

THE ANOSTRACA (CRUSTACEA: BRANCHIOPODA) OF
SOUTHERN AFRICA

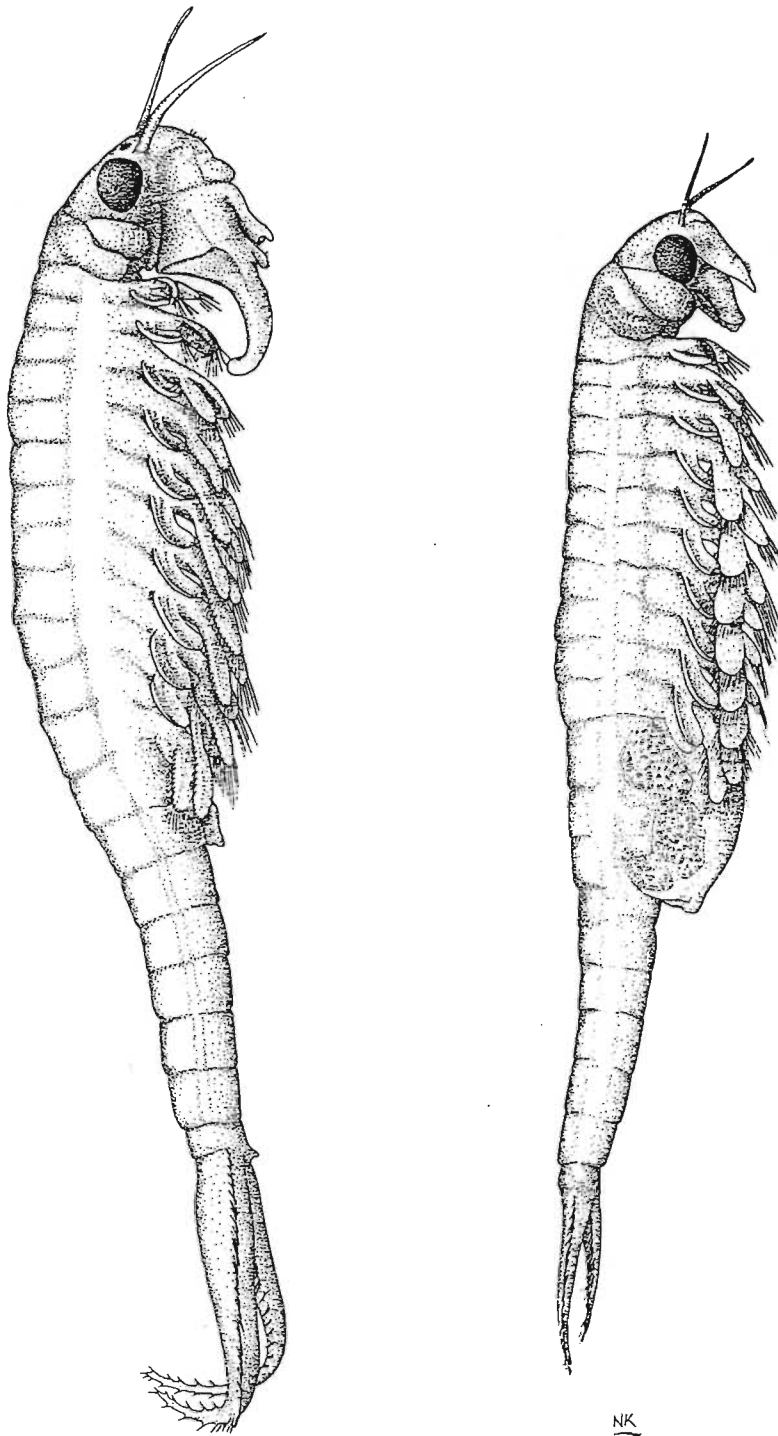
BY

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Branchipodopsis wolfi Daday

Male (left) and female (right); collected from the northern Transvaal, South Africa. Illustration by Nikki Köhly, February, 1994.

PREFACE

This study was carried out in the Department of Zoology & Entomology, University of Natal, Pietermaritzburg, from January, 1990 to March, 1994 under the supervision of Professor C.C. Appleton.

This thesis, unless specifically indicated to the contrary in the text, is my own work and has not been submitted to another university.

M. Hamer

Michelle L. Hamer.

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TABLE OF CONTENTS

	page
Preface	ii
Acknowledgements	iii
Abstract	1
Chapter 1. General Introduction	3
References	14
Key to the southern African Anostracan families	14
Chapter 2. The Streptocephalidae of Africa.	
2.1. A review of African Streptocephalidae. Part 1.	
South of the Zambezi and Kunene Rivers.	
Abstract	18
Introduction	19
Terminology	20
Materials & Methods	18
Taxonomic descriptions	21
Distinction of species groups	41
Key to the male Streptocephalidae	43
Discussion	45
Acknowledgements	46
Localities	47
References	69
2.2. A review of African Streptocephalidae. Part 2.	
North of the Zambezi and Kunene Rivers and Madagascar.	
Abstract	73
Introduction	74
Terminology and abbreviations	74
Materials & Methods	75
Taxonomic descriptions	75
Distinction of species groups	90
Key to the male Streptocephalidae	90
Discussion	91
General discussion	92
Acknowledgements	95
References	110
2.3. Four new <i>Streptocephalus</i> species from south-eastern Africa.	
2.4. A new species of <i>Streptocephalus</i> from Namibia.	

2.5. Additional records of <i>Streptocephalus</i> in southern Africa, with the description of a new species from Zimbabwe.	
Abstract116
Introduction117
Materials & Methods117
Results118
Discussion125
Acknowledgements127
References133
 Chapter 3. A preliminary report on <i>Artemia</i> in southern Africa.	
Abstract135
Introduction136
Materials & Methods139
Results139
Discussion142
Gazetteer148
Acknowledgements149
References149
 Chapter 4. The <i>Branchipodopsis</i> of southern Africa.	
Abstract152
Introduction153
Material & Methods155
Results -	
- Taxonomic descriptions156
Key to the southern African genus <i>Branchipodopsis</i>183
Discussion186
Acknowledgements190
Gazetteer192
References235
 Chapter 5. Three new genera of the family Branchipodidae from southern Africa.	
Abstract239
Introduction240
Material & Methods241
Results242
Discussion247
Acknowledgements250
References261
 Chapter 6. The <i>Branchinella</i> of southern Africa.	
Abstract263
Introduction264
Material & Methods266
Results267
Key to the southern African <i>Branchinella</i>275
Discussion275
Acknowledgements278

Gazetteer278
References284
Chapter 7. Anostracan diversity, biogeography and status in southern Africa.	
Abstract287
Introduction288
The southern African subregion290
Materials & Methods291
Results292
Discussion300
Acknowledgements308
References316
Appendix319

LIST OF FIGURES

	page
Chapter 1.	
Figure 1. General anostracan morphology9
Figure 2. Temporary rockpools, Sehlabatebe10
Figure 3. Animal wallow type temporary pools11
Figure 4. Natural pans in the northern Cape12
Figure 5. Map of southern Africa13
Chapter 2.1.	
Figure 1. Diagram of idealised streptocephalid male antenna and frontal appendage50
Figure 2. Distribution of <i>S. purcelli</i> , <i>S. dendyi</i> , <i>S. dregei</i> , <i>S. cirratus</i> and <i>S. cafer</i>51
Figure 3. Distribution of <i>S. macrourus</i> , <i>S. indistinctus</i> and <i>S. ovamboensis</i>52
Figure 4. Distribution of <i>S. (P) kaokoensis</i> , <i>S. (P) zuluensis</i> , <i>S. gracilis</i> , <i>S. papillatus</i> , <i>S. proboscideus</i> , <i>S. trifidus</i> , <i>S. cladophorus</i> , <i>S. vitreus</i> and <i>S. propinquus</i>53
Figure 5. <i>S. purcelli</i>54
Figure 6. <i>S. dendyi</i>55
Figure 7. <i>S. dregei</i>56
Figure 8. <i>S. cirratus</i>57
Figure 9. <i>S. cafer</i>58
Figure 10. <i>S. indistinctus</i>59
Figure 11. <i>S. macrourus</i>60
Figure 12. <i>S. ovamboensis</i>61
Figure 13. <i>S. gracilis</i>62
Figure 14. <i>S. papillatus</i>63

Figure 15. <i>S. (P) kaokoensis</i>	64
Figure 16. <i>S. (P) zuluensis</i>	65
Figure 17. <i>S. trifidus</i>	66
Figure 18. <i>S. proboscideus</i>	67
Figure 19. <i>S. cladophorus</i>	68

Chapter 2.2.

Figure 1. Map of Africa showing the distribution of <i>Streptocephalus</i> species recorded from the region north of the Zambezi and Kunene Rivers and Madagascar	98
Figure 2. <i>S. rothschildi</i>	99
Figure 3. <i>S. zeltneri</i>	100
Figure 4. <i>S. bouveri</i>	101
Figure 5. <i>S. (P) lamellifer</i>	102
Figure 6. <i>S. (P) sudanicus</i>	103
Figure 7. <i>S. vitreus</i>	104
Figure 8. <i>S. rubricaudatus</i>	105
Figure 9. <i>S. torvicornis</i>	106
Figure 10. <i>S. neumanni</i>	107
Figure 11. <i>S. distinctus</i>	108
Figure 12. <i>S. spinosus</i>	109

Chapter 2.5.

Figure 1. <i>S. gracilis</i>	128
Figure 2. Map of southern Africa showing the distribution of <i>S. spinicaudatus</i> and <i>S. bidentatus</i>	129
Figure 3. Map showing the distribution of <i>S. namibiensis</i> and <i>S. bourquinii</i>	130
Figure 4. <i>S. wirminghausi</i> sp. nov	131
Figure 5. <i>S. wirminghausi</i> and <i>S. bourquinii</i>	132

Chapter 3.

Figure 1. Map of southern Africa showing localities for <i>Artemia</i>	145
Figure 2. <i>Artemia</i>	146
Figure 3. <i>Artemia</i> frontal knob morphology	147

Chapter 4.

Figure 1. Diagram of idealised male antennae illustrating terminology	195
Figure 2. Penes of <i>Branchipodopsis</i>	196
Figure 3. Mouthparts of <i>B. barnardi</i>	197
Figure 4. <i>B. barnardi</i>	198
Figure 5. <i>B. barnardi</i>	199
Figure 6. <i>B. browni</i>	200
Figure 7. <i>B. browni</i>	201
Figure 8. <i>B. dayae</i>	202
Figure 9. <i>B. dayae</i>	203
Figure 10. <i>B. drakensbergensis</i>	204
Figure 11. <i>B. drakensbergensis</i>	205
Figure 12. <i>B. drakensbergensis</i>	206

Figure 13. <i>B. drakensbergensis</i>207
Figure 14. <i>B. drepane</i>208
Figure 15. <i>B. hodgsoni</i>209
Figure 16. <i>B. hodgsoni</i>210
Figure 17. <i>B. hutchinsoni</i>211
Figure 18. <i>B. hutchinsoni</i>212
Figure 19. <i>B. kalaharensis</i>213
Figure 20. <i>B. kalaharensis</i>214
Figure 21. <i>B. kaokoensis</i>215
Figure 22. <i>B. karroensis</i>216
Figure 23. <i>B. natalensis</i>217
Figure 24. <i>B. natalensis</i>218
Figure 25. <i>B. scambus</i>219
Figure 26. <i>B. scambus</i>220
Figure 27. <i>B. simplex</i>221
Figure 28. <i>B. tridens</i>222
Figure 29. <i>B. tridens</i>223
Figure 30. <i>B. tridens</i>224
Figure 31. <i>B. cf. tridens</i>225
Figure 32. <i>B. underbergensis</i>226
Figure 33. <i>B. underbergensis</i>227
Figure 34. <i>B. wolfi</i>228
Figure 35. <i>B. wolfi</i>229
Figure 36. <i>B. wolfi</i>230
Figure 37. <i>B. wolfi</i>231
Figure 38. Map of southern Africa showing the distribution of <i>B. browni</i> , <i>B. drepane</i> , <i>B. hodgsoni</i> , <i>B. kalaharensis</i> , <i>B. kaokoensis</i> , <i>B. karroensis</i> , <i>B. natalensis</i> , <i>B. simplex</i> and <i>B. scambus</i>232
Figure 39. Map of southern Africa illustrating the distribution of <i>B. tridens</i> , <i>B. hutchinsoni</i> and <i>B. drakensbergensis</i>233
Figure 40. Map of southern Africa illustrating the distribution of <i>B. wolfi</i> , <i>B. underbergensis</i> , <i>B. barnardi</i> and <i>B. dayae</i>234
Chapter 5.	
Figure 1. Genus A251
Figure 2. Genus A, thoracopod 5252
Figure 3. Map of southern Africa showing localities for genera A, B and C253
Figure 4. Genus B254
Figure 5. Genus B255
Figure 6. Genus B, thoracopods256
Figure 7. Genus C257
Figure 8. Genus C258
Figure 9. Genus C, thoracopods259
Figure 10. Genus C, egg260

Chapter 6.		
Figure 1. <i>B. spinosa</i>	279
Figure 2. Map of southern Africa showing the distribution of <i>B. spinosa</i> , <i>B. ornata</i> and <i>B. ondonguae</i>	280
Figure 3. <i>B. ornata</i>	281
Figure 4. <i>B. ornata</i> , thoracopods, brood pouch	282
Figure 5. <i>B. ondonguae</i>	283
Chapter 7.		
Figure 1. Map of southern Africa showing major altitudinal regions	309
Figure 2. Map of southern Africa showing distribution of biogeographic category 2	310
Figure 3. Map of southern Africa showing distribution of biogeographic categories 3 and 5	311
Figure 4. Map of southern Africa showing the distribution of biogeographic categories 6, 8 and 10	312
Figure 5. Map of southern Africa showing the distribution of biogeographic categories 4, 7 and 9	313
Figure 6. Map of southern Africa illustrating species richness in two degree grids	314
Figure 7. Aquatic ecoregions as presented by Skelton (1993)	315

LIST OF TABLES

Chapter 1.		
Table 1. Species groups, southern African <i>Streptocephalus</i>	42
Chapter 2.		
Table 1. <i>Streptocephalus</i> species groups, Africa north of the Zambezi and Kunene Rivers and Madagascar	97
Chapter 3.		
Table 1. Frequency of spine groupings on the frontal knob of <i>Artemia</i> from different localities	141
Chapter 4.		
Table 1. Southern African <i>Branchipodopsis</i> species groups	186
Chapter 7.		
Table 1. The southern African anostracan fauna	296
Table 2. Two degree grids of southern Africa with the highest species richness and associated climatic conditions	299

ABSTRACT

The Anostraca are a group of crustaceans belonging to the class Branchiopoda. They are predominantly restricted to temporary, inland waterbodies, which in southern Africa, include rockpools, animal wallows, and large "pans". The anostracan fauna of southern Africa was last examined in detail in 1929 by Barnard, and recent collecting in a number of areas indicated the need to update earlier work. A total of four genera, each belonging to a separate family, and forty-six species, some of which had not previously been described, are presented in this thesis.

The monogeneric family Streptocephalidae is well represented in Africa, and the fauna of Africa south and north of the Zambezi and Kunene Rivers, as well as Madagascar is reviewed. The *Streptocephalus* species are characterised by having an S-shaped antennal process, terminating in a cheliform "hand" region. The species were divided into ten groups based on similarities in antennal process morphology. The descriptions of five new species have been published, and an update on distribution and specimen data for a number of species are presented. An additional, as yet unpublished new species from Zimbabwe is presented.

The genus *Artemia*, although well researched in other parts of the world, has been largely ignored in southern Africa. Bisexual populations occur along the Cape coast, and a set of specimens from Namibia, which includes only females, may indicate that *A. parthenogenetica* is also present on the subcontinent. The frontal knob morphology of the Cape specimens is similar to that of *A. tunisiana* from northern Africa and the Mediterranean.

The family Branchipodidae is characterised by the fusion of the basal joints of the male antennae to form a so-called "clypeus". This family is represented in southern Africa by a diverse fauna of the genus *Branchipodopsis*. Eleven previously described species, as well as five new species are presented. An attempt was made to divide the sixteen species into species groups, as was done for the streptocephalids, but this proved difficult. The taxonomically useful characters in this genus are largely restricted to the basal processes. An additional character, the presence of expansions of the posterior thoracic segments in the females of some species could be useful. Much intraspecific variation in clypeus morphology was evident, particularly in two of the widespread species. *Branchipodopsis* species commonly occur in small pools which fill a number of times during the wet season and this

has probably led to the development of localised adaptations, and intraspecific variation, or even species endemic to very restricted areas.

Three sets of specimens which belong to the family Branchipodidae, but to no known genus, were recently collected from north-eastern Natal, the eastern Cape and the Namib desert in Namibia. These specimens share a single, large process positioned medianly on the fused basal joints, as opposed to a pair of processes in this position. However, the morphology of the penes, and the position and form of other antennal processes could indicate that the specimens are not congeneric. Unfortunately, more material is necessary before the descriptions of two of these possible new genera can be published.

Three species of the genus *Branchinella*, of the family Thamnocephalidae, occur in southern Africa. These species have a well developed frontal process, and fully retractible penes. *Branchinella spinosa* was recorded from the Makgadikgadi Pan in northern Botswana, and was probably introduced to this area from north Africa, or Europe, where it has a wide distribution. The other two southern African species have been collected from few localities, and in small numbers, and this may be connected to cyst hatching processes.

The southern African anostracan fauna exhibits distinct distribution patterns and these appear to be influenced by climate, with rainfall having the dominant influence in the western half of the subcontinent, and temperature influencing distribution in the eastern half. The high altitude Escarpment forms a barrier to the movement of species between the coastal margin and the central plateau region. The formation of the Escarpment could have resulted in vicariance speciation in some anostracans, but in most cases, allopatric speciation appears to have occurred. The type of habitat also influences species distribution in a number of ways. The great anostracan species richness in southern Africa is probably related to the climatic heterogeneity of the subcontinent, as well as the possible origin of two genera in Gondwanaland, and the absence of a Pleistocene glaciation in Africa. Large parts of southern Africa have not been sampled, and the exact status and distribution of many species is uncertain.

CHAPTER 1

GENERAL INTRODUCTION

The Anostraca or fairy shrimps belong to the Class Branchiopoda, a heterogeneous assembly of rather ancient crustaceans, united mainly by their flattened, leaf-like legs. Fryer (1987) revised the branchiopod classification and divided the class into 2 extinct and 8 extant orders. Four of the latter were previously combined as the Cladocera. The other four extant orders, the Anostraca, Notostraca, Spinicaudata and Laevicaudata (the last two were previously combined as the Conchostraca) had been grouped together since Sars (1867) termed them the "Phyllopoda". The last four orders differ from the cladocerans by having a greater number of legs and in the presence of paired compound eyes. The Spinicaudata and Laevicaudata (previously the Conchostraca) possess a bivalved carapace enclosing virtually the entire animal, while the Notostraca have a horseshoe-shaped carapace which covers the head and thoracic region of the trunk. The anostracans are easily distinguished since a carapace of any sort is absent and the eyes are pedunculate and moveable rather than sessile.

Wiggins, Mackay & Smith (1980) suggested that the Branchiopoda evolved from marine ancestors which became adapted to permanent freshwater habitats. The evolution of the jawed fishes in the Devonian period may have resulted in predatory pressure intensive enough to cause the branchiopods to become restricted to transient waters which were free of these fishes, and to eventually become adapted to survive in temporary habitats.

Anostracan morphology

The following characteristics of the Anostraca have been discussed and described in some detail by a number of authors (Linder 1941; Belk 1982; Fryer 1987; Dodson & Frey 1991) but are included here mainly for those not familiar with the group.

The anostracan body is elongate, with 19-27 trunk segments and a telson with caudal furcae or cercopods (Figs 1A-B). Each thoracic segment has a pair of phyllopodous, and largely serially homologous, filtratory limbs. These thoracopods are composed of a respiratory epipodite and one or two exites (referred to as the pre-epipodite/s) proximally, and a distal exopodite, together with a series of five endites and a distal endopodite (Fig. 1C). The borders of the endites, endopodite and exopodite usually have a distinct arrangement of setae. The

metachronal beating of these appendages results in simultaneous respiration, feeding and locomotion.

Posterior to the thoracic limbs are two fused genital segments containing the gonads which extend into the abdomen and in many cases, forward into the preceding thoracic segments. Paired ovaries in the female discharge into a median ovisac (brood pouch) on the ventral surface of the first genital segment (Fig. 1B). The testes lead through paired vas deferens into a pair of penes on the ventral surface of the genital segment of the male (Fig. 1A). The penes are composed of a proximal, usually rigid basal part and an apical, retractable part. In most anostracans reproduction is sexual, and eggs which are able to withstand desiccation are released by the female.

The most conspicuous feature of the head of male anostracans is a pair of well-developed, two-jointed and unsegmented antennae (Fig. 1A) (second antennae) which are used for clasping the female during mating. These antennae develop from a typically biramous larval appendage, in which the endopodite disappears in most species and the exopodite gives rise to the so-called terminal or apical joint of the adult antenna (Linder 1941). A basal joint is formed by the fusion of the coxopodite and basipodite of the larval antenna. Taxonomically significant processes or projections are usually present on or from the basal joint of adults. During development these outgrowths may migrate from the antennae to the head where they often fuse to form a common stem which is usually apically biramous. Such structures are commonly termed frontal appendages. In contrast, the female antennae are simple unjointed structures (Fig. 1B). The antennules of both sexes are similar, uniramous and tubular (Figs 1A-B). Apart from the paired compound eyes, a dorso-median, three-cupped ocellus or naupliar eye is present (Fig. 1A). The labrum is large as are the mandibles which are usually of a grinding and rolling type. The maxillules are reduced to gnathobases and the maxillae are also reduced, consisting only of a single, setulose lobe.

Anostracan habitats in southern Africa

The anostracans have a worldwide distribution, but like the other non-cladoceran branchiopods, most species are restricted to ephemeral, freshwater habitats. Their vulnerability, in particular to fish predators, is one of the major reasons for this restriction. However, by virtue of their drought-resistant eggs, features of their life history and

physiological adaptations, the anostracans are one of the most successful components of the fauna of these unpredictable, and frequently stressful habitats.

In southern Africa a wide range of temporary freshwater habitats is found. Small (1 - 4 m in diameter) and shallow (5 - 20 cm deep) depressions in rocks on top of mountains or rocky outcrops (Figs. 2A-D) are usually quantitatively dominated by anostracans. Animal wallows, presumably formed and enlarged by a combination of the activities of game and wind erosion are temporary pools frequently found in game reserves. These habitats vary in area, depth and vegetation (Figs 3A-C). A series of "pans" or shallow depressions varying from a few square meters to several square kilometres occur in a belt in the arid and semi-arid regions of southern Africa, stretching NNE from Calvinia in the Cape through the northern Cape and western Orange Free State to the Transvaal, with a branch into Namibia and an outlying patch in the eastern Transvaal (King 1967). These pans contain water after rain, but most of the time they are dry, flat, frequently barren and salty floors (Figs 4A-D). King (1967) suggested that they are formed by wind action. Initially, water may have collected in a small depression, causing local disintegration of the underlying sandy or shaly rock. When the water evaporated, wind, perhaps as whirlwinds carried away the disintegration products, very slightly lowering the level of the floor. Over a period of thousands of years, repetition of this process has resulted in an increase in depth and area of the pans. Thomas & Shaw (1991) mentioned that termite activity at the periphery of small waterholes may create subsurface canals and thus contribute to the formation of the larger pans. In addition, termites also accumulate minerals such as sodium and this could attract animals which further contribute to the erosion process. Man-made temporary waterbodies such as roadside ditches and farm dams are also often inhabited by anostracans. A variety of other waterbodies, which do not fit into the above categories, and which are less frequently inhabited by anostracans include heavily reeded and grassed areas (referred to as "vleis" or marshes) which are dry for some period during the year, and pools in dry river beds. Most of the temporary pools in southern Africa are isolated from water sources other than rain, on which they depend for the wet phase.

The southern African subregion has been defined in this study as the area south of the Zambezi and Kunene Rivers which includes South Africa and those independent states within her borders (Swaziland and Lesotho), Namibia (South West Africa), Botswana, Zimbabwe

(Rhodesia) and the southern half of Mozambique (Fig. 5). The climate of this area could be considered semi-arid to arid, with an annual average rainfall of 475 mm as opposed to a world average of 860 mm. In addition to the small quantity, rainfall is usually highly unpredictable and erratic in most parts of southern Africa. A number of climatic regions can be recognised including the Mediterranean of the south-western Cape; a temperate, warm summer, cool winter with year-round rainfall further east; and a subtropical climate in the north-eastern parts of South Africa, Mozambique and Zimbabwe. Along the west coast of the Cape and Namibia, hot, arid desert conditions are prevalent, and in the central region of the subcontinent, there is a semi-arid plateau where winters are cool and dry and summers are hot with some rain.

Research on the anostracan fauna of southern Africa

The order Anostraca currently includes over 200 species, distributed among 24 genera and eight families (Bănarescu 1990). Daday (1910) published the first detailed monograph of the group and this was followed in 1941 with Linder's extensive discussion of the anostracan morphology and an evaluation of the taxonomy. Subsequent to these early works, numerous new species have been described, some of the genera and families revised and the anostracan fauna of certain areas has been studied. There do, however, remain regions of the world in which temporary pools and the anostracan fauna associated with these have not been investigated. Africa south of the Sahara is one such area. The temporary pools of North Africa have been sampled in a number of studies (Rzoska 1961; Thiéry 1987; Dumont, De Walsche & Mertens 1991) but the records from central and southern Africa are largely from the early part of the century. Central Africa, in particular, is poorly known in terms of its anostracan fauna and this is possibly related to the inaccessibility of large areas of this part of the continent as well as political upheaval in many of the countries over the last few decades. The anostracans of southern Africa are better known than those from the areas to the north largely through the contributions of Barnard (1924; 1929; 1935). Sars, based on material sent to him, described a number of new species (1898; 1899; 1905) as did Daday (1908; 1910), and Brady (1913) and Gurney (1904) each recorded a species from one locality. A limited amount of material was collected and identified during Hutchinson, Pickford & Schuurman's (1932) survey of some of the larger temporary pools in the southern Transvaal and even less, considering the large area covered, was collected by the Lund University Expedition to South Africa in 1950 - 1951, the relevant results of which were published by Brehm (1958). During the period between Barnard's work and the 1980's, very little anostracan material was lodged

in museum collections, and there were no significant publications on the anostracan fauna of southern Africa. As a result of the effort by a number of individuals, a considerable amount of material was collected over a wide area during the last decade, but most of this remained unidentified and undocumented. Unfortunately, there are still vast areas which are not easily accessible, such as large parts of Botswana and Zimbabwe as well as areas such as Mozambique, where war has prevented almost any form of survey of the fauna from taking place for the last 27 years.

An earlier study (Hamer 1989) in north-eastern Natal had indicated that the branchiopod fauna of southern Africa required updating. Barnard's (1929) descriptions fitted few of the specimens collected and in this area, for which there were only two previous records of anostracans (Barnard 1929; Rayner & Bowland 1985) these animals were a common and abundant component of the temporary pool fauna. The need to redescribe and illustrate the taxonomically important characters of the anostracan fauna of Africa south of the Zambezi and Kunene Rivers and to identify and describe new species became obvious. The identification of relationships between species, based on morphological similarities is an aspect of anostracan taxonomy which also required investigation. Barnard (1929) did not attempt a zoogeographical analysis of the branchiopods since he believed the records available to him were inadequate for this purpose. The additional material collected recently and surveys of a number of areas has provided sufficient data to allow at least a preliminary analysis of the distribution patterns exhibited by anostracans.

The results of this study have been compiled as a series of manuscripts, two of which have been published, two which are in press and one which has been submitted to a journal and is currently being reviewed. The remainder of the chapters require additional data before they can be considered for publication, but for convenience, they have also been written in manuscript form, following the format of the *Annals of the South Africa Museum* to which future submission of most of these is intended.

KEY TO THE ANOSTRACAN FAMILIES OF SOUTHERN AFRICA

The following key applies to the adult male specimens for the species belonging to the four families of Anostraca found in southern Africa. Each family is represented by a single genus (indicated in brackets) although an additional three genera, previously undescribed, are proposed for the Branchiopodidae.

- 1a. Antennal process from basal joint well developed and S-shaped, terminating in a hand-like cheliform structure, terminal joint much shorter than antennal process

STREPTOCEPHALIDAE.

(*Streptocephalus*) (Chapter 2)

- 1b. Antennal process from basal joint shorter or only slightly longer than terminal joint, not terminating in hand-like structure **2**

- 2a. Terminal joint broad, flattened and blade-like, process on median margin of basal joint a small, rounded knob-shaped structure **ARTEMIIDAE.**

(*Artemia*) (Chapter 3)

- 2b. Terminal joint slender and tubular, basal joint process varying in position and shape **3**

- 3a. Basal joints fused for at least half their length, and antennae more heavily sclerotised than the rest of the body, one to three processes situated on the anterior, median margin of the fused basal joints

BRANCHIOPODIDAE.

(*Branchipodopsis*) (Chapter 4)

- 3b. Basal joints may be fused for a portion of their length, but fused region not heavily sclerotised, process on basal joints not from anterior, median margin, but from dorsal surface of fused basal joints

THAMNOCEPHALIDAE.

