial arena

Deeply excavate in all three species. A lanceolate median papilla, with lobulated margins, is present in *Kassina maculata* and in *K. senegalensis*; a paramedian pair of double villiform papillae is present in *Semnodactylus wealii*.

Lingual papillae

A pair of conical papillae arises from the dorsum of the tongue anlage in all three species; differences in height seem to be species-specific.

Buccal floor arena

Large, and flanked laterally by 5 - 7 tall subconical papillae on either side, in all three species. Pustules are absent in *Kassina senegalensis*, numerous in *K. maculata*, and sparse in *Semnodactylus wealii*.

Buccal pockets

Elliptical to oval, and closed, in all three species. In *Semnodactylus wealii* the anterior margin is deeply grooved. All three species lack prepocket papillae.

Ventral velum

Moderately broad to broad, slightly narrowed medially in *Kassina maculata* and *K. senegalensis*, but not in *Semnodactylus wealii*. Marginal

elaboration is least developed in *Kassina senegalensis*, and most in *Semnodactylus wealii*.

Branchial baskets and filter plates

The branchial baskets are large, rounded, with the major axes directed posterolaterally in all three species. The filter plates are moderately imbricated, with fine, densely folded filter rows and narrow channels.

SPECIES ACCOUNT

Genus *Kassina* Girard, 1853

Kassina Girard, 1853, *Proc. Acad. Nat. Sci. Philadelphia*, 1853:67. Type species by monotypy: *Cystignathus senegalensis* Duméril & Bibron, 1841.

Hylambates Duméril, 1853, *Ann. Sci. Nat.*, 19:162. Type by monotypy: *Hylambates maculatus* Duméril, 1853.

Kassina maculata (Duméril, 1853)

Hylambates maculatus Duméril, 1853, *Ann. Sci. Nat.*, 19:165, pl. 7. Type locality: Zanzibar. Holotype in the Muséum National d'Histoire Naturelle, Paris. Poynton 1964:173, fig. 100. Van Dijk 1966:257, figs.

Kassina poweri Hoffman, 1944, *Soöl. Navors. Nas. Mus. Bloemfontein*, 1:169, figs. 1-3. Type locality: St. Lucia Estuary, Zululand. Holotype in the National Museum, Bloemfontein.

Kassina maculata (Duméril): Passmore & Carruthers 1979:226, figs. Poynton & Broadley 1987:178. Lambiris 1989a:124; 1989v:152, figs. 86 & 87, pl. 18 figs. 1a-c.

ADULT LARYNX (Table 16; Pl. 61, fig. 1)

Material examined: MOZAMBIQUE: NM 3691 (m, SVL 65.3 mm), and NM 3692 (m, SVL 59.6 mm), Maputo. SOUTH AFRICA: NATAL - NM 3695 (m, SVL 62.0 mm), Mboneni Pan, Mkuzi Game Reserve. NM 3703 (m, SVL 58.0 mm) Mtunzini. AJL 2667 (f, SVL 56.6 mm), Bhanga Nek.

Advertisement call: A harsh quack, about 0.6 second long, at about 2.2 kHz (Passmore & Carruthers 1979:226), uttered about once a second for extended periods. Partly submerged males call from emergent vegetation in deep water, at night.

Male larynx:

Pharyngeal mucosa: Thick and somewhat folded, overlying the whole of the arytenoid cartilage.

Arytenoid cartilage: The external margin of the occlusal surface is broadly U-shaped, with a slight apical bulge. The occlusal surface is moderately broad and smooth. The arytenoid valve is a very narrow fold along the internal occlusal margin, extending from the superior pulvinarium to the posterior occlusal notch. The arytenoid shelf is about as wide as the occlusal surface, tapering towards the apices, and

coarsely granular over the posterior half. The elliptical arytenoid fossa is about 0.48x the length of the medial vocal cord.

Vocal cords: The **medial cord** is lorate, the length about 10x the mid-point width. The anterior margin is flanged for most of its length, the flange curving backwards across the cord and towards the superior posterior buttress at about the level of the superior apex of the arytenoid fossa. There are three buttresses -- the superior posterior, and the inferior anterior and posterior, all of which are large and triangular. The **lateral cord** is massive, about the same size as the medial cord, with a superior posterior buttress-like expansion, and with a horizontally rugose inferior insertion. A rather weak, small equatorial frenulum traverses the medial cord and the anterior half of the lateral cord.

Posterior chamber: Rather narrow anteroposteriorly, with a moderately large pulmonary aditus (diameter about 0.3x major axis of chamber).

LARVAL BUCCOPHARYNX (Table 17; Pl. 62, figs. 1a & b)

Identification of larvae: Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 3515; Mkuzi Swamps; stage 36, SVL 26,2 mm, AJL 2681; Empangeni; stage 40, SVL 36,3 mm, AJL ====; Mpophoneni Pan, False Bay Nature Reserve, Lake St, Lucia; stage 40, SVL 30,0 mm, All silver impregnation.

Larval habitat: Deep pans with dense marginal emergent vegetation, and usually at least some central floating vegetation, with a good bottom cover of organic debris. The diet consists of softer macrophytes and algae.

Buccopharyngeal roof

General shape: An inverted T, the stem broadly rectangular and the cross-arm almost square. The width is equal to the height. The buccal roof is most convex centrally, and the prenarial arena is deeply excavate.

Prenarial arena: There is a low, weakly defined, cusped ridge immediately behind the root of the beak, and four papillae (two on

either side) marking out a trapezium in the posterior half of the arena roof immediately anterior to the internal nares. There are two close-set papillae on either lateral wall. The anterior one is low, broad, and flat, with a lobulate border. The posterior papilla (shown in the buccal floor preparation illustrated in fig. 1b, pl. 62) is tall and somewhat fimbriate.

Internal nares: Massive, broadly oval, the minor diameter about 0.53x the major diameter. The nares are set slightly posteromedially. The narial width is about 0.36x the width of the roof at that level, and the internarial distance is about 0.38x the narial width.

Narial valve: The naris is circumscribed by a well-developed rim, the anterior border of which bears mesially a large palpoid papilla that is neither pustulate nor denticulate.

Postnarial arena: A large conical **postnarial papilla** (height about equal to the narial width) arises immediately behind the middle of the posterior narial valve. It is flanked by a pair of conical **lateral ridge papillae**, the anterior margins of which are slightly pustulate; the anteroventral papilla is about half the narial width in height, the posterodorsal one about 1.0 - 1.2x the narial width. The **median ridge** is a low (height about 0.3x width), somewhat rectangular flap, the width about 0.48x the width of the roof at that level, with a rather irregular free margin.

Buccal roof arena: A deep trapezoid, extending from the postnarial arena almost to the dorsal velum. It is flanked on either side by three robust conical papillae, regularly spaced, and slightly diminishing in size posteriorly. The arena contains numerous pustules, which extend beyond its boundaries to cover the whole of the buccal roof.

Dorsal velum: Well developed, of equal width throughout, with a median gap (width about 0.35x length of a velum). The free margin is slightly thickened but bears no appendages.

Glandular ridge: A moderately broad zone, slightly tapered medially, lying immediately behind either velum.

Pressure cushions: Large, triangular (major axis transverse) and coarsely convoluted.

Buccopharyngeal floor

General shape: Irregularly triangular, the sides decidedly undulant. The general surface is concave, with a deeper median depression retrolingually, and the prelingual arena is deeply excavate.

Prelingual papilla: The medial papilla, which arises from about the middle of the arena floor, is lanceolate and lobulate -- three lateral lobes on either side surmounted by an apical lobe, and with a central lobe between the middle lateral pair. The length of the medial papilla is about half the length of the prelingual arena.

Buccal floor arena: Oval, extending from the lingual arena to the ventral velum, but well separated from the buccal pockets. It is bounded laterally by 6 closely spaced conical papillae on either side, set in convex rows, and tallest in the middle of each row. The arena contains about 30 - 35 small pustules; 4 - 5 extend beyond the anterolateral boundaries of the arena.

Buccal pockets: Narrowly oval, closed, shallow, without deeply grooved margins. There are no prepocket papillae.

Ventral velum: Moderately broad, slightly narrowed medially, and with a weakly lobulate free margin. The surface is rather wrinkled laterally.

Branchial baskets: Large and rounded, with the major axes directed posterolaterally.

Filter plates: Large, feebly imbricated, with broad, very finely folded filter rows and narrow channels.

Kassina senegalensis (Duméril & Bibron, 1841)

Cystignathus senegalensis Duméril & Bibron, 1841, *Erpet. Gén.*, 8:418. Type locality: Galam Lakes, Senegal. Syntypes in the Muséum National d'Histoire Naturelle, Paris.

Cassina argyreivittis Peters, 1854, *Mber. Königl. Akad. Wiss. Berlin*, 1854625. Type locality: Cabaceira, Boror. Syntypes in the Zoologisches Museum, Berlin.

Kassina modesta Ahl, 1930, *Zool. Anz.*, 88:281. Type locality: Mariannhill, near Durban.

Kassina senegalensis (Duméril & Bibron): Poynton 1964:175, fig. 101. Passmore & Carruthers 1979:228, figs. Poynton & Broadley 1987:180. Lambiris 1988:51, figs., pl. 6 figs. 3a-c. 1989a:125; 1989b:154, figs. 88 & 89, pl. 18 figs. 2a-d.

Hylambates senegalensis (Duméril & Bibron): Van Dijk 1966:257.

ADULT MALE LARYNX (Table 16; Pl. 61, fig. 2)

Material examined: ZAMBIA: AJL 1151 (m, SVL 40,0 mm, Form 3/Form 1/*modesta*), Kamilonga Farm, 16 km west of Chisamba. ZIMBABWE: AJL 1123 (m, SVL 38,5 mm, Form 3/Form 1), Gem Farm, 34 km NW of Beitbridge. AJL 404 (m, SVL 39,0 mm, Form 1), near Warren Hills Golf Course, Harare. AJL 895 (m, SVL 39,0 mm, Form 1), Munwahuku River, alt. 1400 m, Saffron Walden district. SOUTH AFRICA: TRANSVAAL - LR 2638 (m, SVL 46,0 mm, Form 1), Pilanesburg. NATAL - AJL 2149 (m, SVL 37,6 mm, Form 1), Mkuzi Game Reserve. LR 2625 (m, SVL 35,0 mm) Gillitts (near-topotype of *K. modesta*) EASTERN CAPE - AJL 320 (m, SVL 41,0 mm, Form 3/Form 1), and AJL 317 (m, SVL 36,2 mm, Form 1/*modesta*), near New Cemetery, Grahamstown. AJL 614 (m, SVL 37,9 mm, Form 3/*modesta*), 1,8 km NE of farm "Brak Kloof", Grahamstown district.

Advertisement call: A loud, bell-like "quoip!" about 0.12 second long, showing marked frequency modulation between 1 and 2 kHz (Passmore & Carruthers 11979:28); uttered singly in the later afternoon and at night. Calling follows a well-structured choral sequence, with several frogs responding rapidly to one another so that a ripple of sound spreads rapidly across the veld.

Pharyngeal mucosa: A moderately thick mucosa and very thick submucosa reach the level of the superior pulvinarium. The arytenoid cartilage is covered by a barely visible layer of mucosa.

Arytenoid cartilage: The external margin of the occlusal surface is V-shaped, the internal occlusal margin U-shaped. The smooth occlusal surface is broadest axially. The arytenoid valve is a broad fold on the medial third of the posterior occlusal margin, continuing towards the

pulvinaria as a much narrower fold. The broad segment is slightly corrugated superiorly. The arytenoid shelf is about as wide as the apical portion of the arytenoid cartilage, tapering towards the apices, and coarsely granular over the posterior half. The elliptical arytenoid fossa is about 0.3x the length of the medial vocal cord.

Vocal cords: The **medial cord** is broadly lorate, the length about 5.7x the medial width. The posterior margin bears a strong flange, continuous with the large triangular superior and inferior posterior buttresses. There are no anterior buttresses. The **lateral cord** is small, strongly convex medially, and has a large buttress-like superior expansion. Both cords are traversed by a feeble median frenulum.

Posterior chamber: Compressed anteroposteriorly, with a small pulmonary aditus (diameter about 0.2x the major axis of the chamber).

LARVAL BUCCOPHARYNX (Table 17; Pl. 62, figs. 2a & b)

Identification of larvae: Van Dijk 1966; Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 2438a; stage 38, SVL 15,2 mm, and AJL 2439; stage 38, SVL 18,5 mm; Mboneni Pan, Mkuzi Game Reserve, Silver impregnation.

Larval habitat: Ponds and pans with moderately dense emergent grassy vegetation, and often some central floating vegetation, over a good bottom cover of silt and organic debris. The diet consists of softer macrophytes and algae.

Buccopharyngeal roof

General shape: Outline complex, the inverted U-shaped prenarial arena leading into a transversely elliptical narial and postnarial arena that is demarcated from the buccal cavity proper by a strong lateral constriction. The buccal cavity is slightly expanded posteriorly, continuing without obvious demarcation into the pharynx.

Prenarial arena: A pair of low, rounded paramedian papillae arise from the centre of the arenal roof. A median papilla lies on the posterior boundary of the arena. There are two close-set papillae arising from the posterior half of either lateral wall. The anterior one

is low, broad and flat, with a somewhat ctenate border. It is followed posteriorly by a longer, more cylindrical, papilla with a villose apex.

Internal nares: Massive, broadly oval, the minor diameter about 0.75x the major diameter. The nares are set slightly posteromedially. The narial width is about 0.35x the width of the roof at that level, and the internarial distance is about 0.6x the narial width.

Narial valve: The naris is circumscribed by a low but distinct flap on the posterior and medial margins. The anterior valve is a large palpoid flap with a distinctly pustulate surface.

Postnarial arena: The **postnarial papilla** is smooth and conical, the height being about equal to, or very slightly greater than, the internarial distance. It arises just behind, alnd slightly lateral to, the mid-point of the posterior narial margin. The two **lateral ridge papillae** on either side are conical. The anteroventral papilla is slightly shorter than the internarial distance, the posterdorsal one is larger (height about equal to the narial width), and trilobate apically. The **median ridge** is a broad, low flap (height about 2.3x width), the width about 0.4x the width of the roof between the constrictions. The free margin bears 3 - 4 small pustulations.

Buccal roof arena: Rectangular, occupying the posterior two-thirds of the roof between the postnarial arena and the dorsal velum. It is bounded on either side by three short conical papillae, set rather closely together. The arena contains about 15 - 18 small pustules. Additional pustules spread beyond the arena, over the buccal roof.

Dorsal velum: Moderately broad, well developed, with a median gap about 0.6 of a velum length. The free margin is slightly thickened, but bears no appendages.

Glandular ridge: A well-defined area immediately behind either dorsal velum, interrupted by a median gap.

Pressure cushions: Moderately large, triangular (major axis transverse), and with an alveolate surface. There is no separation onto lateral and medial moieties.

Buccopharyngeal floor

General shape: A U-shaped prelingual arena leads into an irregular buccal cavity with a constriction in the lateral walls just anterior to the buccal pockets.

Prelingual papilla: A medial papilla, arising from the posterior third of the lingual arena, is lanceolate and lobulate -- three short marginal lobules on either side are surmounted by an apical lobe. There is no central lobe. The length of the medial papilla is about half the length of the prelingual arena.

Buccal floor arena: Square, occupying most of the space between the lingual arena and the ventral velum, and approaching the buccal pockets laterally. It is bounded by 4 - 6 regularly-spaced, rather tall conical papillae set in approximately parallel rows. The arena lacks pustules.

Buccal pockets: Broadly oval, closed, shallow, with slightly grooved margins. There are no prepocket papillae.

Ventral velum: Moderately broad, slightly narrowed medially, and with a weakly lobulate free margin. The surface is not wrinkled laterally.

Branchial baskets: Large and rounded, the major axes directed posterolaterally.

Filter plates: Large, feebly imbricated, with very finely folded filter rows and narrow channels.

Genus *Semnodactylus* Hoffman, 1939

Kassina Girard, 1853, *Proc. Acad. Nat. Sci. Philadelphia*, 1853:67. Type species by monotypy: *Cystignathus senegalensis* Duméril & Bibron, 1841.

Hylambates Duméril, 1853, *Ann. Sci. Nat.*, 19:162. Type by monotypy: *Hylambates maculatus* Duméril, 1853.

Semnodactylus Hoffman, 1939, *Soöl. Navors. Nas. Mus. Bloemfontein*, 1:89. Type species by original designation: *Semnodactylus thabanchuensis* Hoffman, 1939.

Notokassina Drewes, 1985, *S. Afr. J. Sci.*, 81:190. Type species by original designation: *Kassina wealii* Boulenger, 1882.

Semnodactylus wealii (Boulenger, 1882)

Cassina wealii Boulenger, 1882, *Cat. Batr. Sal. Brit. Mus.*, 2nd ed., p. 131, pl. 11 fig. 3. Type locality: Kaffraria. Syntypes in the British Museum (Natural History), London.

Kassina wealii Boulenger; Passmore & Carruthers 1979:230, figs.

Kassina wealii quinquevittata Hewitt, 1927, *Rec. Albany Mus.*, 3:409, pl. 24 fig. 4. Type locality: Cape Town. Type in the Port Elizabeth Museum?

Semnodactylus thabanchuensis Hoffman, 1939, *Soöl. Navors. Nas. Mus. Bloemfontein*, 1:90, figs. 1-5. Type locality: Thaba Nchu, Orange Free State. Holotype in the National Museum, Bloemfontein.

Kassina wealii wealii Boulenger; Hoffman, 1942:157.

Kassina wealii fitzsimonsi Hoffman, 1942, *Soöl. Navors. Nas. Mus. Bloemfontein*, 1:158, figs. 36 & 37. Type locality: Wakkerstroom, Transvaal. Holotype in the National Museum, Bloemfontein.

Kassina wealei Boulenger; Poynton 1964:178, fig. 102.

Hylambates wealei (Boulenger); Van Dijk 1966:257.

Notokassina wealei (Boulenger); Drewes 1985:190.

Semnodactylus wealii (Boulenger); Lambiris 1988:53, figs., pl. 6 figs. 4a-c.

ADULT LARYNX (Table 16; Pl. 63, figs. 1 & 2)

Material examined: LESOTHO: AJL 2819 (m, SVL 38.5 mm), Sehlabathebe National Park. SOUTH AFRICA: EASTERN CAPE - AJL 486 (m, SVL 40.0 mm), Coombs, 35 km east of Grahamstown. AJL 492 (m, SVL 38.0 mm), Grahamstown Commonage West. NATAL - AJL 2453 (f, SVL 38.3 mm), Injasuti Outpost, Giant's Castle Game Reserve.

Advertisement call: A loud rattle, about 0.4 second long, at about 2.2 kHz; rapidly trilled initially, much more slowly in the second, longer, phase (Passmore & Carruthers 1979:230). Calls are uttered every few seconds, on cloudy days and at night, in a loose but dense chorus, from among emergent vegetation in the water; or above ground level in grass or even on the lower branches of shrubs close to, or overhanging, water.

Male larynx:

Pharyngeal mucosa: A thin mucosa and deeper submucosa cover the anterodorsal and anteroinferior portions of the arytenoid cartilage, leaving the apex exposed.

Arytenoid cartilage: The external margin of the smooth, moderately broad occlusal surface is roughly arcuate. The internal occlusal margin bears a very narrow arytenoid valve along most of its length. The posterior marginal notch is set very inferiorly, only a short distance above the inferior insertion of the medial vocal cord. The axial width of the arytenoid shelf is about half the width of the occlusal surface. The shelf is smooth and does not taper apically. The narrowly elliptical arytenoid fossa is about 0.3x the length of the medial vocal cord.

Vocal cords: The **medial vocal cord** is narrowly lorate, the length about 10x the medial width. The anterior margin is strongly flanged, and both superior and inferior buttresses are present; the inferior buttresses are somewhat larger than the superior pair. The **lateral cord** is small, largely obscured by the medial cord, and traversed by a distinct frenulum medially.

Posterior chamber: Not compressed anteroposteriorly. The moderately large pulmonary aditus is surrounded by a few poorly defined folds in the lateral wall.

LARVAL BUCCOPHARYNX (Table 17; Pl. 64, figs. 1a & b)

Identification of larvae: Lambiris 1989a, and a series from Stillerust, Kamberg Nature Reserve, Natal (AJL 3516 - 3522, stages 31 - 45), showing the characteristic manus of postmetamorphics at stage 45.

Material examined: SOUTH AFRICA; NATAL - AJL 3518a; stage 38, SVL 18,4 mm, and AJL 3519; stage 38, SVL 20,0 mm; Kamberg Nature Reserve; silver impregnation.

Larval habitat: Pools and shallow to moderately deep pans with fairly dense emergent marginal grassy vegetation, and a bottom cover of silt and organic debris. The diet consists largely of softer macrophytes and algae.

Buccopharyngeal roof

General shape: Outline roughly triangular, but the sides are decidedly undulant, with a constriction behind level of the postnarial arena. The buccal roof is shallowly concave, with a large, well defined oval fossa on either side, lateral to and between the postnarial and buccal roof arenas. The prenarial arena is deeply excavate.

Prenarial arena: The arena roof lacks papillae or pustules. There are two large palpoid lateral wall papillae on either side, separated by a small but definite gap. The anterior papilla is low, broad and flat, with a ctenate margin (taller on the right side only in AJL 2319). The posterior papilla is much taller (about twice the height of the anterior one) and more cylindrical. Both papillae have finely pustulose surfaces.

Internal nares: Massive, broadly oval to rounded, the minor diameter about 0.7 - 0.9x the major diameter. When oval, the nares are orientated slightly posteromedially. The narial width is about 0.4x the width of the roof at that level, and the internarial distance is about 0.28x the narial width.

Narial valve: The valve is a simple flap circumscribing the naris. A slender, conical **prenarial papilla** with a pustulose anterior margin arises from the anterolateral margin of the naris, the apex directed medially.

Postnarial arena: The **postnarial papilla** is conical, with a small papilla at about the mid-point on the anterior margin. Its length is about equal to the narial width. The two conical **lateral ridge papillae** lie ventral to the prenarial papilla. The anterior lateral ridge papilla is small (about 0.7x narial width) and smooth. The posterior papilla is larger (length about 1.5x narial width), more robust, and pustulose on the anterior margin. The **median ridge** is a broad, low flap (height about 0.3x width), the width about 0.4x the width of the roof at that level. The slightly thickened free margin is finely pustulose.

Buccal roof arena: Rectangular, occupying the middle third of the roof between the postnarial arena and the dorsal velum. It is bounded on either side by a pair of small conical papillae of equal height.

Pustulations: A few small pustulations are scattered over the buccal roof, including the buccal roof arena, in the area bounded by the postnarial arena, the lateral fossae, and the posterior border of the

buccal roof arena. The lateral border of each fossa bears three conical pustules.

Glandular ridge: A narrow zone lying immediately before either half of the dorsal velum.

Dorsal velum: A feeble fold on the anterior margin of each pressure cushion. The width of the median gap is only slightly less than the length of either half of the velum.

Pressure cushions: Moderately large, triangular, set transversely, and not divided into distinct lateral and medial moieties. The surfaces are verrucose.

Buccopharyngeal floor

General shape: Roughly triangular, but with very undulant sides. The floor is moderately concave, with a deep prelingual arena.

Prelingual papillae: A pair of double cylindrical papillae arise from the arena floor immediately anterior to the tongue anlage.

Buccal floor arena: Square, occupying most of the space between the lingual arena and the ventral velum, and closely approaching the buccal pockets laterally. It is bounded on either side by 4 - 5 tall, smooth, conical papillae of roughly equal height, spaced approximately equally, and slightly convergent posteriorly. The arena contains 7 - 9 small pustules, concentrated mostly in the mid-line.

Additional papillae and pustules: A few small papillae and pustules occur on the anterior margin of the anterior velum, behind the buccal floor arena.

Buccal pockets: Narrowly oval, closed, moderately deeply recessed, and with deeply grooved margins. There are no prepocket papillae.

Ventral velum: Moderately broad, slightly wider medially than laterally. The thickened free margin bears a group of 4 - 5 short, blunt, close-set lobes medially, flanked laterally by two small, more widely-spaced lobes on either side. Supporting spicules are distinct laterally.

Filter plates: Large, moderately imbricate, with rather narrow, finely folded filter rows and narrow channels.

DISCUSSION

Kassina senegalensis

Drewes (1984:55) remarked that

> "The most perplexing problem in recent years, however, has been the elucidation of the *Kassina senegalensis* complex, a group of closely related savanna forms inhabiting most of Africa."

Poynton & Broadley (1987:181) have made a careful study of material from the Zambeziaca area and have demonstrated that Schiøtz's "Form 1" (*Kassina senegalensis*) and "Form 3" (*sensu* Poynton & Broadley, with a symmetrical occipital break in the lateral stripes and a patch above each eye) show a cline in markings and have no taxonomic value.

Specimens with an interorbital expansion of the dorsal band occur in *Kassina angeli* and in *K. modesta* and this feature is also considered by Poynton & Broadley to have no taxonomic value.

Specimens of *Kassina senegalensis* showing typical "Form 1", "Form 3" (*sensu* Poynton & Broadley), "Form 1 / Form 3" intergrades, and "*angeli/modesta*" interorbital expansions, were selected for examination. (Forms, and their localities, are indicated in the species account.) Also examined were a near-topotype of *Kassina modesta* Ahl, and an example of the larger, more robust population found in the Transvaal.

The larynxes of these specimens were all virtually identical, such few small differences that were noted (e.g. light compression of pharyngeal mucosa) being clearly attributable to preservation artefacts, especially in the less well-prepared alcohol specimens.

Kassina argyreivittis and *K. modesta* cannot be separated from *Kassina senegalensis* on laryngeal characters, but a careful examination of larval buccopharynxes and of larval habitats should be made before making any final pronouncement on their taxonomic status. Unfortunately suitable larval material was not available for study. At present,

however, Poynton seems to be correct in relegating these two taxa to the synonymy of *K. senegalensis*.

The status of *Semnodactylus* Hoffman, 1939

Lambiris (1989a:126) discussed the status of this genus, regarding it as valid but noting that clarification was required.

Although there are marked differences between the calls of *Kassina* and of *Semnodactylus*, the characters examined in this study suggest that the distinctness of *Semnodactylus* could be re-evaluated, using a larger suite of characters than hitherto utilised.

PLATE 61
KASSINA – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

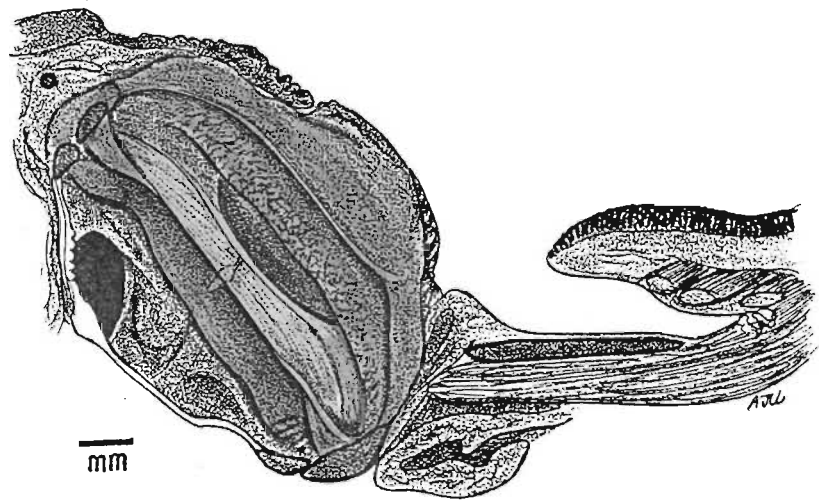


FIG. 1: *Kassina maculata* (Duméril, 1853)
NM 3692 (male), Maputo, Mozambique.

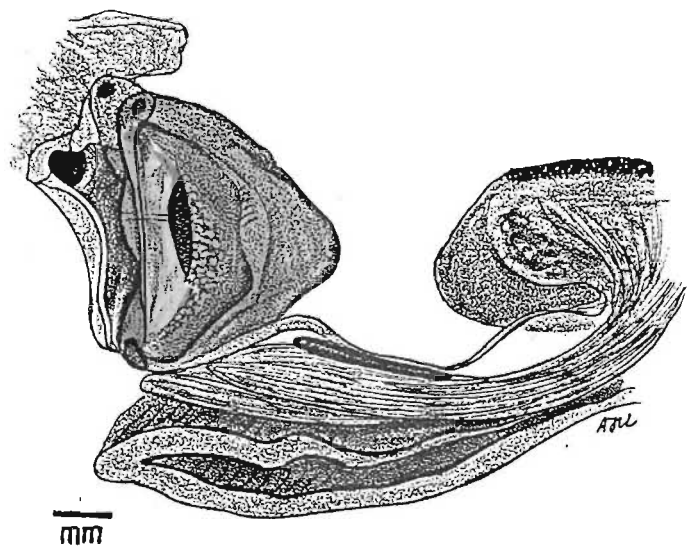


FIG. 2: *Kassina senegalensis* (Duméril & Bibron, 1841)
AJL 320 (male), Near New Cemetery, Grahamstown, Eastern Cape, South Africa.

PLATE 62
KASSINA – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

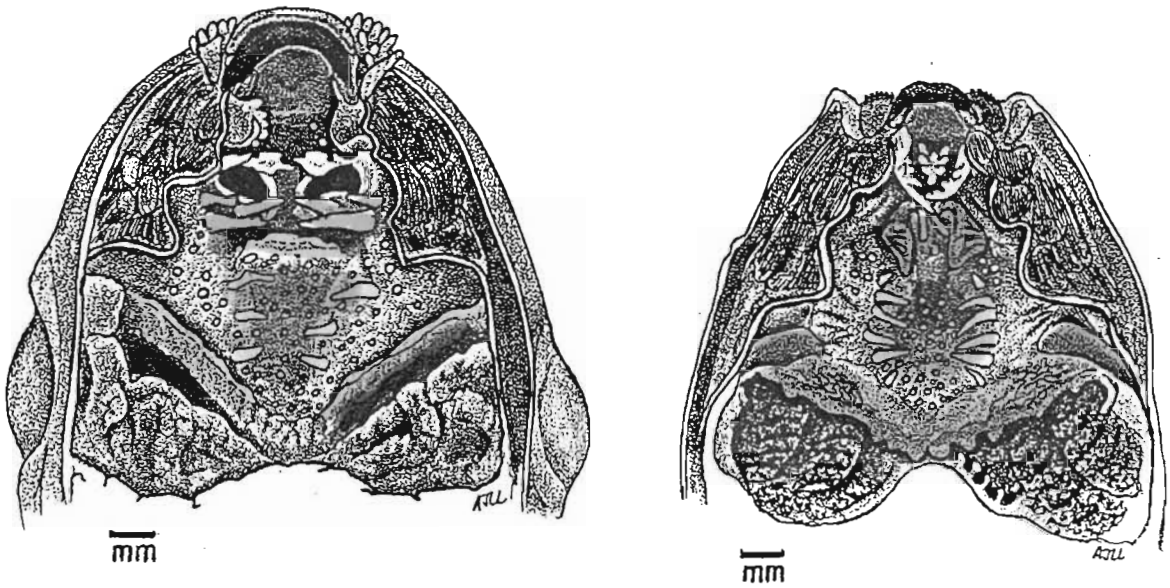


FIG. 1: *Kassina maculata* (Duméril, 1853)
AJL 3515, Stage 36, Mkuzi Swamps, Natal, South Africa.

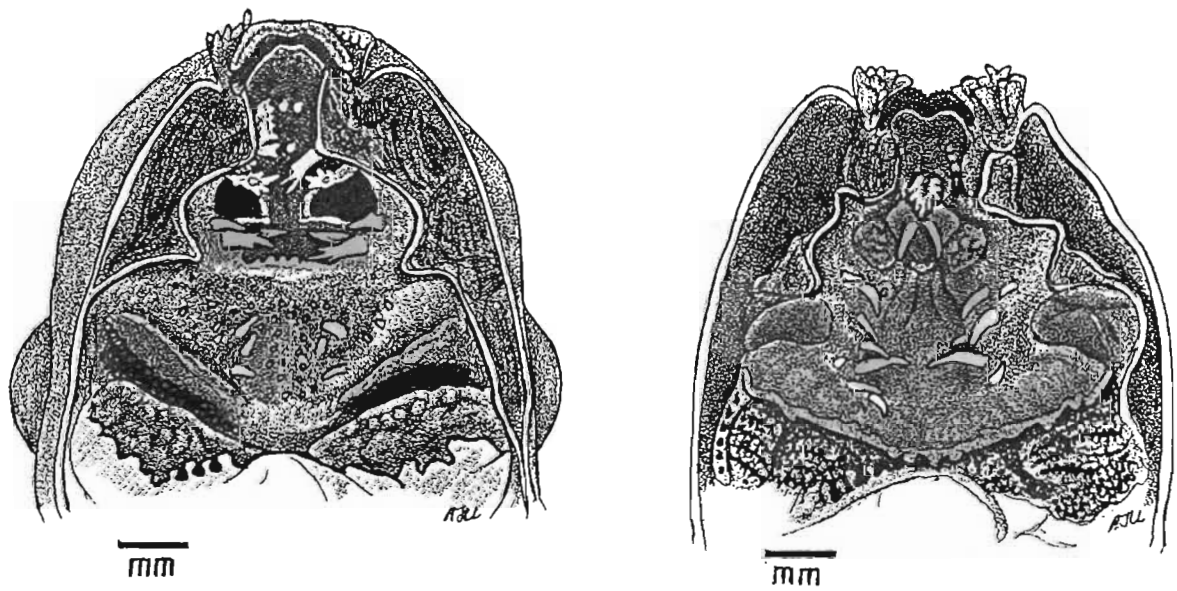


FIG. 2: *Kassina senegalensis* (Duméril & Bibron, 1841)
AJL 2438a, Stage 35, Mboneni Pan, Mkuzi Game Reserve, Natal, South Africa.

PLATE 63
SEMNODACTYLUS – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

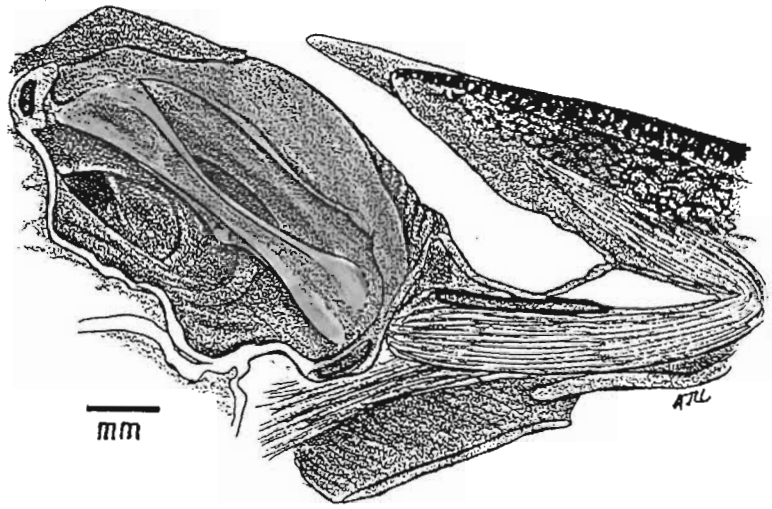


FIG. 1: *Semnodactylus wealii* (Boulenger, 1882)
AJL 492 (male), Grahamstown Commonage West, Eastern Cape, South Africa.

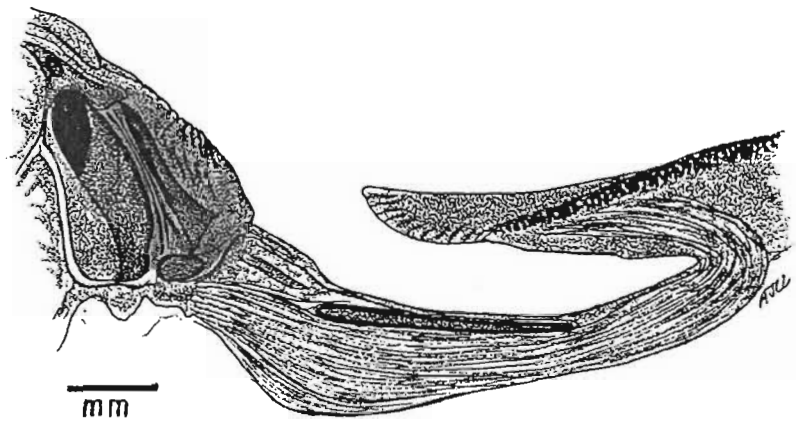


FIG. 2: *Semnodactylus wealii* (Boulenger, 1882)
AJL 2453 (female), Imjasuti Outpost, Giant's Castle Game Reserve, Natal, South Africa.

PLATE 64
SEMNODACTYLUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

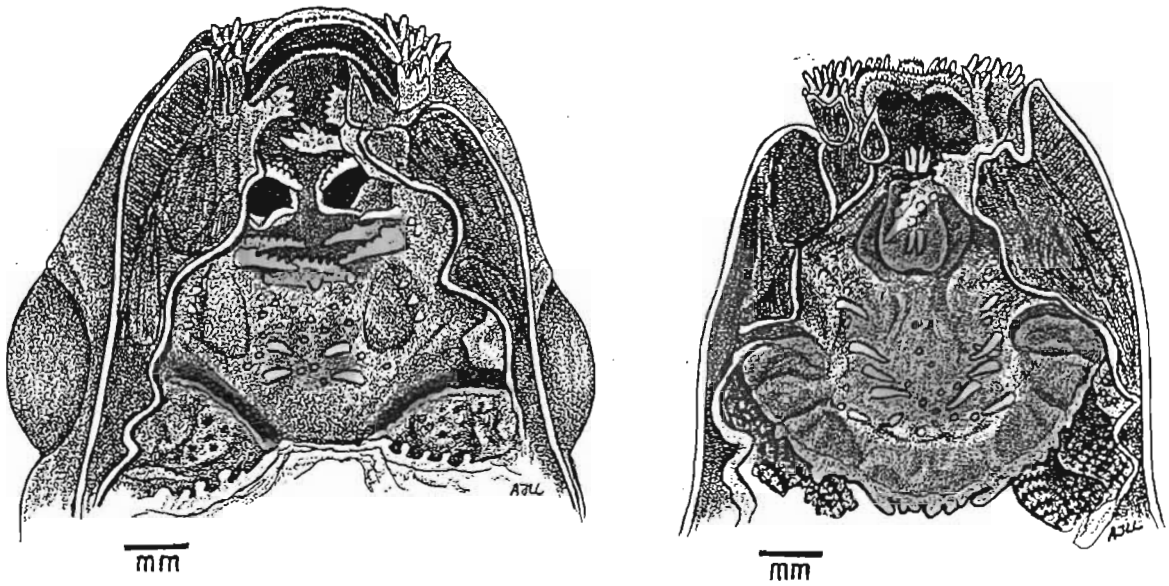


FIG. 1: *Semnodactylus wealii* (Boulenger, 1882)
AJL 3519, Stage 39, Stillerust Vlei, Kamberg Nature Reserve, Natal, South Africa.

TABLE 18. Laryngeal characters:
Afrixalus

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

* = extralimital taxon included for comparison

	INFRA-FLEXURAL PORTION OF ARYTENOID OCCLUSAL SURFACE LESS THAN QUARTER OF TOTAL SURFACE LENGTH	POSTERIOR FLEXURE OF ARYTENOID OCCLUSAL SURFACE V-SHAPED	A DISTINCT ARYTENOID VALVE PRESENT	ARYTENOID SHELF DISTINCTLY TAPERS SUPERIORLY	MAJOR DIAMETER OF ARYTENOID FOSSA GREATER THAN ONE THIRD LENGTH OF MEDIAL CORD	A LARGE SUPERIOR BUTTRESS PRESENT ON THE MEDIAL CORD	LATERAL VOCAL CORD LARGELY COVERED BY THE MEDIAL CORD
Afrixalus spinifrons spinifrons	3	3	3	3	1	3	3
spinifrons subsp. nov. [Pickersgill]	3	3	1	1	3	3	3
*crotalus**	1	3	1	3	3	3	1
aureus	1	1	3	3	3	3	1
delicatus	1	1	3	1	1	3	1
fornasinii	1	1	1	3	3	1	1

Subfamily HYPEROLIINAE Laurent, 1943

Genus *Afrixalus* Laurent, 1944

Megalixalus Günther, 1868, *Proc. Zool. Soc. London*, 1868:485.
Afrixalus Laurent, 1944, *Rev. Zool. Bot. Afr.*, 38:113. Type species by designation of Loveridge 1957: "*Megalixalus fornasinii congicus* Laurent = Hyperolius dorsalis Peters".

CHARACTERS

ADULT LARYNX (Table 18; Pls. 65 & 66)

Character variation in the species examined is summarised in Table 18. An undescribed subspecies of *Afrixalus spinifrons* (Pickersgill, in prep.) is included, as is the extralimital *Afrixalus crotalus*.

Pharyngeal mucosa: In all species examined, except *Afrixalus delicatus*, where it is not clearly defined, the dorsum of the arytenoid cartilage is recessed to acommodate the pharyngeal mucosa. The superior prominentia is bare in all species examined except in *Afrixalus spinifrons* subsp. nov., where it is covered by a conspicuous layer of folded mucosa, and *A. delicatus*, where the overlying mucosa is smooth and thin.

Arytenoid cartilage

The occlusal surface is asymmetrical about the anteroposterior axis. The functional apex (indicated by the posterior occlusal flexure) is markedly hypaxial and the superior portion of the occlusal surface is, consequently, much longer than the inferior portion.

A large superior prominentia is present in all species examined. It is more or less dome-shaped in the dwarf species (*Afrixalus spinifrons, crotalus, aureus* and *delicatus*) but somewhat flattened in *A. fornasinii*.

The inferior portion of the occlusal surface is short, and blends into the inferior pulvinarium vocale, in *Afrixalus spinifrons, crotalus* and *aureus*; it is very short in *A. delicatus* and *A. fornasinii*.

The posterior occlusal flexure is rounded in *Afrixalus spinifrons spinifrons* and *A. crotalus*, and is V-shaped in *A. spinifrons* subsp. nov., *A. aureus, delicatus* and *fornasinii*.

An arytenoid valve is present in *Afrixalus spinifrons* subsp. nov., *A. crotalus* and *A. fornasinii*, but absent in the other species examined.

The arytenoid shelf is wide in *Afrixalus s. spinifrons*, and narrower in the other species examined. In *Afrixalus spinifrons* subsp. nov. and *A. delicatus* it is considerably tapered superiorly, and in *Afrixalus spinifrons* subsp. nov. has a shallow, rather poorly defined fossa behind the flexure.

The arytenoid fossa is more or less oval (broadly lenticular in *Afrixalus spinifrons*) and rather small. Only in *A. s. spinifrons* and *A. delicatus* is its major diameter greater than one-third the length of the medial vocal cord.

Superior and inferior pulvinaria vocalia are well developed in all the species examined.

Medial vocal cord

The medial vocal cord is narrow medially and strongly flared at the insertions. It is traversed by a frenulum in all the species examined.

The posterior margin is slightly to distinctly curved, and flanged. Posterior buttresses are present, but feebly developed, in most of the species examined; they are absent in *Afrixalus spinifrons*.

The anterior margin is strongly concave medially, forming the posterior border of the arytenoid fossa. Anterior buttresses are absent in all the species examined.

A large unguiform superior buttress, immediately anterior to the small posterior buttress, is present in *Afrixalus fornasinii*.

Lateral vocal cord

A discrete well-developed lateral cord is present only in *Afrixalus spinifrons*. It is doubly folded in *A. s. spinifrons*, the anterior fold having a small marginal prominence a little below the mid-line. In *A. spinifrons* subsp. nov. it is broad but simple, and is traversed medially by a thickened band.

In *Afrixalus crotalus*, *delicatus* and *fornasinii* the lateral cord is very narrow, and visible only adjacent to the posterior buttresses. In *A. aureus* even these traces are absent.

Posterior chamber

A weak interadital falciform septum is present on the posterior wall of the posterior chamber in *Afrixalus s. spinifrons*. No other features of diagnostic value could be discerned.

M. hyoglossus

Arises anterior to the cricoid cartilage in all species except *A. aureus*.

LARVAL BUCCOPHARYNX (Pl. 67)

Only the tadpoles of *Afrixalus spinifrons* subsp. nov. and of *A. fornasinii* were available for dissection. Wager's *Afrixalus* tadpoles (now held in the Natal Museum) were so poorly preserved, at the time of collection, as to be useless for the present study.

Differences between the two taxa are quite remarkable. Indeed, the differences are so great and the points in common so few -- if any -- (*vide* Plate 67), that any attempt at a unified comparison becomes meaningless. This problem is addressed further in the Discussion. It is pertinent merely to remark at this point that the buccopharynx of *Afrixalus fornasinii* possesses all the characteristic features of a free-living larva, whilst that of *Afrixalus spinifrons* subsp. nov. approaches that of direct-development larvae!

SPECIES ACCOUNT

Afrixalus spinifrons spinifrons (Cope, 1862)

Hyperolius spinifrons Cope, 1862, *Proc. Acad. Nat. Sci. Philadelphia*, 1862:342. Type locality: Umvoti, Natal. Holotype in the Academy of Natural Sciences, Philadelphia.
Afrixalus spinifrons (Cope): Poynton 1964:182, fig. 105. Van Dijk 1966:257. Passmore & Carruthers 1979:236, figs.
Afrixalus spinifrons spinifrons (Cope): Pickersgill, in prep. Lambiris 1989a:130

ADULT MALE LARYNX (Table 18; Pl. 65, fig. 1)

Material examined: SOUTH AFRICA: NATAL - NM 3994 (m, SVL 19.7 mm), Kwa Mbonambi. NM 5633a (m, SVL 17.2 mm), Pinetown. NM 5634e (m, SVL 19.6 mm), NM 5634h (m, SVL 18.3 mm), and NM 5634k (m, SVL 17.1 mm), Mtunzini.

Advertisement call: A long trilled buzz, about 1.5 seconds long, at about 4 kHz; uttered, in chorus, from short emergent grass in shallow pools and inundated wetlands. (Field observations, Durban district.)

Pharyngeal mucosa: Covers the dorsum of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface broadly U-shaped, the outline of the external margin being modified by a domed superior prominentia and a much smaller triangular inferior prominentia. The internal flexure is very rounded. The occlusal surface is smooth, narrow, and lacks an arytenoid valve. The arytenoid shelf is moderately broad throughout most of its length. The pulvinaria vocalia are very large.

Vocal cords: The **medial cord** is broad, and strongly flared at the insertions. The posterior margin is flanged, and lacks posterior buttresses. There is a rather broad medial frenulum that is itself constricted medially. The **lateral cord** is large, well developed, and thrown into an anterior fold with a small rounded eminence at about the mid-point, and a simple, more strongly concave posterior fold.

Posterior chamber: A weak interadital falciform septum is present on the posterior wall of the posterior chamber. The aditus is small.

LARVAL BUCCOPHARYNX

Well-preserved tadpoles were not available for dissection.

Afrixalus spinifrons subsp. nov. [Pickersgill, in prep.]

Afrixalus spinifrons subsp. A [Pickersgill, in prep.]; Lambiris 1989a:131.

ADULT MALE LARYNX (Table 18; Pl. 65, fig. 2)

Material examined: SOUTH AFRICA: NATAL - NM 3952 (m, SVL 19,2 mm), and NM 3956 (m, SVL 20,2 mm), Cedara. TRANSKEI - NM 5632b (m, SVL 19,8 mm), and NM 5632d (m, SVL 19,0 mm), Port St. Johns. PARATYPES.

Advertisement call: Said to resemble that of *Afrixalus spinifrons spinifrons* very closely. (Pickersgill, in prep.)

Pharyngeal mucosa: Covers the dorsum of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface somewhat V-shaped, the outline of the external margin being modified by a rather triangular superior prominentia, the apex directed ventrally. The inferior portion of the occlusal surface is of uniform width. The internal flexure is broadly V-shaped. There is a narrow arytenoid valve on the posterior margin, above the internal flexure. The arytenoid shelf is strongly tapered superiorly. It has a shallow, rather weakly defined, oval fossa behind the internal occlusal flexure. The pulvinaria vocalia are large.

Vocal cords: The **medial cord** is narrow medially, and strongly flared at the insertions. The posterior margin is flanged, but lacks buttresses. There is a rather broad medial frenulum. The **lateral cord** is broad, with a concave posterior border, and not thrown into folds. It has a rather broad medial frenulum-like thickening.

Posterior chamber: The posterior chamber lacks a falciform posterior septum.

LARVAL BUCCOPHARYNX (Pl. 67, fig. 2)

Identification of larvae: Identification to genus and to "*A. spinifrons* ?" is from Lambiris 1989a. Attribution to this subspecies is circumstantial, being based on material collected at one of the paratype localities listed by Pickersgill, and well outside the range of nominate *spinifrons* (Lambiris 1989a: maps 62, 63).

Material examined: SOUTH AFRICA; NATAL - AJL 3512a; Stillerust Vlei, Kamberg Nature Reserve; stage 39/40, SVL 8,5 mm; silver impregnation.

Larval habitat: An earth scrape, shallow marginally but about one metre deep centrally, with emergent marginal grasses, and some small floating plants in the deeper waters. Water very clear, over a sandstone bottom with sand and organic debris.

Buccopharyngeal roof

General shape: Triangular, base about 0.88x height. Surface concave, slightly more so medially. The prenarial arena is rather deep.