(*Branchinella*) (Chapter 6)

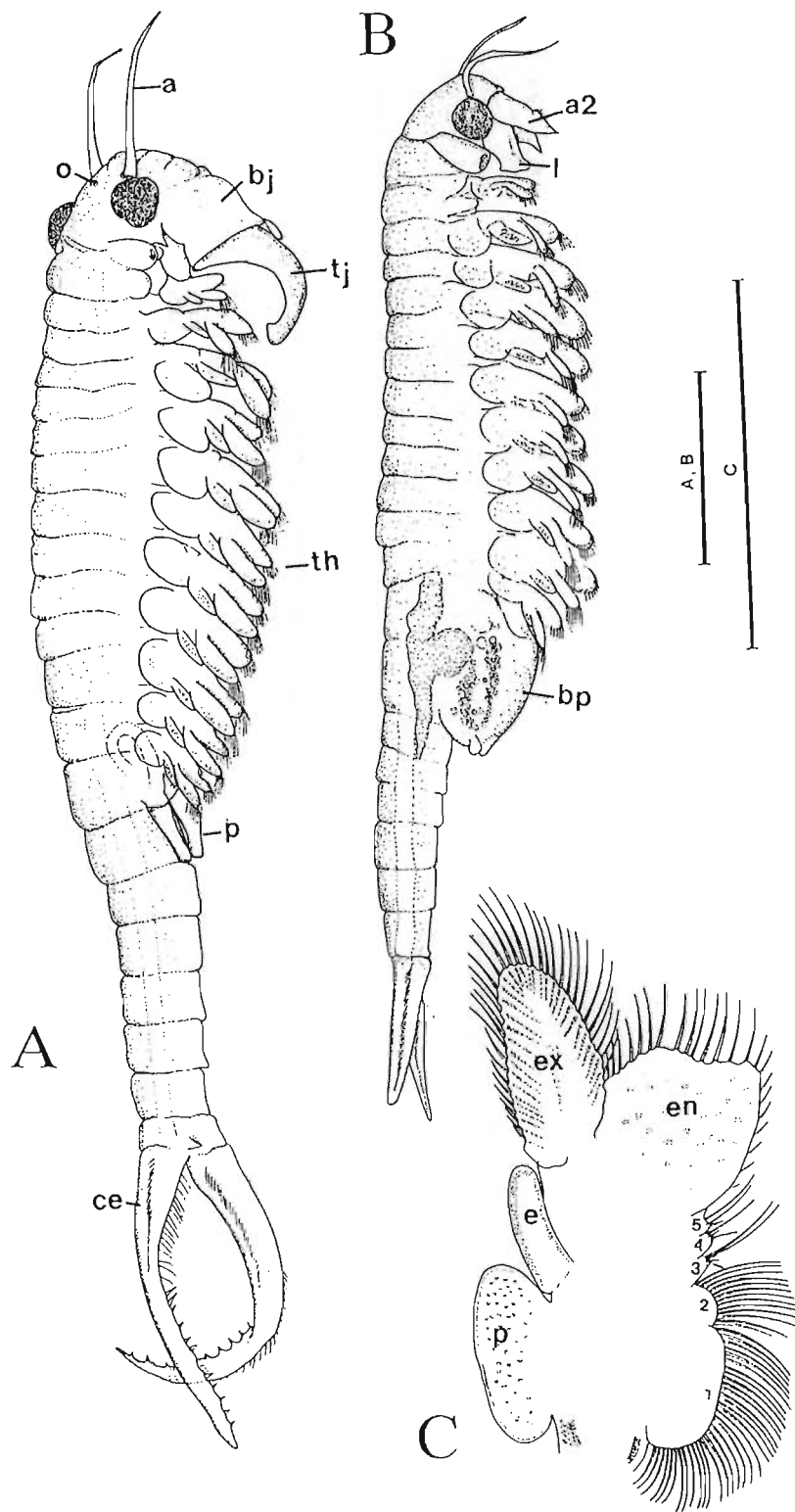


Figure 1. General anostracan morphology. Scale lines represent 1 mm. A = lateral view of adult male; a = antennule, bj = basal joint, ce = cercopods, o = ocellus, p = penes, th = thoracopods, tj = terminal joint. B = lateral view of adult female; a2 = antenna, bp = brood pouch. C = structure of thoracic limb (thoracopod); e = epipodite, en = endopodite, ex = exopodite, p = pre-epipodite, 1-5 = endites.

A



B



C



D





A



B

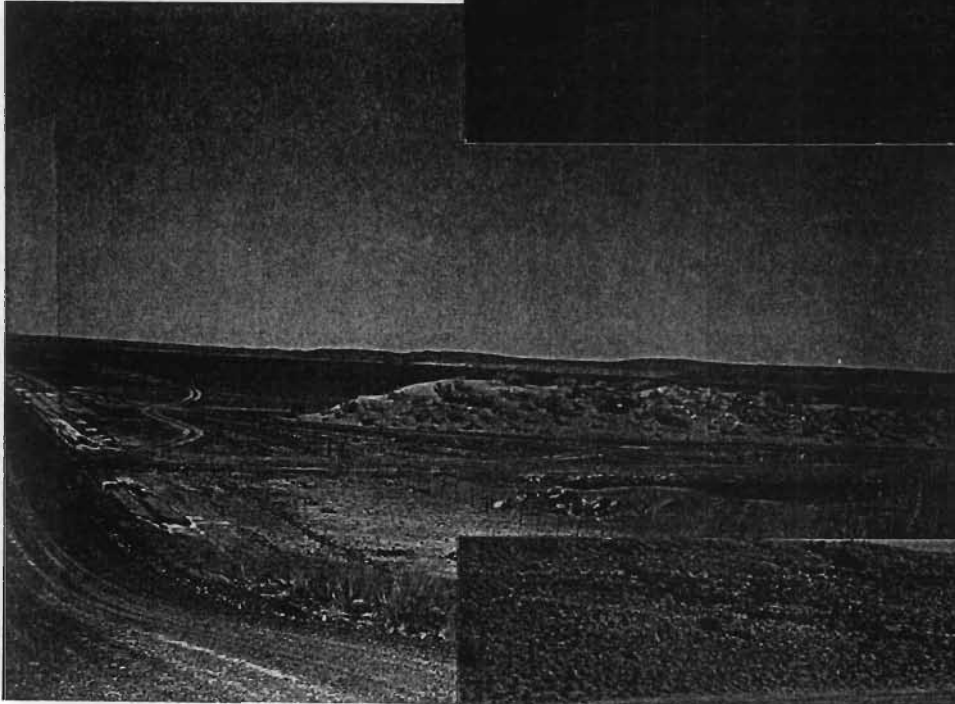
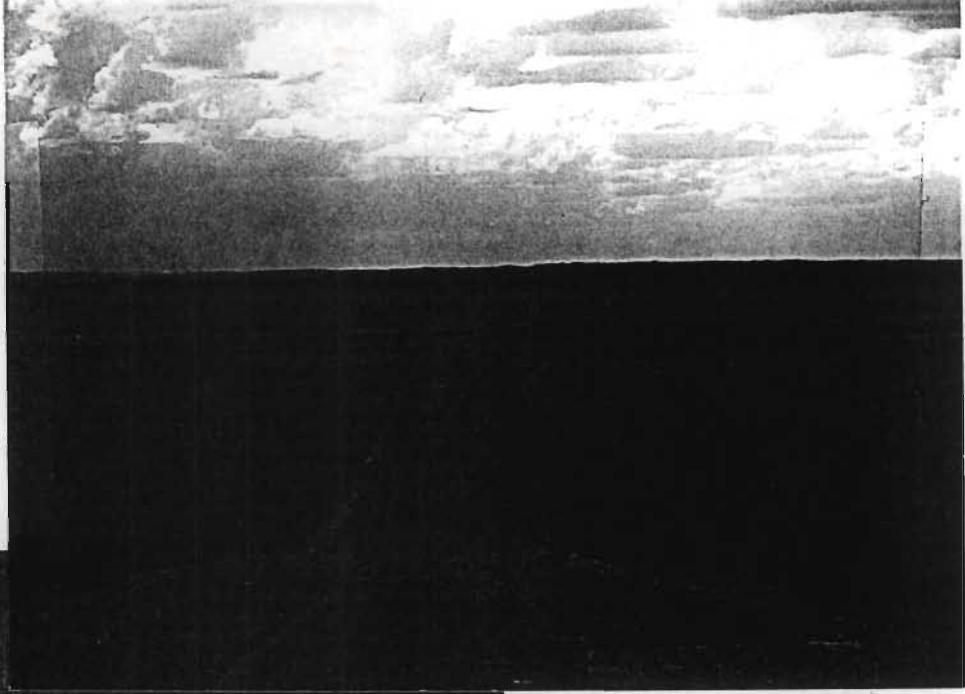


C



D

A



B



C



D

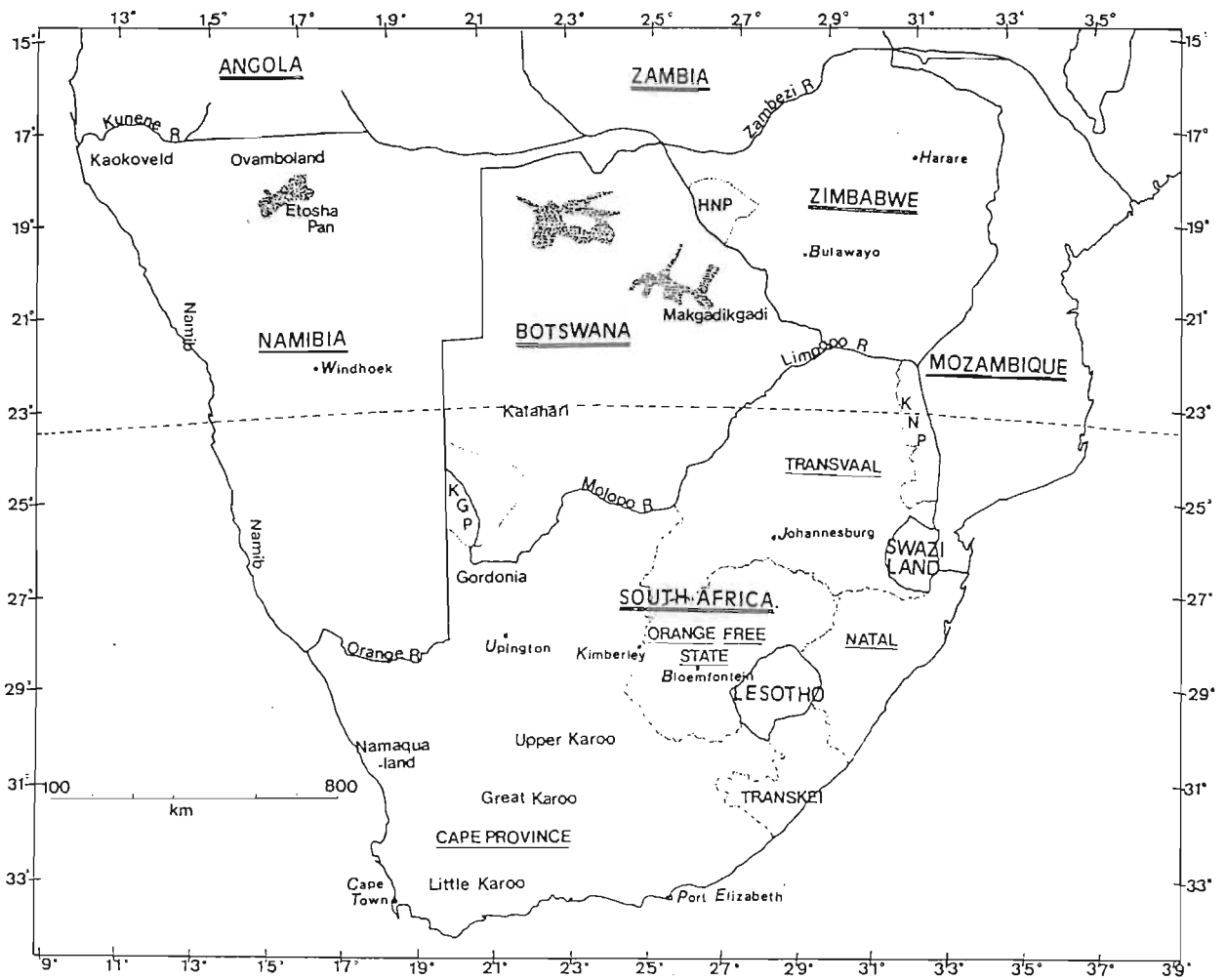


Figure 5. Map of southern Africa illustrating the borders of countries, provinces, relevant regions and cities.

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CHAPTER 2

THE STREPTOCEPHALIDAE OF AFRICA

For the family Streptocephalidae, a manuscript on the fauna of Africa north of the Zambezi and Kunene Rivers and Madagascar has been included. This research was incorporated into the present study because material and species descriptions for the region were examined in order to determine the relationship between those species and the southern African fauna. In addition, there was a need for a single document containing all species recorded, and updated redescriptions of them for this part of Africa.

The manuscripts included in sections 2.1 and 2.2 of this chapter are currently in press in *Archiv für Hydrobiologie* and are presented in the format required by that journal. During the preparation of the manuscripts, five new species of *Streptocephalus* were identified. These were subsequently described in the *Annals of the South African Museum* and form sections 2.3 and 2.4. These are presented in their published form. As a result of continuous collecting throughout the project, a considerable amount of additional material, which includes significant new distribution records for a number of species, as well as a previously undescribed species, has been included in section 2.5 of this chapter.

The manuscripts reviewing the Streptocephalidae of Africa were prepared in conjunction with Dr. Luc Brendonck of the Royal Belgian Institute of Natural Sciences, Department of Freshwater Biology, Brussels, Belgium and formerly of the State University of Gent, Belgium. These manuscripts were included in the Ph.D. thesis of Dr. Brendonck. In order to avoid any complications arising from the duplication of these manuscripts in both theses, a document signed by Dr. Brendonck, stating the contributions of the senior author (M.L. Hamer), is included in the appendix of this thesis.

CHAPTER 2.1.

A REVIEW OF AFRICAN STREPTOCEPHALIDAE (CRUSTACEA: BRANCHIOPODA: ANOSTRACA).

Part 1: South of Zambezi and Kunene rivers.

Abstract

The Streptocephalidae south of the Zambezi and Kunene rivers are reviewed. An attempt is made to construct species groups based on similarities in male antennal and frontal appendage structure. Sixteen *Streptocephalus* species are known from the above region. An additional species, *S. propinquus*, of which no study material was located, could be valid. *Streptocephalus proboscideus* and *S. vitreus*, also occur north of the above rivers. Male antennae, frontal appendage and cercopods are illustrated and the distribution of each species is presented. The southern African streptocephalids are divided into the following nine species groups: 1) *S. purcelli*/*S. dendyi*; 2) *S. dregei*/*S. cirratus*; 3) *S. cafer*/*S. indistinctus*; 4) *S. vitreus*/*S. macrourus*; 5) *S. ovamboensis*; 6) *S. papillatus*/*S. gracilis*; 7) *S. (Parastreptocephalus) zuluensis*/*S. (P.) kaokoensis*; 8) *S. proboscideus*/*S. trifidus*; and 9) *S. cladophorus*. A key, based on male antennal and frontal appendage morphology is presented.

Introduction

The monogeneric anostracan family Streptocephalidae is known from Eurasia, Africa and North America and includes about 50 species. All streptocephalids are characterized by the cheliform 'hand' of the male S-shaped antennal process. The highest species richness is recorded from Africa (BELK, 1984). Since BARNARD's (1929) review in which 13 streptocephalids are listed, the southern African 'phyllopod' fauna has been largely neglected. Examination of museum collections and recent sampling of southern African localities have revealed the need to revise current species descriptions and distribution records in a single document, using standard terminology. In addition, the construction of species groups could reveal phylogenetic relationships for the genus. The southern African region includes South Africa, Namibia, Botswana, Zimbabwe, and southern Mozambique. Unfortunately, little material is available from the latter three countries.

In this paper key-characters of southern African Streptocephalidae are (re-) described and illustrated. The male second antenna usually presents the most useful taxonomic characters. Additional characters presented in this study include the shape and size of the frontal appendage, the shape and setation of the cercopods (caudal furcae), and the presence and location of abdominal processes. Characters not used here but which could be relevant in tracing phylogenetic relationships include male and female genital structures, thoracopods, and mouthparts.

Female structures do not usually present clear-cut interspecific differences and are not included. Recently, however, several authors have investigated the taxonomic potentials of resting egg morphology (MURA et al., 1978; MUNUSWAMY et al., 1985; MURA & THIÉRY, 1986; BELK, 1989; BRENDONCK et al., 1990). This character has been applied with variable success in different branchiopod taxa (see BELK, 1989; BRENDONCK et al., 1990; BRENDONCK et al., 1992). The resting egg morphology of all species under consideration is presented elsewhere (BRENDONCK & COOMANS, in press).

One of the objectives of this study was to use the above mentioned key-characters to establish species groups and to compare these to groupings based on resting egg morphology as presented in BRENDONCK & COOMANS (in press).

Species distributions are given but no detailed zoogeographical analysis is attempted since, at this stage, insufficient data are available.

Terminology

The general morphology and characteristics of the streptocephalids have been discussed by DADAY (1910), BARNARD (1929), LINDER (1941), MOORE (1966), BRTEK (1974), BELK (1982) and BRENDONCK (1990). The terminology used for the different male antennal parts follows LINDER (1941) and BRTEK (1974) and is summarized in Fig. 1. The terminology used to describe frontal appendage morphology when this structure takes the form of distal arms branching off a proximal trunk is based on BELK & PEREIRA (1982).

Materials and methods

List of museums and collections.- The following abbreviations indicate museum collections: AM = Albany Museum (Grahamstown, South Africa); BMNH = British Museum of Natural History (London, England); HNHM = Hungarian Natural History Museum (Budapest, Hungary); MNHN = National Museum of Natural History of France (Paris, France); MNHSI = Museum of Natural History of the Smithsonian Institution (Washington, USA); MNHV = Museum of Natural History of Vienna (Austria); SAM = South African Museum (including BARNARD's 1929 collection) (Cape Town, South Africa); SM = State Museum (Windhoek, Namibia); TM = Transvaal Museum, consisting of BARNARD's 1935 collection from the Vernay Lang expedition to the Kalahari (Pretoria, South Africa); ZMHUB = Zoological Museum of the Humboldt University of Berlin (Germany); ZMUH = Zoological Museum of the University of Hamburg (Germany); ZMUO = Zoological Museum of the University of Oslo (Norway); ZMUU = Zoological Museum of the University of Uppsala (Sweden); ZNM = Zimbabwe National Museum (Bulawayo, Zimbabwe). Specimens collected by Dr. J. Day (University of Cape Town) in the south-western Cape and Namibia were provided by Dr. D. Belk (Our Lady of the Lake University, Texas) and have been catalogued into the Albany Museum collection as has material collected by MH.

Fresh specimens were collected by MH using hand-held dip-nets with a mesh size of 1-2 mm. Specimens were preserved in 70 % ethanol. In some cases, dried pool sediments were rehydrated in the laboratory. Specimens were then cultured until maturity to allow identification.

Drawings were made using a Wild M-5 dissection microscope and drawing tube. Dissected antennae were cleaned and dehydrated in a graded ethanol series. Specimens were then critical point dried, mounted on stubs and coated with gold for scanning

electron microscopical observation. The drawings and SEM's were then used to group species based on common characteristics of, in particular, the hand of the S-shaped antennal process. Only adult specimens were used for study.

Measurements of specimens exceeding 10 mm in length were made using Vernier callipers, while a graticule was used for smaller specimens. All measurements are presented as total body length (mean \pm standard deviation where $n > 10$, or as a range of sizes where $n < 10$), from the front of the head (excluding antennae) to the tip of the cercopods (including setae) for sexually mature specimens. Lengths are only presented for undamaged specimens studied. Antennal length was calculated by totalling the length from the head to the base of the hand of the S-shaped antennal process, and from the latter, in a straight line, to the apex of the thumb.

Except when indicated otherwise, the scale lines in Figs 5-22 equal 100 μm for SEM-pictures and 1 mm for line drawings.

Taxonomic descriptions

Class: Branchiopoda LATREILLE, 1817

Order: Anostraca SARS, 1867

Family: Streptocephalidae DADAY, 1910

Genus: *Streptocephalus* BAIRD, 1852

Type species: *Streptocephalus torvicornis* (WAGA, 1842)

Described as: *Branchipus torvicornis* WAGA, 1842

Abbreviated diagnosis: see BRENDONCK (1990).

Streptocephalus purcelli SARS, 1898

(Fig. 5)

Streptocephalus purcelli SARS, 1898b: 4, pl. 1. - SARS, 1899: 18, pl. 2, figs 3-5. - STEBBING, 1910: 483. - DADAY, 1910: 340, fig. 59. - BARNARD, 1929: 207, fig. 9.

Type material: Type specimens housed in the SAM (SAM 1478, in poor condition). Collector and date unknown.

Type locality: SW Cape, Cape Town, Green Point Common.

Other material examined: SAM A7591: W. Cape, Kamieskroon (Hondeklipbaai). Coll., date unknown. 23 males (14 ± 1.5 mm); 11 females (12.9 ± 1.4 mm) (specimens used for Fig.

5e); SAM 6280: W. Cape, St. Helena, Stompneus. Raised from mud in the laboratory. Coll., date unknown. 7 males (19.5 - 22.1 mm); 6 females (18.2 - 20.8 mm) (specimens used for Fig. 5f); SAM A6278: W. Cape, St. Helena, Stompneus. Raised from mud in the laboratory. Coll., date unknown. 14 males (11.7 ± 1.2 mm); 13 females (10.8 ± 1.2 mm); SAM A7302: W. Cape, Stellenbosch. Coll. de Villiers, 1928. 8 males (18.8 - 23.1 mm); SAM uncat.: SW Cape, Cape Flats, near Epping. Coll. unknown, 1966. 4 males (17.1 - 17.9 mm); 6 females (15.5 - 21.8 mm); AM LEN 63A: W Cape, Yserfontein. Coll: M. Hamer, July, 1990. 4 males (20.8 - 21.9 mm); 7 females (18.1 - 24.4 mm) (specimens used for Fig. 5d); AM LEN 65A: NW Cape, Taaiboskraal, SW of Springbok. Coll: J. Day, 26 August, 1982 (specimens in poor condition); AM LEN 66A NW Cape, Garies. Coll: J. Day, 22 August, 1983. 1 male (head broken); AM LEN 67A SW Cape, Piketburg mountains, 70 km E Saldanha Bay (raised from dried mud). Coll: J. Day, date unknown. 1 male (19.4 mm); SAM 1491: No locality or collection data. 2 males (22.2, 26.1 mm); 2 females (22.5, 24.2 mm) (specimens used for Figs 5a,g); ZMUO F. 19031: W. Cape, Cape Town, Green Point Common. Coll., date unknown. 1 male (10.0 mm) (specimen used for Figs 5b,c)

Redescription: Antenna short (ratio to body length $\pm 0.3:1$). Terminal joint of antenna slightly curved, broad, of average length, and tapering distally to a blunt point. S-shaped antennal process stout and naked (Fig. 5a). Thumb simple, long, broad at base but tapering to an apical point. Spur absent. Angle between proximal and distal parts of anterior part of thumb obtuse (130° - 140°) (Figs 5a,b). Finger weakly curved ventrally, with smooth dorsal margin, approximately half as long as thumb and apically subacute (Figs 5a,b). Tooth, variable in size and shape, situated between finger and thumb. In the Cape Flats (SAM uncat), SAM 1491 and Green Point Common (SAM 1478, ZMUO F.19031) specimens, tooth peg-like with small pointed projections (Figs 5a,c). Other specimens with broader, but less prominent tooth, lacking projections (Fig. 5d).

Frontal appendage short, broad and rounded, either apically indented (Fig. 5e) or pointed (Fig. 5f).

Cercopods slender and tapering, with tips curved outwards. Setae on proximal margins of average length. Distal two thirds lined with curved spines (Fig. 5g). Cercopods of Yserfontein (AM LEN 63A) specimens set with long setae up to the tips.

Distribution: Endemic to the western Cape region with winter rainfall, from the semi-arid north-western localities of Garies and Kamieskroon to the south western area of Cape Town (Fig. 2).

Remarks: BARNARD (1929) described the tooth between the finger and thumb as "more or less prominent digitiform" and illustrated it as large and obvious. The type and Cape Flats specimens conform to BARNARD's (1929) description, but those from the other localities have a much smaller tooth. In addition, the anterior region of the thumb of the Yserfontein specimens is shorter (Fig. 5d), and the cercopods also differ from the others. These differences are not correlated with age, since the Yserfontein specimens were large and mature. It is possible that two species are represented.

Streptocephalus dendyi BARNARD, 1929

(Fig. 6)

Streptocephalus dendyi BARNARD, 1929: 209, fig. 10.

Type material: SAM 6279. Collector: Dendy, 1903. 4 males (15.4 - 19.2 mm); 2 females (15.2, 19.4 mm) (specimens used for Figs 6d,e).

Type locality: SW. Cape, Cape Town, Camp Ground.

Other material examined: SAM A7287: SE Cape, Thornhill, near Port Elizabeth. Coll., date unknown. 9 males (17.1 - 21.8 mm); 6 females (16.8 - 21.2 mm) (specimens used for Figs 6a,b,f); AM LEN 64A: SW Cape, Agulhas region, Bredasdorp. Coll: M.Hamer, July 1990. 2 males (10.4, 8.8 mm); BMNH 1932.2.25.61-64: W. Cape, Cape Town, Rondebosch. Coll., date unknown. 1 male (19.0 mm) (specimen used for Fig. 6c).

Redescription: Antenna short (ratio to body length $\pm 0.27:1$). Terminal joint of antenna stout, short, and slightly curved, tapering to an apical point. S-shaped antennal process slender and naked (Fig. 6a). Thumb simple, broad, and apically pointed, bent approximately half-way along its length. Angle between proximal and distal parts of anterior region of thumb wide ($\pm 150^\circ$). Finger smooth, about four fifths length of thumb, tapered to a blunt apical point (Figs 6b,c). No process between finger and thumb. A low, obscure ridge (r) situated on base of hand (Figs 6b,c).

Frontal appendage short and apically rounded (Fig. 6d).

Telsonic segment with spinose processes on lateral margin (Fig. 6e).

Cercopods stout and tapered with distal half curved outwards. Proximal third of inner margin and tips set with spines. Remainder of cercopods with plumose setae (Fig. 6f). Both cercopodal margins of SAM 7287 specimens set with spines of irregular length up to the tips.

Distribution: Collected from the south-western Cape, Agulhas, and south-eastern Cape

regions only. In the more arid regions of the north-western Cape *S. dendyi* is replaced by *S. purcelli* (Fig. 2).

Remarks: The antenna with simple hand of *S. purcelli* is very similar to that of *S. dendyi*. However, the outgrowths on the telsonic segment and the shape and setation of the cercopods distinguish the two species. Furthermore, the tooth between the thumb and finger in *S. purcelli*, although sometimes reduced, is absent in *S. dendyi*.

Streptocephalus dregei SARS, 1899

(Fig. 7)

Streptocephalus dregei SARS, 1899: 19, pl. 2, figs 6-10 (male), pl. 18, figs 1-2 (female). - GURNEY, 1904: 298, pl. 18, figs 1, 2 (female). - STEBBING, 1910: 483. - DADAY, 1910: 377, fig. 4.

Type material: The type male specimen, SAM A1485, is housed in the SAM but is completely dried. The type female specimen is stored in the BMNH (catalogue no. unknown).

Type locality: No locality specified.

Other material examined: SAM A7597: E Cape, Uitenhage. Coll: Aitkinson, 1938. 18 males (20.6 ± 2.8 mm); 6 females (15.6 - 21.0 mm) (specimens used for Figs 7a,b,d,e); SAM uncat. No data. 2 males (16.8, 17.5 mm); 1 female (16.0 mm); AM AML 112A: E Cape, Somerset East, farm dam. Coll: J.C. Greig, 20 April, 1973. 3 males (17.5 - 18.0 mm); AM AML 212: E Cape, Grahamstown, near Carlisle Bridge, Sunnyside farm dam. Coll: P. Coetzee. 7 April, 1979. 2 males (19.1, 22.0 mm); AM AML 213: E Cape, Somerset East region, Swaershoek. Coll. unknown, 20 April, 1973. 3 males (22.0 - 22.3 mm); 2 females (20.8, 21.5 mm); ZMUH K19632: Port Elizabeth. Coll: J.L. Drège, 19 November, 1897. 1 male (29.0 mm) (specimen used for Fig. 7c).

The following specimens were all dehydrated and were too brittle for examination: SAM 7266 (Blaaukrantz, Kowie Road), SAM 6277 (Willowmore), and SAM A7294 (Kei Road).

Redescription: Antenna of moderate length (ratio to body length $\pm 0.33:1$). Terminal joint of antenna stout, slightly curved, of average length, and apically rounded (Fig. 7a). S-shaped antennal process with triangular flap (f) situated on medial surface proximal to hand (Figs 7b,c). Base of thumb folded medially and anterior margin protruded to form a sharp projection (Figs 7a,b,c). Anterior part of thumb slightly dorsally bent about halfway along its length, distally tapering to an acute apex. Angle between proximal and distal

parts of anterior region of thumb wide ($\pm 150^\circ$). Spur present, separated from anterior part of thumb by rounded tooth (Figs 7a,b,c). Finger broad, about half as long as thumb, apex blunt with ventrally protruded tip (Figs 7a,b,c). Dorsal margin of finger with proximal, short, digitiform tooth followed by a slight bulge (Figs 7b,c).

Frontal appendage, short, narrow and apically rounded with, in some cases, a median indentation. A small, narrow basal process (b.p.) present on either side of the frontal appendage on inner surface of basal joint (Fig. 7d).

Cercopods stout at base but distal half tapered. Outer margin convexly curved with long, plumose setae. Inner margin with proximal patch of long setae, followed by short, broad setae (Fig. 7e).

Spines present on hind margin of abdominal segments 2-7. Approximately eight spines present on the lateral margins of segments 3 and 4. Segments 5, 6 and 7, dorso-laterally set with more prominent spines. Segment 7 with 10-12 spines (Fig. 7f).

Distribution: *Streptocephalus dregei* occurs along the east coast of South Africa, in the area with summer rainfall, not further than 200 km inland and between 31 and 34 lines of latitude (Fig. 2). GURNEY's (1904) locality of Kroonstad in the Orange Free State, also mentioned in BARNARD (1929), is inaccurate. Material collected by Maj. E. Eckersley and identified by Gurney in 1904 as *S. dregei* was examined in the BMNH (BMNH 1904.9.21.114-18) and was found to belong to the closely related *S. cirratus* DADAY.

Streptocephalus cirratus DADAY, 1908

(Fig. 8)

Streptocephalus cirratus DADAY, 1908: 142, fig. 4. - DADAY, 1910: 358, fig. 67. - BARNARD, 1929: 216, fig. 15.

Type material: type specimens in the Paris Museum of Natural History (MNHN Bp. 215).

Collector: E. Simon, 1897. 4 males (14.8-16.9 mm).

Type locality: Orange Free State, Bloemfontein.

Other material examined: SAM A7260: Cape, Karoo, Potfontein. Coll: Miss Starke, 1927. 1 male (28.6 mm); SAM A7293: Transvaal, Rietfontein. Coll: Hutchinson, 1928. 2 males (12.0, 12.2 mm); 8 females (11.0 - 18.0 mm); SAM A7306: S Transvaal, Heidelberg. Coll: Schuurman, January, 1929. 2 males (20.0, 18.8 mm); 2 females (22.8, 23.2 mm) (specimens used for Fig. 8e); SAM A7601: Cape, Karoo, Williston. Coll. unknown, 1939. 1 male (21.0 mm); AM GEN 595D: Orange Free State, Dewetsdorp. Coll. unknown, 29 March, 1961. 6 males (12.5 - 13.8 mm); 2 females (13.0, 14.5 mm) (specimens used for

Figs 8a,b,d); MNHSI cat 75741: locality, collector and date unknown. 1 male (16.0 mm) (specimen used for Fig. 8c).

Redescription: Antenna about one third of total body length (ratio: $\pm 0.36:1$). Terminal joint of antenna short and stout, slightly curved and apically rounded. S-shaped antennal process slender and naked (Fig. 8a). Base of thumb folded medially with anterior margin protruded to form a short projection. Anterior part of thumb short, broad, and with a strong ventral bend about halfway along its length. Distal region tapering to acute apex. Angle between proximal and distal parts of anterior region of thumb 230° - 250° (Figs 8a,b). Spur short, broad and ventrally curved and separated from anterior part of thumb by rounded tooth (Figs 8a,b,c). Finger broad and short with rounded and slightly indented apex (Figs 8b,c). Anterior finger margin unarmed, but a low bulge present about halfway along its length (Fig. 8b).

Frontal appendage short, narrow and apically bifid with narrow, bifid basal processes (b.p.) present at each side on inner surface of basal joint of antenna (Fig. 8d).

Cercopods slender with strongly convex outer margin set with plumose setae. Inner margin with a proximal patch of plumose setae, followed by short, thick setae of irregular length (Fig. 8e).

Spines present on hind margin of abdominal segments 5-7 (Fig. 8f).

Distribution: *Streptocephalus cirratus* occurs in the central, Highveld region of South Africa (Fig. 2).

Remarks: *S. dregei* and *S. cirratus* share a number of characteristics such as the abdominal spines, the pattern of cercopod setation, the short thumb, apically blunt finger, and the flaps on either side of the frontal appendage. These characters indicate closely related species. However, in *S. cirratus*, the basal flaps as well as the abdominal spines are more prominent than in *S. dregei*. In addition, a triangular process proximal to the hand and a distinct tooth on the dorsal margin of the finger are present in *S. dregei* but not in *S. cirratus*.

Streptocephalus cafer (LOVÉN, 1847)

(Fig. 9)

Branchipus cafer LOVÉN, 1847: 433, pl. 5, figs 1-20. - *Branchipus (Streptocephalus) caffer* BRAUER, 1877: 605. - *Streptocephalus propinquus* BRADY, 1913: 470, pl. 38, figs 2-6. - *Streptocephalus cafer* BAIRD, 1852: 21. - STEBBING, 1910: 482. - DADAY, 1910:

392, fig. 79. - BARNARD, 1924: 220. - BARNARD, 1929: 212, fig. 13. - RAYNER & BOWLAND, 1985: 11, fig. 5.

Type material: Type material in Stockholm Museum.

Type locality: Type locality cited in BARNARD (1929) as lat. 26.1/2° S; 29°E (Southern Transvaal).

Material examined: SAM A11595: N Cape, Kimberley. Coll. unknown, February, 1932. 3 males (13.2 - 15.1 mm); 1 female (14.5 mm); AM 4: Zimbabwe, farm dam near Kwekwe. Coll. unknown, January, 1951. 8 males (17.5 - 20.3 mm); 7 females (15.6 - 23.1 mm); AM LEN 68A: NE Natal, Makatini Flats. Coll: M. Hamer, October, 1987. 6 males (15.2 - 21.0 mm); 2 females (18.1, 19.0 mm); AM LEN 69A-75A: E Transvaal, Mala Mala Game Reserve. Coll: W.A. Taylor, June, 1989. 10 males (13.1 -14.9 mm); 10 females (9.8 - 14.9 mm); AM LEN 76A: N Transvaal, Naboomspruit, temporary pool in sandstone rock outcrop. Coll: R. Nanni, 18 March, 1989. 2 males (22.5, 25.0 mm); 4 females (22.0 - 23.0 mm) (specimens used for Fig. 9d); AM LEN 77A: Namibia, 65 km S Mariental. Coll: O. Wirminghaus, 7 April, 1990. 2 males (21.9, 25.0 mm); 2 females (23.4, 24.4 mm) (specimens used for Figs 9a,b,e,f); AM LEN 78A: E Transvaal, Kruger National Park, Skukuza area. Coll: M. Hamer, 25 October, 1990. 12 males (13.4 \pm 1.2 mm); 6 females (13.0 - 15.1 mm); AM LEN 79A: Cape, Karoo, 10km S Carnavon. Coll: M. Hamer, 16 February, 1990. 15 males (13.5 \pm 0.7 mm); 11 females (14.1 \pm 1.1 mm); HNHM I/A-114: Kalahari. 1 male (8.0 mm) (specimen used for Fig. 9c).

Redescription: Antenna of average length (ratio to body length \pm 0.33:1). Terminal joint of antenna recurved and slender, of average length and apically subacute. S-shaped antennal process (Fig. 9a) with large, triangular membranous flap (f) on medial side slightly distal to insertion of terminal joint of antenna (Fig. 9b). Middle part of S-shaped antennal process set anteriorly with similarly-shaped (1 large and 3-6 small) processes (Fig. 9b). Base of thumb folded medially with anterior margin produced to form a projection. Anterior part of thumb geniculate and inflated at bend, distally tapering to an acute point. Angle between proximal and distal parts of thumb 110°-120°. Spur present, separated from anterior part of thumb by small triangular tooth (Fig. 9b). Finger geniculate and apically tapering, about as long as thumb (Figs 9a,b). Anterior margin of finger with proximal ridge ending in a small peak-like tooth, followed by flattened, oval (in dorsal view) and low, distally rounded (in medial view) tooth (Figs 9b,c).

Frontal appendage of moderate length, usually apically bifid (Fig. 9d). In some cases a third, median, shorter process present (Fig. 9e). Two membranous, roughly triangular basal processes (b.p.) with coarse serrations present slightly ventrally on inner side of

basal joint of antenna (Figs 9d,e).

Cercopods stout, tapering, of average length, and with slightly convex outer margin. Plumose setae present on both margins. Dorsal surface of distal third of cercopods set with a row of 8-10 upstanding spines (Fig. 9f).

Distribution: *Streptocephalus cafer*, as stated by BARNARD (1929), is the most widely distributed *Streptocephalus* species in southern Africa (Fig. 3).

Remarks: Some variation was observed in the size of the peak-like tooth on the ridge on the dorsal margin of the finger. In the Makatini specimens (AM LEN 68A) it is small, while in the Mariental specimens (AM LEN 77A) it is distinct and sharp. There is, however, a continuous gradation between these two extremes.

Streptocephalus indistinctus BARNARD, 1924

(Fig. 10)

Streptocephalus indistinctus BARNARD, 1924: 221. - BARNARD, 1929: 217, fig. 6. - BREHM, 1958: 13.

Type material: Type material housed in the SAM (SAM A6692). Collector: K.H. Barnard, 1923. 2 males (21.3, 23.9 mm); 2 females (14.2, 17.0 mm) (specimens used for Figs 10a,b,e).

Type locality: Namibia, Ovamboland, Ongka.

Other material examined: SAM A6696: Namibia, Onambeke. Coll: K.H. Barnard, 1923. 19 males (14.2 ± 0.8 mm); 2 females (13.9, 14.8 mm); SAM A6695: Namibia, Onolongo. Coll: K.H. Barnard, 1923. 3 males (14.0 - 15.3 mm); 5 females (14.2 - 17.0 mm); SAM 5918: Transvaal/Botswana border, Junction of Crocodile and Marico Rivers. Coll: R.W. Tucker, 1918. 8 males (12.5 - 13.5 mm); 7 females (specimens brittle, only 2 measured, 11.8, 12.0 mm) ; SAM A6693: Namibia, Umtekwa. Coll: K.H. Barnard, 1923. 1 male (10.0 mm); 1 female (9.8 mm); ZNM/Cr 25: Zimbabwe, Kazuma Depression (1825B3). Coll: NHMZ/ Falcon College Expedition, 12 April, 1988. 3 males (21.3 - 22.1 mm) (specimens used for Fig. 10d); BMNH 1932.2.25.11-119: Namibia, Ovamboland. 1 male (13.0 mm) (specimen used for Fig. 10c).

Redescription: Antenna of moderate length (ratio to body length: $\pm 0.34:1$). Terminal joint of antenna curved, short and tapering to a subacute apical point (Fig. 10a). S-shaped antennal process with large membranous flap (f) and triangular outgrowths situated

medially, distal to the insertion of terminal joint of antenna (Fig. 10b). Large triangular outgrowth at base of hand, followed by a series of smaller ones (Fig. 10b). Base of thumb medially folded with fold produced to a blunt projection. Anterior part of thumb of moderate length, geniculate, and tapering distal to the bend. Angle between proximal and distal parts of anterior region of thumb 110° - 120° . Spur present, separated from anterior part of thumb either by a triangular (Figs 10a,b,c) or by a rounded tooth (ZNM/Cr 25). Finger stout, geniculate, almost as long as thumb, and tapering apically. Dorsal surface of finger set with low, flat tooth, followed by a blunt, anteriorly-directed digitiform tooth (Figs 10 b,c).

Frontal appendage short and rectangular with rounded corners and a small indentation at the apex (Fig. 10d).

Cercopods of moderate length, almost straight and margins set with long plumose setae along entire length (Fig. 10e).

Distribution: *Streptocephalus indistinctus* appears to be concentrated north of 29° . The single Zimbabwean locality, the localities at the Transvaal/Botswana border and in Bloemfontein (see SEAMAN et al., 1991) and Kakamas (see BREHM, 1958), however, indicate a wider distribution than known to date (Fig. 3).

Remarks: BARNARD (1929) stated that *S. indistinctus* is closely related to *S. distinctus* THIELE, which occurs in Madagascar. Although there are similarities between the hand region of these two species, *S. indistinctus* seems more closely related to *S. cafer*; both species have similar processes on the medial side of the S-shaped antennal process and a similarly-shaped thumb and finger.

Streptocephalus macrourus DADAY, 1908.

(Fig. 11)

Streptocephalus macrourus DADAY, 1908: 143, fig. 5. - DADAY, 1910: 383, fig. 76. - BARNARD, 1924: 219. - BARNARD, 1929: 220, fig. 18. - BARNARD, 1935: 487, fig. 2.

Type material: Male type specimen (20.0 mm) housed in the Paris Museum (MNHN Bp. 222). Female specimen supposedly housed in the SAM but could not be located.

Type locality: Bloemfontein, Orange Free State, South Africa.

Other material examined: SAM A3781: N Cape, Kimberley. Coll: J.H. Power, 1916. 6 males (25.0 - 28.2 mm); 1 female (24.3 mm) (specimens used for Figs 11a,c); SAM A7298: S. Transvaal, Brakpan. Coll: G.H. Hutchinson, 1928. 4 males (18.0 - 20.5 mm);

9 females (17.1 - 20.5 mm) (specimens used for Fig. 11d); SAM A5916: Transvaal/Botswana border, Junction of Crocodile and Marico Rivers. Coll: R.W. Tucker, 1902. 8 males (14.8 - 19.1 mm); TM VLKE 1256: Botswana, N. of Tsotsoroga. Coll: Vernay Lang Kalahari Expedition, 2 July, 1930. Large number of specimens, in poor condition; BMNH 1932.2.25: Namibia, Ovamboland. 1 male (20.0 mm) (specimen used for Fig. 11b).

Redescription: Antenna of moderate length (ratio to body length: $\pm 0.34:1$). Terminal joint of antenna curved, short, and tapering towards the apex (Fig. 11a). Base of thumb folded medially with fold produced to form large pointed projection (Figs 11a,b). Anterior part of thumb long, geniculate and tapering distally to an acute point. Angle between proximal and distal parts of anterior thumb region about 130° - 140° (Fig. 11a). Spur narrow and separated from anterior part of thumb by two, or occasionally three (see BARNARD, 1924) rounded teeth (Fig. 11a). Finger, dorsally curved, about half the length of thumb and with broad and ventrally curved tip. Proximal part of finger with broad, flattened, oval tooth, on which a smaller tooth is situated medially (Fig. 11b).

Frontal appendage narrow, apically rounded and of average length (Fig. 11c).

Cercopods, long (length in relation to body length $\pm 0.30:1$) and slender. First half with convex outer margin, second half concave. First half of inner margin set with plumose setae, distally replaced by short spines of irregular length. Outer margins with plumose setae (Fig. 11d).

Distribution: BARNARD (1929) stated that *S. macrourus* was collected from numerous places in Ovamboland, northern Namibia, but the exact localities are not specified. Additional records include localities in the Transvaal Highveld, Orange Free State and the Kalahari (Fig. 3).

Remarks: The small medial process on the tooth of the finger was not noted by DADAY (1910) nor BARNARD (1929), although this structure is present on all BARNARD's material as well as the type specimen.

BARNARD (1929) observed the similarity between *S. macrourus* and *S. vitreus* BRAUER which occurs in Sudan, Kenya and Zimbabwe. Both species have two rounded teeth separating the anterior part of the thumb from the spur, while thumb and finger are almost identical in shape. The two species differ mainly in the teeth on the dorsal margin of the finger (two or three digitiform teeth in *S. vitreus*) and the setation of the cercopods (*S. vitreus* has plumose setae along the entire length of both margins).

Streptocephalus ovamboensis BARNARD, 1924

(Fig. 12)

Streptocephalus ovamboensis BARNARD, 1924: 220. - BARNARD, 1929: 219, fig. 17. - BREHM, 1958: 14, figs 7-9.

Type material: Type specimens curated in the SAM (SAM A6691). Collector: K.H. Barnard, 1923. 4 males (19.0 - 20.8 mm); 4 females (18.8 - 19.5 mm) (specimens used for Figs 12f,g).

Type locality: Namibia, Ovamboland, Ukualonkathi.

Other material examined: SAM 7594: SE Cape, Oudshoorn. Coll. unknown, August, 1934. 3 males (34.2 - 38.7 mm); 2 females (34.0 - 37.5 mm) (specimens used for Figs 12a,c); SAM A2636: Cape, Karoo, Hanover. Coll., date unknown. 15 males (13.2 ± 1.1 mm); 14 females (12.7 ± 0.7 mm); SAM A6288: N Cape, Gordonia. Coll: Dr. W.M. Borchards, 1909. 9 males (13.8 - 17.4 mm); 1 female (11.1 mm); AM AML 110A: SE Cape, Graaff-Reinet. Coll., date unknown. 55 males (20.6 ± 1.4 mm); 15 females (19.0 ± 1.8 mm); SMN 51318: Namibia, Tstumkwe, rainwater pool outside guest house. Coll: B.A. Curtis, 13 March, 1988. 1 male (12.8 mm); 3 females (15.6 - 16.5 mm); SMN 51339: Namibia, Bushmanland, Maltahöhe, rainwater pool. Coll: B. A. Curtis, 12 March, 1988. 3 males (14.0 - 16.5 mm); 8 females 15.8 - 18.4 mm); AM LEN 77B: Namibia, 65km S Mariental. Coll: O. Wirminghaus, 7 April, 1990. 2 males (23.5, 24.2 mm); 7 females (21.9 - 26.5 mm); AM LEN 80A: N Cape, 4km E Groblershoop. Coll: O. Wirminghaus, April, 1990. 14 males (18.0 ± 1.1 mm); 12 females (17.0 ± 1.5 mm) (specimens used for Figs 12b,d,e); AM LEN 220A: Namibia, Namib desert, Naukluft mountains, 150 km ESE Gobabeb. Coll: Dr. J. Day, 20 December, 1979, 2 males (19.4, 17.8 mm) (lab cultured).

Redescription: Antenna long (ratio to body length $\pm 0.42:1$). Terminal joint of antenna curved, of average length, and apically subacute (Fig. 12a). S-shaped antennal process with 3-4 digitiform projections anteriorly on the basal part (Fig. 12a), followed by a medial row of 8-10 triangular projections on the middle part (Figs 12b,c) and a larger projection proximal to hand (Fig. 12c). Base of thumb folded medially, with spur-like projection on anterior margin (Figs 12c,d). Distal part of thumb with inflation at about one third along length, distal to which thumb curves dorsally and tapers to a subacute point. Single row of similarly-sized and almost evenly-spaced spines present distal to curve of thumb. Angle between proximal and distal parts of anterior region of thumb narrow (100° to 120°) (Figs 12c,d). Spur present, distally flattened and foot-shaped (Fig. 12c). A long, narrow, apically rounded tooth present between anterior part of thumb and spur (Figs 12a,c). Finger broad

and slightly ventrally curved, distally tapering to acute point, and measuring about half the length of thumb (Figs 12a,c,d). Proximal region of finger flattened anteriorly with prominent, flat, tongue-shaped tooth (Figs 12a,e).

Frontal appendage of moderate length, rectangular, and with slight apical indentation (Fig. 12f).

Cercopods stout, outwardly directed and of moderate length, with straight outer margins. Both inner and outer margins set with long plumose setae along entire length (Fig. 12g).

Distribution: *Streptocephalus ovamboensis* is widespread in the arid north-western regions of the Cape Province and in Namibia. BREHM (1958) provided an additional record of this species from a locality north-west of Upington (Fig. 3).

Remarks: BARNARD (1929) noted the similarity between *S. ovamboensis* and the northern African species *S. torvicornis* WAGA (*S. t. torvicornis* and *S. t. bucheti*). *Streptocephalus rubricaudatus* (KLUNZINGER), a north-eastern African species, also seems to be closely related to the above species and has, as in *S. ovamboensis*, lobe-like processes on the dorsal surface of the S-shaped antennal process, a long, curved, spinous thumb, and a similarly-shaped finger.

Streptocephalus gracilis SARS, 1898

(Fig. 13)

Streptocephalus gracilis SARS, 1898a: 17, pl. 2. - STEBBING, 1910: 483. - DADAY, 1910: 352, fig. 65. - BARNARD, 1929: 222, fig. 19.

Type material: One male specimen "raised from dried mud". Type specimen (SAM 1487), completely dehydrated and too brittle to examine.

Type locality: Port Elizabeth.

Material examined: BMNH 1901.12.12.242-243: E Cape, Port Elizabeth. Coll: G.O. Sars, date unknown. 1 male (10.8 mm); 1 female (11.2 mm) (specimens used for Figs 13b,e,f,g); ZMUO F.19032: W. Cape, Cape Town, Green Point Common. Coll., date unknown. 1 male (16.0 mm); 1 female (14.0 mm) (specimens used for Figs 13a,b,c).

Redescription: Antenna long (ratio to body length: $\pm 0.59:1$) and slender. Terminal joint of antenna short, stout, curved and apically rounded (Fig. 13a). S-shaped antennal process with three to four projections on middle part, small and conical in the ZMUO specimens

(Fig. 13a), but large, slender and with irregular lateral margins in the BMNH specimens (Fig. 13b). Base of anterior region of thumb folded, with this fold produced to form a short, prominent projection, with a straight dorsal margin in the ZMUO specimens (Fig. 13c), but with a scalloped margin in the BMNH specimen (Fig. 13e). Distal part of thumb long, curved dorsally and tapering to a subacute apex. Distal part of thumb of BMNH specimen with a slightly crenulate upper margin and a few small, scattered papillae along its length (Fig. 13e). A short process (spur) present on posterior thumb side (Figs 13a,d). Finger broad at base, curved and tapering. Posterior margin of finger with a short, broad process (spur), and with smooth anterior margin (Figs 13a,d).

Short frontal appendage with rounded appearance (Fig. 13f).

Cercopods short, stout and straight, and set with plumose setae along both margins. Distal quarter of inner margin with shorter, spiniform setae (Fig. 13g).

Numerous small spiniform papillae on the dorso-lateral surface of abdominal segments (Fig. 13h).

Distribution: *Streptocephalus gracilis* is probably restricted to the bimodal and winter rainfall areas of the southern and south-western Cape respectively, since specimens have only been collected from Port Elizabeth and Cape Town (Fig. 4).

Remarks: The variability in the morphology of the male antennas of the two specimens examined may indicate separate species. However, additional material is required to draw final conclusions.

Streptocephalus papillatus SARS, 1905

(Fig. 14)

Streptocephalus papillatus SARS, 1905: 4, pl. 1. - STEBBING, 1910: 483. - DADAY, 1910: 343, fig. 61. - BARNARD, 1924: 218. - BARNARD, 1929: 211, fig. 12.

Type material: Type specimens in the collection of G.O. Sars (BARNARD, 1929).

Type locality: Hanover, Cape Province.

Material examined: SAM A7602: Cape, Karoo, Williston. Coll. unknown, 1939. 18 males (19.3 ± 2.3 mm) (specimens used for Figs 14a-d); SAM A5917: Cape, Karoo, Beaufort West division, Hoogeveld. Coll: S.H. Houghton, August, 1917. 3 males (20.5 - 21.4 mm); SAM A6704: Cape, Namaqualand, Kalkfontein South. Coll: J.S. Brown, 1923. 15 males (22.7 ± 1.4 mm); 14 females (19.7 ± 1.6 mm).

Redescription: Antenna long (ratio to body length $\pm 0.71:1$). Terminal joint of antenna short and stout, strongly curved, and with a rounded apex (Fig. 14a). S-shaped antennal process slender with numerous irregular narrow and apically pointed processes along the posterior margin of middle part. Anterior margin of first bend set with 4-5 larger processes mixed with smaller ones (Fig. 14a). Thumb, long and distally recurved, with short, broad base, and narrow, apically pointed anterior process. Thumb triangular in cross section, with a row of digitiform processes on the anterior edge and a row of small papillae at each side (Fig. 15a). Some of the longer processes with short lateral branches or apically bifurcate. Thumb apically tapering and subacute (Fig. 14a). Finger about two thirds of length of thumb and similarly curved. A narrow bifurcate process present on posterior margin. Distal two thirds of finger triangular in cross section, with a single row of long digitiform processes and a series of smaller papillae along its length (Fig. 14a).

Short frontal appendage with rounded appearance, apically bilobed (Fig. 14b).

Cercopods short and stout, with distal third strongly curved inwards. Long, plumose setae present on first two thirds of outer margin, followed by widely spaced, stout, curved setae decreasing in size towards the apex. First third of inner margin set with plumose setae, followed by thick, curved setae with setulose dorsal apices. Distal third of inner margin without setae, but very short spines on dorsal surface of cercopods in this region (Fig. 14c).

Lateral margins of abdominal segments 3-7 covered with digitiform processes of various lengths, decreasing in density on the seventh segment. Sixth segment dorso-medially with large, bifid process with inwardly curved branches (a.p.) (Fig. 14d). Segment 7 with a smaller, unbranched process.

Distribution: *S. papillatus* appears to be confined to the arid northern Cape and Karoo regions of South Africa (Fig. 4).

Remarks: Although *S. papillatus* has a very exclusive appearance, it does share some characteristics with *S. gracilis*, such as the presence of processes on the first bend of the S-shaped antennal process, the shape of hand and thumb, the absence of a typical spur and of teeth on the anterior finger margin, the presence of a ventral spur on the finger and the presence of abdominal protuberances.

Streptocephalus (Parastreptocephalus) kaokoensis BARNARD, 1929

(Fig. 15)

Streptocephalus kaokoensis BARNARD, 1929: 210, fig.11. - *Streptocephalus (Parastreptocephalus) kaokoensis* BRENDONCK et al. 1992: 291, figs 7,8.

Type material: Specimens supposedly housed in the SAM, however, we have been unable to locate these specimens.

Type locality: Kaokoveld, N of Kamanyab (BARNARD, 1929).

Material examined: BMNH 1932.2.25.65-74: Namibia, Kaokoveld. Dissected antenna of male, 1 male (6.0 mm), 1 female (5.5 mm) (specimens used for Figs 15a-d).

Remark: *Streptocephalus (P.) kaokoensis* was recently redescribed (see BRENDONCK et al., 1992) and for this reason, only the illustrations and an abbreviated diagnosis are presented here.

Abbreviated diagnosis.- Cercopods lanceolate and setiferous up to the tips (Fig. 15d). Teeth lacking completely on anterior side of finger of male antenna (Fig. 15b). Small spines present on anterior side of finger, on the base of distal part and spur of thumb (Figs 15b,c.). Frontal appendage conical.

Distribution: *Streptocephalus (P.) kaokoensis* has only been recorded from one locality in Kaokoveld (northern Namibia) (Fig. 4).

Streptocephalus (Parastreptocephalus) zuluensis BRENDONCK and HAMER, 1992

(Fig. 16)

Streptocephalus (Parastreptocephalus) zuluensis BRENDONCK et al. 1992: 287, figs 5,6.

Type material: Type specimens housed in the AM (catalogue no. MLH 17A). Holotype consists of male specimen with head removed and dissected thoracopods mounted in glycerine on a sealed slide. Allotype: 1 female (AM MLH 17B).

Type locality: Temporary pool on the Makatini Flats, north-eastern Natal (Zululand).

Material examined: AM MLH 18 (paratypes): NE Natal, Makatini Flats. Coll: M. Hamer, October, 1987. 6 males (12.3 - 13.8 mm); 5 females (12.9 - 15.0 mm) (specimens used for Figs 16a-f).

Remark: Since *S. (P.) zuluensis* was recently described (see BRENDONCK et al., 1992),

only illustrations of antenna, frontal process and cercopods and an abbreviated diagnosis are presented here (Figs 16 a-f).

Abbreviated diagnosis: Thumb folded medially at base and bifurcate with very long anterior part and shorter, posteriorly projecting and slightly dorsally curved spur (Figs 16a,b). On dorsal (anterior) side, middle part of thumb forming a wide angle ($> 120^\circ$) with distal part, with acute heel showing a spinous projection at the bend. Distal part of anterior end acute and slightly curved. Finger with two strongly developed and irregularly rectangular teeth along the proximal anterior margin (Figs 16b,c). Minute spines on anterior side of finger (Figs 16b,d). Apical part of finger ventrally recurved. Frontal appendage conical (Fig. 16e).

Distribution: *Streptocephalus (P.) zuluensis* has a localized distribution, with records from only three pools on the Makatini Flats (north-eastern Natal) (Fig. 4).

Remarks: *S. (P.) zuluensis* shares a number of characteristics with three other African species, namely *S. (P.) sudanicus*, *S. (P.) lamellifer*, and *S. (P.) kaokoensis*. The similarities between these species and their taxonomic status are discussed in BRENDONCK et al. (1992).

Streptocephalus trifidus HARTLAND-ROWE, 1969

(Fig. 17)

Streptocephalus trifidus HARTLAND-ROWE, 1969: 78, figs 1-3.

Type material: Coll: J.S. Weir, January, 1959 (Holotype male). Paratype material includes 4 males and 4 females from the same locality, as well as two other collections from pools in Wankie (=Hwange) Game Reserve and a collection from a borrow pit in Salisbury (=Harare) in Zimbabwe (December, 1933). All these specimens are housed in the BMNH (HARTLAND-ROWE, 1969).

Type locality: Wankie (=Hwange) National Park, Zimbabwe.

Material examined: BMNH 1969.1.2.2-4: Zimbabwe (Rhodesia), Hwange (Wankie) Game Reserve (Paratypes). 1 male (20.0 mm) (specimen used for Figs 17a,b,c,e); ZNM/Cr 31: Zimbabwe, Lake MacIllwaine, Tiger Bay. Coll. unknown, 28 February, 1976. 5 males (23.2 - 25.5 mm); 3 females (22.0 - 23.1 mm) (specimens used for Fig. 17e); ZNM/Cr 32: Zimbabwe, Lake MacIllwaine, Tiger Bay. Coll. unknown, 28 February, 1976. 1 male (24.5 mm); 4 females (23.0 - 24.5 mm); SAM uncat.: Zimbabwe, Bulawayo, Plumtree. Coll: Eccles, 1954. 1 male (29.5 mm).

Redescription: Antenna of average length (ratio to body length: $\pm 0.34:1$). Terminal joint of antenna slightly curved, of average length, and tapering to a subacute apex (Fig. 17a). S-shaped antennal process (Fig. 17a) with a row of approximately 10-15 digitiform processes on medial surface, proximal to hand (Figs 17b,c). Base of thumb folded medially with proximal rectangular process at base of slightly produced fold (Figs 17b,c). Anterior part of thumb of moderate length, strong dorsal bend about halfway along length, distal to which thumb acutely tapered. Distinct posterior inflation at bend. Angle between proximal and distal parts of anterior region of thumb measuring 110° - 120° . Spur long, slender and separated from anterior part of thumb by small triangular tooth (Figs 17a,b,c). Finger recurved, tapering and reaching up to bend of thumb. Two teeth present on anterior margin of finger; proximal tooth large, angular and folded; distal tooth digitiform, and apically directed (Figs 17a,b,c).

Frontal appendage long (about half the length of the antenna) and trifid. Medial branch shorter and narrower than the two lateral branches. All three branches with dorsal, slightly crenulate ridge (Figs 17a,d).

Cercopods of average length. First two thirds of both margins with plumose setae; distal third of outer margin with widely set spines, inner margin naked (Fig. 17e).

Distribution: *Streptocephalus trifidus* has, to date, been recorded from Zimbabwe only (Fig. 4).

Remarks: HARTLAND-ROWE (1969) stated that *S. trifidus* can be distinguished from all other species of the genus by the frontal appendage, and in particular by its median branch. He stated that it has this feature in common with the west and central African species *S. zeltneri*, but in *S. trifidus* the median branch is about half the length of the lateral branches, while in *S. zeltneri* it measures only a quarter of this length. No median branch was seen on the *S. zeltneri* specimens examined, nor was this structure illustrated in the original description of the species by DADAY (1910). In addition to the difference in frontal appendages, *S. trifidus* has two teeth on the finger and an elongate spur, while *S. zeltneri* has a single tooth on the finger and a very short thumb spur.

Streptocephalus proboscideus (FRAUENFELD, 1873)

(Fig. 18)

Branchipus (Streptocephalus) proboscideus FRAUENFELD, 1873: 189. - BRAUER, 1877: 602, pl. 6, figs 13, 14. - *Streptocephalus proboscideus* DADAY, 1910: 395, fig. 80. - PESTA, 1921: 96. - BARNARD, 1924: 221. - BARNARD, 1929: 223, fig.20. -

BRENDONCK, 1990: 49, figs 1-3.

Type material: Type specimens housed in the Museum of Natural History, Vienna.

Type locality: Sudan, Khartoum.