Prenarial arena: A single conical pustule near the right anterolateral margin (presumably another on the left side is normally also present). The arena is traversed by a large, well-defined inverted chevron-like fold or ridge, the apex at about the middle of the arena and the arms terminating posterolaterally, just anterior to the internal nares. A simple subconical **prenarial papilla** arises from the lateral wall, just anterior to the midpoint of the naris, on the left side. Its length is slightly less than the narial width. (The right papilla was damaged during dissection.)

Internal nares: Obliquely elliptical, orientated anteromedially. The narial width is about 0.39x the width of the roof at that level, and the internarial distance is about 0.44x the narial width.

Narial valve: The nares are circumscribed by a simple continuous flap devoid of ornamentation.

Postnarial arena: A simple cylindrical **postnarial papilla** (length about 0.5x narial width) arises a short distance behind the middle of the posterior narial margin. There are no **lateral ridge papillae**. The **median ridge** is set very far back, a prenarial arena's length behind the nares, and is a small, more or less trapezoid flap (base about equal to height, and both about equal to the internarial distance), with a small apical papilla.

Buccal roof arena: Not demarcated by papillae or pustules, which are (apart from those already described) totally lacking, but may be considered to occupy the shallow inverted trapezoid fossa behind the median ridge.

Dorsal velum: Not present.

Pressure cushions: Continuous across the posterior limits of the buccopharynx. The cushions are broadest laterally, and feebly demarcated from the narrower medial portion by a short groove. The surface is irregularly folded.

Buccopharyngeal floor

A tall trapezoid, the base about equal to the height. The buccal floor is divided longitudinally by a medial ridge, flanked by a narrow, shallow groove which flares out posteriorly. The prelingual arena is moderately deep.

Prelingual papillae: A paramedian pair of short cylindrical papillae, set a short distance apart, arises from the anterior third of the floor. The posterior margin of the arena is bounded by a pair of posteriorly inflected U-shaped folds abutting the tongue anlage.

Lingual papillae: A pair of small, close-set conical pustules arises from the mid-dorsum of the tongue anlage.

Buccal floor arena: Square, occupying the posterior half of the buccal floor. It is bounded on the left side by two very short conical papillae, and a single posterior one on the right (an anterior papilla presumably normally present). There are no pustules on the buccal floor.

Buccal pockets: Narrow, transversely elliptical, deep-set, and apparently open. There are no prepocket papillae.

Ventral velum: Well developed but very delicate, and lacking marginal appendages. There is a massive semilunar cartilaginous support behind the buccal pocket, on either side; supporting spicules are otherwise absent. A small conical velar papilla is present just behind the medial end of either supporting cartilage.

Branchial baskets: Details are not clear in this preparation, but they appear to be rather small and fully occupied by the filter plates.

Filter plates: Only a single filter plate on either side is visible in this preparation. The large, very coarse filter rows, which have only primary folds, are orientated posterolaterally. The channels are correspondingly coarse.

Afrixalus aureus Pickersgill, 1984

Afrixalus brachycnemis brachycnemis (non Boulenger, 1896): Poynton 1964:180, fig. 103 (part). Passmore & Carruthers 1979:236, figs. (part).

Afrixalus aureus Pickersgill, 1984, *Durban Mus. Novit.*, 13:206, figs. 1, 4, 6. Type locality: Mhlatuze Valley, 6 km N. of Eshowe. Holotype in the British Museum (Natural History), London. Lambiris 1989a:132.

ADULT MALE LARYNX (Table 18; Pl. 66, fig. 1)

Material examined: MOZAMBIQUE: NM 3943 (m, SVL 18,6 mm), Maputo, NM 3945 (m, SVL 19,0 mm), Ponto do Calichane. (PARATYPES) SOUTH AFRICA: NATAL - NM 3896 (m, SVL 21,4 mm), Ndumu. (PARATYPE) AJL 2283 (m, SVL 21,0 mm), Mazuwi, Umfolozi Game Reserve.

Advertisement call: Pickersgill (1984:208) describes the call as:

> "... an indistinct, uneven chuckle lasting up to 0,5 s, with pulses in the region of 15-20/s ..."

Pharyngeal mucosa: The mucosa and submucosa are confined to a shallow fossa on the dorsum of the arytenoid cartilage.

Arytenoid cartilage: The occlusal surface is broadly curved, with a very low superior prominentia extending across the anterior margin. The inferior portion of the occlusal surface is triangular. The internal flexure is V-shaped. There is no arytenoid valve. The arytenoid shelf is broad superiorly, and lacks a postflexural fossa. The pulvinaria vocalia are large.

Vocal cords: The **medial cord** is narrow medially, and strongly flared at the insertions. The flange on the posterior margin is continuous with the small, weak posterior buttresses. There is a narrow, well-defined medial frenulum. The **lateral cord** is absent.

Posterior chamber: There is no posterior falciform septum.

LARVAL BUCCOPHARYNX

The tadpole appears to be unknown.

Afrixalus delicatus Pickersgill, 1984

Afrixalus brachycnemis brachycnemis (non Boulenger, 1896): Poynton 1964:180, figs. 103 (part), Passmore & Carruthers 1979:236, figs. (part).

Afrixalus delicatus Pickersgill, 1984, *Durban Mus. Novit.*, 13:211, figs. 3-6. Type locality: St. Lucia village, Natal. Holotype in the British Museum (Natural History), London. Poynton & Broadley 1987:188. Lambiris 1989a:132.

ADULT MALE LARYNX (Table 18; Pl. 66, fig. 2)

Material examined: MOZAMBIQUE: NM 39915 (m, SVL 21 mm), "Pungwe R. x Beira Rd." (PARATYPE). SOUTH AFRICA: NATAL - NM 3890 (m, SVL 21,5 mm), Kwambonambi. NM 3893 (m, SVL 21,5 mm), Mosquito Hill, Mkuzi Swamps. (PARATYPES) AJL 2615 (m, SVL 21,2 mm), Ndumu Game Reserve.

Advertisement call: An abruptly-terminated buzz, about 0.5 - 1 second long, at about 5 - 6 kHz (showing marked frequency modulation); uttered at night, or on overcast days, from dense vegetational cover at or near the water's edge, in close chorus. (Field observations.)

Pharyngeal mucosa: The thin, smooth mucosa and thicker submucosa extend over the dorsum of the arytenoid cartilage, and blend with it apically.

Arytenoid cartilage: The external margin forms a ventrally skewed curve, the superior prominentia being large and dome-shaped, broadest in the lower half. The inferior position of the occlusal surface is very short, and oval. The internal flexure is acutely V-shaped. There is no distinct arytenoid valve, although the posterior margin of the occlusal surface is slightly thickened just above dorsal to the flexure. The arytenoid shelf is markedly tapered superiorly, and lacks a postflexural fossa. The superior pulvinarium vocale is large, the inferior pulvinarium somewhat smaller.

Posterior chamber: There is no posterior falciform septum.

LARVAL BUCCOPHARYNX

No reliably attributable tadpoles were available for study.

Afrixalus fornasinii (Bianconi, 1850)

Euchnemis fornasinii Bianconi, 1850, *Spec. Zool. Mossamb., Rept.*, p. 23, pl. 5 fig. 1, Type locality: Mozambique, Type not traced (Poynton & Broadley 1987:192). Poynton & Broadley 1987:192. Lambiris 1989a:133; 1989b:159, figs. 92 & 93, pl. 18 figs. 4a-c. Steinwarz 1990:53.

Afrixalus fornasinii fornasinii (Bianconi): Poynton 1964:183, fig. 106. Passmore & Carruthers 1979:238, figs.

ADULT MALE LARYNX (Table 18; Pl. 66, fig. 3)

Material examined: SOUTH AFRICA: NATAL - AJL 1923 (m, SVL 40.0 mm), 3.5 km west of Tugela River mouth.

Advertisement call: A series of loud percussive notes at about 2.5 kHz (Passmore & Carruthers 1979:238), repeated about 10 - 12 times a second. Calls are uttered from leaves and reeds, just above water level, at night and on cloudy days. The choral structure is rather loose.

Pharyngeal mucosa: Confined to a shallow fossa on the anterodorsal surface of the arytenoid cartilage.

Arytenoid cartilage: The occlusal surface is very broadly and shallowly calyculate, and narrow. The superior prominentia is low and flattened. The inferior portion of the occlusal surface is very short, and of approximately uniform width. The internal flexure is V-shaped. A narrow arytenoid valve is present above the posterior flexure. The arytenoid shelf is not tapered superiorly, and lacks a postflexural fossa. The superior pulvinarium vocale is larger than the inferior pulvinarium.

Vocal cords: The **medial cord** is narrow medially, and widely flared at the insertions. The narrow posterior flange is continuous with the small, weakly developed posterior buttresses. The cord is divided vertically into two portions by a medial fold originating from a large unguiform buttress immediately anterior to the superior posterior buttress. The **lateral cord** is greatly reduced and almost entirely covered by the medial cord, with only the apices of the posterior margins visible.

Posterior chamber: There is no posterior falciform septum.

LARVAL BUCCOPHARYNX (Pl. 67, figs. 2a & b)

Identification of larvae: Lambiris 1989a, and a series from False Bay Nature Reserve, Lake St. Lucia, Natal (AJL 2693 - 2705, stages 34 - 46), showing markings diagnostic of adults from stage 45.

Material examined: AJL 2695a; stage 36, SVL 11,6 mm; and AJL 2697a; stage 38, SVL 11,3 mm; False Bay Nature Reserve; silver impregnation.

Larval habitat: Moderately deep to deep pans with dense emergent marginal reed beds and grasses, often with some floating vegetation more centrally, and with a rich bottom layer of organic debris. The diet consists of soft macrophyte material and small algae.

Buccopharyngeal roof

General shape: A tall trapezoid, the base about equal to the height. The roof is shallowly concave, and the prenarial arena is rather deep.

Prenarial arena: A narrow ridge traverses the roof immediately behind the root of the upper beak. A U-shaped row of pustules (three separate ones on either side, and about 5 - 6 confluent pustules medially) are arranged anteriorly and laterally, behind the transverse ridge.

Internal nares: Elliptical, orientated slightly posteromedially. The narial width is about 0.4x the width of the roof at that level, and the internarial distance is about 0.43x the narial width.

Narial valve: A low flap circumscribing the naris, and bearing a short subconical papilla at about the mid-point on the anterior flap. The posterior margin is grooved.

Postnarial arena: A conical **postnarial papilla** (height about equal to the narial width), with a slightly pustulate anterior margin, arises behind the mesial half of the naris. It is flanked by two similar **lateral ridge papillae, equal, to slightly larger, in size. The median ridge** is a low arcuate flap, the base about 0.6x the width of the roof at that level. The free margin is thickened, but devoid of ornaments. Three pustules lie immediately anterior to the median ridge, between the posterior lateral ridge papillae.

Buccal roof arena: Demarcated by four stout conical papillae (two on either side) arranged in an inverted trapezium, and containing 16 - 20 small pustules. Additional pustules extend beyond the arena towards the median ridge.

Glandular ridge: A well defined ridge anterior, and parallel to, the dorsal velum on each side. It is coarsely pustulate.

Dorsal velum: A weak fold on either side, with a small median gap.

Pressure cushions: Triangular, the major axes directed posteromedially. The surfaces are longitudinally ridged.

Buccopharyngeal floor

General shape: Roughly trapezoid, the base slightly less than the height. The surface is convex, slightly more so medially. The prelingual arena is moderately deep.

Prelingual papillae: A short bifurcate papilla arises just behind the centre of the arena floor. A larger, more complex bifurcate papilla, each arm itself bifid, lies immediately anterior to the tongue anlage. Between these papillae is a short, simple cylindrical papilla. A slender subconical papilla, slightly pustulate on the anterior apical margin, arises from the middle of the lateral wall on either side.

Lingual papillae: A pair of tall, close-set cylindrical papillae arises from the mid-dorsum of the tongue anlage.

Buccal floor arena: Demarcated by a posteriorly convergent row of three conical papillae on either side, the anterior two more closely spaced than the second and third. The first and third papillae are of approximately equal size; the second is somewhat taller.

Pustulations: The whole of the buccal floor behind the lingual arena, including the buccal pockets and the ventral velum, is covered with a moderately dense scattering of dark verrucosities.

Buccal pockets: Oval, shallow, closed, and with rather deeply grooved margins.

Ventral velum: Rather broad, and divided into five segments (one median, two paramedian on either side) by a continuous series of arched cartilaginous supports. The free margin is thickened and has five or six regularly-spaced, but very small, lobes.

Branchial baskets: Moderately large, somewhat triangular, the major axes directed posteromedially.

Filter rows: Weakly fimbriated. The rows are directed posteromedially, and have secondary folds. The channels are rather narrow.

DISCUSSION

Poynton & Broadley (1987) present a detailed discussion of the numerous problems that arise in any attempt to treat the dwarf *Afrixalus* species, and Lambiris (1989a:130) expressed considerable reservations about the validity of the three southern African species described by Pickersgill (1984).

These difficulties stem from the fact that the diagnostic features generally used (e.g. markings, extent of skin asperities, shape of gular disc) are frequently poorly defined or ambiguous. Advertisement calls are invaluable in indicating taxonomically different populations in the field, but are of little value where the majority of museum specimens are concerned.

Adult laryngeal morphology appears to be a useful diagnostic tool in the taxa examined here, and may well contribute to an elucidation of the currently intractable problems involving the more northerly species, particularly the *Afrixalus brachycnemis / A. pygmaeus* complex.

The *Afrixalus spinifrons* subspecies

Pickersgill's as yet unpublished subspecies of *Afrixalus spinifrons* is said to differ from the nominate form in having a less bulbous snout, smaller asperities, and reduced markings, but Lambiris (1989a:131) commented that intergradation in these features rendered distinction difficult. However, internal laryngeal morphology separates the two taxa very satisfactorily (Pl. 65, figs. 1 & 2) and I now have no doubt that Pickersgill was correct in recognising two forms.

The *Afrixalus aureus / crotalus / delicatus* group

Lambiris (1989a:130) expressed reservations about the validity of these species, using Pickersgill's names only for taxonomic stability.

Once again, internal laryngeal morphology readily and consistently serves to identify Pickersgill's species, irrespective of the state of external diagnostic features, and show them to be valid taxa (Plate 65, fig. 3; Plate 66, figs. 1 & 2). It would appear that the live specimens from Ndumu Game Reserve considered by Lambiris (1989a:132) to be *Afrixalus aureus* on the basis of their markings were in fact *A. delicatus* with *aureus*-like markings -- a situation which seems to occur occasionally.

Afrixalus fornasinii

Steinwarz (1990:51) examined the larynx of *Afrixalus fornasinii*, comparing it with those of a number of European Bufonid, Ranid and Hylid genera. He examined only the external morphology -- that is, the cricotracheal, arytenoid and hyoid cartilages, and the extrinsic laryngeal muscles. He considered (p. 58) that

> "The [laryngeal] skeleton, then, is most similar to that of the abovementioned Hylidae and Bufonidae, whereas the musculature is most like that of the Hylidae and Ranidae. In the overall structure of the skeletal and muscular elements of the larynx, *A. fornasinii* resembles the Hylidae more closely than the Ranidae."

Curiously enough, Steinwarz did not compare the larynx of *Afrixalus fornasinii* with that of any other African Hyperoliid, and his conclusions are, consequently, difficult to understand.

Comparison of internal laryngeal morphology shows that, apart from the highly specialised Leptopeline species examined, the larynx of *Afrixalus fornasinii* is far closer to those of the other Hyperoliid genera and species treated here than to those of the Bufonidae and the Ranidae.

The generic status of the dwarf *Afrixalus* species

The amount of larval *Afrixalus* material examined in this study is insufficient for any meaningful treatment of taxonomic relationships. However, differences between the buccopharynxes of *Afrixalus spinifrons*

subsp. nov. and of *Afrixalus fornasinii* are so remarkable that some comment is called for.

It is immediately apparent, simply from consulting the plates, that in all the other taxa examined in this study, there are strong intrageneric similarities in adult larynxes and larval buccopharynxes, and equally distinct intergeneric differences. (These have not been discussed in detail, for classification above the species level was not one of the proximal aims of this study.)

Had adult frogs shown morphological differences of the magnitude occurring in the larval buccopharynxes of these two species, they would assuredly have been assigned to two different genera. It is obviously premature to suggest generic separation on such insufficient material, but the possibility of such separation should at least be considered if additional material, when available, shows a consistent difference between the dwarf and larger species of *Afrixalus*. The collection of more material for such a further study is to be undertaken as a matter of urgency.

PLATE 65
AFRIXALUS - ADULT HYOLARYNXES
Median sagittal section, View into left half, Anterior to right.

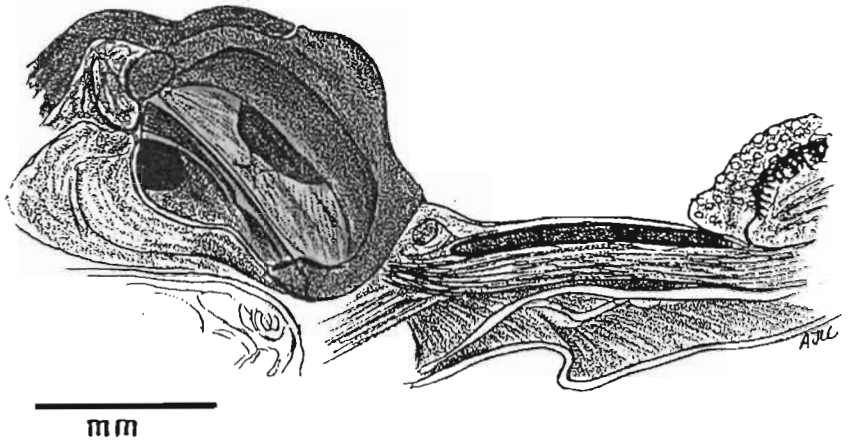


FIG. 1; *Afrixalus spinifrons spinifrons* (Cope, 1862)
NM 5634k (male), Mtunzini, Natal, South Africa.

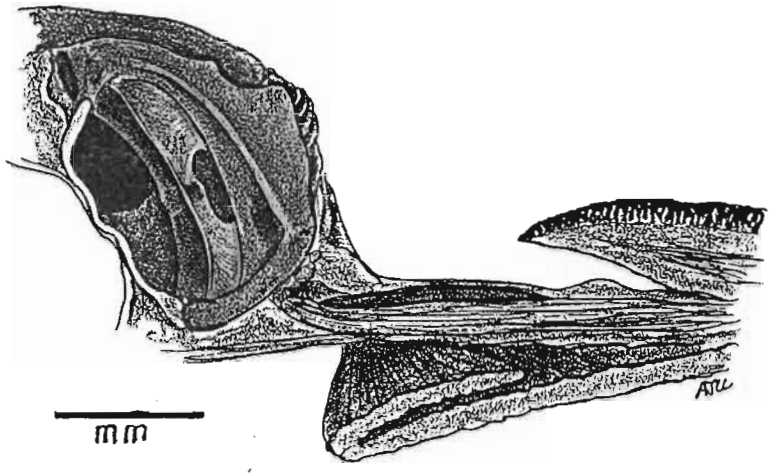


FIG. 2; *Afrixalus spinifrons* subsp. nov. - Pickersgill, in prep.
NM 33632d (male), Port St. Johns, Transkei, South Africa.

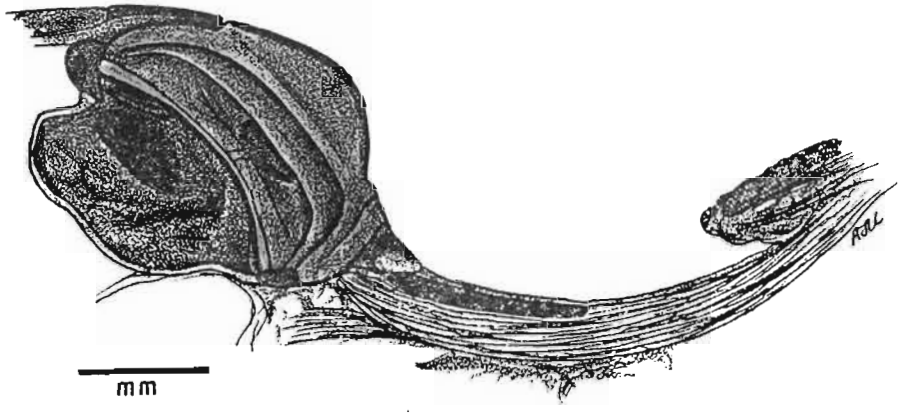


FIG. 3; *Afrixalus crotalus* Pickersgill, 1984
AJL 1857 (male), Mutare, Zimbabwe.

PLATE 66
AFRIXALUS – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

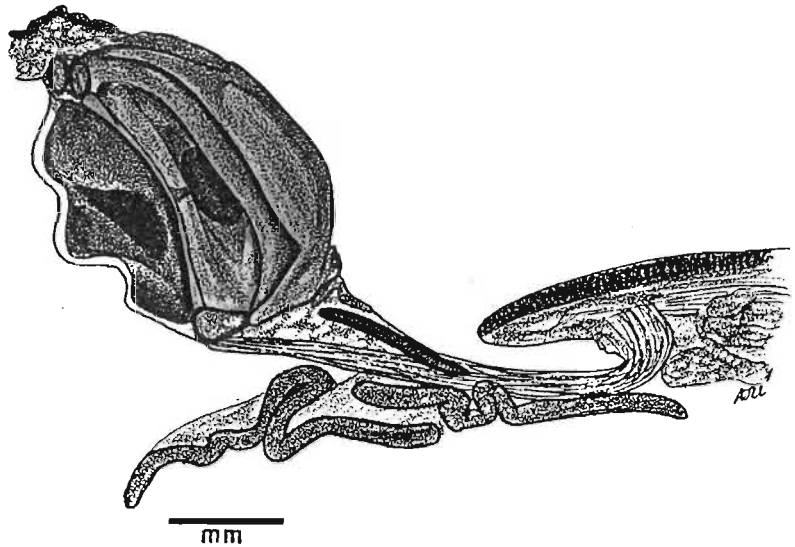


FIG. 1: *Afrixalus aureus* Pickersgill, 1984
AJL 2283 (male), Mazuwi, Umfolozi Game Reserve, Natal, South Africa.

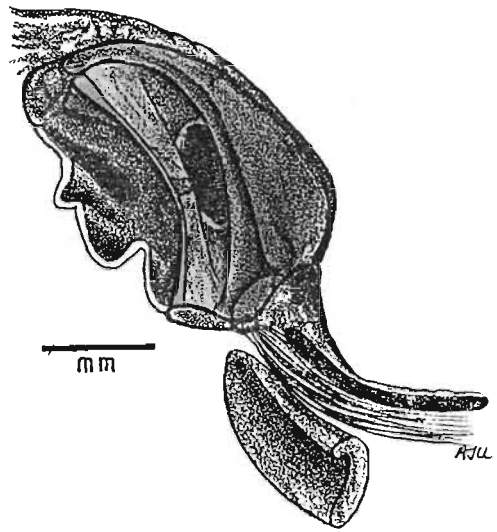


FIG. 2: *Afrixalus delicatus* Pickersgill, 1984
AJL 2615 (male), Mahemane, Ndumu Game Reserve, Natal, South Africa.

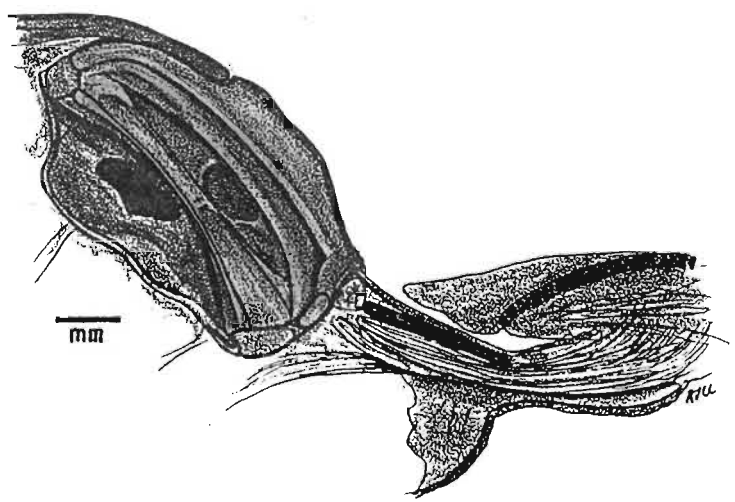


FIG. 3: *Afrixalus fornasinii* (Bianconi, 1850)
AJL 1923 (male), 3.5 km west of Tugela River Mouth, Natal, South Africa.