Material examined: SAM A6007: Namibia, Ovamboland, Onambeke. Coll. K.H. Barnard, 1926. 8 males (15.9 - 17.1 mm). SAM A3777: Border Botswana and South Africa, Molopopo River. Coll. Marawat, 1915. 4 males (19.0 - 20.5 mm); 5 females (17.2 - 19.0 mm); SAM uncat: Namibia, 11km from Okaukuejo. Coll. unknown, 11 March, 1976. Very large number of specimens. 20 males measured (14.2 ± 1.9 mm); 21 females measured (15.7 ± 3.4 mm) (Figs 18a,c,e from these specimens). SMN 51327: Namibia, Bushmanland, Gautscha Pan. Coll. B.A. Curtis, 17 March, 1988. 1 mature male (15.0 mm); 1 mature female (16.3 mm); SMN 51337: Namibia, Etosha National Park, Fisher's Pan. Coll. R. Jessnitz, 11 June, 1986. 4 males (15.0 - 15.8 mm); AM SWA 74A, 84D, 84E: Namibia, Nyai-Nyai pan near Tsumkwe (1500m). Raised from dried mud sample. Coll: F.M. Chutter, 19 August, 1962. 6 males (10.3 - 19.3 mm); 4 females (9.3 - 11.3 mm). BMNH 1932.25.151-155: N Cape, Achabdam. Coll., date unknown. 1 male (36.0 mm) (specimen used for Figs 18b,d). AM LEN 102A: Cape, 110 km NW Upington, Abiekwasputs. Raised from dry mud. Coll: J. Day, 11 December, 1979. 1 male (14.0 mm).

Remark: Since *S. proboscideus* was recently redescribed (see BRENDONCK, 1990), only illustrations of the antenna, frontal appendage and cercopods and an abbreviated diagnosis are presented here (Figs 18a-e).

Abbreviated diagnosis: Male frontal appendage very long, rolled up ventrally between antennae and with bifid apex (Fig. 18a). S-shaped part of male antenna with numerous digitiform processes at first bend, and large triangular process distal to hand (Figs 18a,b,c). Two broad, digitiform teeth on anterior margin of finger (Fig. 18d). Truncal and abdominal segments smooth. Brood pouch reaching last abdominal segment in full grown females. Cercopods setiferous up to the tips (Fig. 18e).

Distribution: *Streptocephalus proboscideus* is restricted to the arid and semi-arid regions of Namibia and the northern Cape. This is the only streptocephalid occurring in southern Africa with extensions as far north as Egypt/Sudan (Fig. 4).

Remark: The presence of processes on the medial surface of the S-shaped antennal process and the teeth on the finger may indicate a relationship between *S. trifidus* and *S.*

proboscideus.

Streptocephalus cladophorus BARNARD, 1924

(Fig. 19)

Streptocephalus cladophorus BARNARD, 1924: 222. - BARNARD, 1929: 225, fig. 21.

Type material: Type specimens housed in the SAM (SAM A6702). Collector: K.H. Barnard, 1923. 14 males (11.7 ± 1.6 mm); 14 females (11.4 ± 1.5 mm).

Type locality: Namibia, Ovamboland, Owuthija.

Other material examined: SAM A6703: Namibia, Ukualonkathi. Coll: K.H. Barnard, 1923. 3 males (15.1 - 19.2 mm); 3 females (12.3 - 20.0 mm); SAM A6701: Namibia, Onambeke. Coll: K.H. Barnard, 1923. 14 males (11.2 ± 1.4 mm); 12 females (10.3 ± 1.1 mm) (specimens used for Fig. 19b); SAM 5935: Cape, Vryburg. Coll: J.S. Brown, 1918. 9 males (13.0 - 16.2 mm); 6 females (10.0 - 13.9 mm) (specimens used for Figs 19a,c-e); SAM A7307: S Transvaal, Heidelberg. Coll: Miss Schuurmann, date unknown. 4 males (12.2 - 14.2 mm); 3 females (12.6 - 13.9 mm); SAM 6698: Namibia: Ovamboland, Ondongua. Coll. K.H. Barnard, 1921. 10 males (10.1 ± 0.9 mm); 15 females (11.4 ± 3.3 mm); SAM 6699: Namibia: Eunda, Coll. K.H. Barnard, 1921, 2 males (11.9 , 12.5 mm); 2 females (11.4, 11.0 mm); ZNM Cr/25: Zimbabwe, Kazuma Depression. Coll: NHMZ Expedition, 12 April, 1988. 6 males (16.9 - 18.8 mm); MNHSI cat. 75741: Namibia, Ovamboland. 1 male (16.0 mm) (specimen used for Figs 19d,f).

Redescription: Antenna long (ratio to body length $\pm 0.4:1$). Terminal joint of antenna slightly curved, of average length and with a blunt apex. S-shaped antennal process slender (Fig. 19a). A small, triangular (Namibia, Fig. 19b) or long and bifid (Transvaal and Zimbabwe specimens, Fig. 19c) projection ventro-medially at the base of each antenna. Basal part of antenna with two to three small papillae on medial surface (Fig. 19d). Thumb folded medially at base, ventral margin of anterior part notched about halfway along the length and distally tapering (Fig. 19e). Angle between proximal and distal regions of anterior part of thumb wide (180°). Thumb spur ventrally curved, broad, and tapering. Acute angle between anterior part of thumb and spur (Figs 19a,d). Finger long (about two thirds the length of thumb), slender and tapering (Figs 19d,e). Small rounded tooth on anterior margin at base of finger (Fig. 19e). Some specimens with two teeth (Fig. 19d,f), the proximal tooth consistently larger and roughly triangular, and distal one slender and

digitiform in appearance.

Frontal appendage elaborate, about one third the length of the body (but shorter in the Zimbabwe and Transvaal specimens). Two lateral branches (1VL/VL) and a third, apically bifurcate one (1A) branching off proximal part (trunk). Ventral margin of trunk with long, slender projections, also present in decreasing length along each of the branches. Apical processes occurring in all planes (Fig. 19a).

Cercopods stout and straight, of moderate length (ratio to body length $\pm 0.17:1$), and with long plumose setae along both margins (Fig. 19g).

Distribution: *Streptocephalus cladophorus* is widely distributed in northern Namibia with additional populations between 26° and 27°S in the Transvaal, North-western Cape and one locality in Zimbabwe (Fig. 4).

Remarks: BARNARD (1929) noted the presence of a second tooth on the dorsal margin of the finger, and although it is absent in the type specimens, it is present on some other material examined by him. The variation in the teeth on the finger, the shape of the basal process and the length of the frontal appendage may indicate different species. The Namibian specimens all have long frontal appendages and conical basal processes, and the Zimbabwean and Transvaal specimens have short frontal appendages and bifid basal processes. The presence of a second tooth on the finger, however, is a character present in some populations of both groups. A more detailed investigation is necessary to determine whether intraspecific variation or separate species are involved.

The unique appearance of the hand region of *S. cladophorus* separates it from all other streptocephalids, even those with elaborate frontal appendages.

Additional remarks:

Besides the above species, a species from the region north of the Zambezi and Kunene Rivers occurs in southern Africa:

Streptocephalus vitreus (BRAUER, 1877)

This is predominantly a central and east African species that has also been recorded from Hwange National Park (Zimbabwe) (Fig. 4) (WEIR, 1969). It is illustrated and redescribed in HAMER et al. (in press).

Two other species may also be valid which would increase the number of streptocephalid species in southern Africa to eighteen:

Streptocephalus distinctus THIELE, 1907

Known from Madagascar, but 1 tube with specimens in the HNHM apparently from the Kalahari (South Africa) (FORRO & BRTEK, 1984). These specimens have not been examined, but it is unlikely that this is an accurate report. This species is illustrated and described in HAMER et al. (in press).

Streptocephalus propinquus BRADY, 1913

Streptocephalus propinquus BRADY, 1913: 470, p 138, figs 2-6.

BRADY (1913) described this species from a pool on the summit of Inkenjeni mountain, Mahlabatini, Zululand (Fig. 4). The illustrations by BRADY (1913) of the male antenna indicate that the specimens resemble *S. cafer*, but BRADY stated that the studied specimens were immature. BARNARD (1929) agreed with this observation and considered *S. propinquus* a synonym of *S. cafer* or *S. indistinctus*. BRTEK (1974), on the other hand, considered it a valid species since enough key-characters are clear from the original drawings. No material of this species could be found.

Distinction of species groups

Different sets of characters can be distinguished as listed in the caption of Table 1. Species were grouped according to these types as presented in Table 1. Species groups A,B,F, and I occur exclusively in southern Africa, while for the other types, corresponding species were found north of Zambezi and Kunene rivers, and in Madagascar.

Table 1. Sorting of southern African *Streptocephalus* species, based on male antennal and frontal appendage morphology. Species groups with no northern African representatives are indicated with thick lines.

A: hand simple, thumb without spur, absence of teeth on finger; B: short and non-tapering, apically broad finger, processes at antennal base, rounded tooth between thumb and spur, spines on dorso-lateral margins of abdomen; C: thumb and finger geniculate or distinctly bent, 1 or 2 teeth on finger, finger apically tapered; D: thumb and spur separated by 2 rounded teeth, finger, short, broad, and dorsally curved; E: thumb spinulose, digitiform processes on S-shaped antennal process, triangular process on medial surface, proximal to hand; F: finger with ventral spur, absence of teeth on dorsal margin of finger, digitiform process on S-shaped antennal process; G: thumb not separated from spur by tooth, finger with spinules on dorsal margin; H: finger with two teeth (of which distal one conical), finger distally recurved, frontal appendage large, well developed; I: narrow angle between thumb and spur, no tooth between thumb and spur, finger long, slender, almost straight and tapered, frontal appendage elaborate.

A	B	C	D	E	F	G	H	I
<i>S.purcelli</i> (Fig. 5)	<i>S.dregei</i> (Fig. 7)	<i>S.cafer</i> (Fig. 9)	<i>S.macrourus</i> (Fig. 11)	<i>S.ovamboensis</i> (Fig. 12)	<i>S.gracilis</i> (Fig. 13)	<i>S. (P.) kaokoensis</i> (Fig. 15)	<i>S.trifidus</i> (Fig. 17)	<i>S.cladophorus</i> (Fig. 19)
<i>S.dendyi</i> (Fig. 6)	<i>S.cirratus</i> (Fig. 8)	<i>S.indistinctus</i> (Fig. 10)	<i>S.vitreus</i> (part 2, Fig. 7)		<i>S.papillatus</i> (Fig. 14)	<i>S. (P.) zuluensis</i> (Fig. 16)	<i>S.probooscideus</i> (Fig. 18)	

Key to the male Streptocephalidae

- 1 a. Thumb with spur or posterior process 3
b. Thumb without spur or posterior process 2
- 2 a. Blunt triangular, peg-like tooth between finger and thumb, telsonic segment with smooth lateral margins *S. purcelli* (Fig. 5)
b. Tooth between finger and thumb absent, telsonic segment with lateral processes *S. dendyi* (Fig. 6)
- 3 a. Finger apically blunt, without distinct bend, abdominal segments 3-7 with spines on hind margins 4
b. Finger apically acute/subacute, spines, if present, not restricted to hind margins of abdominal segments 5
- 4 a. Triangular process on medial side of S-shaped antennal process proximal to hand, finger with distally rounded digitiform tooth on anterior margin *S. dregei* (Fig. 7)
b. Triangular process proximal to hand on medial side of S-shaped antennal process absent, finger without distinct digitiform tooth on anterior margin *S. cirratus* (Fig. 8)
- 5 a. Digitiform or triangular processes on medial or anterior surface of S-shaped antennal process 9
b. S-shaped antennal process without processes 6
- 6 a. Dorsal margin of finger with numerous small spinules 7
b. Finger without spinules on dorsal margin 8
- 7 a. Thumb with distinct, proximal heel, finger with 2 teeth on dorsal margin *S. (P.) zuluensis* (Fig. 16)
b. Thumb without heel, finger without teeth on dorsal margin *S. (P.) kaokoensis* (Fig. 15)
- 8 a. Frontal appendage small/ medium length, simple, two rounded teeth separating

- thumb and spur *S. macrourus* (Fig. 11)
- b. Frontal appendage large and elaborate, teeth between thumb and spur absent
S. cladophorus (Fig. 19)
- 9 a. Finger with ventral spur, teeth on dorsal margin of finger absent 10
b. Finger without ventral spur, one or two teeth present on dorsal margin of finger 11
- 10 a. Finger and thumb with numerous, long papillae, basal and middle parts of S-shaped antennal process papillate *S. papillatus* (Fig. 14)
b. Finger and thumb without, or with few small, papillae, 4-5 papillae on middle part of S-shaped antennal process only *S. gracilis* (Fig. 13)
- 11 a. Frontal appendage $> 1/3$ length of S-shaped antennal process 12
b. Frontal appendage $< 1/3$ length of S-shaped antennal process 13
- 12 a. Frontal appendage trifid, without papillae *S. trifidus* (Fig. 17)
b. Frontal appendage apically bifid, with numerous papillae along its length
S. proboscideus (Fig. 18)
- 13 a. Medial row of conical processes (8-10) on middle part of S-shaped antennal process, thumb spinulose *S. ovamboensis* (Fig. 12)
b. Conical processes not present on S-shaped antennal process, if present, processes in the form of triangular flaps, thumb not spinulose 14
- 14 a. Frontal appendage bifid or trifid, serrated basal flaps present, finger with single, broad, flat tooth with peaked ridge proximally *S. cafer* (Fig. 9)
b. Frontal appendage single, basal flaps absent, two distinct teeth on dorsal margin of finger *S. indistinctus* (Fig. 10)

Discussion: Streptocephalidae south of Zambezi and Kunene rivers

The streptocephalid fauna of southern Africa is a diverse but distinct one. No clear-cut similarity was found between the southern African, the North American, and Asian streptocephalids. *Streptocephalus moorei* BELK from North America and *S. ovamboensis* have a row of projections along the thumb, and a narrow angle with notch between thumb and spur. Furthermore, they both have conical processes on the dorso-lateral surface of the middle part of the S-shaped antennal process. *Streptocephalus similis* BAIRD from North and Central America, has an antennal morphology which would, apart from the absence of a tooth between the thumb and spur, place it in group C with *S. cafer* and *S. indistinctus*. The Indian species *S. simplex* and *S. dichotomus* have a more prominent finger than thumb; this character is not shown by any of the southern African species.

Two of the nine groups created for the southern African species are enigmatic: *S. cafer* (group C) shares the basal process character with group B. *S. dregei* of the latter group, on the other hand, has a similar hand region (except for the shape of the finger) to group C. Group H, comprising *S. trifidus* and *S. proboscideus* could be split into two separate groups based on the difference in the shape of the thumb and spur and tooth separating these. In the other species groups, however, there is a minimum of overlap in key characters.

There is little correlation between the species groups based on cysts and those on antennal morphology (see BRENDONCK & COOMANS, in press). Only group G (*S. (Parastreptocephalus) kaokoensis*/*S. (P.) zuluensis*) and group E with *S. ovamboensis* as the only representative correspond. This discrepancy results from the inclusion of a large number of species in the first two 'cyst-groups' (see BRENDONCK & COOMANS, in press) as a result of a large overlap in cyst patterns as well as intra-specific variability.

A detailed discussion of the distribution and zoogeography of the southern African streptocephalids would be premature, as vast areas still remain to be investigated. Discussion of relationships between species from the region north of the Zambezi and Kunene rivers and those from the south, and aspects of diversity, dispersal and speciation are presented in the second part of this study (see HAMER et al., in press).

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LOCALITIES: SOUTHERN AFRICAN STREPTOCEPHALIDAE

SOUTH AFRICA

CAPE PROVINCE:

Cape Town, Camp Ground	33°54'S 18°24'E
Cape Town, Green Point Common	33°54'S 18°24'E
Kamieskroon, Hondeklipbaai	30°25'S 17°17'E
Kakamas	28°47'S 20°38'E
Williston	31°21'S 20°55'E
Abiekwasputs, 110km NW Upington	27°18'S 20°06'E
St. Helena, Stompneus	32°45'S 17°56'E
Stellenbosch	33°50'S 18°52'E
Cape Flats, near Epping	33°55'S 18°33'E
Yserfontein	33°20'S 18°10'E
Taaiboskraal, SW of Springbok	29°40'S 17°48'E
Garies	30°34'S 17°59'E
Piketberg mountains, 70km E Saldanha Bay	32°S 18°E
Thornhill near Port Elizabeth	31°58'S 26°30'E
Agulhus, Bredasdorp	34°35'S 20°E
Cape Town, Rondebosch	33°57'S 18°28'E
Uitenhage	33°45'S 25°22'E
Somerset East	32°40'S 25°35'E
Grahamstown	33°16'S 26°35'E
Somerset East region, Swaershoek	32°30'S 25°E
Port Elizabeth	34°S 25°E
Kowie Road, Blaaukrantz	33°20'S 26°44'E
Willowmore	33°12'S 23°29'E
Kei Road	32°42'S 27°32'E
Karoo, Potfontein	30°11'S 24°07'E
Karoo, Williston	31°20'S 20°50'E
Kimberley	28°45'S 24°45'E
Carnarvon, 10Km S	31°10'S 22°08'E
Oudshoorn	33°37'S 22°12'E
Hanover	31°05'S 24°26'E
Gordonia	27°30'S 20°30'E
Graaff-Reinett	32°15'S 24°35'E
Grobbershoop, 4km E	28°55'S 22°05'E
Beaufort West Division, Hoogeveld	32°22'S 22°35'E
Namaqualand, Kalkfontein South*	29°S 17°E
Achabdam*	27°30' 20°E
Moloppo River	28°S 20°30'E
Vryburg	26°58'S 24°45'E

TRANSVAAL

Heidelberg	26°30'S 28°23'E
Mala Mala Game Reserve	24°45'S 31°30'E
Naboomspruit	24°40'S 28°23'E
Kruger National Park, Skukuza area	25°03'S 31°38'E
Junction of Crocodile and Marico Rivers	24°12'S 26°52'E
Brakpan	26°14'S 28°21'E
Rietfontein#	

ORANGE FREE STATE

Bloemfontein	29°07'S 26°14'E
Dewetsdorp	29°35'S 26°40'E
Kroonstad	27°40'S 27°13'E

NATAL

Makatini Flats	27°24'S 32°10'E
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BOTSWANA

Tsotsoroga, N	18°S 24°E
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ZIMBABWE

Kwekwe	25°18'S 29°48'E
Kazuma Depression	18°15'S 25°35'E
Hwange (=Wankie) Game Reserve	18°S 26°E
Harare (Salisbury)	17°43'S 31°05'E
Lake MacIlwaine, Tiger Bay	17°S 30°E
Plumtree	20°10'S 28°43'E

NAMIBIA

Mariental, 65km S	25°10'S 17°50'E
Naukluft mountains	24°15'S 16°15'E
Ovamboland, Ongka*	18°S 15°E
Onambeke	18°10'S 15°50'E
Onolongo (Eholongo)?	18°17'S 14°52'E
Umtekwa*	
Tstumkwe	19°37'S 20°30'E
Maltahohe	24°50'S 16°59'E
Kaokoveld, N Kamanyab	19°36'S 14°50'E
Fisher's Pan	18°45'S 17°00'E
Bushmanland, Nyae-Nyae Pan	19°45'S 20°28'E
Gautscha Pan	19°S 20°E
Owuthija (Omuthiya river)?	18°30'S 17°05'E
Ukualonkathi*	
Ondongua	17°51'S 15°59'E
Eunda	17°31'S 14°39'E
Okaukuejo	19°11'S 15°50'E
Namib Naukluft Park, 150km ESE Gobabeb	24°15'S 15°34'E

* Those localities marked by an asterisk could not be found on any maps. In some cases the co-ordinates for the region (eg. Ovamboland) are given.

? Localities marked by a question mark could not be found but it is possible that this is a result of a different spelling or interpretation of the place name. The possible correct locality is presented in brackets after the locality given in the text.

The co-ordinates for Rietfontein could not be identified with certainty since at least 15 localities with the same name exist in the Transvaal

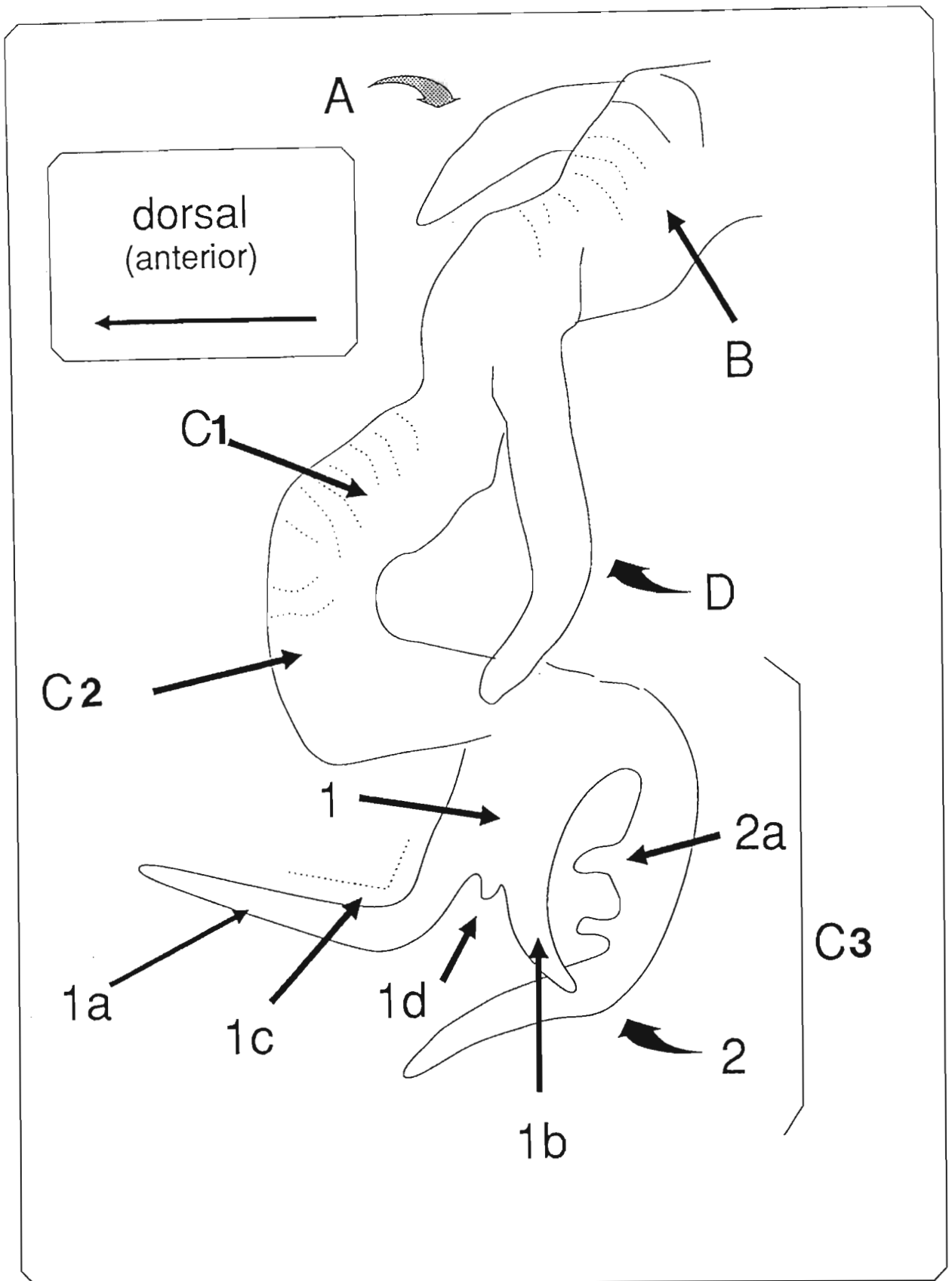


Fig. 1. Diagram of idealised streptocephalid male antenna and frontal appendage summarizing terminology used in text and figures; A = frontal appendage (process); B = basal joint of antenna; C = S-shaped antennal process; C1 = basal and C2 = middle region of S-shaped antennal process; C3 = hand (apical region of S-shaped antennal process); C3-1 = thumb; C3-1a = anterior part of thumb; C3-1b = posterior process (spur) of thumb; C3-1c = angle between proximal and distal parts of anterior region of thumb; C3-1d = tooth between anterior and posterior part (spur) of thumb; C3-2 = finger; C3-2a = tooth (teeth) on anterior surface of finger; D = terminal joint of antenna.

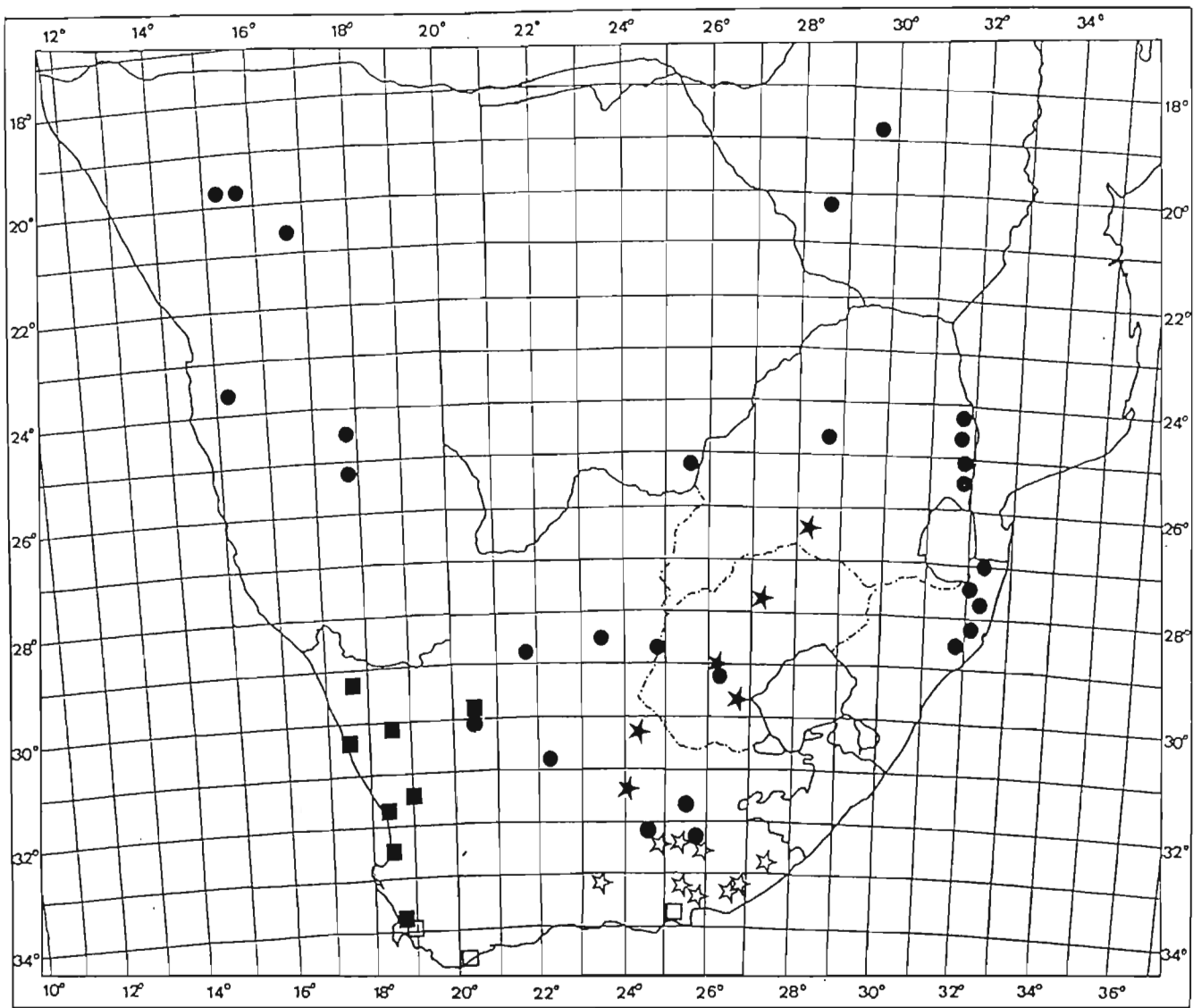


Fig. 2. Distribution of **■** *S. purcelli*, **□** *S. dendyi*, **☆** *S. dregei*, **★** *S. cirratus*, and **●** *S. cafer*.

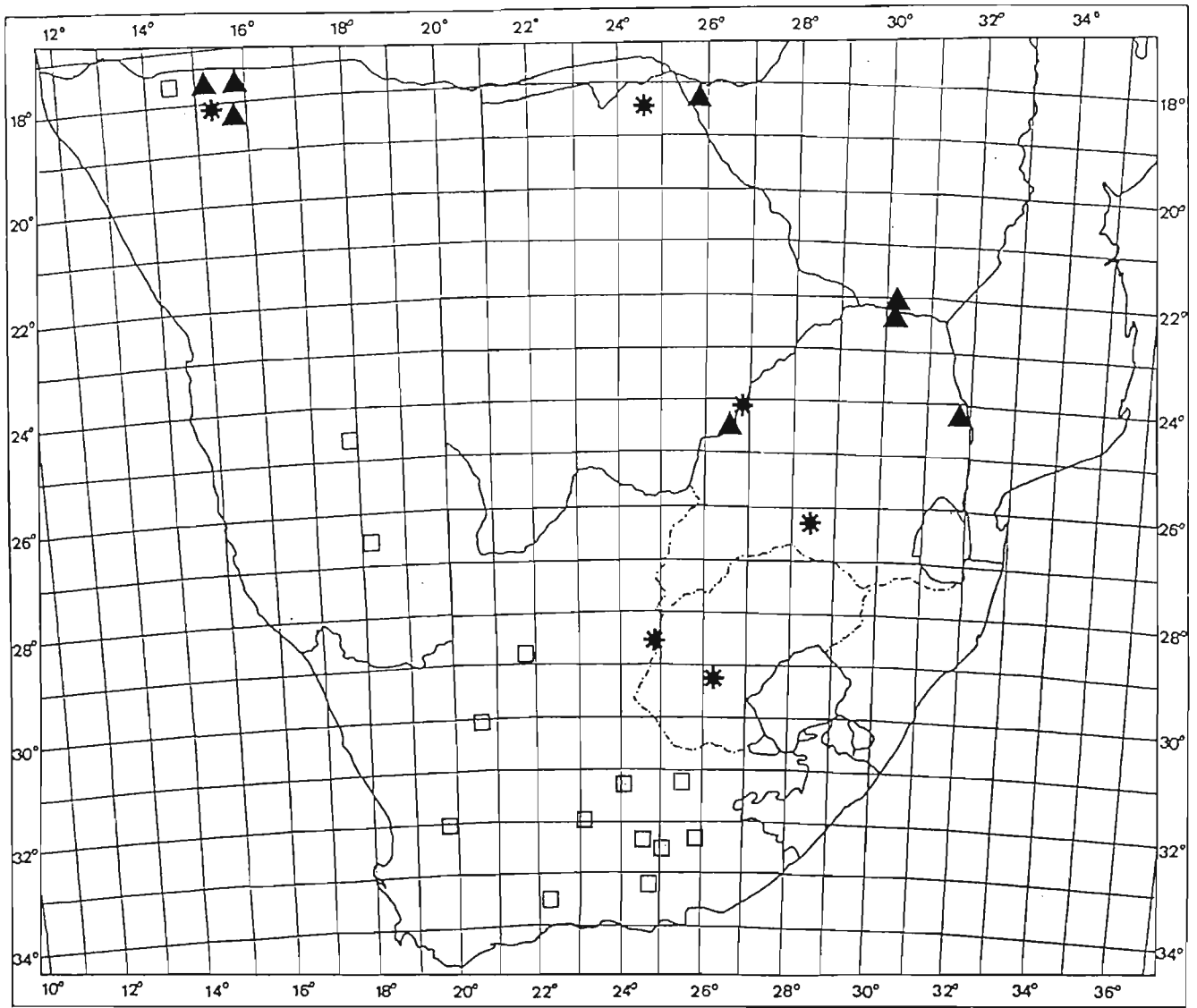


Fig. 3. Distribution of * *S. macrourus*, ▲ *S. indistinctus* and □ *S. ovamboensis*.