PLATE 67
AFRIXALUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

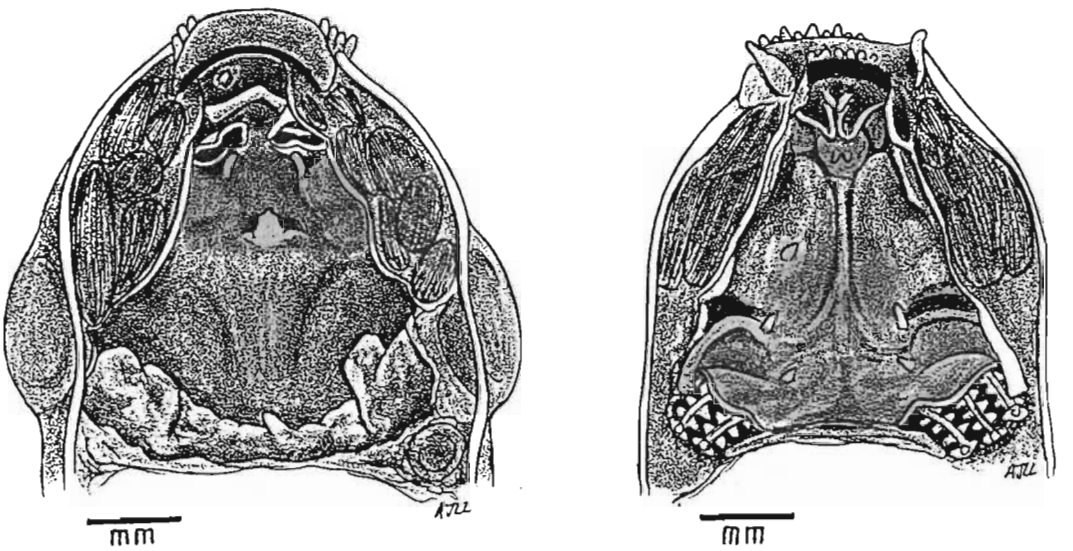


FIG. 1: *Afrixalus spinifrons* subsp. nov. – Pickersgill, in prep.
AJL 3512a, Stage 39/40, Stillerust Vlei, Kamberg Nature Reserve, Natal, South Africa.

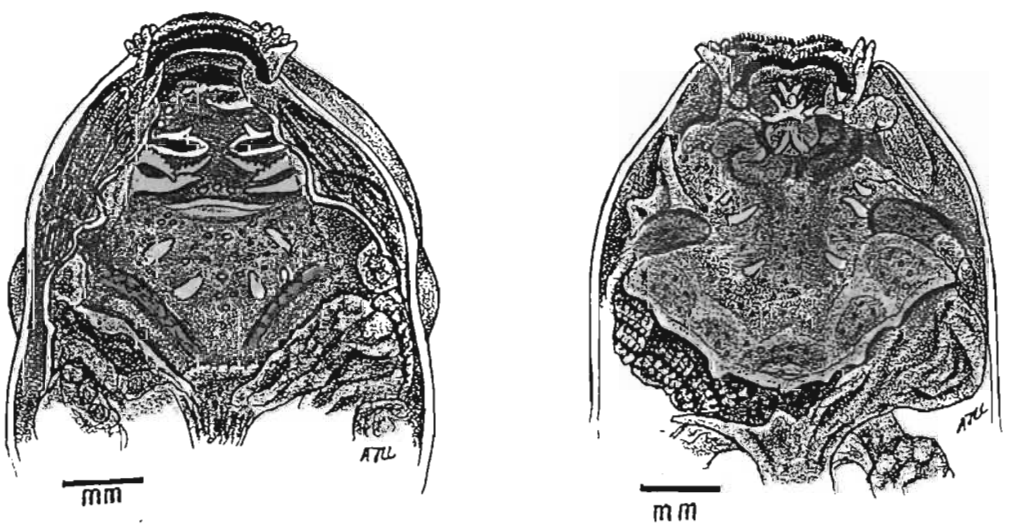


FIG. 2: *Afrixalus fornasinii* (Bianconi, 1850)
AJL 2697, Stage 38, False Bay Nature Reserve, Lake St. Lucia, Natal, South Africa.

TABLE 19. Laryngeal characters: *Hyperolius*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	DORSUM OF ARYTENOID CARTILAGE RECESSED TO RECEIVE PHARYNGEAL MUCOSA	SUPERIOR PROMINENTIA MASSIVE AND CONSPICUOUS	A DISTINCT ARYTENOID VALVE PRESENT	POSTERIOR OCCLUSAL MARGIN HAS A DISTINCTLY V-SHAPED NOTCH	ARYTENOID SHELF HAS A DOUBLE STEP	ARYTENOID SHELF STRIATED OR RUGOSE AT ANTERIOR BORDER OF FOSSA	POSTERIOR MARGIN OF MEDIAL VOCAL CORD DISTINCTLY FLANGED ALONG ITS ENTIRE LENGTH	NO LARGE BUTTRESSES PRESENT ON THE MEDIAL VOCAL CORD	ALL, OR NEARLY ALL, OF THE LATERAL VOCAL CORD CLEARLY VISIBLE	LATERAL VOCAL CORD HAS A BULBOUS INFERIOR BUTTRESS
Hyperolius semidiscus	1	1	1	1	3	3	3	3	1	3
argus	3	3	1	3	3	3	3	1	1	3
tuberilinguis	1	1	3	3	3	3	1	1	1	3
pusillus	3	3	1	3	3	3	1	1	1	3
nasutus	1	3	1	1	3	3	1	1	3	3
pickersgilli	3	1	3	1	3	3	1	1	1	3
marmoratus verrucosus	1	1	3	1	1	1	1	1	1	3
marmoratus marmoratus	1	1	1	1	1	1	1	3	1	1
marmoratus taeniatus	1	1	1	1	3	1	1	1	1	1

Genus *Hyperolius* Rapp, 1842

Eucnemis (non Ahrens) (part) Tschudi, 1838, *Classif. Batr.*, p. 76. Type species not designated.

Hyperolius Rapp, 1842, *Archiv. für Naturg.*, 8:289. (Substitute name for *Eucnemis* Tschudi, preoccupied.) Type species by monotypy: *Hyperolius marmoratus* Rapp, 1842.

Crumenifera Cope, 1862, *Proc. Acad. Nat. Sci. Philadelphia*, 1862:343. Type species by monotypy: *Crumenifera pusilla* Cope, 1862.

Rappia Günther, 1864, *Zool. Rec.*, 1:130. (Substitute name for *Hyperolius* Rapp, thought to be preoccupied by *Uperolia* Gray.)

CHARACTERS

ADULT LARYNX (Table 19, Pls. 68 - 70)

Character variation in male larynxes of the species examined is summarised in Table 19. Sexual dimorphism is slight, the female larynx differing from that of the male only in small matters of detail.

Surface of the arytenoid cartilage

A dorsal fossa receives the pharyngeal mucosa in all the species examined. It is very shallow, and barely definable, in *Hyperolius argus* and *H. pusillus*, but deeper and more sharply defined (in approximately increasing order) in *Hyperolius pickersgilli*, *nasutus*, *tuberilinguis*, *semidiscus*, *marmoratus marmoratus*, *marmoratus verrucosus*, and *marmoratus taeniatus*.

Symmetry of the arytenoid cartilage

Symmetry about the anteroposterior axis is variable. Approximate symmetry is shown in the larynxes of *Hyperolius argus*, *H. pusillus* and *H. pickersgilli*. Those of the other species are asymmetrical, most markedly so in *Hyperolius semidiscus* and the *Hyperolius marmoratus* subspecies, least so in *H. nasutus*.

Prominentia vocalia

A distinct flexure in the posterior margin of the occlusal surface is taken to define the functional apex of the occlusal surface, and thus to differentiate between superior and inferior prominentiae. Where there is no such flexure, any prominentia present is taken to be superior.

The superior prominentia is massive in all the species examined excepting *Hyperolius argus*, *H. pusillus* and *H. nasutus*.

Only in *Hyperolius marmoratus verrucosus* is the surface of the superior prominentia thrown into folds; in the other taxa examined it is quite regular.

A small but distinct inferior prominentia vocale is present in *Hyperolius marmoratus verrucosus* (also thrown into folds), *H. m. taeniatus*, *H. m. marmoratus* and *H. pusillus* (listed in order of decreasing size).

Shape of the posterior occlusal margin

The posterior occlusal margin is broadly and shallowly calyculate in *Hyperolius argus* and *H. pusillus*, irregularly so in *h. tuberilinguis*, and indented with a more or less well-defined flexure in *Hyperolius nasutus*, *pickersgilli*, the *marmoratus* subspecies, and *H. semidiscus* (listed in approximate order of increasing flexural acuteness).

Arytenoid shelf

Two features appear to be of special interest. The arytenoid shelf has a double step in *Hyperolius m. marmoratus* and *H. m. verrucosus*. (It is absent, or not strongly developed, in the specimens of *H. m. taeniatus* examined.)

That portion of the arytenoid shelf forming the anterior border of the arytenoid fossa bears numerous well-defined, short, closely-spaced, transverse striations in the *Hyperolius marmoratus* subspecies, but not in other members of the genus, examined in this study.

Arytenoid fossa

The arytenoid fossa is, for the most part, narrowly oval. It is almost round in *Hyperolius tuberilinguis*, and in *Hyperolius pusillus* the inferior border tapers acutely.

Medial vocal cord

The fundamental pattern is that of a flat cord with a strongly concave anterior margin delimiting the posterior border of the arytenoid

fossa; widely flared insertions; and a gently curved, weakly flanged, posterior margin with superior and inferior buttresses.

The cord is only slightly constricted, and rather broad medially, in *Hyperolius semidiscus*, *nasutus*, *pickersgilli* and *H. marmoratus taeniatus*. It is moderately constricted medially in *Hyperolius argus*, *H. pusillus* and *H. marmoratus marmoratus*. It is strongly constricted, and very narrow medially, in *Hyperolius tuberilinguis* and *H. marmoratus verrucosus*.

A frenulum is present in all the species examined. It is broadly triangular in *Hyperolius semidiscus* and *H. m. marmoratus*, and narrow in the other taxa examined.

Large posterior buttresses are present only in *Hyperolius semidiscus* and *H. marmoratus marmoratus*.

Lateral cord

A lateral cord is present in all the taxa examined. The posterior border is slightly convex in *Hyperolius argus*, but concave to a greater or lesser degree in the other taxa examined. The extent to which the lateral cord is exposed or covered by the medial cord shows consistent interspecific variation -- details are most clearly seen by consulting the plates directly.

Posterior chamber

The posterior chamber is anteroposteriorly compressed in all the taxa examined. No features of taxonomic value could be discerned.

M. hyoglossus

The m. hyoglossus arises beneath the inferior portion of the cricoid cartilage in all the taxa examined.

LARVAL BUCCOPHARYNX (Table 20; Pls. 72 - 73)

Reliably identified and adequately preserved larvae of only five taxa were available for dissection in this study -- *Hyperolius semidiscus*, *H. tuberilinguis*, *H. pusillus*, *H. nasutus* and *H. marmoratus marmoratus*.

TABLE 20. Buccopharyngeal characters: *Hyperolius*

0 = UNKNOWN
1 = TRUE
2 = VARIABLE
3 = FALSE
4 = INAPPLICABLE

	PRENARIAL ARENA TRAVERSED BY CURVED ROW OF DISCRETE PUSTULES	ANTERIOR NARIAL FLAP BEARS ONE OR TWO PAPILLAE	ANTERIOR NARIAL FLAP BEARS A PALPOID PAPILLA	FREE MARGIN OF MEDIAN RIDGE SERRATE OR DENTICULATE	A POSTARENAL GLANDULAR PATCH PRESENT AS WELL AS PREVELAR GLANDULAR RIDGE(S)	POSTARENAL GLANDULAR PATCH DIVIDED MEDIALLY	INFRALABIAL ARENA BEARS A LARGE MEDIAL PAPILLA	BUCCAL FLOOR ARENA BOUNDED BY MORE THAN TWO PAPILLAE ON EITHER SIDE	SPICULES OF VENTRAL VELUM PROMINENT	FREE MARGIN OF VENTRAL VELUM BEARS WELL DEFINED APPENDAGES
Hyperolius semidiscus	1	1	3	1	1	3	3	1	1	1
tuberilinguis	3	3	3	1	1	1	1	3	1	3
pusillus	1	3	1	1	1	3	3	2	3	1
nasutus	1	1	3	3	3	4	1	1	1	1
marmoratus marmoratus	3	1	3	3	3	4	1	1	3	3

Prenarial arena

An arcuate row of pustules is present in all taxa examined except in *Hyperolius marmoratus marmoratus*, where they are replaced by a transverse ridge separating the anterior third from the remainder of the arena.

The row of pustules is smallest and most feebly developed in *Hyperolius semidiscus*. In *H. pusillus* it consists of close-set groups of two or three pustules on a simple arena roof, while in *H. nasutus* they are arranged in groups of three or four, borne on a well defined arched ridge. In *H. tuberilinguis* the pustules are more or less confluent.

Nares and narial valves

The nares are transversely elliptical (rather widely so, in *H. pusillus*) in all the taxa examined.

The narial valve consists of a single rim encircling the naris, the posterior margin being unadorned with appendages. The anterior margin is denticulate in *Hyperolius tuberilinguis*, and bears a single papilla in *H. semidiscus* and in *H. m. marmoratus*. A pair of short papillae are present in *H. nasutus*, and in *H. pusillus* the papilla is palpoid.

Postnarial arena

The taxa examined differ principally in matters of detail, having a common pattern of a single conical, anteriorly pustulose, postnarial papilla flanked by a pair of similar lateral ridge papillae.

The median ridge shows clearer interspecific variation. The free margin is serrate in *Hyperolius semidiscus*, finely lobulate in *H. tuberilinguis*, denticulate in *H. pusillius*, and smooth in *H. nasutus* and in *H. m. marmoratus*.

Buccal roof arena

The arena is of moderate size, and bounded laterally by two (*Hyperolius semidiscus, pusillus, nasutus, m. marmoratus*) or three (*H. tuberilinguis*) smooth, conical papillae.

Pustules in the arena are few in *Hyperolius semidiscus, H. pusillus* and *H. m. marmoratus*, more mumerous in the other species examined.

Additional pustules occur on the buccal roof, beyond the arena boundaries, in *Hyperolius tuberilinguis*, *pusillus*, *nasutus* and (very few) in *H. m. marmoratus*.

Glandular areas

A glandular ridge immediately anterior to the dorsal velum is present in all the taxa examined. It is a narrow band of approximately uniform width in *Hyperolius semidiscus* and *H. m. marmoratus*. It is narrowly interrupted medially in *H. nasutus*, and broadly so in *H. pusillus*. In *Hyperolius tuberilinguis* it takes the shape of a broad, low, inverted triangle.

Additional glandular areas are present in *Hyperolius semidiscus* (an oval patch immediately behind the buccal roof arena), *H. tuberilinguis* (an oblique, pustulate, narrow ridge on either side of the buccal roof arena), and in *H. pusillus* (a broad crescent behind the buccal roof arena).

Ventral velum

The ventral velum is moderately well developed in all the taxa examined. It is virtually continuous medially in *Hyperolius semidiscus* and *H. tuberilinguis*, narrowly interrupted in *H. nasutus* and *H. m. marmoratus*, and broadly interrupted medially in *H. pusillus*.

Pressure cushions

Narrow, transversely elongate, and essentially featureless in all the taxa examined.

Prelingual arena and papillae

Pustules are present on the floor of the arena only in *Hyperolius semidiscus* (a pair on either side, equatorially) and *H. pusillus* (a row of separate pustules just behind the root of the beak).

A subconical or cylindrical median papilla, arising from the floor of the arena, just anterior to the tongue anlage, is present in *Hyperolius tuberilinguis* and *H. m. marmoratus*. A stout, apically trifid cylindrical papilla, arising from the middle of the arena floor, is

present in *Hyperolius nasutus*. The other species examined lack prelingual arena floor papillae.

Lingual papillae

Lingual papillae are small, paired, conical paramedian structures arising from the mid-dorsum of the tongue anlage in all taxa examined. They do not show features of clear diagnostic use.

Buccal floor arena

The buccal floor arena is large (occupying 0.75 or more of the area between the lingual arena and the ventral velum) in *Hyperolius semidiscus, tuberilinguis, nasutus* and *H. m. marmoratus*. It is shallower, but broad, in *H. nasutus*.

It is bounded by three conical papillae on either side in all the taxa examined except in *Hyperolius tuberilinguis*, which has only two on either side. Where three papillae are present, the third (posteriormost) is usually more widely separated than the first two. The papillae are usually more or less equal in height; where there is inequality, the tendency seems to be for the first one to be smaller.

Pustules cover the buccal floor arena and extend beyond its borders in all the taxa examined. In *Hyperolius semidiscus, H. tuberilinguis* and, to a lesser extent, *H. m. marmoratus*, they extend even onto the ventral velum.

Buccal pockets

The buccal pockets are transversely oval and rather deeply set in all the species examined. In *Hyperolius semidiscus, pusillus* and *nasutus* the anterior margins are widely to very widely, and deeply, incised. Prepocket papillae are absent.

Ventral velum

The ventral velum is broad and well developed in all the taxa examined. It is of approximately uniform width throughout in *Hyperolius m. marmoratus* and *H. pusillus*, broadest mesially in *H. semidiscus* and *H. tuberilinguis*, and constricted mesially in *H. nasutus*.

The free margin is feebly lobulated in *Hyperolius tuberilinguis* and *H. m. marmoratus*, and more elaborately so in the other species examined. The differences in detail are consistent between species, and are best seen by consulting the plates directly. Full descriptions are given in the Species Account.

Supporting spicules are very prominent, throwing the surface of the velum into characterisitic folds, in *Hyperolius semidiscus* and *H. tuberilinguis*. They are well developed, but not so prominent, in *H. nasutus*, and still less conspicuous in *H. pusillus* and *H. m. marmoratus*.

Branchial baskets and filter plates

The branchial baskets are rather large and rounded. The filter plates are moderately imbricate, and the rather broad filter rows have at least secondary folds. The channels are narrow to moderately wide. They were not studied in detail in this investigation.

SPECIES ACCOUNT

Hyperolius semidiscus Hewitt, 1927

H*Hyperolius horstockii semidiscus* Hewitt, 1927, *Rec. Albany Mus.*, 3:410, pl. 24 fig. 7, Type locality: Mariannhill, Natal. Syntypes in the Port Elizabeth Museum.
Hyperolius semidiscus Hewitt: Poynton 1964:185, fig. 108. Van Dijk 1966:257. Passmore & Carruthers 1979:244, figs. Lambiris 1989a:137.

ADULT MALE LARYNX (Table 19; Pl. 69, fig. 1)

Material examined: SOUTH AFRICA: NATAL - AJL 1830 (m, SVL 31.5 mm), and AJL 1831 (m, SVL 29.0 mm), 1 km west of Merrivale Station, Merrivale.

Advertisement call: A harsh, trilled croak, at about 2.7 kHz and about 0.2 second long (Passmore & Carruthers 1979:244); uttered, in chorus, from reeds growing in water, at night.

Pharyngeal mucosa: A thin mucosa and deeper submucosa covering the dorsum of the arytenoid cartilage, lying in a deep, well defined fossa.

Arytenoid cartilage: The superior prominentia is large and smooth. The rather narrow occlusal surface bears an arytenoid valve on its posterior margin, extending from the superior pulvinarium to the posterior flexure, which is acutely V-shaped. The arytenoid shelf is broadest inferiorly, and is narrowly tapered superiorly. The arytenoid fossa is long and narrow, its diameter about 0.45x the length of the medial vocal cord.

Vocal cords: The **medial cord** is moderately broad medially. The posterior margin is weakly flanged above the level of the frenulum, and has a large superior, but no inferior, buttress. The frenulum is large and triangular, the apex directed posteriorly. The **lateral cord** is large, with a strongly concave posterior margin, and broadly flared at the insertions.

LARVAL BUCCOPHARYNX (Table 20; Pl. 71, figs. 1a & b)

Identification of larvae: Tadpoles reared from eggs laid by identified adults.

Material examined: SOUTH AFRICA; NATAL - AJL 3532a; Mariannhill; stage 39, svl 16,7 mm; silver impregnation.

Larval habitat: Shallow ponds and pans with emergent grassy vegetation, and a bottom cover of organic debris. The diet appears to consist of soft macrophyte tissues and algae.

Buccopharyngeal roof

General shape: Somewhat dome-shaped. The surface is more or less regularly concave, with a deeper prenarial arena.

Prenarial arena: A short, slightly curved row of small pustules (about 4) traverse the arena at about its midpoint.

Internal nares: Transversely elliptical. The narial width is about 0.39x the width of the roof at that point, and the internarial distance is about 0.57x the narial width.

Narial valve: A simple flap circumscribing the naris, bearing a simple cylindrical papilla (the height equal to the narial width) on the anteromedial border. The posterior margin is not deeply grooved.

Postnarial arena: The **postnarial papilla** is robust, conical, and pustulose anteriorly. Its height is about equal to the narial width, and it arises a short distance behind the medial half of the naris. It is flanked by two conical **lateral ridge papillae**, the anterior margins of which are somewhat serrate. The anterior papilla is about 0.6x the height of the posterior one. The **median ridge** is a roughly semicircular flap, the base about 0.25x the width of the roof at that level. The free margin is finely serrate.

Buccal roof arena: A wide, low, inverted trapezoid, bounded on either side by two conical papillae, the anterior ones larger than the posterior. The arena contains about 7 small pustules, and about 7 extend beyond the anterior limits of the arena.

Glandular areas: An oval glandular patch (diameter about half that of the buccal roof arena) lies immediately behind the buccal roof arena. A narrow, continuous glandular ridge lies immediately anterior to the dorsal velum.

Dorsal velum: Moderately well developed, but low, and lacking marginal ornamentation. It is virtually uninterrupted medially.

Pressure cushions: Narrowly triangular, set slightly posteromedially, and almost in contact medially.

Buccopharyngeal floor

General shape: Roughly triangular. The floor is more or less regularly concave.

Prelingual papillae: There is a pair of small pustules, set equatorially, on either side of the prelingual arena floor.

Lingual papillae: Two small, close-set mid-dorsal conical papillae.

Buccal floor arena: Large, occupying the area between the lingual arena and the ventral velum. It is bounded on either side by three tall conical papillae with pustulose anterior margins. The first and second papillae are set closer together than the second and third, and the first papilla is shorter than the other two. The arena contains numerous small pustules, which extend posteriorly beyond its limits onto the ventral velum.

Buccal pockets: Rather small, oval, and deeply set. The anterior margins are widely and deeply grooved. There are no prepocket papillae.

Ventral velum: Well developed, broadest medially, and with four prominent, equally-spaced supporting spicules that throw the velum into arcuate folds between them. The free margin is slightly thickened and bears a group of six closely-set short, rounded lobes medially, and another pair at about the mid-point of either side. The velum between the margin and the spicular folds is granular.

Branchial baskets: Large, rounded, with the major axes directed posterolaterally.

Filter plates: Moderately imbricate. The filter rows have secondary folds, and the channels are narrow.

Hyperolius argus Peters, 1854

Hyperolius argus Peters, 1854, *Monatsber. könig. Akad. Wiss. Berlin*, 1854:628. Type locality: Boror, northern Mozambique. Type apparently lost (Poynton & Broadley 1987:199). Poynton 1964:187, fig. 110 (part). Passmore & Carruthers 1979:246, figs. Poynton & Broadley 1987:199. Lambiris 1989a:137; 1989b:163, fig. 94, pl. 19 figs. 1a-e.

Hyperolius flavoviridis Peters, 1854, *Monatsber. könig. Akad. Wiss. Berlin*, 1854:628. Type locality: Boror, northern Mozambique. Location of type not ascertained.

Hyperolius tetensis Peters, 1854, *Monatsber. könig. Akad. Wiss. Berlin*, 1854:628. Type locality: Tete, Mozambique. Location of type not ascertained.

Rappia platycephala Pfeffer, 1893, *Jahrb. der Hamb. Wissensch. Anst.*, 10:96, pl. 1 fig. 2. Type locality: Quilimane [i.e., Quelimane, Mozambique]. Syntypes destroyed.

Hyperolius puncticulatus puncticulatus (non Pfeffer, 1893): Poynton 1964:109 (part).

Hyperolius puncticulatus (non Pfeffer, 1893): Van Dijk 1966:257.

ADULT MALE LARYNX (Table 19; Pl. 68, fig. 2)

Material examined: SOUTH AFRICA: NATAL - AJL 3066 (m, SVL 32,0 mm), St. Lucia Village, Lake St. Lucia. NM 7516 (m, SVL 34,0 mm), and NM 7519 (m, SVL 30,2 mm), Yellowwood Park, Durban.

Advertisement call: A short cluck, about 0.03 second long, at about 3.2 kHz (Passmore & Carruthers 1979:246), uttered two or three times a second for extended periods. Calls are made from floating water lily leaves (sometimes from reeds), in chorus, at night.

Pharyngeal mucosa: A thin mucosa and submucosa cover the superior portion of the arytenoid cartilage, lying in a barely defined fossa.

Arytenoid cartilage: There are no distinct prominentiae apicales. The arytenoid valve is well developed, and blends with the posterior border of the arytenoid shelf inferiorly. The shelf is of approximately uniform width throughout. The arytenoid fossa is broadly oval, its diameter about 0.28x the length of the medial vocal cord.