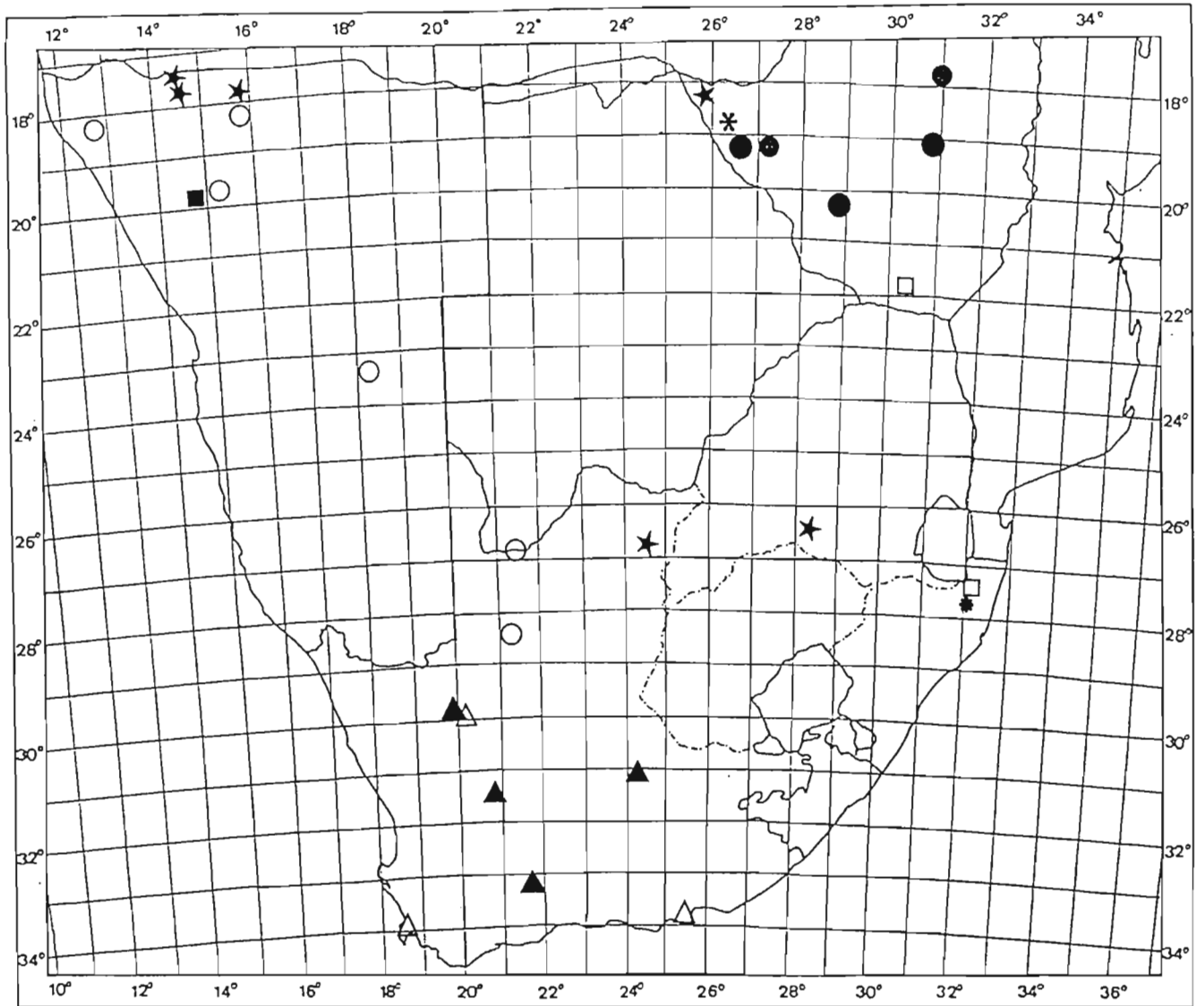


Fig. 4. Distribution of ■ *S. (P.) kaokoensis*, □ *S. (P.) zuluensis*, △ *S. gracilis*, ▲ *S. papillatus*, ○ *S. proboscideus*, ● *S. trifidus*, ★ *S. cladophorus*, ✱ *S. vitreus* and ✱ *S. propinquus*.

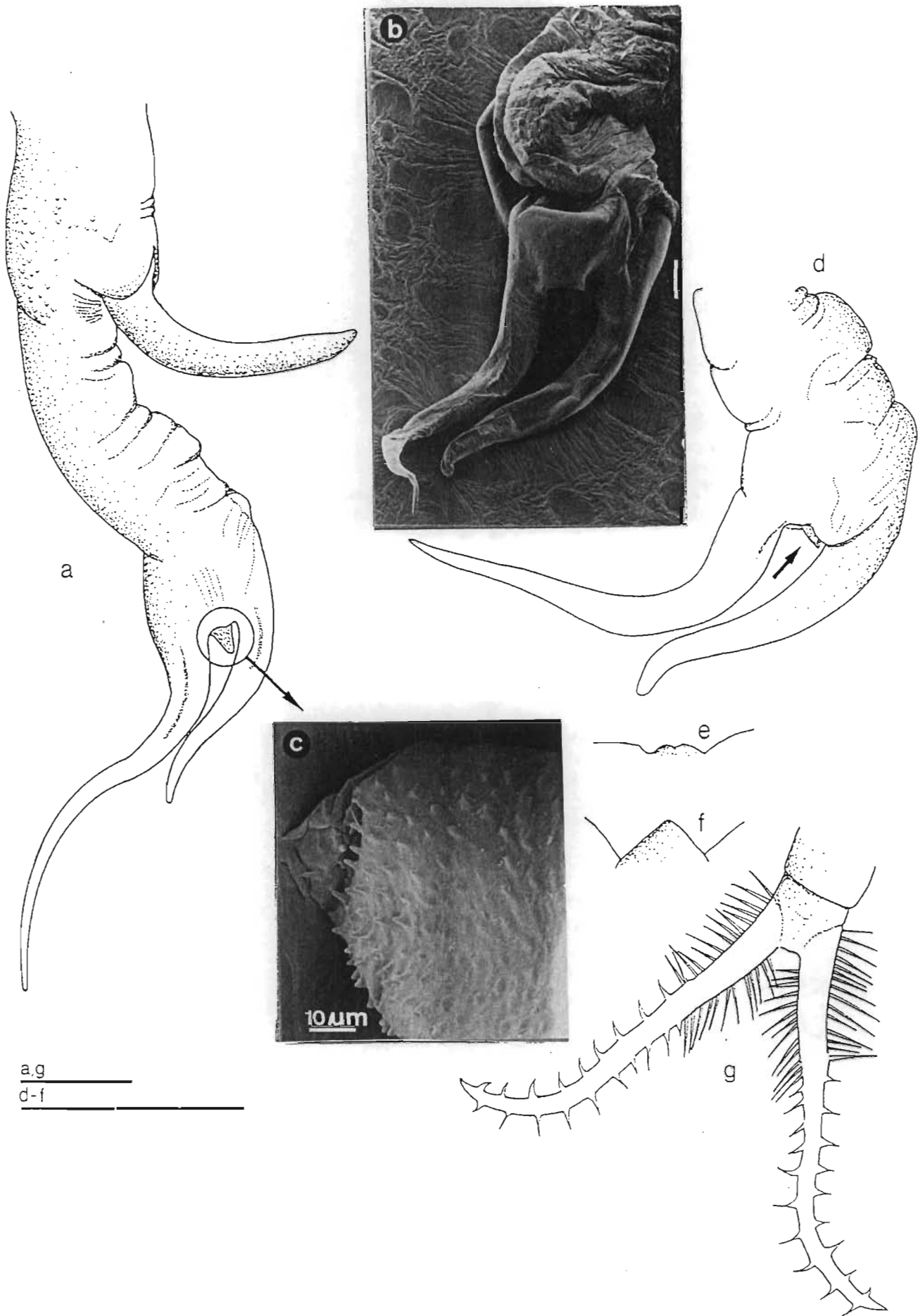


Fig. 5. *S. purcelli* (male); a: lateral view of left antenna; b: medial view of right antenna; c: detail of tooth separating thumb and finger; d: lateral view of (left) hand region (Yserfontein specimens); e: frontal appendage (Kamieskroon specimens); f: frontal appendage (Stompneus specimen); g: cercopods, dorsal view.

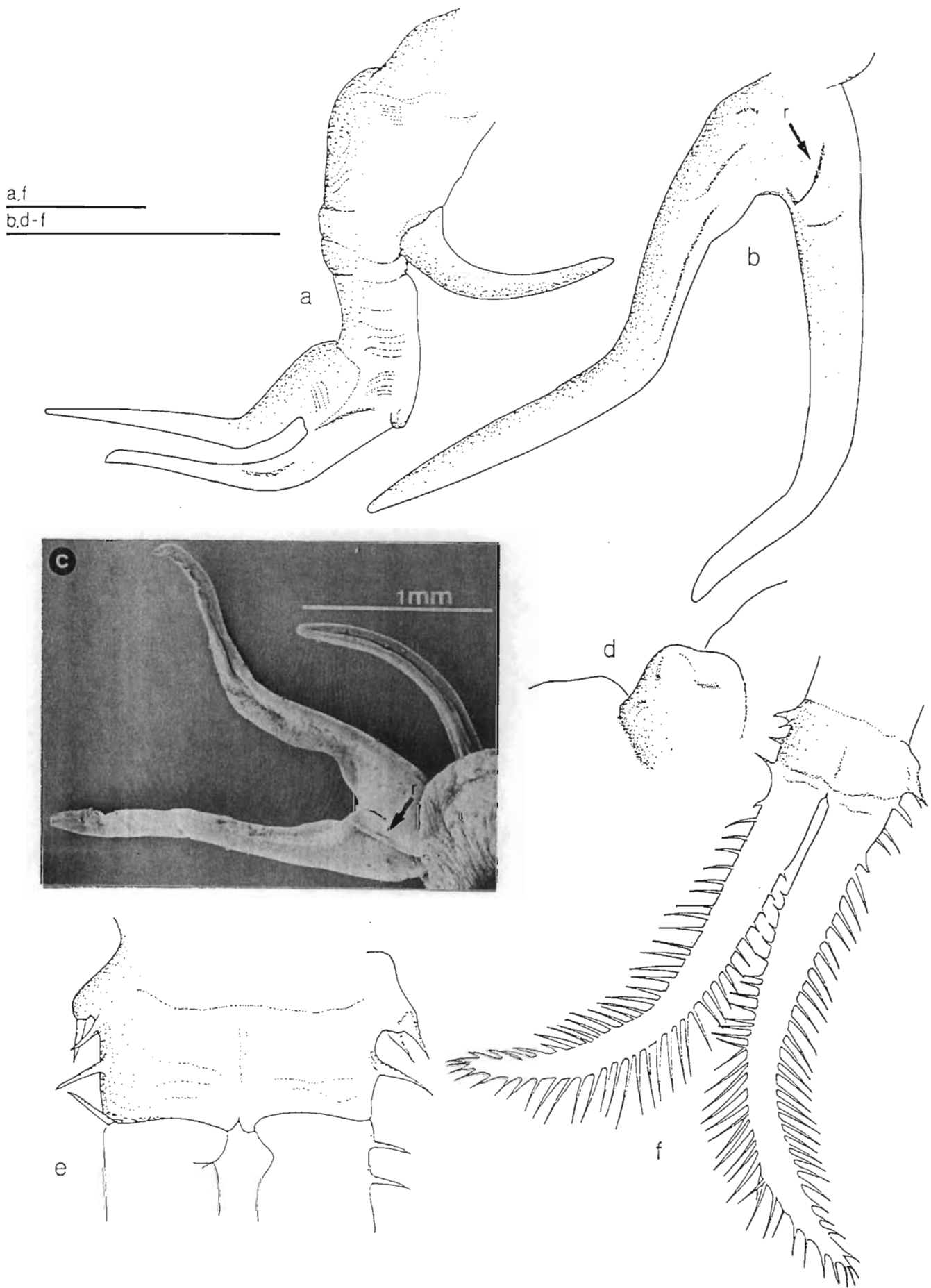


Fig. 6. *S. dendyi* (male); a: lateral view of left antenna; b: lateral view of (left) hand region; c: medial view of (right) hand region; d: frontal appendage; e: telsonic segment; f: cercopods, dorsal view. r = ridge.

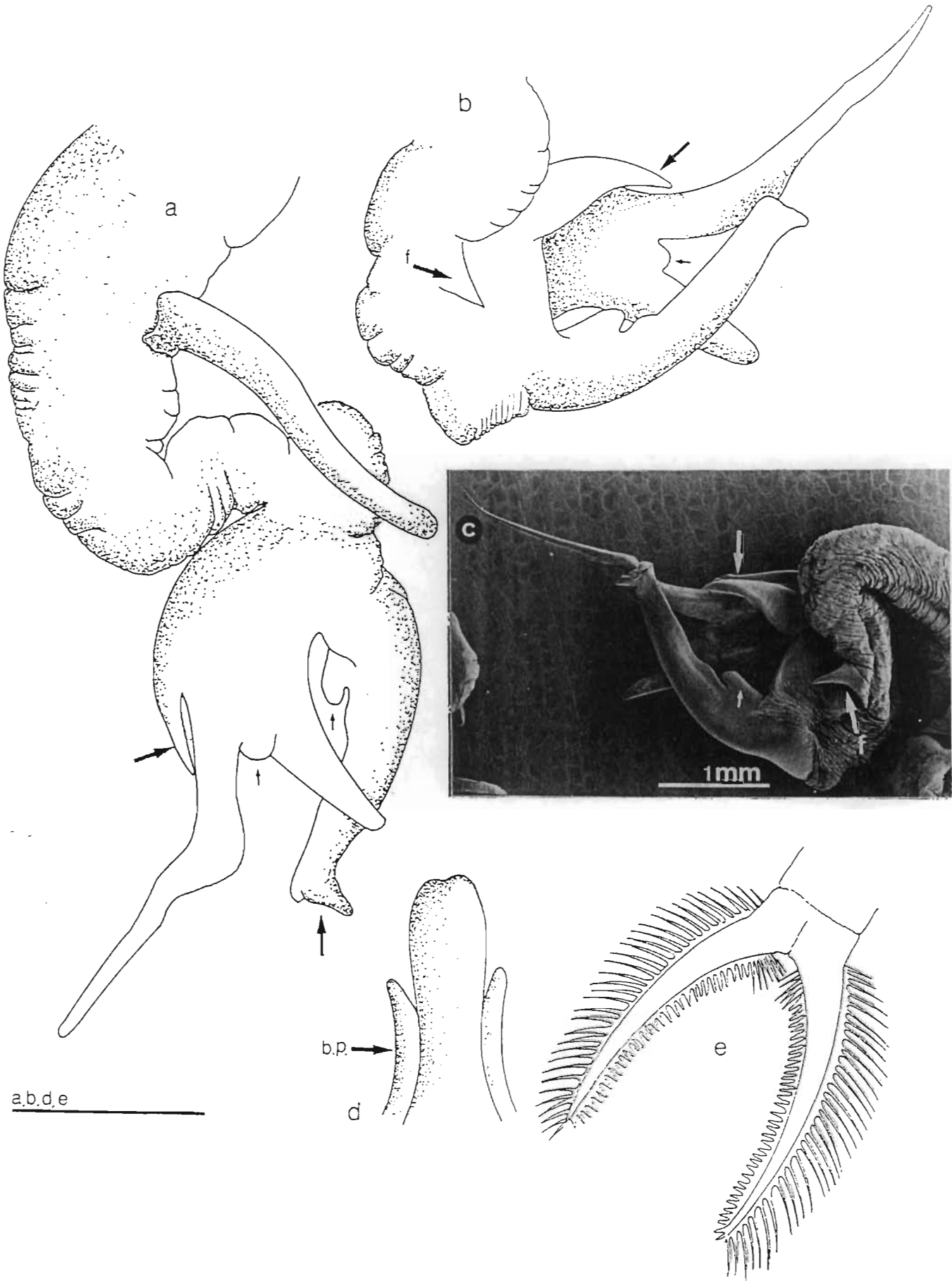


Fig. 7. *S. dregei* (male); a: lateral view of left antenna; b: medial view of left antenna; c: medial view of right antenna; d: dorsal view of frontal appendages and basal processes; e: cercopods; f: dorsal view of abdominal segments 2-8 and telson. f = membranous flap; b.p. = basal process.

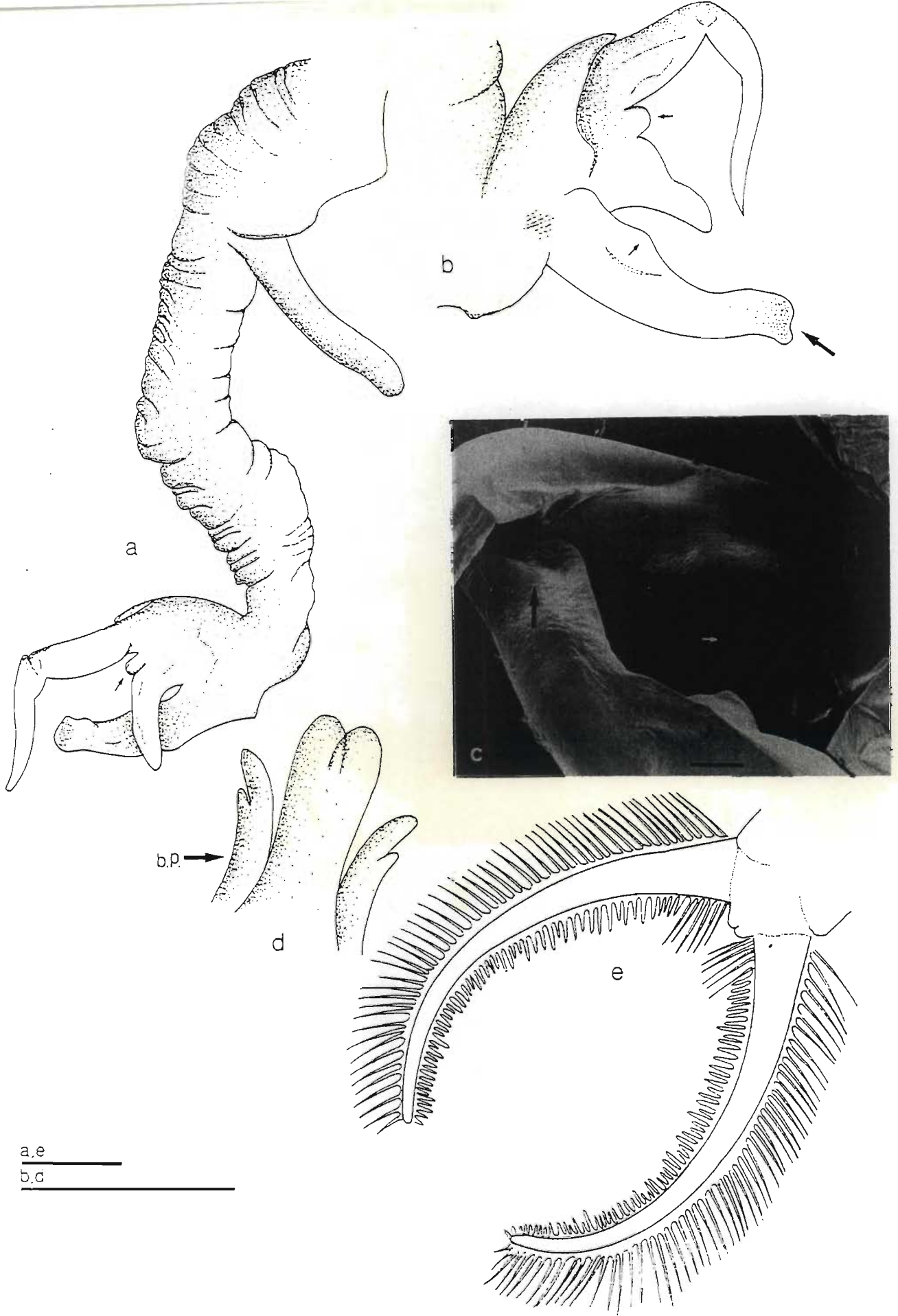


Fig. 8. *S. cirratus* (male); a: lateral view of left antenna; b: medial view of left hand region; c: detail of hand region median view, right antenna; d: frontal appendage and basal processes; e: cercopods; f: dorsal view of abdominal segments 5-7. b.p. = basal process.



Fig. 9. *S. cafer* (male); a: lateral view of left antenna; b: medial view of left antenna; c: medial view of dorsal margin of finger showing teeth (right antenna); d: frontal appendage (bifid form) and basal processes; e: frontal appendage (trifid form) and basal processes; f: cercopods. f= membranous flap; b.p. = basal process.

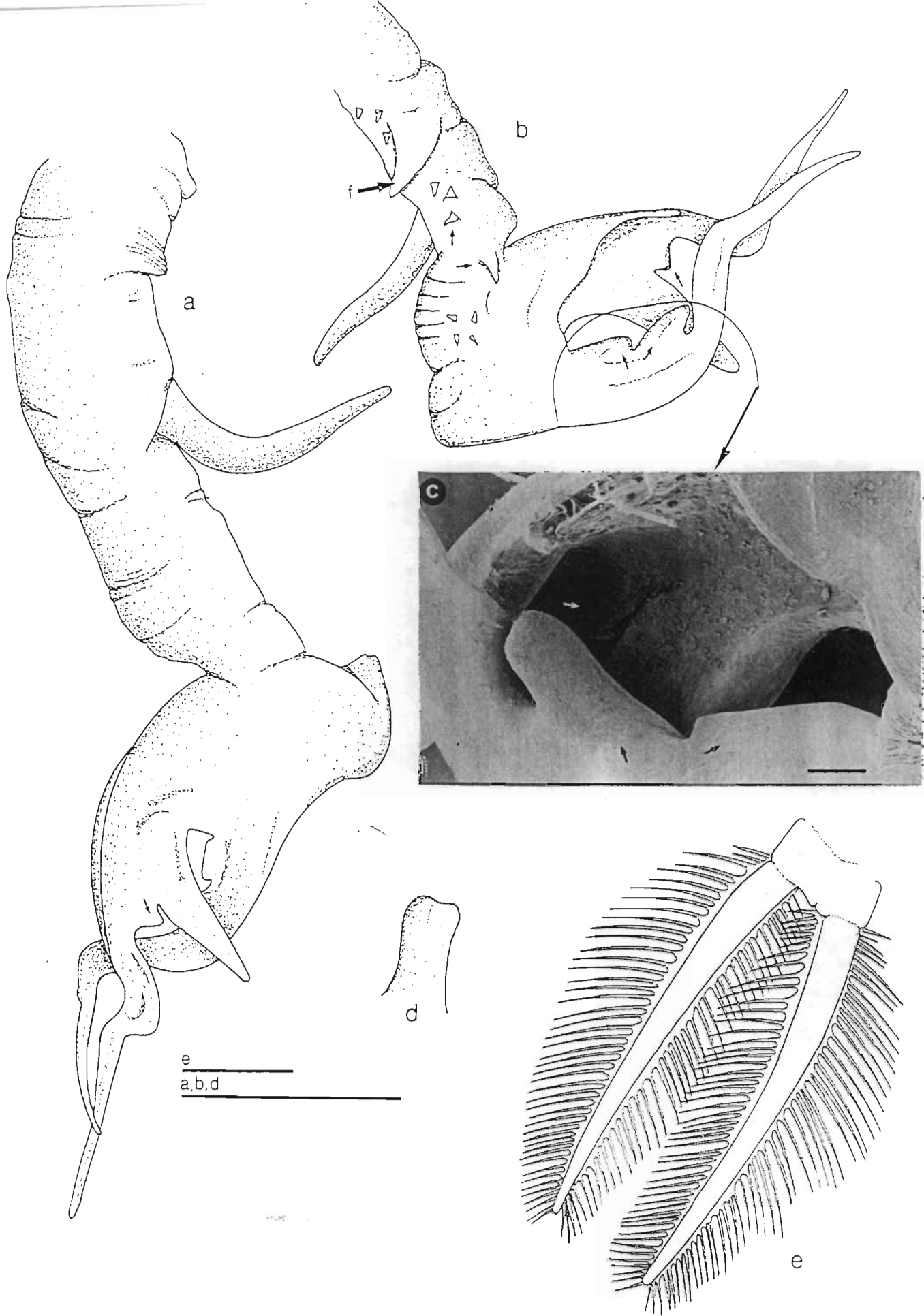


Fig. 10. *S. indistinctus* (male); a: lateral view of left antenna; b: medial view of left antenna; c: medial view of dorsal margin of finger showing teeth (right antenna); d: frontal appendage; e: cercopod. r = membranous flap.

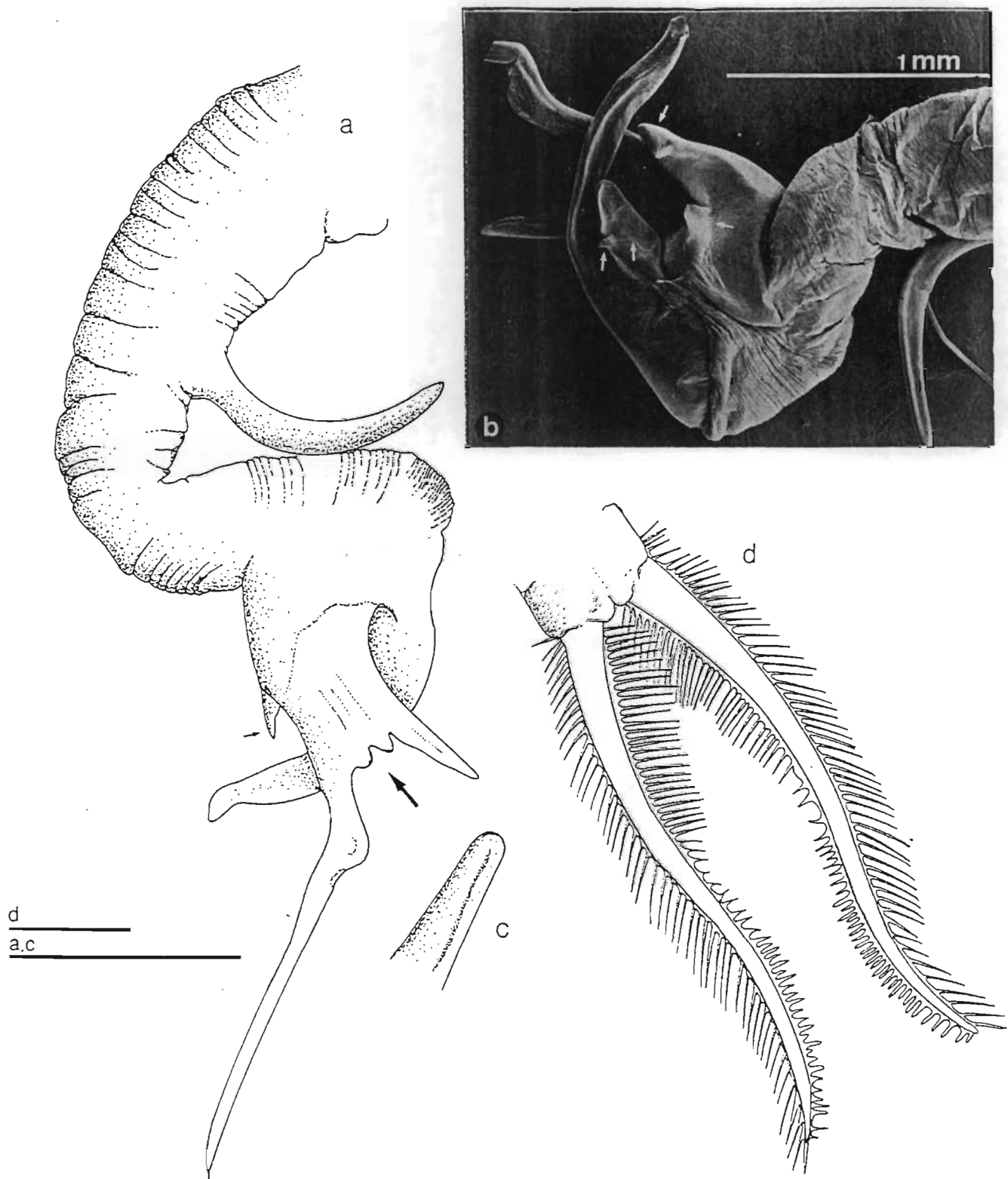


Fig. 11. *S. macrourus* (male); a: lateral view of left antenna; b: medial view of right antenna; c: frontal appendage; d: cercopods.