Vocal cords: The **medial cord** is rather narrow medially. The posterior margin is not flanged, and there are no buttresses. The **lateral cord** is shorter than the medial cord, and its posterior margin is slightly convex. The frenulum traverses both cords.

LARVAL BUCCOPHARYNX

No material suitable for dissection was available.

Hyperolius tuberilinguis A. Smith, 1849

Hyperolius tuberilinguis A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App., p. 26. Type locality: "Country to the eastward of the Cape Colony". "No discoverable type material" (Poynton & Broadley 1987:194). Poynton 1964:189, fig. 111. Van Dijk 1966:257. Passmore & Carruthers 1979:248, figs. Poynton & Broadley 1987:194. Lambiris 1989a:139; 1989b:164, figs. 95, 96, pl.19 figs. 2a-g.

Hyperolius concolor (non Hallowell, 1844): Cope 1862:124. Boulenger, 1882:124.

Hyperolius coccotis Cope, 1862, *Proc. Acad. Nat. Sci. Philadelphia*, 1862:342. Type locality: Umvoti, Natal. Holotype in the Academy of Natural Sciences, Philadelphia.

Rappia sansibarica Pfeffer, 1893, *Jahrb. der Hamburg. Wissensch. Anst.*, 10:97, pl. 2 fig. 4. Type destroyed.

Hyperolius mossambicus Parker, 1930, *Proc. Zool. Soc. Lond.*, 1930:479, pl. 1 fig. 1. Type locality: "Fambani river, Mozambique." Holotytpe in the British Museum (Natural History), London.

Hyperolius kivuensis smaragdinus Laurent, 1947, *Ann. Mag. Nat. Hist.*, 14:292. Type locality: Charre, Mozambique. Holotype in the British Museum (Natural History), London.

ADULT LARYNX (Table 19; Pl. 68, fig. 3)

Material examined: SOUTH AFRICA: NATAL - AJL 2471 (m, SVL 29,0 mm), 1 km east of Makhamisa Gate, Umfolosi Game Reserve. AJL 2884 (m, SVL 30,5 mm), Futululu. AJL 1912 (f, SVL 33,0 mm), Darnall.

Advertisement call: A loud tap, about 0.03 second long, at about 3 kHz (Passmore & Carruthers 1979:248) uttered once or twice, with long pauses between calls, from reeds growing in water. There is a loose choral structure.

Male larynx:

Pharyngeal mucosa: Moderately thick and folded; lies in a well-defined fossa on the dorsum of the arytenoid cartilage.

Arytenoid cartilage: A large, rather low prominentia extends over most of the anterior surface; its superior margin forms a distinct lip to the pharyngeal mucosal fossa. The posterior margin of the occlusal surface is slightly convex medially, and lacks a valve. The arytenoid shelf is not tapered superiorly. The arytenoid fossa is rounded, the diameter about 0.22x the length of the medial vocal cord.

Vocal cords: The **medial cord** is very narrow medially, and very broadly flared at the insertions. The anterior margin is slightly flanged. The posterior margin is flanged along its entire length, and there is a small superior posterior buttress. The frenulum is a narrow

medial band. The **lateral cord** is well developed, but partly obscured by the medial cord, and the insertions are not widely flared. There is a small conical medial prominence on the posterior margin.

LARVAL BUCCOPHARYNX (Table 20; Pl. 71, fig. 2a & b)

Identification of larvae: Lambiris 1989a, 1989b.

Material examined: SOUTH AFRICA; NATAL - AJL 3523; Lake Sibayi; stage 39, SVL 19,6 mm; silver impregnation.

Larval habitat: Moderately deep ponds and pans with rather dense marginal emergent reeds and grasses, with a good bottom cover of silt and organic debris. The diet consists of soft macrophyte tissues and algae.

Buccopharyngeal roof

General shape: Irregularly triangular, with a strong constriction on either side behind the postnarial arena. The roof is more or less concave, more markedly so medially than laterally. The prenarial arena is deeply excavate.

Prenarial arena: A curved row of large pustules, more or less confluent, lies a short distance behind the root of the beak. There are one or two small pustules posterolaterally.

Internal nares: Transverse, elliptical. The narial width is about 0.3x the width of the roof at that level, and the internarial distance is about 0.86x the narial width.

Narial valve: The anterior valve is a low flap, denticulate on the medial half. The posterior valve is a simple, low flap.

Postnarial arena: The **postnarial papilla** (height about equal to the internarial distance) is stout, slightly flattened conical, and somewhat serrated apically. It arises a short distance behind the middle of the naris. It is flanked by two **lateral ridge papillae** which are stout, conical, and denticulate on their anterior margins. The anterior papilla is short (about 0.6x the internarial distance), the posterior papilla much larger (length about 1.5x the internarial distance). The **median**

ridge is a semicircular flap, the base about 0.4x the width of the roof at that level. The free margin is finely lobulate.

Buccal roof arena: An inverted trapezoid bounded on either side by three regularly spaced, subequal, conical papillae. The arena contains about 16 scattered small pustules. Additional pustules extend beyond the borders of the arena anterolaterally.

Glandular areas: An oblique narrow glandular ridge, with a single row of rather regularly spaced pustules, flanks the arena on either side, lateroposteriorly. A large triangular glandular ridge, immediately anterior to the dorsal velum, traverses almost the whole buccal roof posteriorly. The surface is finely granular.

Dorsal velum: Moderately well developed, but low and lacking marginal ornamentation. It is virtually uninterrupted medially.

Pressure cushions: Long and narrow, set slightly posteromedially, and almost in contact medially.

Buccopharyngeal floor

General shape: Irregularly triangular. The surface is shallowly concave, with a deeper prelingual arena.

Prelingual papillae: A median papilla, flanked on either side by a small basal pustule, arises immediately before the tongue anlage. A short but robust cylindrical papilla, fimbriated apically, arises from the base of the lateral wall, posteriorly, on either side.

Lingual papillae: Two small, close-set, slightly curved conical papillae.

Buccal floor arena: Large, occupying most of the space between the lingual arena and the ventral velum. It is bounded on either side by two short, robust, smooth conical papillae of approximately equal size. There are about 12 small, widely scattered pustules in the arena. Additional pustules extend beyond the arena, and onto the ventral velum.

Buccal pockets: Oval, closed, and with a distinct marginal rim. The margins are not deeply grooved. There are no prepocket papillae.

Ventral velum: Broad, semicircular, deepest medially. There are two prominent supporting spicules on either side, with the velum thrown into conspicuous arcuate folds between them. There is a pair of small conical papillae, one on either side of the midline, anteriorly. The free margin

is thickened and bears three tiny projections on either side of a slightly larger paramedian pair.

Branchial baskets: Moderately large and rounded, fully occupied by the filter plates.

Filter plates: Large, moderately strongly imbricate. The filter rows are finely folded and the channels are rather wide.

Hyperolius pusillus (Cope, 1862)

Crumenifera pusilla Cope, 1862, *Proc. Acad. Nat. Sci. Philadelphia*, 1862:343. Type locality: Umvoti, Natal. Holotype in the Academy of Natural Sciences, Philadelphia.

Hyperolius microps Günther, 1864, *Proc. Zool. Soc. Lond.*, 1864:311, pl. 1 figs. 3-4. Type locality: Port St. Johns. Syntypes in the McGregor Museum, Kimberley.

Hyperolius pusillus (Cope): Poynton 1964:191, fig. 112. Van Dijk 1966:257. Passmore & Carruthers 1979:250, figs. Poynton & Broadley 1987:205. Lambiris 1989a:140; 1989b:167, figs. 97 & 98, pl. 20 figs. 1a-c.

ADULT MALE LARYNX (Table 19; Pl. 69, fig. 1)

Material examined: SOUTH AFRICA: NATAL - AJL 2146 (m, SVL 21.4 mm), Gwambane Hide, Mkuzi Game Reserve. AJL 2882 (m, SVL 21.5 mm), Fulululu. AJL 3109 (m, SVL 17.5 mm), St. Lucia Game Park, Lake St. Lucia.

Advertisement call: A short (about 0.03 second) tick at about 5.8 kHz (Passmore & Carruthers 1979:25), uttered about 1.5 seconds apart, from water lilies or other floating vegetation, usually at night, in close chorus.

Pharyngeal mucosa: A very thin layer on the dorsum of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface shallowly and broadly calyculate, lacking prominentiae apicales. The arytenoid valve is well developed, and extends across the whole posterior occlusal margin. The arytenoid shelf is rather broad and of more or less uniform width. The arytenoid fossa is narrow, rounded superiorly but tapered inferiorly, and extends along the inferior half of the arytenoid shelf.

Vocal cords: The **medial cord** is a tall narrow trapezoid above the level of the arytenoid fossa, and more triangularly shaped inferiorly. The posterior margin is flanged along its length. There are no buttresses. The **lateral cord** is well developed, but rather narrow, and the inferior insertion is hidden by the lower part of the lateral cord. The broad frenulum traverses the whole of the lateral cord medially.

LARVAL BUCCOPHARYNX (Table 20; Pl. 72, fig. 1a & b)

Identification of larvae: *Det.* Wager, from a captive-reared series of known parentage; Port St. Johns, Transkei. (NM 5648.)

Material examined: SOUTH AFRICA; TRANSKEI - NM 5648a; Port St. Johns; stage 39/40, SVL 12.6 mm; silver impregnation.

Larval habitat: Shallow to moderately deep pools or pans with moderately dense marginal emergent grasses, sedges and reeds.

Buccopharyngeal roof

General shape: Broadly triangular, with very irregular sides. The roof is shallowly concave, with a rather deep prenarial arena.

Prenarial arena: A curved row of pustules, arranged in three close-set pairs, lie just below the root of the beak.

Internal nares: Transverse, broadly elliptical. The narial diameter is about 0.42x the width of the roof at that level, and the internarial distance is about 0.50x the narial width.

Narial valve: The naris is circumscribed by a low simple flap, which bears a short, broad palpoid papilla on the middle of the anterior border.

Postnarial arena: The **postnarial papilla** is tall (slightly longer than the narial width), conical, and with a finely serrated anterior margin. The two close-set **lateral ridge papillae** on either side are subequal in height, about 0.5x the narial width, conical, with serrated anterior margins. The **median ridge** is a triangular flap (base about 0.4x width of roof at that level) with a strongly denticulate free margin.

Buccal roof arena: An inverted trapezoid, bounded on either side by a pair of smooth conical papillae, the anterior one about twice the height of the posterior papilla. There are about 19 pustules scattered about the arena, with about the same number extending beyond its lateral and anterior borders.

Glandular areas: A crescentic pustulose ridge lies just behind the posterior border of the buccal roof arena, extending almost across the buccal roof. There is also a granular glandular ridge immediately anterior to either half of the dorsal velum.

Dorsal velum: Moderately well developed, but low and simple, with a medial gap about equal in width to the length of a velum.

Pressure cushions: Small, narrow, feebly developed and widely separated medially.

Buccopharyngeal floor

General shape: Roughly triangular, and shallowly concave. The prelingual arena is deeply excavate medially.

Prelingual papillae: A row of five pustules lies immediately below the root of the beak. A flat lateral wall papilla with rolled, serrate edges, arises from the posterior border of the arena on either side.

Lingual papillae: Not present in this specimen.

Buccal floor arena: Transversely rectangular, occupying the anterior half of the area between the lingual arena and the ventral velum. It is bounded on either side by two (left) or three (right) smooth conical papillae, slightly taller posteriorly. There are about 10 widely scattered pustules in the arena, and about 20 laterally and posteriorly beyond its boundaries.

Buccal pockets: Oval, deeply set, with very widely and deeply grooved anterior margins. There are no prepocket papillae.

Ventral velum: Broad, well developed, and of approximately uniform width throughout. There are two rather inconspicuous supporting spicules on either side, and the velum is not thrown into arcuate folds between them. The free margin has a group of about 8 more or less confluent lobules on the middle third, largest medially, and an indefinite number of smaller, less well defined projections more laterally, especially on the left side.

Branchial baskets: Shallowly rounded, and completely occupied by the filter plates.

Filter plates: Large, weakly imbricate. Details are not clear in this specimen, but the rows appear to be quite finely folded.

Hyperolius nasutus Günther, 1864

Hyperolius nasutus Günther, 1864, *Proc. Zool. Soc. Lond.*, 1864:482, pl. 33 fig. 3, Type locality: Duque du Bragança, Angola. Holotype in the British Museum (Natural History), London. Van Dijk 1966:257, Passmore & Carruthers 1979:252, figs. Poynton & Broadley 1987:206. Lambiris 1989a:141; 1989b:169, figs. 99 & 100, pl. 20 figs. 2a-d.

Rappia nasuta (Günther): Boulenger 1882:127.

Hyperolius poweri Loveridge, 1938, *Proc. Biol. Soc. Washington*, 51:213. Type locality: Umvoti River, near Stanger, Natal. Location of holotype not ascertained.

Hyperolius nasutus nasutus Günther: Poynton 1964:192, fig. 113.

ADULT MALE LARYNX (Table 19; Pl. 69, fig. 2)

Material examined: ZIMBABWE: AJL 402 (m, SVL 24.7 mm), Warren Hills, Harare. SOUTH AFRICA: NATAL - NM 4436 (m, SVL 23 mm), and NM 4443 (m, SVL ==), Umvoti River, between Pietermaritzburg and Greytown.

Advertisement call: A harsh trilled chirp about 0.25 second long, at about 5.7 kHz (Passmore & Carruthers (1979:252), uttered repeatedly about once a second, from reeds and sedges growing in water; at night, in chorus.

Pharyngeal mucosa: Thin, overlying a thicker submucosa, and confined to a fossa on the dorsum of the arytenoid cartilage.

Arytenoid cartilage: No distinct prominentia apicales. A well developed arytenoid valve extends across the whole of the posterior occlusal margin. The arytenoid shelf is moderately broad, and tapers superiorly. The arytenoid fossa is elliptical, the diameter about 0.27x the length of the medial vocal cord.

Vocal cords: The **medial cord** is broad medially, and only moderately flared at the insertions. The posterior margin is flanged along its length, and feebly expanded at the insertions into weak buttresses. The frenulum is a rather narrow, slightly curved, band. The **lateral cord** is narrow and largely hidden by the medial cord, only the posterior margins of the expanded insertions being clearly visible.

LARVAL BUCCOPHARYNX (Table 20; Pl. 72, fig. 2a & b)

Identification of larvae: Based on a series from Stillerust Vlei, Kamberg Nature Reserve, Natal (AJL 3526 - 3536, stages 34 - 45; 28 January 1987), showing the characteristic white dorsolateral stripe,

distinctly edged black, with dorsal spotting; and the pointed snout characteristic of adults, at stage 44/45.

Material examined: SOUTH AFRICA; NATAL - AJL 3528a; Stillerust Vlei, Kamberg Nature Reserve; stage 37, SVL 15.3 mm; silver impregnation.

Larval habitat: Shallow to moderately deep ponds or quiet streams, with fairly dense marginal emergent grasses, and a light bottom cover of silt and organic debris. The diet consists largely of algae, with soft macrophyte tissues forming a lesser part.

Buccopharyngeal roof

General shape: An inverted T, the stem extending from the prenarial arena to the postnarial arena, the arms including the buccal cavity proper and the pharynx. The surface is gently concave, with a rather deep prenarial arena.

Prenarial arena: A broad shelf lies behind the beak, extending across the anterior 0.4 of the arena. It is separated by a rather broad, deep, curved groove from a posterior eminence, the anterior border of which bears two groups of three closely-spaced pustules anteriorly, and one group of four, on either side, laterally. Three or four pustules are present on the surface of the posterior eminence.

Internal nares: Transverse, elliptical. The narial diameter is about 0.37x the width of the roof at that level, and the internarial distance is about 0.69x the narial width.

Narial valve: The naris is circumscribed by a simple flap, the anterior margin of which bears two short, closely-spaced conical papillae at about the mid-point.

Postnarial arena: The **postnarial papilla** is a tall (height about 1.1x narial diameter), smooth, conical papilla. There are two **lateral ridge papillae**, the anterior being shorter and more or less cylindrical; the posterior being longer, conical, and (on the left side) with a serrated anterior margin.

Buccal roof arena: An inverted trapezium, bounded on either side by a pair of subequal smooth, conical papillae.

Pustulations: Pustulations extend across the whole of the buccal roof. They are largest in and around the buccal roof arena, and tiny, little more than fine verrucosities, laterally and posteriorly.

Glandular ridge: A well-developed band lying immediately anterior to the dorsal velum, and virtually uninterrupted medially.

Dorsal velum: Moderately well developed, and narrowly interrupted medially. The free margins are smooth.

Pressure cushions: Moderately large, and widely separated medially.

Buccopharyngeal floor

General shape: Roughly triangular. An X-shaped retrolingual fossa extends backwards into the anterior half of the buccal floor arena. The prelingual arena is rather deeply excavate.

Prelingual papillae: There are no pustules on the arena floor. A flattened papilla, fimbriated apically, arises from the middle of the arena floor. It is flanked laterally by a broad, flat palpoid papilla with a papillate apex, on either side.

Lingual papillae: A pair of moderately tall cylindrical papillae, arising from the mid-dorsum of the tongue anlage.

Buccal floor arena: An inverted trapezium, bounded on either side by three smooth, conical papillae. The first and second are spaced more closely than the second and third, and the first is the shortest.

Pustulations: Pustulations cover the whole of the buccal floor arena and extend beyond it, posteriorly, to the ventral velum. The whole buccal floor is covered with minute, scattered verrucosities.

Buccal pockets: Oval, deep-set, closed, and with deeply incised anterior margins. There are no prepocket papillae.

Ventral velum: Broad and well developed, constricted medially. There are four equally-spaced supporting spicules; the velum is not thrown into folds between them. The free margin is thickened and bears short lobules, three on either side flanking a close-set group of six, three on either side of the midline.

Branchial baskets: Large and rounded, almost completely occupied by the filter plates.

Filter plates: Moderately broad and only slightly imbricate. The filter rows are finely folded, and the channels are narrow.

Hyperolius pickersgilli Raw, 1982

Hyperolius pickersgilli Raw, 1982, *Durban Mus. Novit.*, 13:117, pl. 1 figs. 1-3. Type locality: Avoca, north of Durban. Holotype in the Natal Museum, Pietermaritzburg. Lambiris 1989a:142.

ADULT MALE LARYNX (Table 19; Pl. 69, fig. 3)

Material examined: SOUTH AFRICA: NATAL - NM 6657 (m, SVL 18,9 mm), Avoca, HOLOTYPE.

Advertisement call: A quiet creak, about 0.7 second long, at about 3 kHz, sometimes preceded by a shorter (0.3 second) call (Raw 1982:123). The call is uttered at night, from sedges growing in water.

Pharyngeal mucosa: A thin mucosa and thicker submucosa overlie the arytenoid cartilage anterodorsally. There is no distinct mucosal fossa.

Arytenoid cartilage: There is a single apical prominentia. The posterior occlusal margin is distinctly squared-off medially, and bears a well-developed, but narrow, arytenoid valve. The arytenoid shelf is moderately broad and is not tapered at the apices. The arytenoid fossa is small and oval, about 0.3x the length of the medial vocal cord.

Vocal cords: The **medial cord** has a short, strongly curved anterior margin, and the insertions are widely flared. The posterior margin is strongly flanged, the flange being feebly expanded towards the insertions into minute buttresses. The frenulum is a rather broad band. The **lateral cord** is broad and well developed, with a rather straight posterior margin.

LARVAL BUCCOPHARYNX

No tadpoles were available for examination.

Hyperolius marmoratus verrucosus A. Smith, 1849

Hyperolius verrucosus A. Smith, 1849, *Illus. Zool. S. Afr., Rept.*, App., p. 26. Type locality: "Kaffirland". Locality of holotype not ascertained.

Hyperolius marmoratus pondoensis FitzSimons, 1930, *Ann. Transvaal Museum*, 14:43. Type locality: Port St. Johns. Holotype in the Transvaal Museum.

Hyperolius marmoratus verrucosus A. Smith: Poynton 1964:195, fig. 114. Passmore & Carruthers 1979:254, fig. Lambiris 1989a:143.

Hyperolius marmoratus (non Rapp, 1842): Van Dijk 1966:257 (part?).

ADULT LARYNX (Table 19; Pl. 70, fig. 1)

Material examined: SOUTH AFRICA: EASTERN CAPE - AJL 322 (m, SVL 28.2 mm), New Cemetery, Grahamstown. AJL 399 (m, SVL 28.5 mm), Humansdorp. AJL 400 (m, SVL 30.0 mm), Witelbos. AJL 240 (f, SVL 30.2 mm), Grahamstown.

Advertisement call: A piercing chirp about 0.12 second long, at about 3 kHz (Passmore & Carruthers 1979:254), showing frequency modulation. Calls are uttered in close chorus, at night, from reeds growing in water.

Male larynx:

Pharyngeal mucosa: Thin, over a deep submucosa, in a well-defined fossa on the dorsum of the arytenoid cartilage.

Arytenoid cartilage: A massive superior prominentia is present, the anterior margin of which is thrown into conspicuous folds. The rather broad occlusal surface lacks an arytenoid valve. The arytenoid shelf is broad, and double-stepped. The middle portion of the posterior margin bears a number of strong, short, horizontal striations. The arytenoid fossa is oval.

Vocal cords: The **medial cord** is very narrow medially, and is widely flared at the insertions. The posterior margin is strongly flanged, and bears a small, weak superior buttress. The **lateral cord** is well developed, fully visible along its length, and has a concave posterior border. The narrow frenulum traverses both cords medially.

LARVAL BUCCOPHARYNX

Tadpoles were not available for dissection.

Hyperolius marmoratus marmoratus Rapp, 1842

Hyperolius marmoratus Rapp, 1842, *Arch, Naturgesch.*, 8:289, pl. 6 figs. 1, 2. Type locality: Natal. Type not traced (Frost 1985:213). Van Dijk 1966:257 (part).

Hyperolius cinctiventris Cope, 1862, *Proc, Acad, Nat, Sci, Philadelphia*, 1862:341. Type locality: Umvoti. Holotype in the Academy of Natural Sciences, Philadelphia.

Hyperolius sugillatus Cope, 1862, *Proc, Acad, Nat, Sci, Philadelphia*, 1862:342. Type locality: Umvoti. Holotype in the Academy of Natural Sciences, Philadelphia.

Rappia marmorata (Rapp): Boulenger 1882:121 (part).

Hyperolius marmoratus marmoratus Rapp: Poynton 1964:196, fig. 115. Passmore & Carruthers 1979:254, fig. Lambiris 1989a:144.

ADULT LARYNX (Table 19; Pl. 70, fig. 2)

Material examined: SOUTH AFRICA: NATAL - AJL 1834 (m, SVL 25,5 mm), 1 km west of Merrivale Station, Merrivale. AJL 1996 (m, SVL 27/7 mm), Umtamvuna Nature Reserve. AJL 2066 (m, SVL 27,2 mm), Bluff Nature Reserve. AJL 1924 (f, SVL 27,0 mm), 3,5 km west of Tugela River Mouth.

Advertisement call: A piercing chirp about 0.12 second long, at about 3 kHz (Passmore & Carruthers 1979:254), showing frequency modulation. Calls are uttered in close chorus, at night, from reeds growing in water.

Male larynx:

Pharyngeal mucosa: Rather thick and folded, overlying a deeper submucosa, and contained in a well defined fossa on the dorsum of the arytenoid cartilage.

Arytenoid cartilage: A massive superior prominentia is present. The posterior occlusal margin is straight, and bears a well-developed arytenoid valve, narrow inferiorly but broad superiorly, and merging insensibly into the superior pulvinarium. The moderately broad arytenoid shelf is double-stepped, and the middle of the posterior margin bears a series of short, strong, transverse striations. The arytenoid fossa is oval.

Vocal cords: The **medial cord** is moderately narrow medially, and widely flared at the insertions. The posterior margin is flanged, and has a small, triangular superior posterior buttress, and a massive inferior posterior buttress. The **lateral cord** is large, well developed,

and has a massive, bullous prominence on the inferior insertion. The rather broad frenulum traverses both cords medially.

LARVAL BUCCOPHARYNX (Table 20; Pl. 73, fig. 1a & b)

Identification of larvae: Captive-reared from identified parents.

Material examined: SOUTH AFRICA; NATAL - AJL 2185; Umvoti Vlei Nature Reserve; stage 40, SVL 18,0 mm; silver impregnation.

Larval habitat: Moderately deep pools or pans, with fairly dense to dense marginal reeds, and a good bottom cover of silt and organic debris. The diet consists of soft macrophyte tissues and algae.

Buccopharyngeal roof

General shape: More or less triangular, with a constriction below the level of the postnarial arena. The surface is concave, with posterolateral eminences behind the buccal roof arena. The prenarial arena is deeply excavate.

Prenarial arena: A narrow ridge traverses the arena about one third the way back behind the beak. A pair (one on either side) of smooth, slender, subconical lateral wall papillae arise at about the midpoint of the arena walls, the apices directed medially.

Internal nares: Narrowly elliptical, transverse. The narial width is about 0.42x the width of the roof at that level, and the internarial distance is about 0.37x the narial width.

Narial valve: A simple flap, bearing a very short cylindrical papilla at about the middle of the anterior margin.

Postnarial arena: The **postnarial papilla** is about 0.7x the narial diameter and conical, with a feebly serrated anterior margin. There are two **lateral ridge papillae**. The anterior one is short (subequal to the postnarial papilla), and slightly serrated on the anterior margin; the posterior one is longer (about equal to the narial diameter) and pustulate apically. The **median ridge** is trapezoid, the base about 0.3x the width of the roof at that level, and with a smooth margin.

Buccal roof arena: Roughly rectangular, bounded on either side by a pair of conical papillae, the posterior one smaller than the anterior

papilla. There are about 20 small pustules within the arena, and about 6 extending a little distance beyond the posterior margin, between the posterolateral eminences.

Glandular ridge: A broad, well-developed, verrucose ridge traversing the buccal roof immediately before the dorsal velum.

Dorsal velum: Well developed and rather broad laterally, tapering and narrowly interrupted medially.

Pressure cushions: Narrow, triangular, transversely orientated, and narrowly separated medially.

Buccopharyngeal floor

General shape: Trapezoid, with a narrow apex. The floor is generally concave, with a deeper retrolingual fossa and a rather deeply excavate prelingual arena.

Prelingual papillae: A smooth, cylindrical median papilla arises from the arena floor immediately before the tongue anlage. It is flanked by a single conical lateral wall papilla on either side, the anterior margin of which is densely pustulate.

Lingual papillae: Two moderately small, smooth, cylindrical papillae arising from the mid-dorsum of the tongue anlage.

Buccal floor arena: Deeply rectangular, bounded on either side by three smooth, conical papillae. The first and second are more closely spaced than the second and third, and the first is the smallest. There are about 12 small verrucosities in the arena, concentrated medially.

Additional verrucosites: Extend posteriorly beyond the buccal floor arena, onto the ventral velum.

Buccal pockets: Oval, oblique, the major axes orientated posterolaterally; closed, with narrowly but deeply incised anterior margins. There are no prepocket papillae.

Ventral velum: Broad, of more or less uniform width. Supporting spicules are not prominent. The thickened free margin bears three tiny, equally-spaced swellings on either side of the midline.

Branchial baskets: Somewhat triangular, the apices directed posterolaterally, and only partially occupied by the filter plates.

Filter plates: Details are not clear in this preparation.

Hyperolius marmoratus taeniatus Peters, 1854

Hyperolius taeniatus Peters, 1854, *Mber. Akad. Wiss. Berlin*, 1854:628. Type locality: Boror, Mozambique. Holotype in the Zoologisches Museum Berlin.

Hyperolius citrinus Günther, 1864, *Proc. Zool. Soc. Lond.*, 1864:311, pl. 27 fig. 2. Type locality: Zambezi. Holotype in the British Museum (Natural History), London.

Hyperolius granulosus Peters, 1866, *Mber. Akad. Wiss. Berlin*, 1866:891. Type locality: Capanga, east of Tete. Syntypes in the Zoologisches Museum, Berlin.

Hyperolius variegatus Peters, 1882, *Sitzungb. der Ges. Naturf. der Freunde zu Berlin*, 1882:8. Type locality: Cabaceira, Quelimane, Boror. Syntypes in the Zoologisches Museum, Berlin.

Rappia marmorata (non Rapp, 1842): Pfeffer 1893:27.

Hyperolius marmoratus taeniatus Peters: Poynton 1964:197, fig. 116. Passmore & Carruthers 1979:254, fig. Lambiris 1989a:146; 1989b:177, figs. 104 & 105, pl. 23 figs. 1a-f.

Hyperolius marmoratus (non Rapp, 1842): Van Dijk 1962:257 (part).

ADULT MALE LARYNX (Table 19; Pl. 70, fig. 3)

Material examined: SOUTH AFRICA: NATAL - AJL 2284 (m, SVL 29,5 mm), Mazuwi, Umfolosi Game Reserve. AJL 2497 (m, SVL 30,8 mm), Chaka's Pits, Umfolosi Game Reserve. AJL 2683 (m, SVL 28,3), Vryheid Nature Reserve.

Advertisement call: A piercing chirp about 0.12 second long, at about 3 kHz (Passmore & Carruthers 1979:254), showing frequency modulation. Calls are uttered in close chorus, at night, from reeds growing in water.

Pharyngeal mucosa: Fairly thick, over a deeper submucosa, and contained in a deep fossa on the dorsum of the arytenoid cartilage, the inferior lip of which is strongly reflexed.

Arytenoid cartilage: A massive superior prominentia is present. The posterior occlusal surface is more or less straight, and bears a rather stout arytenoid valve, the superior portion of which widens and blends insensibly with the superior pulvinarium. The arytenoid shelf is not, or only very slightly, stepped, and the middle of its posterior margin bears a number of short, strong, transverse striations. The arytenoid fossa is oval.

Vocal cords: The **medial cord** is broad medially, and widely flared at the insertions. The posterior margin is flanged, and slightly dilated at the insertions, but lacks discrete buttresses. The frenulum is large and triangular, the apex directed anteriorly. The **lateral cord** is well

developed, but largely hidden by the medial cord. The posterior margin is slightly concave, and has a small bullous exapansion on the inferior insertion.

LARVAL BUCCOPHARYNX

No material suitable for dissection was available for study.

DISCUSSION

Adult laryngeal morphology

Few representatives of this large genus have been examined in the present study. As it happens, the Natal species of *Hyperolius* present relatively few major taxonomic problems as compared with the situation in other parts of the genus's range.

Adult laryngeal morphology shows clear, consistent, species-specific differences that support current taxonomic conclusions within the study area. It is possible that laryngeal characters could prove useful in helping identify problem specimens which have borderline external morphological characters, particularly in details of webbing and of colour patterns -- a not uncommon occurrence in the genus.

It is really further afield, especially with the central and northern African species, that the possible taxonomic usefulness of laryngeal characters will best be tested. They may well prove helpful in resolving problems in such groups as, for example, *Hyperolius kivuensis* and *H. quinquevittatus*; male *Hyperolius argus*, *H. mitchelli* and *H. puncticulatus*; *Hyperolius viridis*, *H. nasutus* and *H. benguellensis*; *Hyperolius benguellensis* and *H. granulatus*; and, of course, the *Hyperolius marmoratus* subspecies.

Of the *Hyperolius marmoratus* subspecies, Poynton & Broadley remark (1987:213):

> "The delimitation of nearly all currently recognised subspecies of *marmoratus* is, it must be admitted, still largely a matter that remains open to question. At present the different taxa are characterised by dorsal colour pattern, as recognised in mainly small samples from scattered localities, without the biological significance of this patterning being at all clear, and without taking into account other features such as lateral subdermal darkening which, if used as taxonomic characters, could produce conflicting classifications."

The three subspecies examined in this study showed (rather surprisingly, in view of the remarkable similarities of their advertisement calls) distinct and consistent differences in laryngeal

morphology, and these characters may prove to be of value even in this difficult complex.

However, a full study of *Hyperolius marmoratus* larynxes needs to be undertaken that shall include not only typical specimens from the centre of each subspecies' range, but also from marginal populations -- especially from populations that show complete transitions from one forms' pattern to another.

The significance of the peculiar striations on the posterior margin of the arytenoid shelf in the *Hyperolius marmoratus* subspecies is not quite clear. It may be associated with the distinct frequency modulation of the call (not a feature of the calls of the other *Hyperolius* species examined), but this is at present mere conjecture.

Larval buccopharyngeal characters

Lambiris (1989a:40) was unable to distinguish, in the key to the Natal *Hyperolius* tadpoles, between *Hyperolius tuberilinguis, semidiscus* and *argus*, or between *Hyperolius pusillus* and *H. nasutus*, on the basis of external morphological characters, even though specimens from known parents were available for examination.

Buccopharyngeal characters, however, have here proved effective in readily separating specimens of *Hyperolius semidiscus* and *H. tuberilinguis*, and of *H. pusillus* and *H. nasutus*.

Tadpoles of *Hyperolius marmoratus* subspecies suitable for dissection, other than those of *H. m. marmoratus*, were unfortunately not available for study, and the taxonomic value of buccopharyngeal characters in this group still remains to be examined.

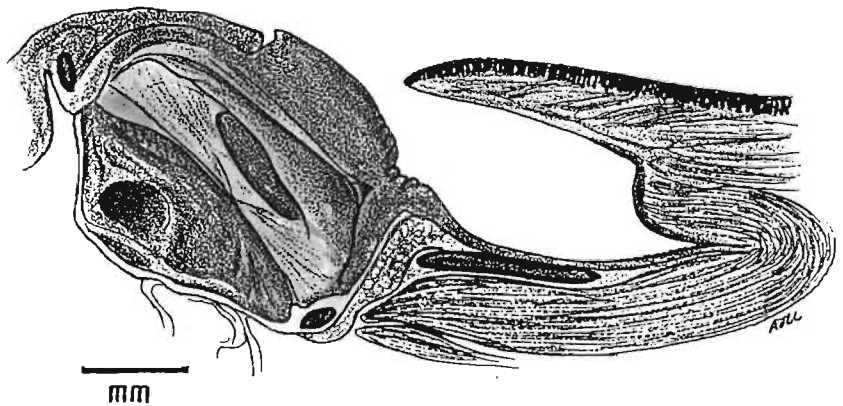


FIG. 1: *Hyperolius semidiscus* Hewitt, 1927
AJL 1831 (male), 1 km west of Merrivale, Natal, South Africa.

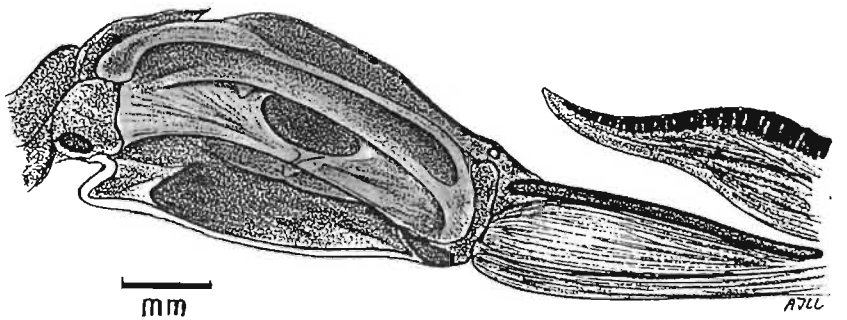


FIG. 2: *Hyperolius argus* Peters, 1854
AJL 3066 (male), St. Lucia Estuary, Natal, South Africa.

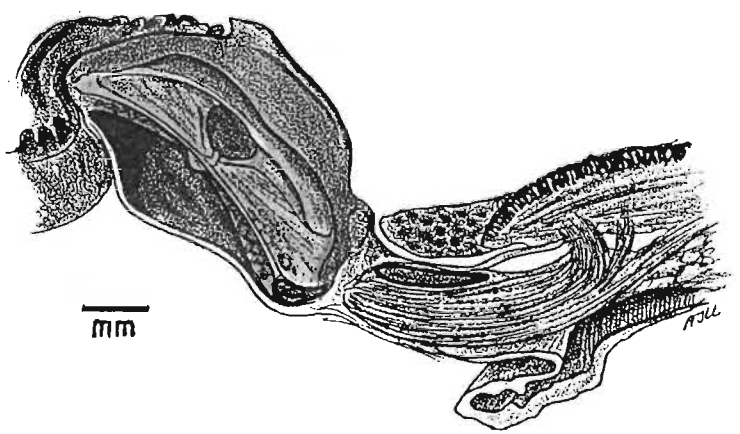


FIG. 3: *Hyperolius tuberilinguis* A. Smith, 1849
AJL 2884 (male), Futululu, Natal, South Africa.

PLATE 68
HYPEROLIUS - ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

PLATE 69

HYPEROLIUS – ADULT HYOLARYNXES

Median sagittal section. View into left half. Anterior to right.

FIG. 1: *Hyperolius pusillus* (Cope, 1862)
AJL 2282 (male), Futululu, Natal, South Africa.

FIG. 2: *Hyperolius nasutus* Günther, 1864
AJL 402 (male), Warren Hills, Harare, Zimbabwe.

FIG. 3: *Hyperolius pickersgilli* Raw, 1982
NM 6657 (male), Avoca, north of Durban, Natal, South Africa. HOLOTYPE.

PLATE 70
HYPEROLIUS – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

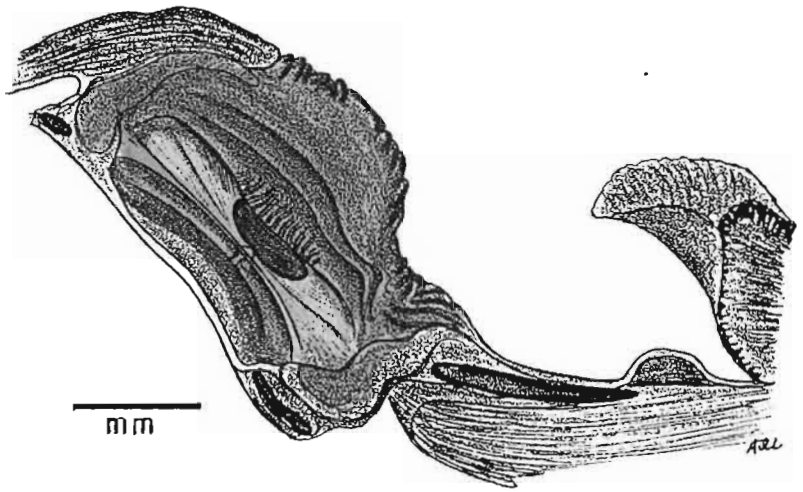


FIG. 1: *Hyperolius marmoratus verrucosus* A. Smith, 1849
AJL 399 (male), Humansdorp, Eastern Cape, South Africa.

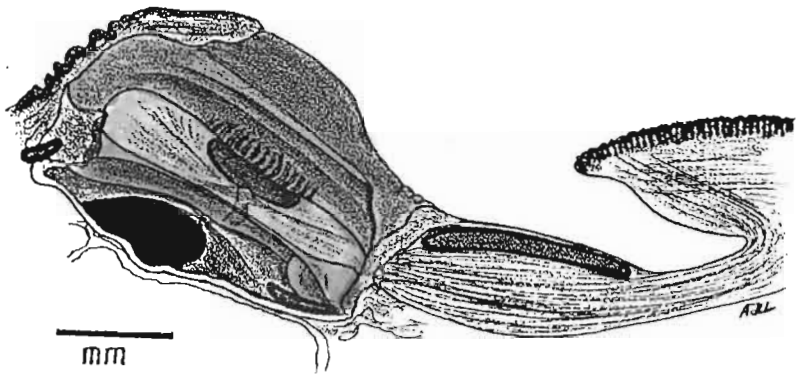


FIG. 2: *Hyperolius marmoratus marmoratus* Rapp, 1842
AJL 2066 (male), Bluff Nature Reserve, Natal, South Africa.

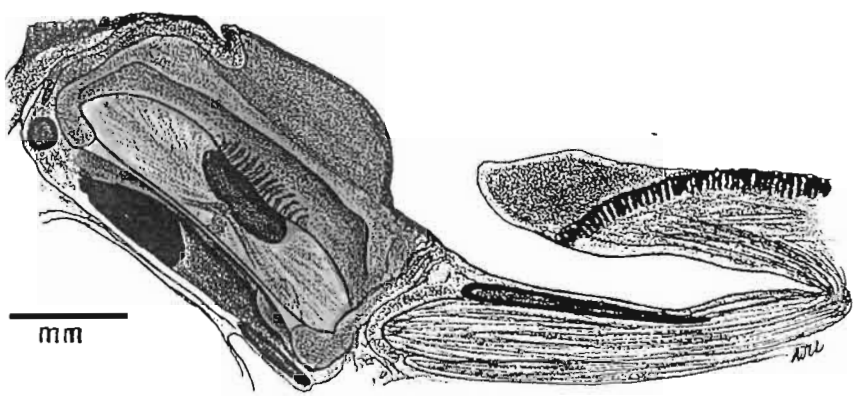


FIG. 3: *Hyperolius marmoratus taeniatus* Peters, 1854
AJL 2683 (male), Vryheid Nature Reserve, Natal, South Africa.

PLATE 71

HYPEROLIUS – LARVAL BUCCOPHARYNXES

Roof on left, floor on right.

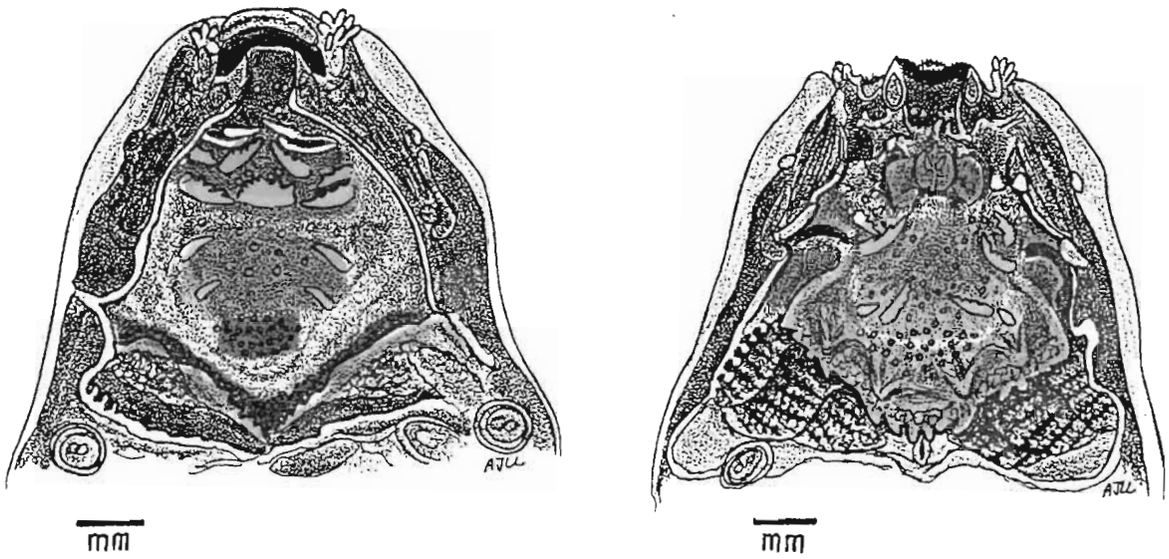


FIG. 1; *Hyperolius semidiscus* Hewitt, 1927
AJL 3532a, Stage 39, Mariannhill, Natal, South Africa.

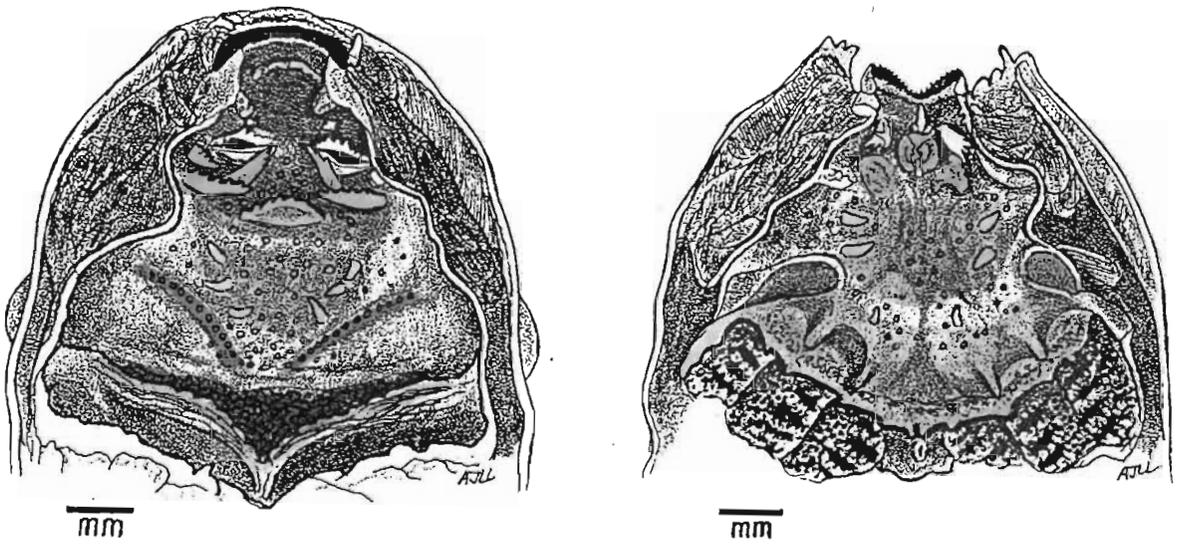


FIG. 2; *Hyperolius tuberilinguis* A. Smith, 1849
AJL 3523a, Stage 39, Lake Sibayi, Natal, South Africa.

PLATE 72
HYPEROLIUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

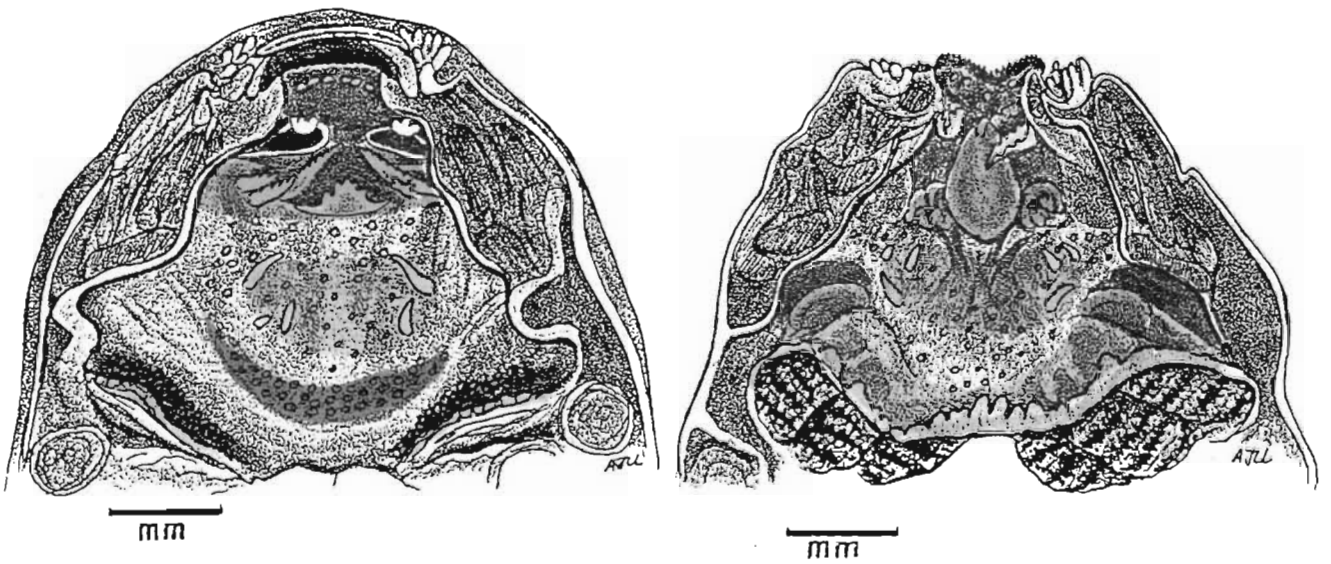


FIG. 1: *Hyperolius pusillus* (Cope, 1862)
NM ----, Stage 39/40, Port St. Johns, Transkei, South Africa.

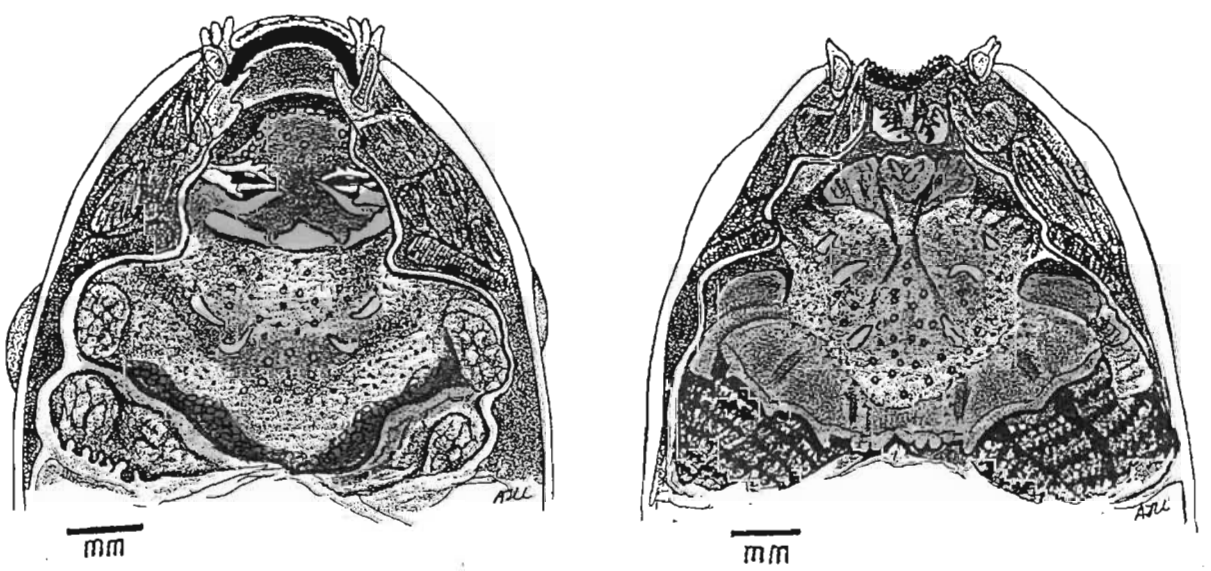


FIG. 2: *Hyperolius nasutus* Günther, 1864
AJL 3528a, Stage 37, Stillerust Vlei, Kamberg Nature Reserve, Natal, South Africa.