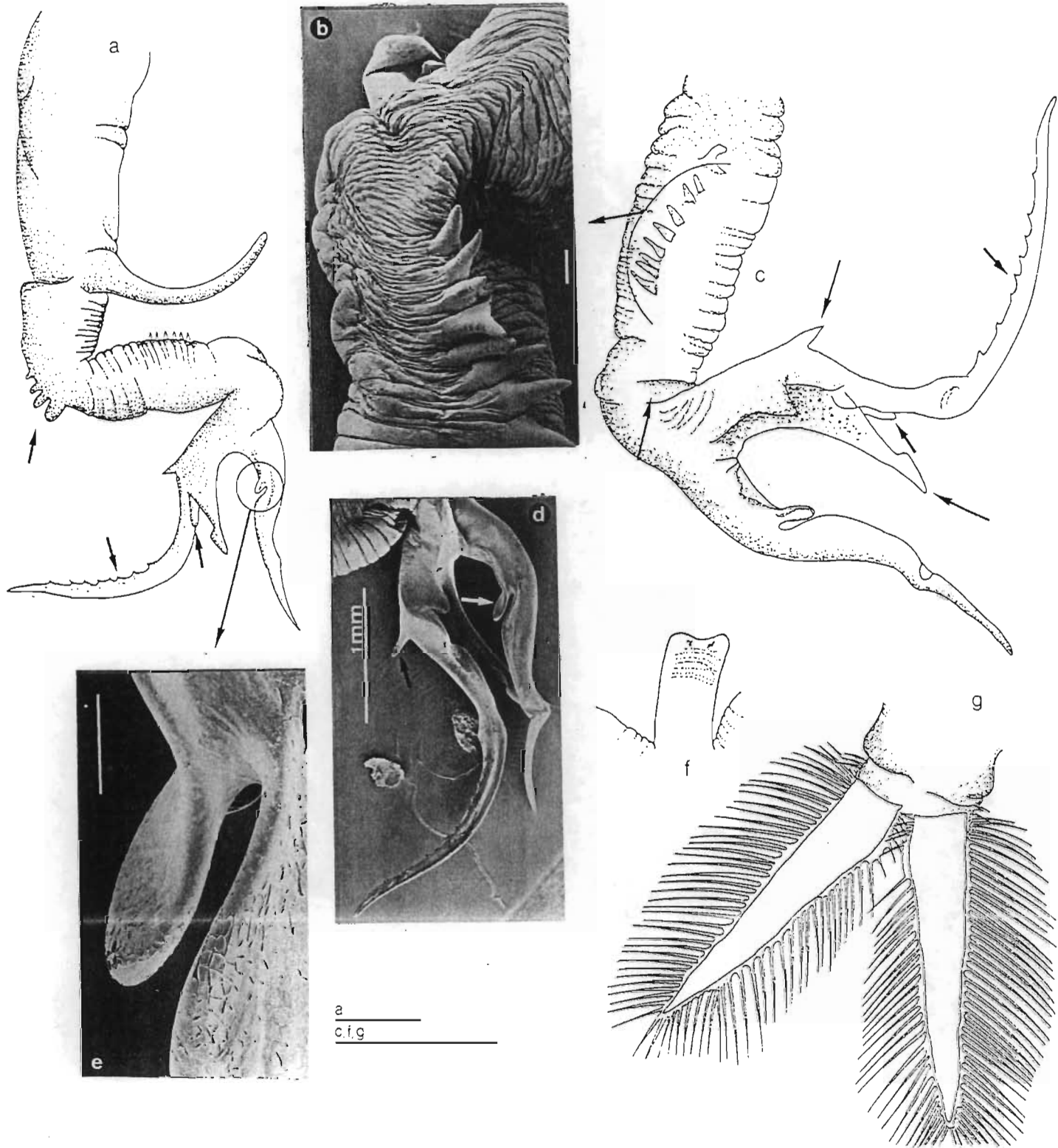


Fig. 12. *S. ovamboensis* (male); a: lateral view of left antenna; b: medial view of middle part of S-shaped antennal process; c: medial view of left antenna; d: medial view of right hand region; e: detail of tooth on dorsal margin of finger (right antenna); f: frontal appendage; g: cercopods.

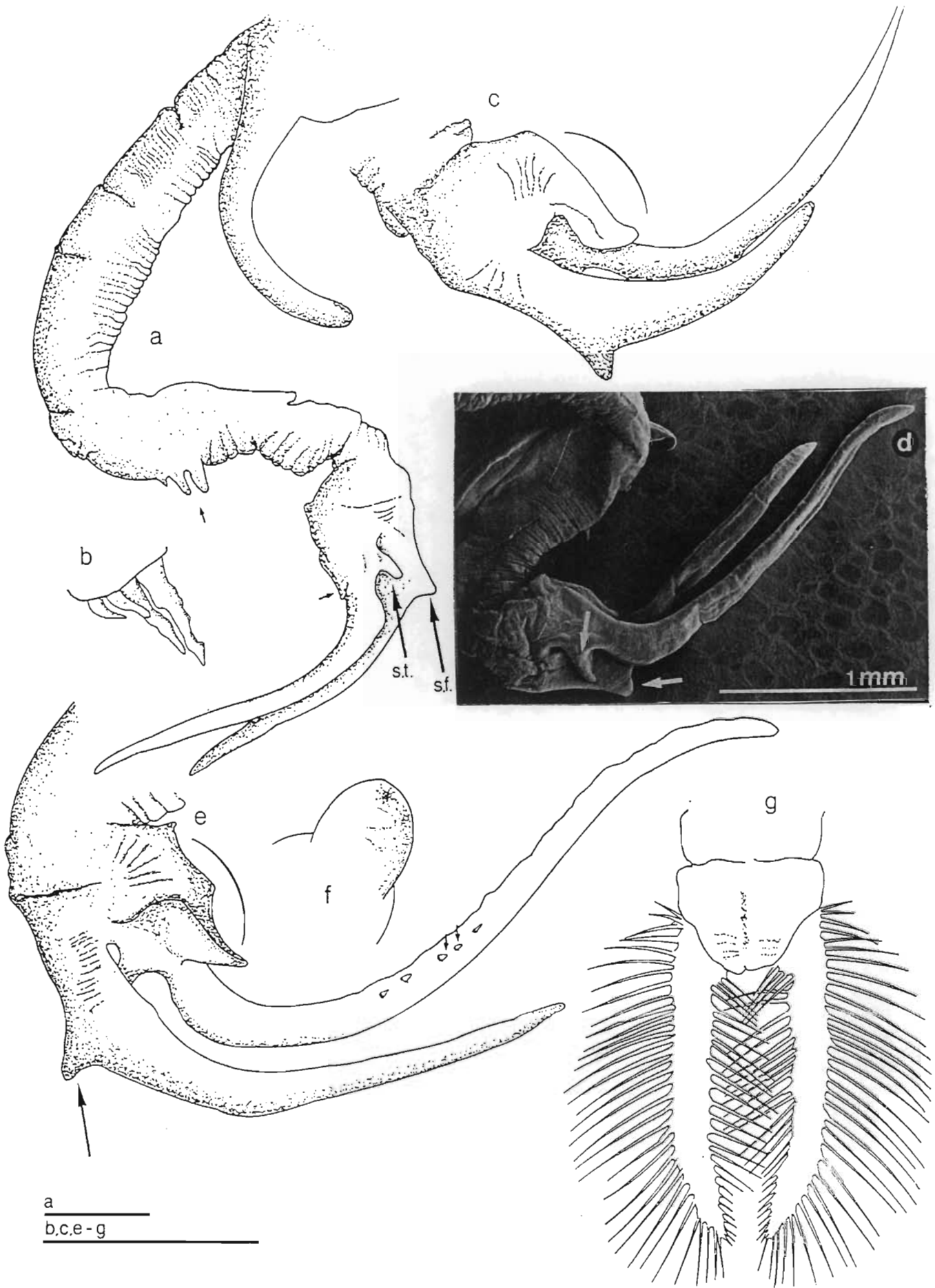


Fig. 13. *S. gracilis* (male); a: lateral view of left antenna; b: processes on anterior margin of S-shaped antennal process (BMNH specimen); c: medial view of left hand region of antenna (ZMUOF specimen); d: lateral view of right antenna; e: medial view of left hand region (BMNH specimen); i: frontal appendage; g: cercopous; h: dorsal view of abdominal segments 4, 5. s.t.

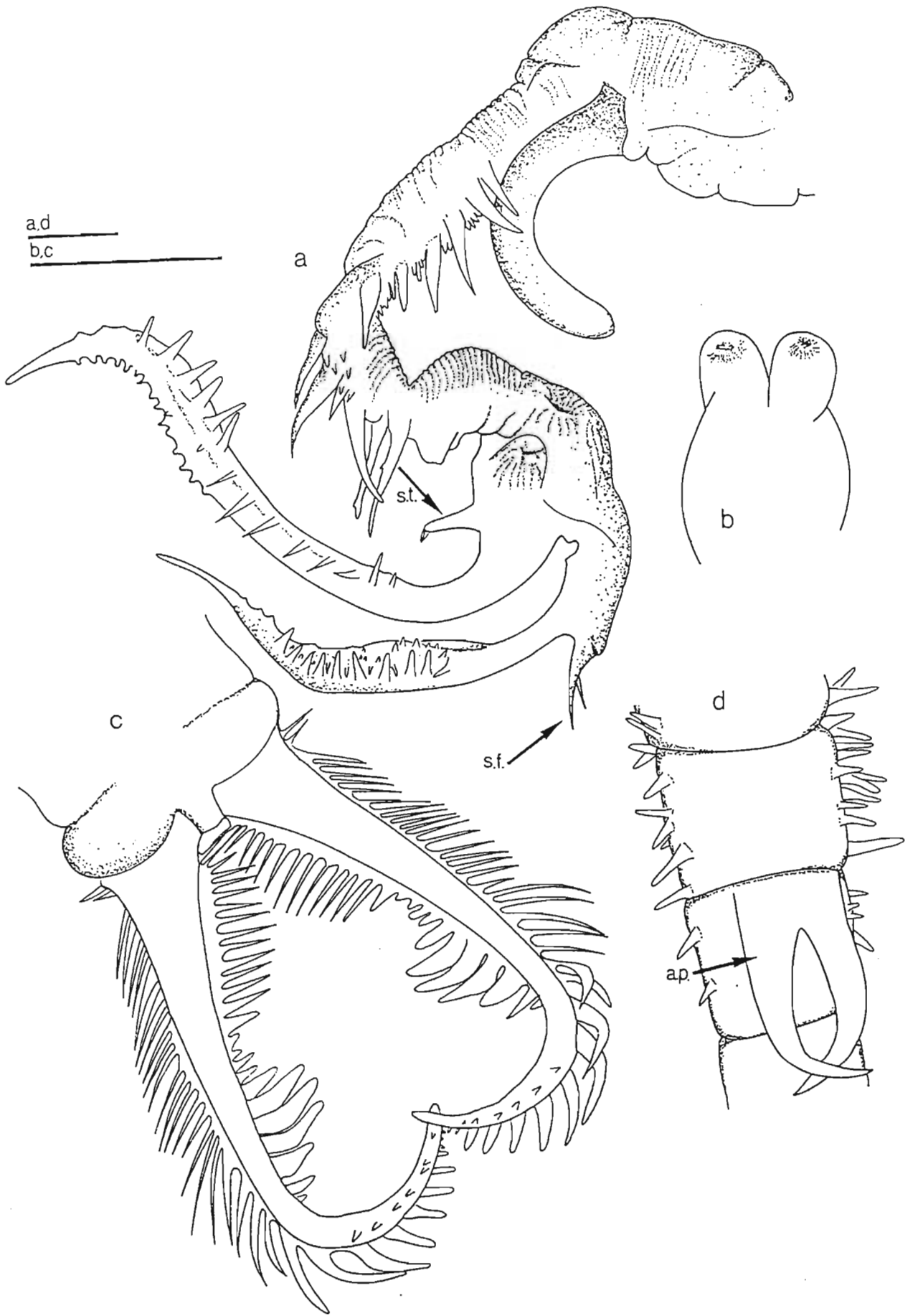


Fig. 14. *S. papillatus* (male); a: lateral view of left antenna; b: frontal appendage; C: cercopods; D: abdominal appendages. a.p. = abdominal process. s.f. = finger spur; s.t. = thumb spur.

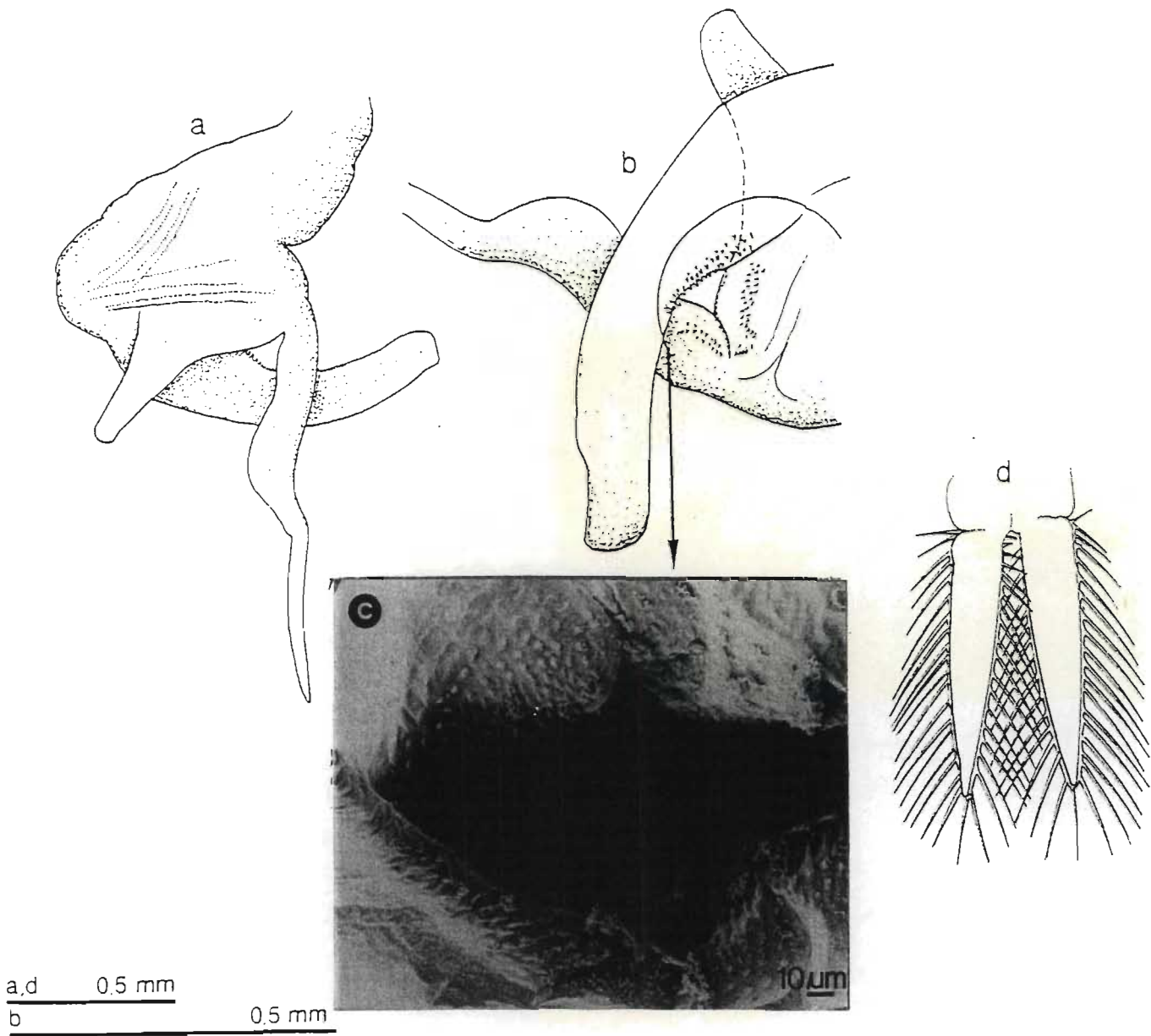


Fig. 15. *S. (P.) kaokoensis* (male); a: lateral view of right antenna (drawn after BRENDONCK et al., 1992); b: medial view of left hand region; c: detail of spinules on finger and basal region of thumb; d: cercopods.

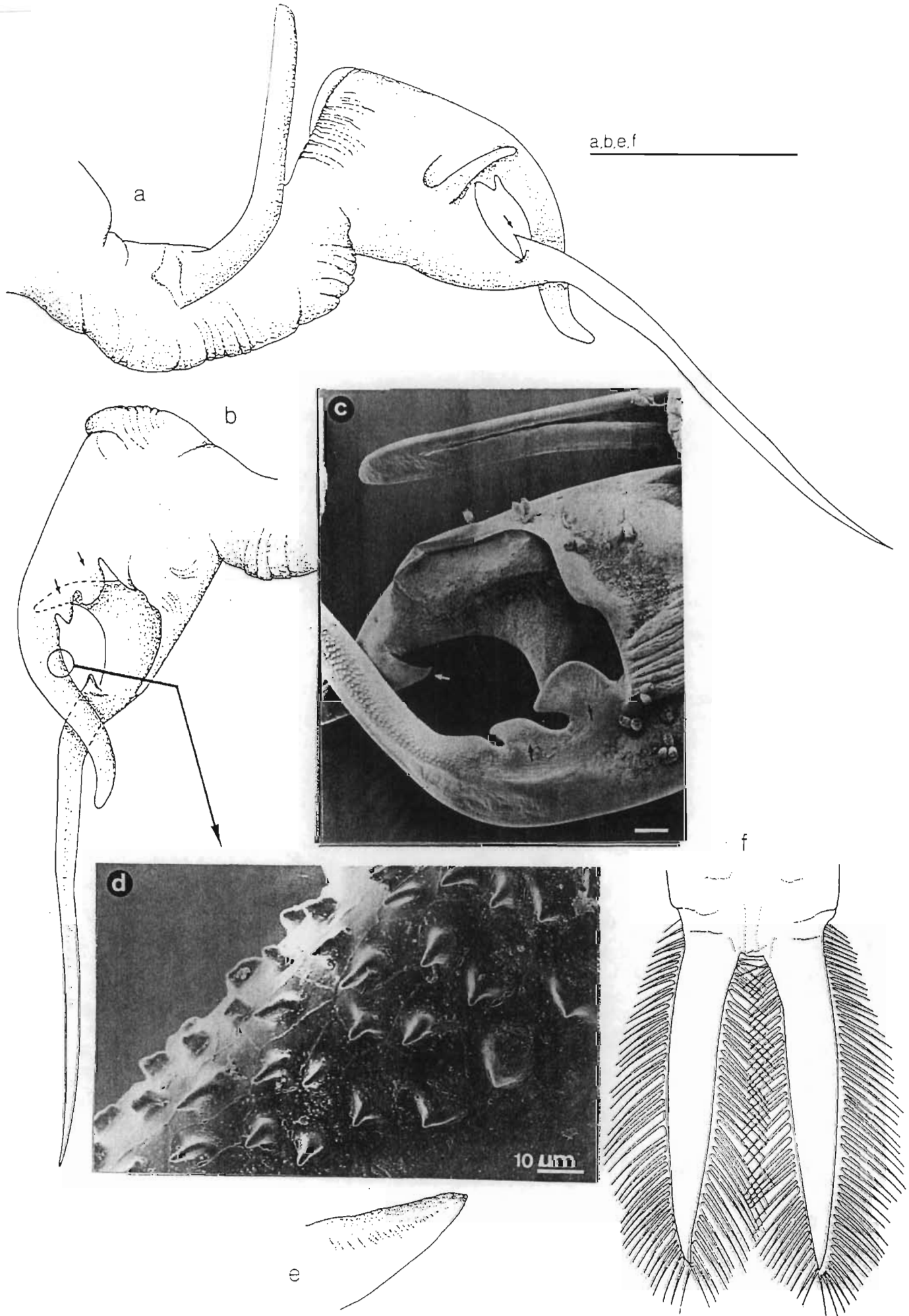


Fig. 16. *S. (P.) zuluensis* (male); a: lateral view of left antenna; b: medial view of left hand region; c: medial view of right hand region; d: detail of spinules on dorsal margin of finger; e: frontal process; f: cercopods.

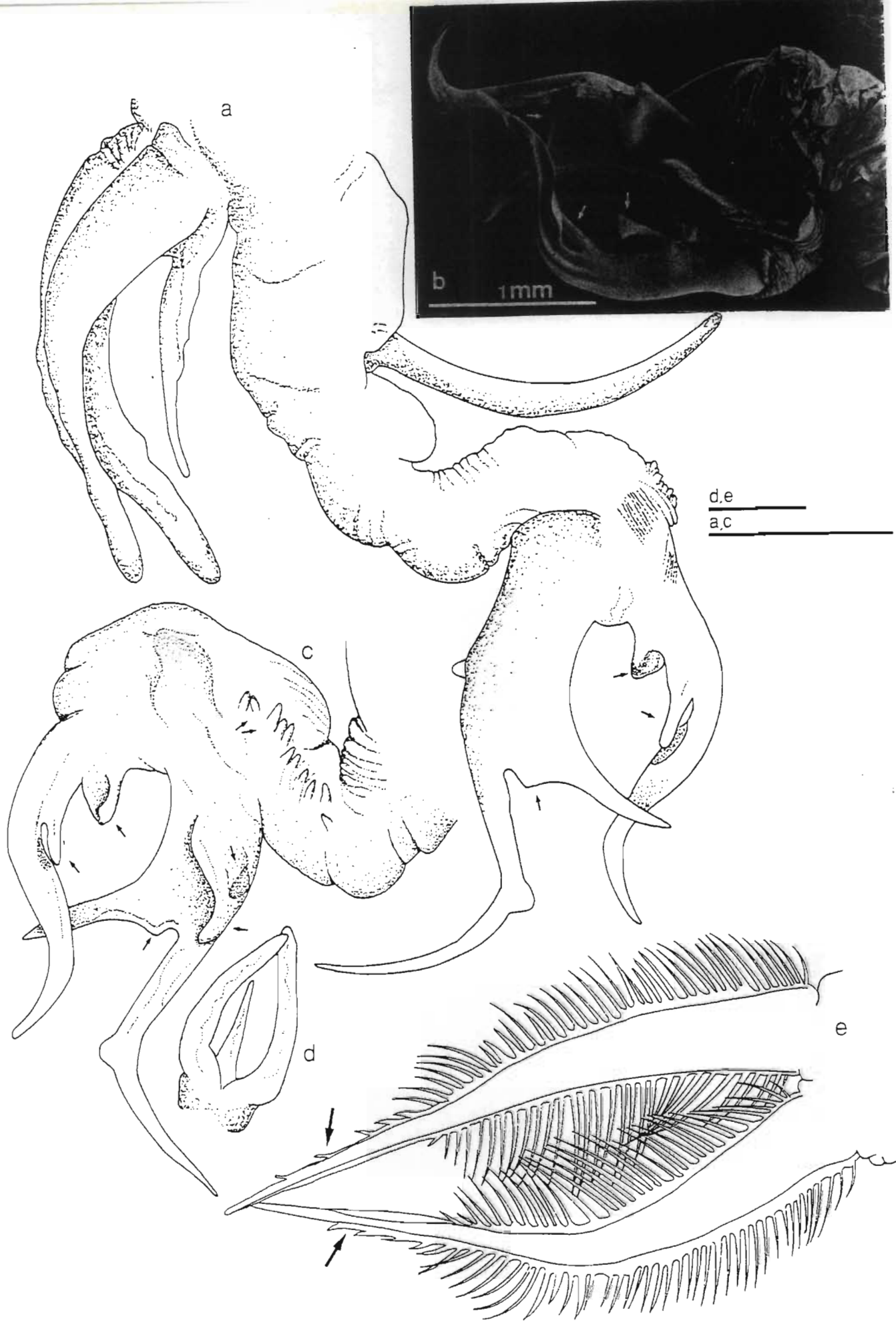


Fig. 17. *S. trifidus* (male); a: lateral view of left antenna, and frontal appendage; b: medial view of right antenna; c: medial view of left antenna; d: frontal appendage (dorsal view); e: cercopods.

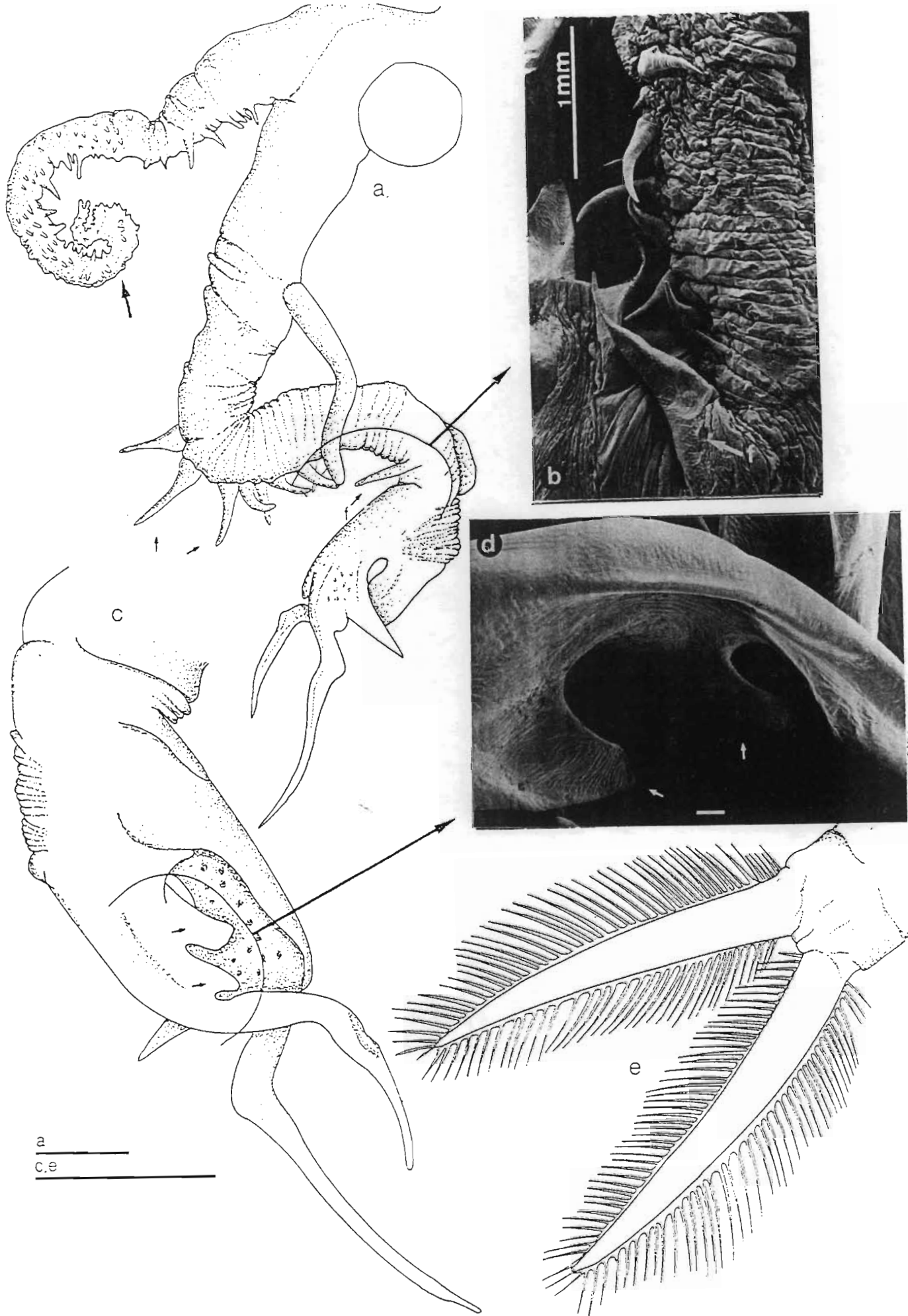


Fig. 18. *S. proboscideus* (male); a: lateral view of left antenna and frontal appendage; b: medial view of S-shaped antennal process proximal to hand; c: medial view of left hand region; d: medial view of teeth on dorsal margin of finger (right antenna); e: cercopods. f= membrannus flange

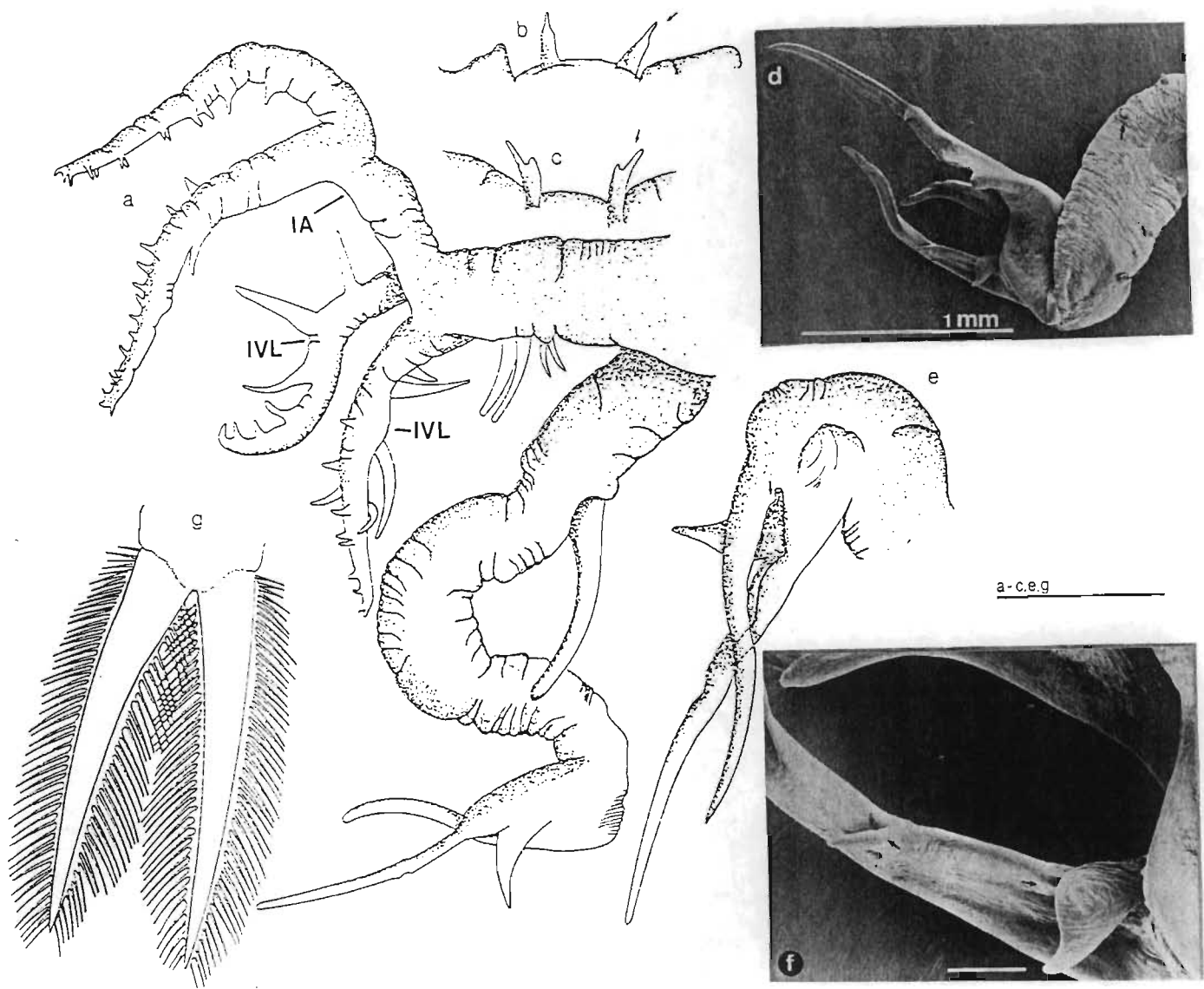


Fig. 19. *S. cladophorus* (male); a: lateral view of left antenna and frontal appendage; b: basal processes (Namibian specimens); c: basal process (Transvaal and Zimbabwean specimens); d: medial view of right antenna; e: medial view of left hand region; f: detail of teeth on dorsal margin of finger (MNHSI specimen); g: cercopods. 1VL = ventro-lateral branches of frontal appendage; 1A = anterior branch on trunk of frontal appendage (after BELK & PEREIRA (1982)).

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CHAPTER 2.2.

A REVIEW OF AFRICAN STREPTOCEPHALIDAE (CRUSTACEA: BRANCHIOPODA: ANOSTRACA).

Part 2: North of Zambezi and Kunene Rivers, and Madagascar

Abstract

The African Streptocephalidae reported from the region north of the Zambezi and Kunene rivers and from Madagascar are reviewed. An attempt is made to delineate species groups based on similarities in male antennal and frontal appendage structure and to compare them with southern African representatives. Furthermore, species groups based on adult characters are compared with those based on egg morphology. Comments on dispersal, streptocephalid origin, and diversity are also addressed. Twelve *Streptocephalus* species from the above region are considered. *Streptocephalus vitreus* and *S. proboscideus* occur south of the above rivers also. For an additional six species no material could be located and for some of them the taxonomic validity is uncertain. Six species groups are constructed. For five groups, 1) *S. vitreus*, 2) *S. neumanni*/*S. proboscideus*, 3) *S. torvicornis*/*S. rubricaudatus*, 4) *S. (Parastreptocephalus) lamellifer*/*S. (P.) sudanicus*, and 5) *S. distinctus*/*S. spinosus*, related species were found in southern Africa. Only the *S. rothschildi*/*S. zeltneri*/*S. bouvieri* group has an exclusive set of characters. At least 27 of the approximately 50 known streptocephalids occur in Africa. This high diversity could result from massive adaptive radiation in a warm continent with great habitat diversity or from the genus originating in Africa.

Introduction

Most published information on the *Streptocephalus* species of Africa north of the Zambezi and Kunene rivers and of Madagascar is restricted to single countries or regions (GAUTHIER, 1933, 1938; MONOD, 1950, 1969a, 1969b), to descriptions of a small number of species (BRAUER, 1877; THIELE, 1904, 1907), or is in the form of monographs including species from several continents (DADAY, 1910a; LINDER, 1941). BRTEK (1974) provided a summary of African species sharing antennal characteristics but no figures or distribution patterns were included. The need for a single document, using uniform terminology to review the key-characters of all species recorded from the region under discussion, their interspecific relationships, and their distribution, is evident.

A total of ten species recorded from Africa north of the Zambezi and Kunene rivers and a further two from Madagascar will be considered, as will the validity of an additional six species. Unfortunately, large areas have not yet been sampled, rendering the present revisions incomplete.

Several taxonomic works (DADAY, 1910a; BARNARD, 1929; LINDER, 1941; MOORE, 1966) emphasized the efficiency of using only secondary reproductive structures for taxonomy and considered cercopods, penes, body armature, thoracopods and female morphology of only limited importance. Recently, the importance of branchiopod egg morphology in taxonomy has received much attention (GILCHRIST, 1978; MURA et al., 1978; MURA & THIERY, 1986; BELK, 1989; BRENDONCK et al., 1990; BRENDONCK et al., 1992).

Our objectives are to examine relationships among the African streptocephalids and to create species groups based on similarities in male antennal and frontal appendage morphology. These species groups will then be compared to groupings based on resting egg morphology as presented in BRENDONCK & COOMANS (in press b). Aspects of dispersal, streptocephalid origin, diversity, and interspecific relationships will also be addressed.

Terminology and abbreviations

See part 1 (HAMER et al., in press)

Materials and methods

List of museums and collections.- see part 1 (HAMER et al., in press).

The head or left antenna and frontal appendage were dissected and drawn using a Wild M-5 stereo dissection microscope and drawing tube. Scanning electron micrographs (SEM's) of antennal structures, and measurements were made following the procedure presented in BRENDONCK (1990) and HAMER et al. (in press). The drawings and SEM's were then used to group species based on common characteristics of, in particular, the hand of the S-shaped antennal process. Only adult specimens were used for study.

Information on the type material was, where possible, taken from the actual information on specimen bottles, from the original description (DADAY, 1910a), or from FORRO & BRTEK (1984). Locality data presented on specimen containers or in some old publications is, however, often incomplete or inadequate. These localities have not been plotted on the distribution map and are represented in the text by a '?'.

Except when indicated otherwise, the scale lines in Figs 2-22 equal 100 μm for SEM-pictures and 1 mm for line drawings.

Taxonomic descriptions

Class: Branchiopoda LATREILLE, 1817

Order: Anostraca SARS, 1867

Family: Streptocephalidae DADAY, 1910

Genus: *Streptocephalus* BAIRD, 1852

Type species: *Streptocephalus torvicornis* (WAGA, 1842)

Described as: *Branchipus torvicornis* Waga, 1842

Abbreviated diagnosis: see BRENDONCK (1990).

Streptocephalus rothschildi DADAY, 1908

(Fig. 2)

Streptocephalus rothschildi DADAY, 1908: 144, fig. 6. - DADAY, 1910a: 388, fig. 78.

Type material: Collected in 1904 by Baron de Rothschild, housed in MNHN, Paris.

Type locality: Abyssinia (Ethiopia), Tehoba.

Material examined: HNHM I/A-112: 1 male (15 mm) (specimen used for Fig. 2b); MNHN Bp 235: 1 male (15 mm) (specimen used for Figs 2a,b).

Abbreviated redescription: Antenna of average length. Terminal joint of antenna stout, slightly sigmoid and apically rounded (Fig. 2a). Hand broad and simple (Figs 2a,b). Thumb of average length, tapered and apically sub-acute. Spur absent. Angle between proximal and distal regions of anterior part of thumb measuring $\pm 180^\circ$ (Figs 2a,b). Finger dorsally curved and broad at base, almost same length and shape as thumb with large, rounded tooth on dorsal margin (Figs 2a,b).

Frontal appendage broad, of average length, apically bifid and with each branch acutely pointed (Fig. 2c).

Distribution: Ethiopia (Abyssinia): Tehoba (DADAY, 1908, HNHM I/A-112); Soullouki and Ouardy (DADAY, 1908). East-Africa: Menabella (DADAY, 1908) (Fig. 1).

Remarks: The HNHM specimen had, in contrast to Fig. 2a, a short, blunt thumb. DADAY (1908), however, gave no additional relevant information and more material is therefore required before the importance and extent of this variation can be determined.

Streptocephalus rothschildi shares some important antennal characteristics with *S. bouvieri* and *S. zeltneri*. The single large tooth on the finger, and the overall similarity in the shape of the hand may indicate a close relationship between these three species. In addition, the frontal appendage of *S. rothschildi*, although not as elaborate as in the other two species, is nevertheless well developed and apically branched.

DADAY (1910a) noted the similarity between *S. rothschildi* and the South African *S. purcelli* SARS. Both species have simple hands and a thumb without spur. However, a single, large tooth separates the thumb and finger in *S. purcelli* while in *S. rothschildi*, a tooth is situated on the anterior margin of the finger. Other important differences between these species are noted in the form of their frontal appendage and abdomen. We can therefore conclude that, based on antennal morphology, *S. rothschildi* is closer to the *S. bouvieri*/*S. zeltneri* group than to the South African *S. purcelli*/*S. dendyi* species group.

Streptocephalus zeltneri DADAY, 1910

(Fig. 3)

Streptocephalus zeltneri DADAY, 1910a: 396-399, fig. 81. - MONOD, 1969b: 506, figs 11-13.

Type material: Collected in 1906 by F. de Zeltner. Curated in MNHN, Paris (Bp. 225). 1 male, cercopods damaged (8 mm).

Type locality: Sudan, Yelimane (DADAY, 1910a).

Other material examined: MNHN Bp 237: 1 male (17 mm) (specimen used for Figs 3a,b,c)

Abbreviated redescription: Antenna of moderate length. Terminal joint of antenna curved and tapered, broad at base, and with bulge on the upper margin (Fig. 3a). Single, large, tooth-shaped flap (f) ventromedially at junction of basal joints of antennae and frontal appendage (Fig. 3a). Medial row of 7-8 small processes on middle part of S-shaped antennal process; another horizontally orientated row of 5-6 processes proximal to hand (not on figure). Hand simple with broad base. Thumb long, slightly ventrally curved, and tapering to a sharp apical point. Angle between proximal and distal regions of anterior part of thumb $\pm 180^\circ$. Short, blunt, spur (Fig. 3a). Finger dorsally bent, proximally broad with large, blunt triangular tooth (Figs 3a,b), followed by distinct bulge, distal to which finger tapers to narrow apex. Finger approximately two thirds length of thumb (Fig. 3a).

Frontal appendage long (one quarter length of antenna), bifid, with outer margins of each branch convexly curved. Inner margin set with two small projections; the first near the base of each branch and the second about halfway along its length (Fig. 3c).

Distribution: Senegal: pool at Ndilla dam, close to Linguere (MNHN Bp 237). Sudan: Goumbou ? (MNHN Bp 226); Yelimane ? (MNHN Bp 225).

Remarks: In *S. zeltneri* and *S. bouvieri*, there is no evidence to consider the proximal process of the thumb as a spur, since it may equally well be regarded as a large tooth. However, because of its characteristic location at the ventral base of the thumb, it is referred to as a 'spur' here.

Streptocephalus bouvieri DADAY, 1908

(Fig. 4)

Streptocephalus bouvieri DADAY, 1908: 140, fig. 3. - DADAY, 1910a: 399, fig. 82.

Type material: Collected in 1904 by Dr. I. Decorse. Housed in MNHN, Paris (Bp. 211), 1 male (10 mm).

Type locality: Central Africa, Chad: Kousseri, Mission Chari-Chad.

Other material examined: BMNH 1927.10.19.1-3. 1 male (15 mm) (specimen used for Figs 4a,b,c).

Abbreviated redescription: Antenna of moderate length (ratio to body length $\pm 0.33:1$). Terminal joint of antenna curved, distally tapering to subacute point (Fig. 4a). Large, tooth-shaped flap ventro-medially at junction of basal joints of antennae and frontal appendage (not on figure). S-shaped antennal process with two bluntly triangular processes on median surface proximal to hand (not on figure). Base of hand short and broad. Thumb simple, slightly curved, long and tapered to a point (Figs 4a,b). Angle between proximal and distal regions of anterior part of thumb measuring $\pm 150^\circ$. Spur a small blunt bulge (Figs 4a,b). Finger broad, distally slender, measuring approximately two thirds length of thumb, and with large, acute triangular tooth on proximal, anterior margin (Figs 4a,b).

Frontal appendage long (about two thirds length of antenna) with trunk divided into two branches. Each branch with short, ventrally curved process basally. Ventral margin of two main branches set with single row of small processes (Fig. 4c).

Distribution: Northern Uganda: Zaipi; E. Madi (BMNH specimens). Chad: Kousseri, Mission Chari-Chad (type locality) (Fig. 1).

Remarks: *Streptocephalus bouvieri* and *S. zeltneri* share a number of antennal characteristics. The shape of thumb and spur, the single, prominent tooth on the anterior margin of the finger, as well as the presence of projections on middle region of the S-shaped antennal process and the well developed frontal appendage suggest a close relationship.

Streptocephalus (Parastreptocephalus) lamellifer THIELE, 1900

(Fig. 5)

Streptocephalus lamellifer THIELE, 1900: 565, figs 1-4. - DADAY, 1910a: 346, fig. 62. -

Streptocephalus (Parastreptocephalus) lamellifer BRENDONCK et al., 1992: 289, figs 7,8.

Type material: Collected in 1894 by Alluaud. Type specimens housed in ZMHUB.

Type locality: Tanzania, Sumpf der Massai Njika.

Material examined: HNHM I/A-96: 1 male (12 mm) (specimen used for Figs 5b,c); MNHN Bp 221: 1 male (11 mm) (specimen used for Fig. 5a); AML 219: 5 males (13 - 15 mm).

Remark: Since the general morphology of *S. (P.) lamellifer* has recently been redescribed in detail by BRENDONCK et al. (1992), only illustrations of the antenna (Figs 5a-c) and an abbreviated diagnosis are presented here.

Abbreviated diagnosis: Male frontal appendage of moderate size and conical. Cercopods lamella-like. Thumb of hand with very long and acute apex, curved dorsally (Fig. 5a). Anterior (dorsal) margin of finger set with two large teeth and numerous small spines (Figs 5b,c). Apex of finger ventrally curved (Figs 5a,b,c).

Distribution: Kenya: Samburu (HNHM I/A-96); temporary pool alongside Tana river, near Kamburu (AML 219). Tanzania: Sumpf der Masai Nyika (MNHN Bp 221) (Fig. 1).

Streptocephalus (Parastreptocephalus) sudanicus DADAY, 1910

(Fig. 6)

Streptocephalus sudanicus DADAY, 1910b: 261, fig. 5. - MONOD, 1969b: 509, figs 14,15. - *Streptocephalus (Parastreptocephalus) sudanicus* BRENDONCK et al., 1992: 283, figs 1-4.

Type specimens: Collected in 1908 by D. F. de Zeltner and housed in the MNHN, Paris.

Type locality: Niore (Sudan, Mali, or Senegal).

Material examined: HNHM I/A-115: 1 male (20 mm) (specimen used for Figs 6a-d).

Remark: Since the general morphology, of *S. (P.) sudanicus* has recently been redescribed in detail in BRENDONCK et al. (1992), only illustrations of the antenna (Figs 6a-d) together

with an abbreviated diagnosis are presented here.

Abbreviated diagnosis: Frontal appendage of male of moderate size, conical, with acute apex. Cercopods setiferous to the tips. Thumb of hand of antenna with very long and acute apex, curved dorsally (Fig. 6a). Anterior margin of finger set with two small teeth and numerous small spines (Figs 6a,c). Apex of finger ventrally curved (Figs 6a,b).

Distribution: Mali (or Senegal): Nioro (HNHM I/A-115). Senegal: Ndilla dam near Linguere (MONOD, 1969b). Mali: Gao-Mopti. Burkina Faso (BRENDONCK et al., 1992) (Fig. 1).

Remarks: The antennae of *S. (P.) kaokoensis*, *S. (P.) zuluensis* and *S. (P.) lamellifer* and *S. (P.) sudanicus* show a number of remarkable structural similarities which clearly unite them in a subgenus (*Parastreptocephalus*) and separate them from the remainder of the genus (BRENDONCK et al., 1992).

Streptocephalus vitreus (BRAUER, 1877)

(Fig. 7)

Branchipus (Streptocephalus) vitreus BRAUER, 1877: 601, pl. 5, figs 11a,c; pl. 6, figs 12a,b. - *Streptocephalus vitreus* THIELE, 1900: 567. - DADAY, 1910a: 385, fig. 77. - GAUTHIER, 1939: 132, fig. 1. - MONOD, 1969a: 50, figs 4-5, 6-8.

Type material: Collected by Herr Marno. Museum housing type specimens unknown.

Type locality: Central Africa, Tura and el Khadra, Bahr el Abiad.

Material examined: MNHV 6817: 1 male (no measurement) (specimen used for Figs 7c,e); ZMHUB 10254: 1 male (18 mm) (specimen used for Figs 7f,h); MNHN Bp 245: 1 male (12 mm); AML 219: 10 males (12 - 15 mm) (specimens used for Figs 7a,b,d,g); BMNH 1934.2.8.178-200: 2 males (no measurements); BMNH 1959.3.2.1: 1 male. BMNH 1920.9.10.1-10: 1 male (no measurement); BMNH 1964.9.3.1: 2 vials, 4 males (no measurements).

Abbreviated redescription: Antenna of average length (ratio to body length \pm 0.3:1). Terminal joint of antenna weakly curved, ending in subacute point (Fig. 7a). Hand region of S-shaped antennal process well developed. Anterior region of thumb folded proximally with fold produced to form a projection (Figs 7b,c). Thumb long, apically acute, with

distinct bend and distal straight and slender region (Figs 7a,b). Angle between proximal and distal parts of anterior region of thumb $\pm 120^\circ$. Spur apically narrow, and separated from thumb by two, occasionally three, rounded teeth (Figs 7a,d). Broad and dorsally curved finger measuring approximately half the length of thumb, and with subacute, curved apex (Figs 7b,c). Anterior margin of finger with small, or indistinct digitiform tooth followed by large, anteriorly-directed tooth with basal, small process on median side (Figs 7b,e,f).

Frontal appendage slender, of average length, apically rounded (Fig. 7g) or with median indentation (Fig. 7h).

Distribution: Zimbabwe: Wankie (= Hwange) National Park (BMNH 1969.1.2.6-7). Kenya: Nairobi (HILDREW, 1985), Pickfords, Lake Naivasha (BMNH 1934.2.8.178-200); Riuru (BMNH 1983.103), Tana River; Kamburu (AML 219). Sudan: Khartoum (MNHV 6817); Tura el Khadra (Bahr el Abiad) (Soudan-Nilotique) (MONOD, 1969a); El Fasher, Khor pool (BMNH 1920.9.10.1-10). Tanzania: Traung, Surnefood (ZMHUB 10252); Massai Njika (ZMHUB 10252); Kilimandjaro (ZMHUB 11234); Irangi (Iringa) (MONOD, 1969a); East of Irangi (Iringa) (ZMHUB 10253); Dodoma township (BMNH 1959.3.2.1). Chad: Kousseri, Fort Lamy, Mission Chari-Tchad (MNHN Bp 239); Zakouma National Park (MNHN Bp 245; MONOD, 1969a); Massacori Mission Chari-Tchad (MNHN Bp 240); Mortcha (MONOD, 1969a) (Fig. 1).

Remarks: Variation was observed in the teeth on the dorsal margin of the finger. The proximal tooth is longer and more slender and the distal tooth broader and more rounded in some material (AML 219 specimens, Fig. 7b). Furthermore, specimens with both two and three teeth separating thumb and spur were found in the same population in the AM material (Figs 7a,d). A similar phenomenon was observed by BARNARD (1935) in a population of *S. macrourus* DADAY from the Kalahari in Botswana. The relevance of this variation needs to be investigated but more material is necessary to draw conclusions. The antennae of *S. vitreus* and *S. macrourus* share a number of important morphological characteristics, in particular the shape of anterior and posterior parts (spur) of thumb, and the finger. In addition, the teeth separating anterior part of thumb and spur are, in both species, unlike those of any other *Streptocephalus* species. The above similarities have also been noted by DADAY (1910a), BARNARD (1929) and MONOD (1969a).

Streptocephalus rubricaudatus (KLUNZINGER, 1867)

(Fig. 8)

Branchipus rubricaudatus KLUNZINGER, 1867: 23, Tab. 4. - BRAUER, 1877: 605. -
Streptocephalus torvicornis var. *rubricaudatus* DADAY, 1910a: 365, fig. 69. -
Streptocephalus rubricaudatus HARTLAND-ROWE, 1968: 319, fig. 1. - BRTEK, 1974: 1,
figs 1-7. - MERTENS & DUMONT, 1989: 211.

Type material: Type material housed in the MNHN, Paris.

Type locality: Kosseir in Egypt (DADAY, 1910a).

Material examined: BMNH 1972.II.22.3: 1 male (15 mm) (specimen used for Figs 8a-e);
BMNH 1903.2.19.1-3: 1 male (28 mm).

Abbreviated redescription: Antenna long (ratio to body length \pm 1:1.3). Terminal joint of antenna broad and apically subacute. Anterior margin of basal part of S-shaped antennal process set with a series of digitiform, irregularly shaped processes, distally increasing in size (Figs 8a,b,c). Median surface of middle part set with row of triangular teeth (3-4) (Fig. 8c). Prominent narrow, triangular flap (f) situated on median surface proximal to hand (Figs 8c,d). Base of hand long and slender with proximally folded thumb. Anterior part of thumb very long, dorsally curved, with a row of spines along dorsal margin (Figs 8a,c,e). Angle between proximal and distal parts of anterior region of thumb \pm 100°. Spur short, broad, ventrally curved and apically acute, separated from anterior part of thumb by narrow, prominent tooth (Fig. 8a). Finger approximately one quarter the length of thumb, proximally broad, and tapering to apical point. Proximal anterior region of finger with broad, flattened area, followed by a slender, digitiform tooth with small, basal tooth on its medial surface (Figs 8c,d).

Frontal appendage short, broad and apically blunt (Fig. 8f).

Distribution: Sudan: Rain puddle near Omdurman (BMNH 1903. 2.19). Libya: Guelta near Trou Aonatron Tibetsi (BMNH 1972.11.22.3); Guelta near Zowar (BRTEK, 1974). Egypt: Kosseir ? (DADAY, 1910a); Wady Sikait ? (HARTLAND-ROWE, 1968). Algeria: Oued Djerat, south of Illizi (MERTENS & DUMONT, 1989); Oued Tabaraket, north of Djanet (MERTENS & DUMONT, 1989) (Fig. 1).

Remarks: BRTEK (1962) synonymized KLUNZINGER's description of *S. rubricaudatus* with

S. torvicornis since no type material was assigned to the former species. HARTLAND-ROWE (1968), BRTEK (1974), and MERTENS & DUMONT (1989), however, pointed out the important differences between them and considered *S. rubricaudatus* and *S. torvicornis* distinct but closely related species.

Streptocephalus torvicornis torvicornis (WAGA, 1842)

(Fig. 9)

Branchipus torvicornis WAGA, 1842: 261, Tab. 11, figs 1-4. - BRÜHL, 1860: 120. - CHYZER, 1861: 77, Tab. 6, figs 3-7, Tab. 7, fig. 5. - FRIC, 1866: 557. - BRAUER, 1877: 606, Tab. 6, fig 15. - CLAUS, 1886: 267. - DADAY, 1890: 289. - *Streptocephalus torvicornis* BAIRD, 1852: 20. - DADAY, 1910a: 366, fig. 69 - HARTLAND-ROWE, 1968: 319, fig. 2. - MONOD, 1969b: 506. - THIERY, 1986: 152. - ROUX & THIERY, 1988: 228, figs 2b-e. - DUMONT et al., 1991: 203, figs 1,3.

Type specimens: unknown

Type locality: Exact type locality unknown but WAGA (1842) mentioned Warsovia as a locality in his original description.

Material examined: HNHM I/A-101: 1 male (8 mm) (specimen used for Figs 9c,d,e,f); MNHN Bp. 227: 1 male (15 mm) (specimen used for Figs 9a,b,g); 1 male with antennae removed (17mm).

Abbreviated redescription: Antenna of moderate length. Terminal joint of antenna long, slender, moderately curved and apically acute (Fig. 9a). S-shaped antennal process with medial row of digitiform processes on middle part (Figs 9b,c). Large, triangular flap (f) present on medial surface proximal to hand region (Fig. 9b). Proximal medial fold of anterior thumb region with notched margin and fold produced to form a sharp projection (Figs 9b,d). Distal thumb region of moderate length, with distinct bend, dorsal surface set with row of short spines and apically acute (Figs 9a,d,e). Angle between proximal and distal regions of anterior part of thumb $\pm 100^\circ$. Spur long, slender, dorsally curved and separated from anterior thumb region by sharp triangular tooth (Figs 9a,b). Finger proximally broad, approximately four fifths the length of thumb, dorsally curved and tapered to apical point (Fig. 9b). Anterior margin of finger with small, digitiform tooth, followed by anteriorly-directed, conical tooth with median, basal, small process (Figs 9b,d,f).

Frontal appendage short, broad, and anteriorly rounded (Fig. 9g).

Distribution: Widely distributed in North Africa, Europe and Asia, including Hungary, Russia, Poland, Austria, Bohemia, and Germany (DADAY, 1910a; FLOESSNER, 1972). North African localities include: Sahara: Redir de tfedit (HNHM I/A-101). Algeria: Guelt es Stel (MNHN Bp. 227); Sahara Atlas, (DUMONT et al., 1991); Tassilli n'Aijer, Hoggar, Tanezruft. Mauritania: Adrar. Chad: Tibesti (DUMONT et al., 1991). Niger: Air mts (DUMONT et al., 1991), Western Sahara: Tunisia (GAUTHIER, 1928, 1931) (Fig. 1).

Remarks: THIERY (1986) noted variability in shape and spination of the thumb. DADAY (1910a) recognized two varieties of *S. torvicornis*, the one redescribed here he referred to as *S. t. torvicornis* and the other as *S. t. bucheti*.

Streptocephalus torvicornis bucheti DADAY, 1910

Streptocephalus torvicornis bucheti DADAY, 1910a: 367, fig. 70. - THIERY, 1986: 152. - ROUX & THIERY, 1988: 227, fig. 2. - DUMONT et al., 1991: 203.

Type material: Type material collected by G. Buchet in 1901 and housed in the MNHN, Paris (Bp. 251, 2 females, 1 male in poor condition).

Type locality: Morocco, "Daia de Sidi Kassem et Arzilla".

Other material examined: HNHM I/A-109: 1 male (28 mm).

Distribution: Morocco: Daia de Sidi Kassem (MNHN Bp. 250); Near Arzilla (MNHN Bp. 251) (Fig. 1).

Remarks: There has been some confusion about the status of this subspecies. ROUX & THIERY (1988) pointed out the major differences from *S. t. torvicornis*: the proportion of the thumb distal to the bend and the length of the spur is 2.5:1 in *S. t. bucheti* and in *S. t. torvicornis* it is 3.5:1. In this publication, *S. t. bucheti* was also considered a subspecies. The teeth on the anterior margin of the finger do show minor differences. The proximal tooth is more upright in *S. t. torvicornis* and the large distal tooth has a convex margin in *S. t. bucheti* while it is flat or slightly concave in *S. t. torvicornis*. However, insufficient evidence was found to consider both taxa as independent species.

DUMONT et al. (1991) attribute the differences to interpopulation variability and

furthermore show that ROUX & THIERY's (1988) criteria cannot be used to separate specimens into two distinct morphological types.

Streptocephalus neumanni THIELE, 1904

(Fig. 10)

Streptocephalus neumanni THIELE, 1904: 371, figs 1-7. - DADAY, 1910a: 406, fig. 84.

Type material: Type specimens collected in 1900. Specimens housed in the HHNM (10 spp).

Type locality: Ethiopia: Harro Rufa in Ennia Galla-Land.

Material examined: ZMHUB 11137: 1 male (immature specimen); ZMUU: 1 male (17 mm) (specimen used for Figs 10a-c).

Abbreviated redescription: Antenna of moderate length. Terminal joint of antenna slender, curved and apically rounded (Fig. 10a). Anterior region of thumb proximally folded, with fold produced to form a projection (Fig. 10b). Thumb broad, distal part bent ventrally approximately halfway along its length and tapering to a sub-acute point (Figs 10a,b). Angle between proximal and distal regions of anterior part of thumb $\pm 140^\circ$. Spur large, tapered and separated from thumb by prominent, blunt tooth (Fig. 10a). Finger broad, recurved, half as long as thumb, and distally tapering to sub-acute apex (Figs 10a, b). Dorsal margin of finger set with two teeth, a proximal, small, conical and anteriorly-directed one, followed by a large, blunt triangular tooth (Fig. 10b).

Frontal appendage long and elaborate. Stout trunk with two lateral branches (1L/L) and one anterior arm (1A). Distal two thirds of each lateral branch (1L/L) bifid. Sub-branches of lateral branches 1L/L and arm 1A with sharp spines along dorsal surface (Fig. 10c).

Distribution: The only African locality for *S. neumanni* is that of the type specimens in Ethiopia/Abbyssinia (Fig. 1). This locality, however could not be found on any map. Other localities are Arabia: Sirah Batawil, Fisarab, Hadramaut (BMNH specimens); E. Aden protectorate: Jolebeid, near Wadi Dam (BMNH specimens); W. Aden protectorate: Rassais, Wadi Habib (BMNH specimens); Aden protectorate: Jebel Jihat (BMNH specimens).

Remarks: The elaborate frontal appendage of *S. neumanni* resembles that of *S. cladophorus* BARNARD. Both species have a distinct basal region with spiniform papillate lateral branches. The distal region of the frontal appendage in *S. neumanni*, however, is single, while in *S. cladophorus* it is bifid. Furthermore, the hand regions of the two species do not show any similarities. The hand of *S. neumanni* shows a closer resemblance to that of the Zimbabwean *S. trifidus* HARTLAND-ROWE, which also has a large, branched frontal appendage. The long, unbranched, papillate frontal appendage, and similar hand region of *S. proboscideus* also indicates a possible relationship between it and *S. neumanni*.

Streptocephalus distinctus THIELE, 1907

(Fig. 11)

Streptocephalus distinctus THIELE, 1907: 291, Tab. 1, fig. 2, Tab. 2, figs 8-10, 12. - DADAY, 1910a: 379, fig. 75.

Type material: Type specimen in Berlin Museum, collected by Sikova.

Type locality: Madagascar, Annanarivo.

Material examined: ZMUH K 19630. 1 male (16 mm); HNHM I/A-113. 1 male (16 mm); HNHM I/A-110. 1 male (19 mm) (specimen used for Figs 11a-e).