PLATE 73
HYPEROLIUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

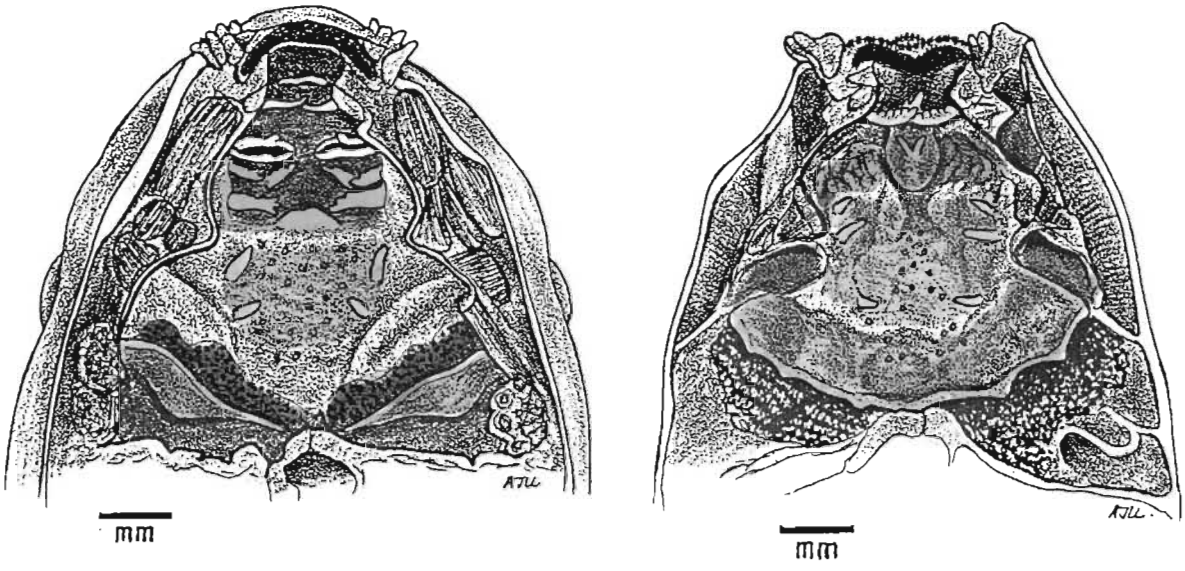


FIG. 1: *Hyperolius marmoratus marmoratus* Rapp, 1842
AJL 2185, Stage 40, Umvoti Vlei Nature Reserve, Natal, South Africa.

Family HEMISOTIDAE Cope, 1867

Genus *Hemisus* Günther, 1867

Hemisus Günther, 1858, *Cat. Batr. Sal. Brit. Mus.*, p. 47. Type species by monotypy: *Engystoma guttatum* Rapp, 1842.

CHARACTERS

ADULT LARYNX (Pl. 74)

The larynxes of the two species examined show their greatest difference in the shape of the occlusal surface of the arytenoid cartilage. There is a strong similarity in the structure of the vocal cords. Sexual dimorphism is marked, the female larynx being smaller and simpler in structure, especially in lacking a lateral vocal cord.

Arytenoid cartilage

The occlusal surface in *Hemisus guttatus* lacks well defined prominentiae apicales, and the internal margin is widely U-shaped. The external occlusal margin in *Hemisus m. marmoratus* is squared off by large prominentiae, and the internal occlusal margin is V-shaped.

Medial vocal cord

In both species the medial cord is flared at the insertions and narrowed medially. The posterior margin is narrowly flanged in *Hemisus guttatus*, and very thickened in *H. m. marmoratus*. There are no buttresses in either species. A broad frenulum is clearly discernible in *H. guttatus*, but not in *H. m. marmoratus*.

Lateral cord

The general appearance of the lateral cord is the same in both species. The anterior margin, which lies behind the posterior margin of the medial cord, is produced anteriorly medially, in a frenulum-like extension reaching under the medial cord. The lateral cord is proportionally larger in *H. guttatus* than in *H. m. marmoratus*.

Posterior chamber

The posterior chamber lacks any features of taxonomic use in either species. The pulmonary aditus is massive, but lacks cartilaginous rims.

LARVAL BUCCOPHARYNX (Pl. 75)

The buccopharynxes of the two species examined have much in common, and only the salient features are summarised here.

Prenarial arena

A large raised shelf is present posteromedially in both species. It bears a series of pustules on the anterior and lateral margins, the nature and arrangement of which seem to be species-specific. Additional pustules are present on the general surface of the shelf in both species, and also over the anterior portion of the arena in *Hemisus m. marmoratus*.

Nares and narial valves

The nares are narrowly elliptical, and directed posteromedially in both species. The narial valve is a continuous flap circumscribing the naris, and bearing a papilla on the anterior margin, in both species. The posterior margin is moderately deeply grooved.

Postnarial arena

There are two papillae on either side, postnarially. These could be interpreted as a postnarial papilla in close association with a single lateral ridge papilla, or as two postnarial papillae, since they both arise behind the middle of the naris. On the other hand, the lateral ridge is well developed and extends quite far medially, so they could just as well be interpreted as two lateral ridge papillae, the postnarial papillae being absent. In view of the position of their bases I have here called them both postnarial papillae and assumed the lateral ridge papillae to be lacking.

The median ridge is smooth in *Hemisus guttatus*, finely lobulated in *Hemisus m. marmoratus*.

Buccal roof arena

The arena is small. It is bordered laterally and posteriorly by conical papillae that show a distinct tendency to bifurcate apically. Pustules are confined to the arena in *Hemisus m. mamrmoratus*, but extend beyond its boundaries in *H. guttatus*.

Additional papillae and pustulations

Small conical papillae are present lateral to the postnarial arena in *Hemisus guttatus*, but not in *H. m. marmoratus*.

In both species, small papillae are present on the buccal walls lateral to the buccal roof arena, as also are pustules in *Hemisus guttatus*. In *H. m. marmoratus* the papillae form a row on the lateral margin of a moderately large, shallow, oval fossa on either side of the buccal roof arena.

A small dense verrucose patch is present behind the buccal roof arena in *Hemisus guttatus*.

Glandular ridge

A continuous V-shaped band, immediately anterior to the dorsal velum, in both species.

Prelingual arena

Pustules are present on the arena floor in both species, as is a small palpoid lateral wall papilla on either side.

Lingual papillae

The lingual papillae are reduced to a pair of small pustules arising from the mid-dorsum of the tongue anlage. The paralingual cushions are also pustulate in both species.

Buccal floor arena

Large, occupying most of the space between the lingual arena and the ventral velum. It is bounded laterally and posteriorly by a rather irregularly arranged row of conical papillae, and is pustulate, in both species.

Buccal pockets

Large, oval (*H. guttatus*) to pyriform (*H. m. marmoratus*), closed, and with a rather deeply incised anterior margin. Prepocket pustules are present in both species.

Ventral velum

Large and well developed, with prominent supporting spicules. The velum is thrown into distinct folds between the spicules, in *Hemisus guttatus*; these folds are less obvious in *H. m. marmoratus*.

The free margin in both species bears rather long, well developed lobules, described in detail in the Species Account, below.

Branchial baskets and filter plates

The branchial baskets are large and rounded, more or less completely occupied by the filter plates.

The filter plates are moderately imbricate. The filter rows are finely folded, and there are partial rows intercalated between the complete rows.

SPECIES ACCOUNT

Hemisus guttatus (Rapp, 1842)

Engystoma guttatum Rapp, 1842, *Arch. Naturgesch.*, 8:290, pl. 6 figs. 3 & 4. Type locality: Natal. Type not traced (Frost 1985:109).
Hemisus guttatum (Rapp): Poynton 1964:166, fig. 93. Van Dijk 1966:256.
Hemisus guttatus (Rapp): Lambiris 1989a:148.

ADULT LARYNX (Pl. 74, figs. 1 & 2)

Material examined: SOUTH AFRICA: NATAL - AJL 2901 (m, SVL 43,0 mm), Gunjaneni, Hluhluwe Game Reserve. AJL 3083 (f, SVL 55,0 mm), St. Lucia Estuary.

Advertisement call: A quiet trill about 1.5 seconds long, at about 3 kHz, uttered from the mouth of a burrow, or under a clump of grass. Calls are made individually, at night or on overcast days. (Field observations.)

Male larynx:

Pharyngeal mucosa: Thick, villose, over a relatively thin submucosa, and covering the dorsum of the arytenoid cartilage.

Arytenoid cartilage: Occlusal surface basically U-shaped, the external margin rather squared-off, the internal margin regularly curved. There is a narrow arytenoid valve on the posterior occlusal margin, with a hypaxial anterior projection across the occlusal margin. The arytenoid shelf is about as wide as the occlusal surface. The arytenoid fossa is lenticular in outline, and rather deep.

Vocal cords: The thin, transparent **medial cord** has a strongly concave anterior margin which forms the posterior border of the arytenoid fossa. The posterior margin is slightly concave, with a narrow but distinct flange. There are no buttresses. The frenulum is broad. The **lateral cord** is broad and well developed. It lies posterior to the medial cord, and the anterior margin is strongly biconcave, the medial portion produced forwards into a frenulum-like band that extends forwards and under the medial cord. The superior and inferior anterior insertions of the lateral cord also curve forwards and under the medial cord.

LARVAL BUCCOPHARYNX (Pl. 75, Fig. 1a & b)

Identification of larvae: Lambiris 1989a.

Material examined: SOUTH AFRICA: NATAL - AJL 3531a; Hillcrest; stage 39/40, SVL 19,7 mm; silver impregnation.

Larval habitat: Initially in an underground chamber just above water; subsequently in a shallow pool, with a rather silted bottom. The gut contains small algae.

Buccopharyngeal roof

General shape: Triangular, the base about 1.17x the height. The surface is concave medially, raised posteriorly and laterally; the large, deep prenarial arena has a raised shelf posteromedially.

Prenarial arena: The arena shelf has three separate pustules on either lateral margin, and a row of confluent pustules on the anterior margin; there are 7 pustules scattered irregularly over the general surface of the shelf, but not elsewhere in the arena.

Internal nares: Obliquely elliptical, orientated posteromedially. The narial width is about 0.31x the width of the roof at the level of the anterolateral narial angles, and the internarial distance is about 1.2x the narial width.

Narial valve: A low, simple flap circumscribing the naris, and bearing a cylindrical papilla with a pustulose apex arising from the anterolateral margin. The posterior margin is weakly grooved.

Postnarial arena: There are two large (height about 1.4x narial length), conical **postnarial papillae** on either side, the bases set a little distance behind the middle of the nares. The anterior papilla has a pustulose surface, and both have somewhat serrated anterior margins. The posterior papilla is slightly larger than the anterior one. The **medial ridge** is trapezoid, the base about 0.25x the width of the roof at that level, and the free margin is smooth.

Buccal roof arena: Flanked on either side by 6 (left) or 7 (right) conical papillae, largest anteriorly, and with a tendency to bifurcate apically. There are about 20 irregularly scattered pustules in the arena.

Additional papillae and pustules: The lateral buccal walls have about 5 small conical papillae on either side. Pustules are also scattered over the buccal roof lateral to the buccal roof arena and the postnarial arena. There is a small patch of dense verrucosities behind the buccal roof arena, medially.

Glandular ridge: A well-defined continuous band traversing the buccal roof immediately before the dorsal velum. The surface is verrucose.

Dorsal velum: Low and narrow, but well defined, and narrowly interrupted medially. The free margin is finely serrate.

Pressure cushions: Rather small, and rounded. The surface is thrown into irregular folds.

Buccopharyngeal floor

General shape: Roughly triangular, with irregularly undulant lateral walls. The surface is moderately concave, with a deeper prelingual arena.

Prelingual papillae: The arena floor has a transverse row of four closely-spaced pustules on either side of the midline, a little behind the root of the beak, and a single one on either side of the midline at about the middle of the arena floor. A fimbriate lateral wall papilla arises on either side, in the posterior third of the arena.

Lingual papillae: A pair of close-set pustules on the mid-dorsum of the tongue anlage.

Buccal floor arena: Roughly circular, and bounded laterally by conical papillae, tallest posteriorly. There are about 25 small pustules scattered irregularly around the arena, with others extending beyond its boundaries and onto the dorsal velum medially.

Buccal pockets: Oval, orientated posterolaterally, closed, rather deep set, and with deeply incised anterior margins. Five or six prepocket pustules or short papillae are present on either side.

Ventral velum: Broad and well developed. There are four prominent, equally-spaced supporting spicules, with the velum thrown into folds around their posterior apices. The velum is also transversely wrinkled between the middle pair of spicules. The slightly thickened free margin

bears three rather closely-spaced long, well developed lobes on either side of a more slender paramedian pair.

Branchial baskets: Large and rounded.

Filter plates: Large, moderately imbricate, and with finely folded filter rows. Partial filter rows are intercalated between the complete rows.

Hemisus marmoratus marmoratus (Peters, 1854)

Engystoma marmoratum PQeters, 1854, *Mber. Königl. Akad. Wiss. Berlin*, 1854:628, Type locality: Cabaceira, Mozambique. Syntypes in the Zoologisches Museum, Berlin.
Hemisus marmoratus (Peters): Van Dijk 1966:256.
Hemisus marmoratum (Peters): Trewavas 1933:486, figs. 66 & 67. Poynton 1966:166, fig. 93. Passmore & Carruthers 1979:212, figs.
Hemisus marmoratum marmoratum (Peters): Poynton & Broadley 1985a:529.
Hemisus marmoratus marmoratus (Peters): Lambiris 1989a:149; 1989b:184, figs. 109 & 110, pl. 24 figs. 2a-c.

ADULT LARYNX (Pl. 74, fig. 3)

Material examined: SOUTH AFRICA: NATAL - AJL 2365 (m, SVL 26.4 mm), Gwambane, Mkuzi Game Reserve. ZIMBABWE: AJL 829 (f, SVL 37.0 mm), Kutama Mission. AJL 941 (f, SVL 30.2 mm), Nyanyana River Mouth, Lake Kariba.

Advertisement call: A long, quiet buzz at about 4 kHz, lasting several seconds (Passmore & Carruthers:212), uttered at night, from the mouth of a burrow near water.

Male larynx:

Pharyngeal mucosa: Rather thin, and finely villose, over a deeper submucosa, covering the dorsum of the arytenoid cartilage.

Arytenoid cartilage: The external margin is broad and squared-off by large superior and inferior prominentiae apicales, which have somewhat corrugated surfaces. The posterior occlusal margin is V-shaped, and lacks a distinct arytenoid valve. The arytenoid shelf is broad. The arytenoid fossa is narrowly elliptical, and deep.

Vocal cords: The **medial cord** is robust and has a short, strongly concave anterior margin. The posterior margin is strongly concave, and greatly thickened, but lacks buttresses. There is no distinct frenulum. The **lateral cord** is moderately broad and well developed. It lies well posterior to the medial cord. The anterior margin is concave, with a narrow median frenulum-like projection that extends forwards under the medial cord.

LARVAL BUCCOPHARYNX (Pl. 75, fig. 2a & b)

Identification of larvae: Lambiris 1989a.

Material examined: SOUTH AFRICA; NATAL - AJL 3533a; Msinga Hide, Mkuzi Game Reserve; stage 37, SVL 17,4 mm; silver impregnation.

Larval habitat: Initially in an underground chamber just above water level; subsequently in a shallow pool with a silted bottom.

Buccopharyngeal roof

General shape: Roughly triangular, the base about 1.3x the height. The floor is moderately concave,and has a large, shallow, oval fossa on either side of the buccal roof arena. The prenarial arena is deeply excavate and has a raised shelf posteromedially. The shelf bears a shallow median groove in the posterior half.

Prenarial arena: The arena shelf has three separate pustules on either lateral border, and seven closely-spaced papillae along the anterior margin. There are five pustules on the surface of the shelf -- three around the apex of the median groove, and one on either side posteriorly. Other pustules are scattered over the arena anterior and lateral to the shelf.

Internal nares: Obliquely elliptical, orientated posteromedially. The narial width is about 0.43x the width of the roof at the level of the anterolateral narial angles, and the internarial distance is about 0.6x the narial width.

Narial valve: A low, simple flap bearing a large conical papilla with a slightly pustulose anterior margin, arising from about the midpoint of the anterior border. The posterior margin is moderately deeply grooved.

Postnarial arena: There are two large, conical **postnarial papillae** on either side, the bases set a little behind the middle of the nares. The anterior margin of both is pustulose. The anterior papilla is larger (height about equal to narial width) than the posterior one (height about 0.6x narial width). The **median ridge** is arcuate, the base about 0.32x the width of the roof at that level, and the free margin is finely lobulate.

Buccal roof arena: Bounded on either side by a curved row of 5 conical papillae, diminishing in size posteriorly, and with a tendency

to be slightly bifurcate apically. The arena contains 16 rather irregularly scattered pustules.

Additional papillae: There are four close-set papillae on the lateral margin of either fossa flanking the buccal roof arena.

Glandular ridge: A well-defined continuous band traversing the buccal roof immediately before the dorsal velum. The surface is verrucose.

Dorsal velum: Low and narrow, with lobulate free margins, and narrowly interrupted medially.

Pressure cushions: Large, triangular, orientated transversely and narrowly separated medially. The surfaces are thrown into irregular folds.

Buccopharyngeal floor

General shape: Triangular, the base about 1.2x the height. The surface is moderately concave, with a deeper prelingual arena. The arena floor is traversed by an irregular fold posteriorly.

Prelingual papillae: Two large paramedian pustules are flanked by three smaller ones on either side. There is a large palpoid lateral wall papilla posteriorly on either side.

Lingual papillae: A pair of close-set pustules on the mid-dorsum of the tongue anlage.

Buccal floor arena: A large oval, bounded laterally and posteriorly by an irregularly arranged series of smooth conical papillae. The arena contains 18 scattered pustules, concentrated medially.

Buccal pockets: Large, pyriform, closed, and narrowly grooved anteriorly. There are five small prepocket pustules on the right side (left side damaged).

Ventral velum: Broad and well developed. There are three equally-spaced, prominent spicules on either side of a median spicule, but the velum is not thrown into distinct folds around the spicules. The thickened posterior margin bears a broad median flap with a papillate border; this is closely flanked on either side by a large conical papilla and, more laterally, by two similar but more widely spaced appendages.

Branchial baskets: Large, rounded, with the axes directed posterolaterally. They are almost fully occupied by the filter plates.

Filter plates: Large, moderately imbricate, with finely folded filter rows (secondary and tertiary folds) intercalated with partial rows. The channels are narrow.

PLATE 74
HEMISUS – ADULT HYOLARYNXES
Median sagittal section. View into left half. Anterior to right.

FIG. 1: *Hemisus guttatus* Rapp, 1842
AJL 2091 (male). Gunjaneni, Hluhluwe Game Reserve, Natal, South Africa.

FIG. 2: *Hemisus guttatus* Rapp, 1842
AJL 3083 (female). St. Lucia Estuary, Natal, South Africa.

FIG. 3: *Hemisus marmoratus marmoratus* (Peters, 1854)
AJL 2365 (male). Gwambane, Mkuzi Game Reserve, Natal, South Africa.

PLATE 75
HEMISUS – LARVAL BUCCOPHARYNXES
Roof on left, floor on right.

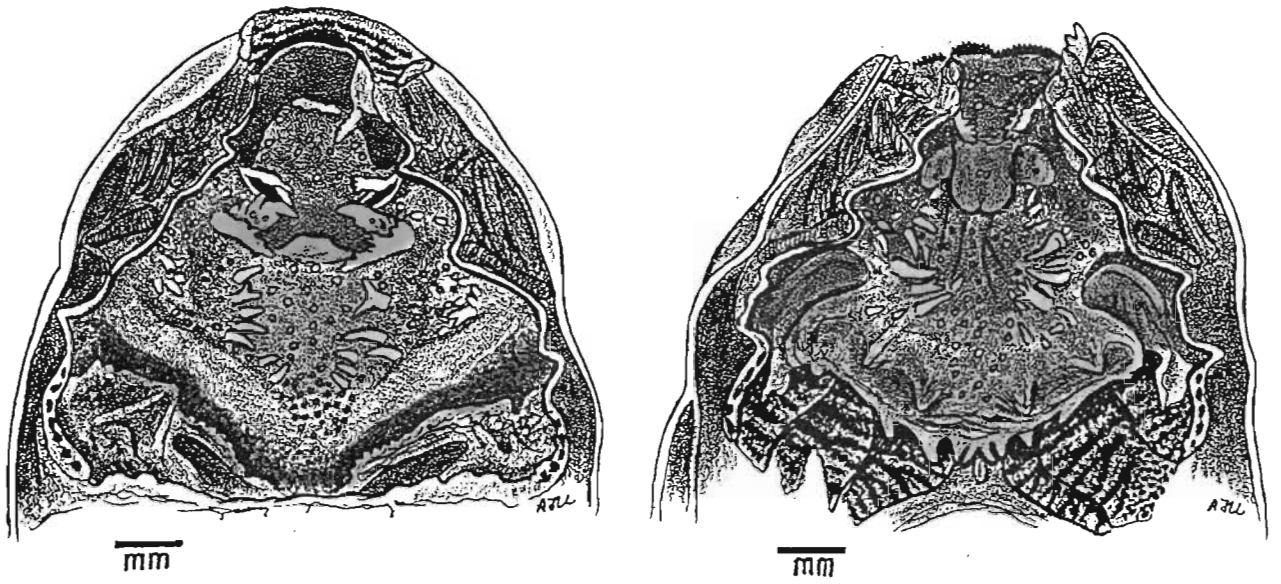


FIG. 1; *Hemisus guttatus* Rapp, 1842
AJL 3531a, Stage 39/40, Hillcrest, Natal, South Africa.

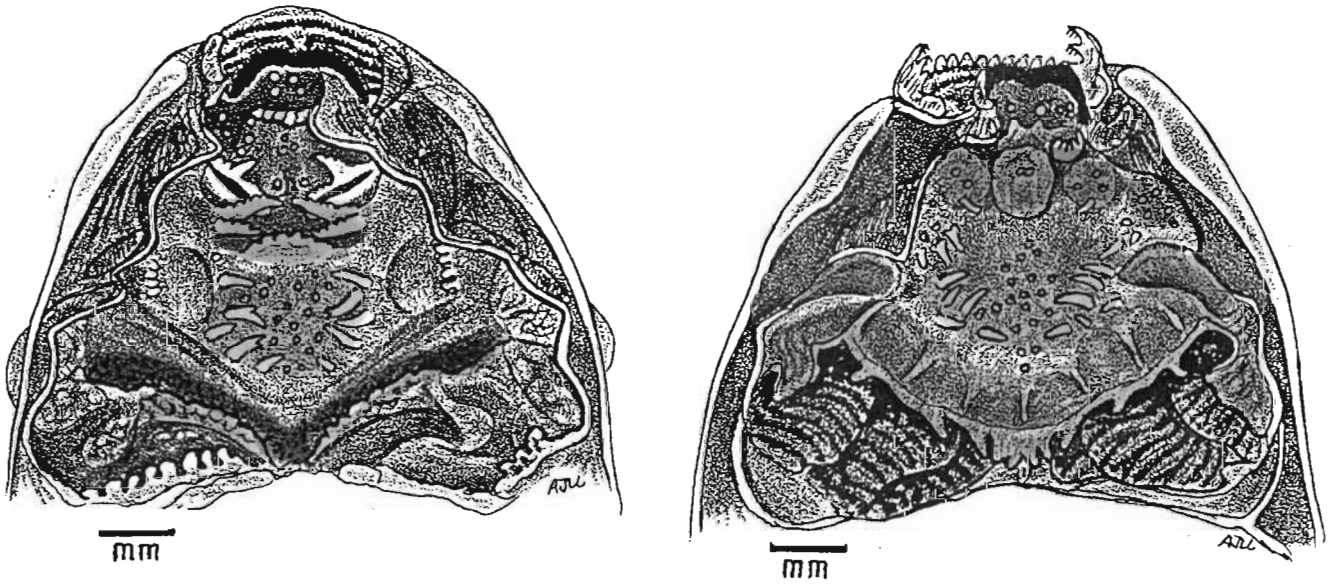


FIG. 2; *Hemisus marmoratus marmoratus* (Peters, 1854)
AJL 3533a, Msinga Hide, Mkuzi Game Reserve, Natal, South Africa.

CHAPTER 5

CONCLUSION

"Das Wenige verschwindet leicht dem Blick,
Der vorwärts sieht, wie viel noch übrig bleibt,"
-- Goethe,

5.1 General remarks

This study has been undertaken with two principal aims in mind -- firstly, to examine and describe adult laryngeal and larval buccopharyngeal morphology in a reasonably wide selection of southern African amphibians; and secondly, to ascertain whether these character sets tend to confirm or refute taxonomic conclusions based on more traditional morphological and vocal characters.

The fundamental approach of this study is the investigation of these character suites as purely taxonomic adjuncts. I have deliberately and specifically excluded all consideration of behavioural, ecological and evolutionary aspects; and while recognising their importance, shall not touch upon them even in this final chapter. They deserve more careful consideration in their own right than can be given here.

It must be emphasised at the outset that the principal aim of this study is not to solve specific taxonomic problems, although some issues do seem, *en passant*, to have been resolved or at least clarified. Rather, this investigation is to be considered no more than a preliminary survey of sets of characters not previously applied in southern African Anuran taxonomy, and an attempt to assess their potential use at taxonomic tools.

As indicated in the introduction, this study has been confined principally to the amphibians of Natal, which were recently the subject of a more traditionally-based survey, and which thus provide a convenient framework for comparisons and discussion.

It will be observed that the Natal Bufonidae have been treated in considerably more detail than the other taxa, especially with regard to sexual dimorphism, female larynxes being illustrated more extensively than in other genera. Furthermore, tadpoles of all the species occurring in Natal were available for dissection -- something unfortunately not true of most of the other genera treated. Such detailed treatment for all the species considered in this survey, though highly desirable, was impossible within the time and financial constraints of the present investigation (especially with regard to the collection of suitable larval material), but was done in this family to indicate the kind of approach that eventually should be done for all taxa.

5.2 The nature of adult laryngeal morphology

As far as I have been able to ascertain, no similar extensive study of internal laryngeal morphology as a taxonomic adjunct has been undertaken before. Blume (1930) investigated microscopic anatomy and surface features in some detail, but attended to gross internal structure somewhat cursorily. Trewavas (1933) similarly paid scant attention to internal morphology; and Martin (1972), who considered the internal structure of the larynx in detail, did so only with reference to the mechanics of vibration. Steinwarz (1990) considered only external asspects of the laryngeal skeleton and the extrinsic musculature. It would seem, then, that this aspect of the present study has of necessity to be considered somewhat in isolation, since there appears to be no other investigation with which it can be directly compared.

The principal findings on the general nature of adult laryngeal morphology which emerge from this study are:

1. Each of the species and subspecies examined has a characteristic internal laryngeal structure that may be used for diagnostic purposes.

The male larynxes of all but one of the species examined (*Cacosternum poyntoni*, known only from the female holotype) have been described and figured in the text to this end.

2. Within any species or subspecies, there is sexual dimorphism, to a greater or lesser degree, in internal laryngeal morphology; but in either sex there is very little intraspecific variation.

Sexual dimorphism has been illustrated in detail in the Bufonid taxa discussed, and in less detail in most of the other genera treated, to give an idea of the nature of such dimorphism. For the purposes of this study the taxonomic value of the female larynx was, generally, not considered.

3. The female larynx shows consistent interspecific variation and intraspecific stability in internal morphology, and can be used, like that of the male larynx, for diagnostic purposes.

Although this aspect was not addressed in detail in the text, the female larynx is just as useful taxonomically as the male larynx. Ideally, any atlas of Anuran larynxes would illustrate those from both sexes for diagnostic purposes.

4. Internal laryngeal morphology shows a definite overall agreement of general characteristics at the genus level, but less so at the family level.

This aspect was not treated in the present study, being considered beyond the scope and principal aims of the investigation.

5.3 The nature of larval buccopharyngeal morphology

The studies by Wassersug (1976; 1980) and by Inger (1985) have clearly established the nature and taxonomic value of larval buccopharyngeal morphology. It merely needs to be stated here that the larvae of those southern African taxa examined here show similarly useful features, as described and illustrated in the text.

I have tried to base descriptions on several specimens of each species, where possible, in order to have at least a basic idea of the

nature of intraspecific variation, but much more work still needs to be done in this respect. As noted above (Section 5.1), the tadpoles of many species are not known (or not reliably identified); in some instances, material may be available but is in such poor condition as not to be usefully dissectable. Nevertheless, the preliminary findings appear to be very promising.

5.4 Taxonomic results

In general, internal laryngeal characters fit in well with those external morphological and vocal characters defining the species currently recognised in the study area (e.g. Poynton 1964; Passmore & Carruthers 1979; Channing 1979; Lambiris 1989a).

Larval buccopharyngeal characters have also proved to be of immense value. Inger (1985:1) remarked that

> "... herpetologists have almost shunned anuran larvae as sources of taxonomical, ecological and evolutionary information. I suspect this has occurred because, superficially, tadpoles have an even more circumscribed morphological compass than adults and because they are more difficult to manipulate as preserved specimens."

While it may be a little more difficult to dissect a small tadpole than to examine the webbing of a large frog, such skills can readily be achieved with practice, and the set of characters available are actually more quickly obtained, and are visually far more distinctive, than the extensive set of external features outlined by Van Dijk (1966). This is not to suggest that oral disc structure, tooth row formulae and the rest should be abandoned, merely that buccopharyngeal characters should not be neglected because of any supposed difficulty in displaying them.

In a number of instances, external characters (particularly in preserved material) do not permit easy or confident identification of some adult specimens -- for example, *Bufo g. gariepensis* and *B. gariepensis nubicolus* in the Lesotho highlands; *Rana angolensis*, *R. dracomontana* and *R. fuscigula*; *Cacosternum nanum* and *C. parvum*; and the

dwarf *Afrixalus* species in Natal. Laryngeal morphology has proved to be an effective and reliable way of identifying such specimens.

Similarly, the tadpoles of some species cannot, at present, be separated on external characters -- for example, *Ptychadena mascareniensis* and *P. mossambica*; *Phrynobatrachus natalensis* and *P. acridoides*; *Cacosternum nanum* and *C. parvum*; and many of the *Hyperolius* species. On the material (admittedly very incomplete) presently available, buccopharyngeal morphology appears to provide a satisfactory means of identifying such tadpoles, as can be seen by consulting the plates and the text.

In other cases, taxonomic problems have been recognised but have not been satisfactorily resolved using more traditional characters or approaches. Some of these cases, and the consequences of examining adult laryngeal and/or larval buccopharyngeal characters, are discussed directly.

Tadpoles of *Xenopus l. laevis* and *X. muelleri* are usually distinguished by the orientation of the external nares, the narial / internarial ratio, and internarial pigmentation. These characters are not always clear and some specimens cannot be satisfactorily identified. Buccopharyngeal morphology provides more distinctive and more reliable characters for separation, and may well prove invaluable in distinguishing between the tadpoles of the central African species.

The genus *Heleophryne* has barely been touched upon in this study, all but *H. natalensis* being confined to the Western Cape. The remarkable differences in larval buccopharyngeal morphology shown between *Heleophryne natalensis* and *H. rosei* (Plate 4) suggest that these characters may be of great value in elucidating the taxonomic problems posed by the various species in this genus.

Laryngeal morphology convincingly demonstrates that *Bufo garmani* Meek and *Bufo poweri* Hewitt are separate taxa (a conclusion independently arrived at by Channing [1991] on the basis of sonagraphic

analyses). The status of *Bufo pseudogarmani* Hulselmans has still to be investigated, but it is possible that laryngeal characters will prove useful here as well. The status of *Bufo pusillus* Mertens has been controversial for many years, and the general tendency has been to regard it as a synonym of *Bufo maculatus* Hallowell (e.g. Tandy & Keith 1972; Passmore & Carruthers 1979; Poynton & Broadley 1988). Examination of the larynx shows distinct differences and *Bufo pusillus* is here regarded as a distinct species. Tadpoles of *Bufo maculatus* from West Africa were unfortunately not available for examination.

Similarly, the validity of *Breviceps maculatus* as a species appears to be confirmed by laryngeal morphology, as does the separation of "Species A" suggested by Lambiris 1989a. If the tadpole of *Breviceps pentheri* is at all typical, buccopharyngeal morphology of tadpoles in this genus will prove to be taxonomically valueless at the species level. However, the degree of reduction of buccopharyngeal structures in direct-development larvae in general may show useful patterns above the species level (see discussion of *Arthroleptella* and *Anhydrophryne*, below).

The two subspecies of *Pyxicephalus adspersus* recognised by Parry (1982), which are sometimes difficult to separate, are easily identified by differences in laryngeal morphology, and larval buccopharyngeal characters are even more distinctive -- these latter differences are undoubtedly reflections of the very different habitats in which the larvae live.

Laryngeal characters have also proved invaluable in separating the more difficult specimens of *Tomopterna cryptotis*, *T. krugerensis* and *T. marmorata*, where size, markings and ambiguous subarticular tubercle shape sometimes makes identification uncertain.

Poynton (1964:129) remarked of *Ptychadena m. mascareniensis*:

> "It appears to be impossible to separate African material referred to this form from Mascarene material on morphological grounds alone. However, the identification of the African material as *mascareniensis* is here considered to be purely a matter of nomenclatural makeshift, which can last

only as long as purely morphological criteria are used. It is not believed that one and the same subspecies covers such a vast area."

Ptychadena m. mascareniensis, as generally recognised, now proves to be separable into at least two taxa in south-eastern Africa, but which of these (if either) is the same as Duméril & Bibron's species, has not yet been established. Indeed, laryngeal material from the whole of the species' range needs to be examined.

A little more surprising was the revelation that *Ptychadena taenioscelis* also appears to consist of two sibling species, and this raises interesting questions about the genus as a whole. Some of these points are addressed in the discussion of the genus, in the main body of the text.

Lambiris (1989a:93) considered *Rana dracomontana* "a poorly characterised species", and it is pleasing to confirm, on unambiguous larngeal and larval buccopharyngeal morphological grounds, that this species is indeed a valid taxon, and that the reservations which I expressed earlier were unjustified.

Quite unexpected was the discovery that *Rana vertebralis* Hewitt, as recognised by Lambiris (1989a:94) is in fact a complex of three sibling species. *Rana umbraculata* Bush proves to be a valid species, and a third, as yet unnamed, species occurs in the Lesotho highlands. While the laryngeal and buccopharyngeal material available demonstrates the existence of three species quite clearly, many the older museum specimens are in poor condition and collection of fresh material is necessary before a formal revision of the group can be undertaken.

The genus *Strongylopus* is particularly in need of more detailed investigation than was possible in this study. In particular, the status of the various colour morphs of *Strongylopus g. grayii* (A. Smith) and *S. grayii rhodesianus* (Hewitt), which seem to be correlated with habitat type, needs to be considered more carefully. Since the tadpole habitats in forest and in woodland are likely to differ in small but important details, larval buccopharyngeal morphology may well play an important

part in elucidating taxonomic problems in this genus. Adults of the tadpole of "Species A" described here are unknown, but it seems certain that these tadpoles represent an undescribed taxon.

The Phrynobatrachine genera presented some quite unexpected problems, several of which were exacerbated by the lack of larval material or, in the case of *Cacosternum poyntoni*, of adult male larynxes.

Cacosternum nanum Boulenger and *C. parvum* Poynton show such marked differences in laryngeal morphology that they are treated here as separate species.

Cacosternum striatum FitzSimons is a valid species, but my earlier concept of it (1989a:111) proves to have been erroneous. The Boston and Sehlabathebe specimens included under this species (Lambiris 1989a) are in fact a separate taxon, and laryngeal differences suggest that it belongs in a genus of its own. The recognition of a new genus on such slender grounds may seem unjustified, but is parallelled in Drewes' diagnosis (1985:190) of *Notokassina*: "A kassinoid genus distinct from all other Hyperoliid frogs by presence of the zygodactylous manus."

Larval buccopharynxes of *Anhydrophryne* and *Arthroleptella* revealed, surprisingly enough, more structures than are present in the tadpoles of *Breviceps* and suggest that overall trends may be valuable above the species level in evolutionary studies. Whether features diagnostic at the species level are present in all three *Arthroleptella* species, and in *Arthroleptis* tadpoles (no dissectable material of which was available for this study) remains to be seen.

Larynxes of the *Leptopelis* species examined differ markedly from those of the other Hyperoliid taxa included in this study, in the elaborate nature of the arytenoid cartilage and medial vocal cord. On the other hand, the larval buccopharynx of *Leptopelis natalensis* (the only species examined) has the same general facies as those of the other Hyperoliid larvae examined, which raises some interesting questions

about the systematic significance of the overall morphology of the larynx in this genus.

The genera *Kassina* and *Semnodactylus* show no major differences in either adult laryngeal or larval buccopharyngeal characters, others than those at the species level. The case for retaining *Semnodactylus* as a separate genus needs to be re-evaluated, using a larger suite of characters.

The several forms currently assigned to the synonymy of *Kassina senegalensis* (Duméril & Bibron) have proved especially intractable. I have not been able to find any laryngeal differences to support the recognition of *Kassina argyreivittis* Peters or of *K. modesta* Ahl, despite the apparent differences in markings and in general habitus. Larvae of these forms were not available for examination, and a final opinion should perhaps be withheld until such material is available.

The dwarf *Afrixalus* species *Afrixalus aureus*, *A. delicatus* and *A. crotalus* described by Pickersgill were considered by Lambiris (1989a:130) to be of doubtful validity, and *A. crotalus* was referred to the synonymy of *A. brachycnemis* (Boulenger) in a review of the frogs of Zimbabwe (Lambiris 1989b:157). Examination of the laryngeal morphology of Pickersgill's species shows that they are indeed valid taxa, and that laryngeal characters serve to distinguish them even when markings and skin asperities are poorly preserved or absent. Reliably attributable tadpoles of these species are not, unfortunately, available at present.

Laryngeal characters have proved to be very useful in separating specimens of *Hyperolius* which cannot be easily identified by external characters, and may be invaluable in helping identify preserved specimens that have lost essential details of colours and markings.

Positively identified tadpoles of most of the *Hyperolius* species included in this study are not currently available, but those that have been examined show clear diagostic differences that readily distinguish

one form from another, even when they cannot be separated on external characters.

In closing, we may recall Goethe's words and affirm that the little we have done does indeed fade into insignificance when we look ahead and see how much remains to be done. If, however, this study is judged useful in providing a basis for further research, its goal will have been achieved.

Τέλος δεδωκώς, θεῶν σοὶ χάριν φέρω

REFERENCES

BISHOP, P.J., 1985: A new species of *Arthroleptella* in South Africa. *S. Afr. J. Sci.*, 81:209

BLUME, W., 1930: Studien am Amphibien. *Morpholog. Jahrbuch*, 65:307-464.

BRANCH, W.R. (ed.), BAARD, E., HAACKE, W.D., JACOBSEN, N., POYNTON, J.C., & BROADLEY, D.G. (sub-eds.), 1988: A provisional and annotated checklist of the herpetofauna of southern Africa. *J. Herp. Soc. Afr.*, 34:1-19.

CHANNING, A., 1972: A description of *Bufo pusillus* tadpoles (Anura: Bufonidae). *Ann. Natal Mus.*, 21(2):509-511.

CHANNING, A., 1973: A description of *Bufo pardalis* tadpoles (Anura: Bufonidae). *Zool. Afr.*, 8(2):153-156.

CHANNING, A., 1978: A new *Rana* from the Lesotho plateau (Amphibia: Anura). *Ann. Natal Mus.*, 23(2):361-365.

CHANNING, A., 1979: Ecological and systematic relationships of *Rana* and *Strongylopus* in southern Natal (Amphibia: Anura). *Ann. Natal Mus.*, 23(3):797-831.

CHANNING, A., 1991: The distribution of *Bufo poweri* in southern Africa. *S. Afr. J. Zool.*, 26(2):81-84.

DE VILLIERS, C.G.S., 1929: Some features of the early development of *Breviceps*. *Ann. Transvaal Mus.*, 13(3):142-151.

DREWES, R.C., 1984: A phylogenetic analysis of the Hyperoliidae (Anura): Treefrogs of Africa, Madagascar, and the Seychelles Islands. *Occ. Pap. Calif. Acad. Sci.*, 139:1-70.

DREWES, R.C., 1985: A case of paraphyly in the genus *Kassina* Girard, 1853 (Anura: Hyperoliidae). *S. Afr. J. Sci.* 81:186-191.

DUELLMAN, W., & TRUEB, L., 1986: *Biology of Amphibians*. McGraw-Hill, New York.

FITZSIMONS, V., 1947: Descriptions of new species and subspecies of reptiles and amphibians from Natal, together with notes on some other little known species. *Ann. Natal Mus.*, 11:(1):111-137, pls. 1-3.

FROST, D.R. (ed.), 1985: *Amphibian Species of the World. A taxonomic and geographic reference*. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas, U.S.A.

GRISWOLD, C., 1987: The African members of the trap-door spider family Migidae (Araneae: Mygalomorphae) 1: The genus *Moggridgea* O.P. Cambridge, 1875. *Ann. Natal Mus.*, 28(1):1-118.

INGER, R.F., 1985: Tadpoles of the Forested Regions of Borneo. *Fieldiana: Zoology* New Series, No. 26: v + 1-89.

LAMBIRIS, A.J.L., 1987: Description of the tadpole of *Strongylopus hymenopus* (Boulenger, 1920) (Amphibia: Anura: Ranidae) and a key to described southern African tadpoles of the genus. *Ann. Natal Mus.*, 28(2):455-462.

LAMBIRIS, A.J.L., 1988: *Frogs and Toads of the Natal Drakensberg*, Ukuhlamba Series, No. 3, University of Natal Press, Pietermaritzburg.

LAMBIRIS, A.J.L., 1989a: A review of the Amphibians of Natal, *Lammergeyer*, 39:1-210.

LAMBIRIS, A.J.L., 1989b: *The Frogs of Zimbabwe*, Monografie X, Museo Regionale di Scienze Naturali, Torino.

LAMBIRIS, A.J.L., 1990, Management of Herpetological Collections, pp. 13-25, *In*: Herholdt, E.M. (ed.), *Natural history collections: their management and value*, Transvaal Museum Special Publication No. 1, Transvaal Museum, Pretoria.

MARTIN, W.F., 1972: Evolution of vocalisation in the genus *Bufo*, Chap. 15, pp. 279-309, *In*: Blair, W.F. (ed.), Evolution in the genus *Bufo*, University of Texas Press, Austin and London.

NOBLE, G.K., 1927: The value of life history data in the study of the evolution of the Amphibia, *Ann. New York Acad. Sci.*, 30:31-128.

ORTON, G.L., 1953: The systematics of vertebrate larvae, *Syst. Zool.*, 2:63-75.

ORTON, G.L., 1957: The bearing of larval evolution on some problems in frog classification, *Syst. Zool.*, 6:79-86.

PARRY, C.R., 1982: A revision of southern African *Pyxicephalus* Tschudi (Anura: Ranidae), *Ann. Natal Mus.*, 25:281-292.

PASSMORE, A., 1988: Epithelial specialisations of the Anuran larynx, *Proc. Electron Microsc. Soc. Sthn. Afr.*, 18:75-76.

PASSMORE, N.I., & CARRUTHERS, V.C., 1979: *South African Frogs*, Witwatersrand University Press, Johannesburg.

PETERS, J.A., & DONOSO-BARROS, R., 1970: Catalogue of the Neotropical Squamata, Part II, Lizards and Amphisbaenians, *United States Nat. Mus. Bull.* 279, viii + 293 pp.

PICKERSGILL, M., 1984: Three new *Afrixalus* (Anura: Hyperoliidae) from south-eastern Africa, *Durban Mus. Novit.*, 13:203-220.

POYNTON, J.C., 1963: Descriptions of Southern African amphibians, *Ann. Natal Mus.*, 15:319-332.

POYNTON, J.C., 1964: The Amphibia of Southern Africa: a faunal study, *Ann. Natal Mus.*, 17:1-334.

POYNTON, J.C., 1970: Guide to the *Ptychadena* (Amphibia: Ramnidae) of the southern third of Africa, *Ann. Natal Mus.*, 20:365-375.

POYNTON, J.C., 1985: Nomenclatural revision of southeast African treefrogs of the genus *Leptopelis* (Amphibia: Hyperoliidae), *S. Afr. J. Sci.*, 81:466-468.

POYNTON, J. C., & BROADLEY, D.G., 1985a: Amphibia Zambesiaca 1, Scolecomorphidae, Pipidae, Microhylidae, Hemisidae, Arthroleptidae, *Ann. Natal Mus.*, 26:503-553.

POYNTON, J.C., & BROADLEY, D.G., 1985b: Amphibia Zambesiaca 2, Ranidae, *Ann. Natal Mus.*, 27:115-181.

POYNTON, J.C., & BROADLEY, D.G., 1987: Amphibia Zambesiaca 3. Rhacophoridae and Hyperoliidae. *Ann. Natal Mus.*, 28:161-229.

POYNTON, J.C., & BROADLEY, D.G., 1988: Amphibia Zambesiaca 4. Bufonidae. *Ann. Natal Mus.*, 29:447-490.

SCHMIDT, P., 1852: Beschreibung zweier neuen Reptilien, aus dem naturhistorischen Museum zu Hamburg. *Abh. Geb. Naturf. Hamburg*, 2:168-171.

STARRETT, P.H., 1973: Evolutionary patterns in larval morphology. Chap. 7, pp. 251-271. *In*: Vial, J.L. (ed.), *Evolutionary Biology of the Anurans*. University of Missouri Press, Columbia.

STEINWARZ, D., 1990: Morphology of the larynx of the banana frog *Afrixalus fornasinii* (Bianconi) (Anura). *Amphibia-Reptilia*, 11:53-59.

TANDY, R.M., & KEITH, R., 1972: *Bufo* of Africa. Chap. 9, pp. 119-170. *In*: Blair, W.F. (ed.), Evolution in the genus *Bufo*. University of Texas Press, Austin and London.

TREWAVAS, E., 1933: The hyoid and larynx of Anura. *Phil. Trans. Roy. Soc. Lond.*, 222b:401-527.

VAN DIJK, D.E., 1966: Systematic and field keys to the families, genera and described species of southern African Anuran tadpoles. *Ann. Natal Mus.*, 18:231-286.

VAN DIJK, D.E., 1971. A further contribution to the systematics of southern African Anuran tadpoles - the genus *Bufo*. *Ann. Natal Mus.*, 21:71-76.

WAGER, V.A., 1986. *Frogs of South Africa. Their fascinating life stories*. Delta Books, Cape Town.

WASSERSUG, R.J., 1976. Oral morphology of Anuran larvae: terminology and general description. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas*, 48:1-23.

WASSERSUG, R.J., 1980: Internal oral features of larvae from eight anuran families: functional, systematic, evolutionary and ecological considerations. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas*, 68:1-146.

APPENDIX I

ADDITIONAL MATERIAL EXAMINED

The descriptions of adult hyolarynxes and of larval buccopharynxes were made from dissections of catalogued museum specimens. The provenance of this material is listed, for each taxon examined, in the main text.

Development of dissection and staining techniques was, necessarily, dependent on the use of specimens not forming part of any permanent research collection. This material, which included specimens of both sexes and a wide range of sizes (postmetamorphics) or developmental stages (larvae) also provided the basis for the remarks on variation in Chapters 2 and 3. The uncatalogued material examined, which was not indicated in the main text, is listed here. The breeding status of adult males was determined by the state of the nuptial pads and of the testes.

Adult hyolarynxes

TAXON	BREEDING MALE	NON-BREEDING MALE	BREEDING FEMALE	NON-BREEDING FEMALE
Xenopus l. laevis	10	12	4	4
Bufo gutturalis	12	10	8	8
Bufo garmani	6	5	3	3
Bufo rangeri	10	10	6	6
Schismaderma carens	12	12	8	7
Tomopterna natalensis	6	6	3	3
Ptychadena anchietae	3	3	2	2
Rana angolensis	12	14	9	8
Phrynobatrachus natalensis	10	10	7	4
Hyperolius m. marmoratus	5	3	1	1

Larval buccopharynxes

TAXON	NUMBER OF SPECIMENS	GOSNER STAGES
Xenopus l. laevis	25	25 - 38
Bufo gutturalis	ca 40	28 - 40
Schismaderma carens	ca 40	28 - 40
Rana angolensis	25	25 - 41
Strongylopus g. grayii	28	26 - 41