Abbreviated redescription: Antenna of moderate length. Long terminal joint of antenna with very slender distal region and curved apex (Fig. 11a). Hand of S-shaped antennal process with bent digitiform process on ventral margin proximal to finger (Figs 11a,b,c). Anterior region of thumb proximally folded, with fold produced to form blunt projection (Figs 11b,c). Distinct bend close to basal thumb region (Fig. 11a). Remainder of thumb long, slender, and apically acute (Fig. 11a). Angle between proximal and distal parts of anterior region of thumb 130°-140°. Spur slender and tapered, separated from anterior part of thumb by distinct, blunt tooth. Finger slender and recurved, measuring about four fifths the length of thumb (Fig. 11a). Proximal part of dorsal margin of finger with large, triangular tooth with irregular anterior margin followed by a low, ridge-like tooth (Figs 11b,c,d).

Frontal appendage slender, of moderate length and with apical indentation (Fig. 11e).

Distribution: Known from Fort Dauphin, S-Madagascar (ZMUH K 19630) and from the type locality which is probably Antananarivo (Fig. 1). Specimens in the HNHM were reported

to be from the Kalahari in Southern Africa (FORRO & BRTEK, 1984) but the identity of these specimens has not been verified.

Remarks: In the general appearance of the antenna, *S. distinctus*, resembles the southern African species group consisting of *S. cafer* and *S. indistinctus*. The characteristic process on the posterior margin of the hand region and the arrangement of a large tooth, followed by a small one on the finger, however, distinguishes *S. distinctus* to some extent from this group.

Streptocephalus spinosus DADAY, 1908

(Fig. 12)

Streptocephalus spinosus DADAY, 1908: 146, fig. 7. - DADAY, 1910a: 355, fig. 66.

Type material: Type specimens housed in the MNHN, Paris (MNHN Bp. 238). Additional material in the HNHM may be paratypes. All specimens are in very poor condition.

Type locality: Madagascar: Catat.

Other material examined: HNHM I/A-99. 1 male (specimen used for Fig. 12a-c).

Abbreviated redescription: Antenna of moderate length. Terminal joint of antenna weakly sigmoid and apically blunt (Fig. 12a). S-shaped antennal process with prominent bulge on posterior margin proximal to hand (Fig. 12a). Hand region elongated, thumb with two folds, both produced to form a projection on the anterior margin; first of these smaller than second (Figs 12a,b). Anterior and distal part of thumb dorsally bent, long, slender and apically acute. Spur weakly dorsally curved and separated from anterior part of thumb by small, blunt triangular tooth (Figs 12a,b). Finger dorsally curved, broad, approximately half the length of thumb, and with sub-acute and slightly curved tip. Dorsal margin of finger set with a proximal large triangular tooth, followed by an anteriorly-directed conical tooth (Figs 12a,b).

Frontal appendage of moderate length, broad and apically rounded (Fig. 12c).

Distribution: No details of locality other than "Catat, Madagascar" are presented in DADAY's (1910a) description, or on the museum labels (Fig. 1).

Remarks: As for the other Madagascan species *S. distinctus*, *S. spinosus* shares some

characteristics with the *S. cafer* species group from southern Africa, but it also has unique features, such as the two teeth on the anterior margin of the thumb and the two, subequal teeth on the finger.

The spine on the ventral/posterior margin of the hand illustrated by DADAY (1910a) was not observed in the HMNH specimens, but this may be due to the poor condition of this material. If this spine is present, a relationship between *S. distinctus* and *S. spinosus* could be suggested.

Additional remarks:

Besides the species redescribed above, seven additional species have been recorded from the geographical region under discussion. In some cases, their validity is questionable:

Streptocephalus proboscideus (FRAUENFELD, 1873)

Originally described from Khartoum (Sudan) (Fig. 1). It is extensively redescribed and its distribution discussed in BRENDONCK (1990) and also illustrated in HAMER et al. (in press).

Streptocephalus annanarivensis (THIELE, 1907)

Streptocephalus distinctus annanarivensis THIELE, 1907: 292.

In his original description of *S. distinctus*, THIELE (1907) described and illustrated a subspecies, *S. d. annanarivensis* from Annanarivo (Madagascar) (Fig. 1). The latter has no distinct projection on the ventral margin proximal to the hand as in *S. distinctus*. Furthermore, two large teeth are present on the finger. DADAY (1910a) suggested that THIELE was dealing with *S. similis* BAIRD. BRTEK (1974), however, considered *S. annanarivensis* a valid species. No material of this species could be found.

Streptocephalus bimarisis GURNEY, 1909

Streptocephalus bimarisis GURNEY, 1909: 285, pl. 8, fig. 3, pl. 10, fig. 12. - DADAY, 1910a: 376.

GURNEY described this species from Oued Tindja (30 miles N.W. of Tunis) (Fig. 1), Tunisia. He presented the frontal process as a short, rostral structure. The second antennae are small and the hand region consists of two subequal dactyli (finger and thumb), each with a small rounded process on the inner face at its base. No material of this species could be found.

Streptocephalus chappuisi BREHM, 1935

Streptocephalus chappuisi BREHM, 1935: 162, figs 13-15.

Recorded from Kenya, Machacos (Fig. 1). Antenna with thumb and finger of similar shape, both with large rounded process on inner surface near base. Finger shorter than thumb. This species may be identical or very similar to *S. bimarisi*. Since no study material was available, it is impossible to conclude whether it is a valid species or a synonym of *S. bimarisi*. According to BRTEK (1974), it is a dubious species since descriptions are based on juveniles with no clearly developed key-characters.

Streptocephalus gauthieri BRTEK, 1974

Streptocephalus (Streptocephalopsis) sp. GAUTHIER, 1939: 134-136, figs 2a-c.

GAUTHIER (1939) described and illustrated a *Streptocephalus* species and BRTEK (1974) considered it, from this description, to be a valid species. It resembles *S. rothschildi* in antennal morphology and in the frontal appendage, although the latter structure is longer in *S. gauthieri*. It is likely that this is a valid species, but without study material this cannot be confirmed. These specimens were collected in Tunisia-Chad, La Mortcha (between Fada and Oum Chalouba) (Fig. 1).

Streptocephalus jakubskii GROCHMALICKI, 1921

The only available study material is the type material, housed in the BMNH. These specimens were, however, immature and the male antennae are not fully developed. Consequently, without adult material, it is difficult to consider it a valid species. Specimens were collected from the Usangu-steppe (Tanzania) (Fig. 1). The reference in which this species is described could not be located.

Streptocephalus rugosus BREHM, 1960

Streptocephalus rugosus BREHM, 1960: 49, figs 4-10.

Described from Anjohimavo, Madagascar (Fig. 1). Although not cited in the list of known streptocephalids by Brtek (1974), sufficient characters are presented in the original description to consider it a valid species. No material of this species could be found.

Distinction of species groups

Using the different sets of characteristics as outlined for the southern African species (HAMER et al., in press) and listed in the caption of Table 1, the species of Africa north of Zambezi and Kunene rivers and of Madagascar were grouped as presented in Table 1.

Species group J has a set of characters which occurs exclusively in the northern region, while for the other groups, corresponding southern African streptocephalids were found.

Key to the male Streptocephalidae

- 1 a. Hand simple, thumb without spur, or spur \geq width of proximal region of thumb 2
b. Hand well developed, thumb with distinct spur, spur $<$ width of proximal region of thumb 4
- 2 a. Thumb with very short spur or with bluntly triangular tooth on ventral/posterior margin 3
b. Thumb spur absent *S. rothschildi* (Fig. 2)
- 3 a. Finger with blunt tooth, frontal appendage bifid, each branch with only 2 small processes on inner margin *S. zeltneri* (Fig. 3)
b. Finger with acute tooth, frontal appendage with 2 main branches, each with a shorter, curved lateral branch, and a ventral row of small processes
S. bouvieri (Fig. 4)
- 4 a. Tooth between thumb and spur absent 5
b. Tooth separating thumb and spur 6
- 5 a. Two large, rounded teeth on anterior margin of finger, angle between anterior region of thumb and spur *S. (P.) lamellifer* (Fig. 5)
b. Two small teeth on anterior margin of finger, distal one triangular, angle between anterior region of thumb and spur $< 140^\circ$ *S. (P.) sudanicus* (Fig. 6)

- | | | |
|----|---|--|
| 6 | a. Frontal appendage short or medium, simple | 7 |
| | b. Frontal appendage long and elaborate | 11 |
| 7 | a. One tooth between thumb and spur | 8 |
| | b. 2/3 rounded teeth separating thumb and spur | <i>S. vitreus</i> (Fig. 7) |
| 8 | a. A series of processes present on middle part of S-shaped antennal process, distal region of anterior part of thumb spinulose, triangular process on medial side of S-shaped antennal process, proximal to hand | 9 |
| | b. S-shaped antennal process without processes, anterior part of thumb smooth | 10 |
| 9 | a. Finger about 0.3x length of thumb, series of processes on curved part of S-shaped antennal process distally increasing in size | <i>S. rubricaudatus</i> (Fig. 8) |
| | b. Finger about 0.6-0.9x length of thumb, series of processes on curved part of antennal process of equal size | <i>S. torvicornis</i> (Fig. 9) |
| 10 | a. Thumb with single basal fold produced to form a single projection. First tooth on dorsal margin of finger larger than second | <i>S. distinctus</i> (Fig. 11) |
| | b. Thumb with two basal folds produced to form two projections. Teeth on dorsal margin of finger subequal | <i>S. spinosus</i> (Fig. 12). |
| 11 | a. Frontal appendage without lateral branches, series of processes on median process | <i>S. proboscideus</i> (see HAMER et al., in press, Fig. 18) |
| | b. Frontal appendage with 2 lateral branches, processes on curved part of S-shaped antennal process absent | <i>S. neumanni</i> (Fig. 10). |

Discussion: Streptocephalidae north of Zambezi and Kunene rivers and from Madagascar

The streptocephalid fauna of Africa north of the Zambezi and Kunene rivers and of Madagascar is morphologically distinct from that of other continents. *Streptocephalus torvicornis*, however, occurs throughout Europe and in large parts of Asia, and will not be considered in the following comparison. Only *S. spinifer* GURNEY, from Ceylon and India, shows similarity in the antennal hand region and in the frontal appendage with *S. zeltneri*

and *S. bouveri* of group J.

Difficulties in assigning the present species to groups were similar to those encountered for the southern African species (see HAMER et al., in press). The Madagascan species *S. distinctus* and *S. spinosus* share some characters with members of group C to which they were assigned. These species, however, could equally well be allocated to an additional and distinct group. Examination of additional characters may help to group the Madagascan streptocephalids more accurately in the future. *Streptocephalus neumanni* shows some similarities to the species of group H which includes *S. trifidus* and *S. proboscideus*. The shape of the finger and thumb and tooth separating it from the spur may, however, separate *S. neumanni* from the remainder of the group. The other *Streptocephalus* species north of Zambezi and Kunene rivers, could be assigned with less ambiguity to species groups. The creation of a tenth group, containing only northern African species was necessary to accommodate the closely related *S. rothschildi*, *S. bouvieri* and *S. zeltneri*.

General discussion: adult morphology in African Streptocephalidae

The *Streptocephalus* species of both defined African regions show some similarities. Five of the ten species groups (groups C, D, E, G, H) include species from both regions. The southern African fauna has four 'endemic' groups while the rest of the continent only has one exclusive group (group J). The regional distribution of five groups and the occurrence in both regions of only two (viz. *S. proboscideus* and *S. vitreus*) of the 27, possibly 34, *Streptocephalus* species indicates that dispersal and successful colonization are not as common as could be expected for organisms with drought-resistant, easily transportable resting eggs. Ecological factors prevailing in new habitats may frequently eliminate new arrivals. For example, it is unlikely that *S. dendyi* and *S. purcelli*, which occur in the winter rainfall regions of the western Cape, South Africa (see HAMER et al., in press) would survive if eggs were dispersed to arid regions of the continent where summer pool temperatures were exceedingly high. Some species, for example *S. vitreus*, *S. torvicornis*, and *S. proboscideus*, on the other hand, must have a wide ecological tolerance since they have successfully colonized a range of habitats over large areas.

The division of the African *Streptocephalus* species into species groups may not only help in tracing evolutionary and zoogeographical patterns, but future research may

even justify the division of the large genus into a number of genera or subgenera based on these species groups. BANARESCU (1990) stated that without knowledge of species groups, it is difficult to analyze the zoogeography of the family. To date, inter-species relations in the genus have not yet been fully examined. The division of *Streptocephalus* into three subgenera based on the frontal appendage by DADAY (1910a) was rejected by both BARNARD (1929) and LINDER (1941). Recently, the southern African *S. (P.) zuluensis*, *S. (P.) kaokoensis*, and two species (*S. (P.) lamellifer* and *S. (P.) sudanicus*) from northern/central Africa were presented as a subgenus (*Parastreptocephalus*) based on the similarities of male antennae and frontal appendage and resting eggs (BRENDONCK et al., 1992). In the present study, not all groupings were clear-cut as some species share characters with other species groups. Further research on additional characters and the application of genetic methods are necessary before a final division of the genus can be attempted.

The characters traditionally used for the identification of streptocephalids namely the male antenna, the frontal appendage, and the cercopods were most valuable for this study. The construction of African *Streptocephalus* species groups was, however, mainly based on antennal characters, such as the shape of the finger and thumb, the presence and shape of teeth on these structures, presence or absence and shape of the spur and the number of teeth separating it from the anterior thumb region, and the presence and shape of processes on the curved part of the S-shaped antennal process. The length and shape of the frontal appendage were used to a lesser extent, as were abdominal processes and the setation and shape of the cercopods in the species of the northern region. The importance of the antenna as a key-feature in streptocephalid taxonomy could be related to the process of 'specific mate recognition'. BELK (1991) suggested that receptive females select males using tactile cues provided by the antennae and frontal appendage. The hand region of the antenna, in particular, appears to be the first structure reflecting morphological changes related to speciation, and even small differences in this structure often indicate separate species (BELK, pers. comm.). The frontal appendage, however, can be misleading when examining species relationships since its configuration may be similar in species with completely different antennae as exemplified by *S. cladophorus* and *S. proboscideus*. Both species have long and papillate frontal appendages, but their hand regions show little resemblance. This is also true for *S. cladophorus* and *S. neumanni*. Similarly, the elaborate frontal appendages of *S. bouvieri* and *S. zeltneri* resemble that of *S. trifidus*, but again, the antennal hand region of the last species is very different from

that of the two former ones. However, several *S. cladophorus* populations were found with differences in the length of the frontal appendage but with identical hand regions. On the other hand, in the *S. rothschildi*/*S. bouvieri*/*S. zeltneri* group, only the latter two members have well developed frontal appendages, but all three species have a simple hand with a small, or no thumb spur and a single large tooth on the finger. In contrast, the hand of the *S. neumanni*/*S. proboscideus*/*S. trifidus* group is well developed and shows no resemblance to that of the former species group, but all three representatives also have elaborate frontal appendages. Cyst morphology is another branchiopod character currently receiving much attention, but it appeared to be of only limited value in assessing interspecific relationships (see BRENDONCK & COOMANS, in press a,b). Cyst morphology can, however, provide a useful additional character when examined in combination with other morphological features. However, the species groups based on cyst morphology as presented in BRENDONCK & COOMANS (in press a,b), show little correlation with the classification based on antennal morphology as shown here. The problems associated with the grouping based on cyst morphology appeared to be the high level of intra-specific variability and the reoccurrence of patterns in completely different taxa. It should however be noted that even species groups based on antennal and frontal appendage morphology remain tentative at this stage. This is particularly true for the species described from Africa north of the Zambezi and Kunene rivers and from Madagascar, since only limited study material was available.

Of the approximately 50 known *Streptocephalus* species, between 27 and 34 occur in Africa. This high diversity of African streptocephalids raises questions about the origin and age of the genus. BELK (1984) presumed a Laurasian origin of *Streptocephalus* because of its absence from South America and Australia which suggests that the genus moved into Africa after the break-up of Gondwana-land and showed a major adaptive radiation there. WIMAN (1979) and BANARESCU (1990), however, suggested an African origin for the genus, mainly because of its high diversity in this continent. Neither hypotheses, however, can, as yet, be falsified mainly because of the lack of anostracan fossils (TASCH, 1969). If BELK's (1984) idea is correct, however, the reason for the high species diversity in Africa still remains unclear. BELK (1977) suggested climatic zonation and habitat heterogeneity as important factors influencing anostracan diversity. The wide range of climatic regions in southern Africa for example, including amongst others, Mediterranean regions with winter rainfall in the southwestern Cape, desert regions in Botswana and Namibia, and subtropical climates in north-eastern Natal, provides large

habitat diversity. In addition, there are regions with vastly different elevations and consequently climatic regimes. However, since North America also has a range of climatic zones and habitats, the question remains why only about eleven *Streptocephalus* species occur there. An important point was raised by BARNARESCU (1990) who stated that *Streptocephalus* is the most thermophilous genus; it is absent from cold areas, most species live in the subtropical zone, and those from temperate countries develop mainly during the warm season. In this context, the vast African regions with high mean temperatures should offer more potential for colonization and speciation in *Streptocephalus* than North-America.

Dispersal by resting eggs is a key-process for successful colonization of new habitats. Potential dispersal agents are discussed in BRENDONCK et al. (1990). The relatively large number of species, and the regional distribution of some streptocephalids, may be an indication that populations are easily isolated and gene flow restricted and that dispersal and/or colonization are not frequently successful. The disjunct nature of ponds, gene flow and population differentiation in such habitats have been discussed by WIMAN (1979). It is remarkable that most of the closely related African species have small, if any, areas of sympatry (e.g. *S. macrourus* and the East African *S. vitreus*, and *S. dregei* and *S. cirratus*), and areas where members of the same species group co-occur (e.g. *S. purcelli*, and *S. dendyi*) are rare. Since sexual isolation between closely related species appears to be uncommon (WIMAN, 1979), reduced fitness of the hybrid offspring may cause the disjunct nature of localities of related species.

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Table 1. Sorting of *Streptocephalus* species north of Zambezi and Kunene rivers and of Madagascar, based on male antennal and frontal appendage morphology. Species group with no southern African representatives is indicated with thick lines.
 C: thumb and finger curved, 1 or 2 distinct teeth on finger, finger apically tapered; D: thumb and spur separated by 2 rounded teeth, finger short, broad, and dorsally curved; E: thumb spinulose, digitiform processes on S-shaped antennal process, triangular process on medial surface, proximal to hand; G: thumb not separated from spur by tooth, finger with spinules on dorsal margin; H: finger with two teeth (of which distal one conical), finger distally recurved, frontal appendage long, well developed; J: hand simple, spur (if present) reduced and not separated from thumb by tooth, single large tooth on finger, frontal appendage branched.

C	D	E	G	H	J
<i>S. distinctus</i> (Fig. 11)	<i>S. vitreus</i> (Fig. 7)	<i>S. rubricaudatus</i> (Fig. 8)	<i>S. (P.) lamellifer</i> (Fig. 5)	<i>S. neumanni</i> (Fig. 10)	<i>S. rothschildi</i> (Fig. 2)
<i>S. spinosus</i> (Fig. 12)		<i>S. torvicornis</i> (Fig. 9)	<i>S. (P.) sudanicus</i> (Fig. 6)	<i>S. proboscideus</i> (part 1, Fig. 18)	<i>S. zeltneri</i> (Fig. 3)
					<i>S. bouvieri</i> (Fig. 4)

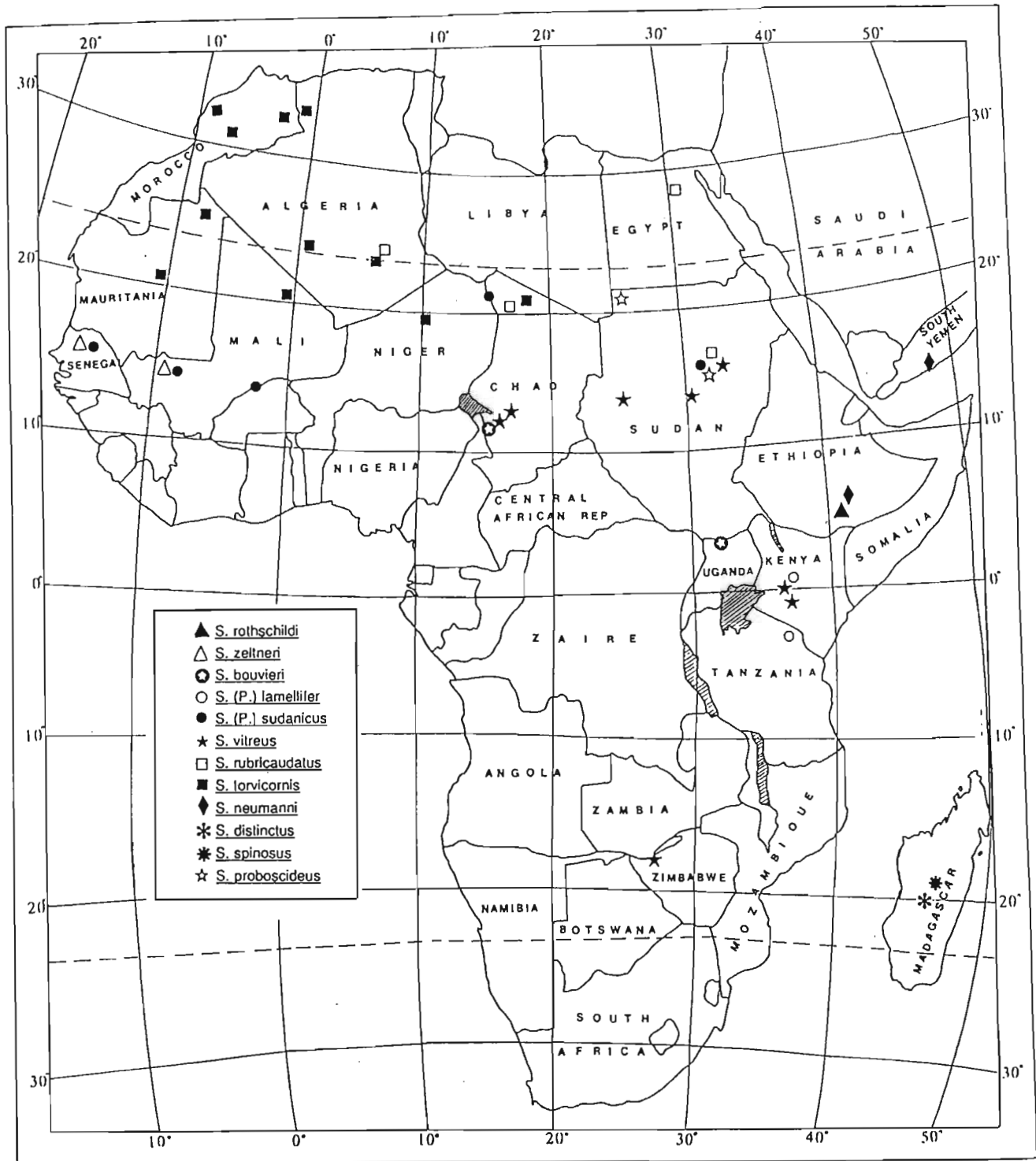


Fig. 1. Map (tentative) of Africa showing the distribution of *Streptocephalus* species recorded from the region north of the Zambezi and Kunene Rivers and from Madagascar.

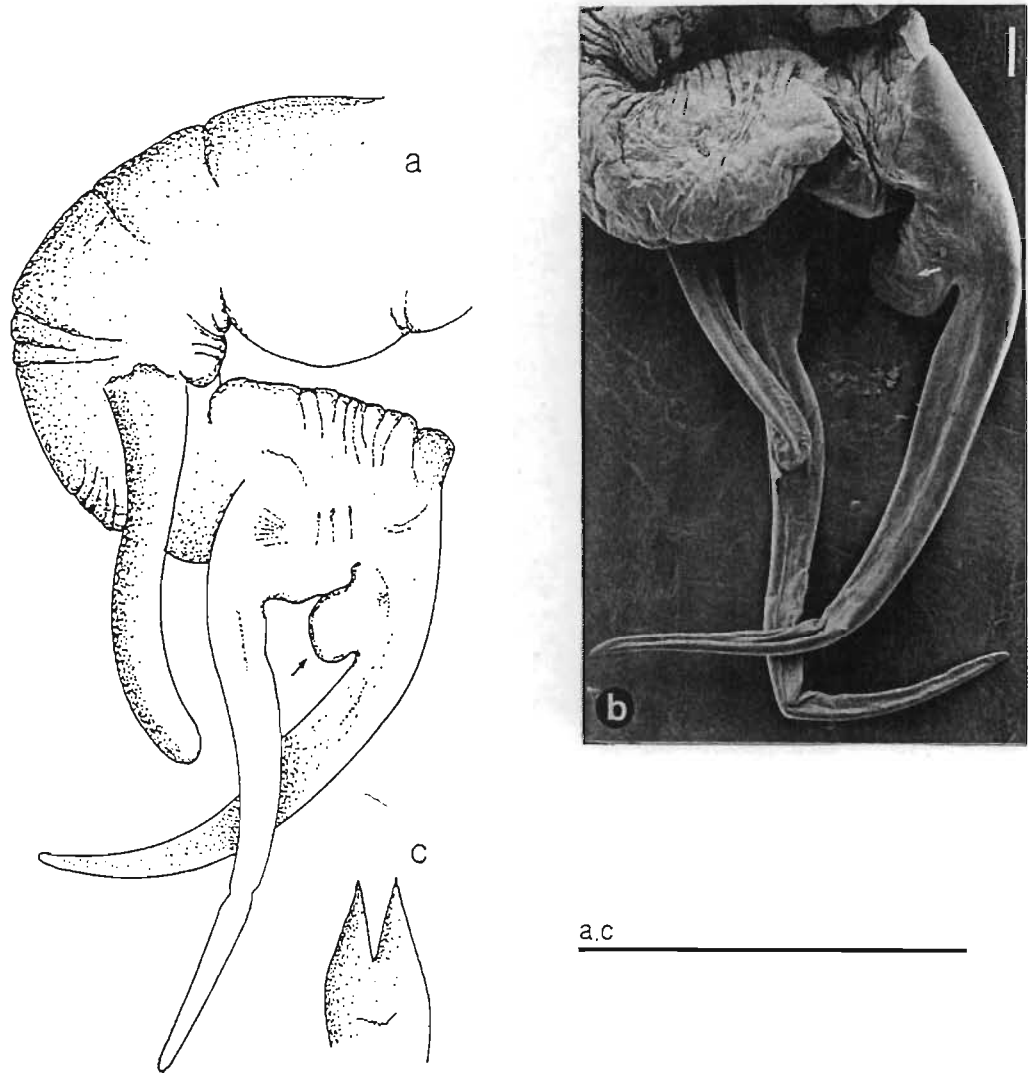


Fig. 2. *S. rothschildi* (male); a: lateral view of left antenna; b: medial view of right antenna; c: dorsal view of frontal appendage.

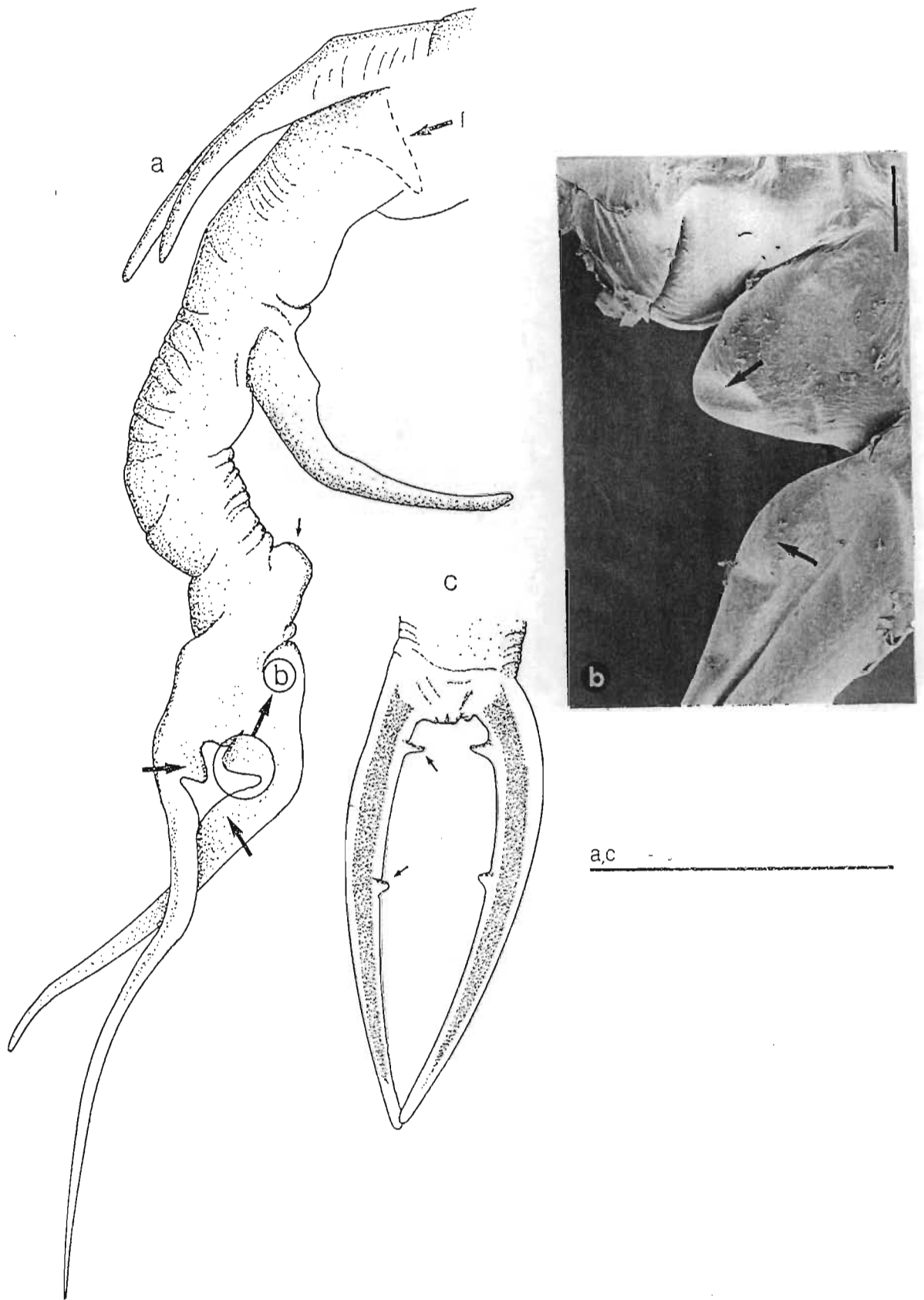


Fig. 3. *S. zeltneri* (male); a: lateral view of left antenna and frontal appendage; b: medial view of right finger showing tooth; c: dorsal view of frontal appendage. f = membranous flap.

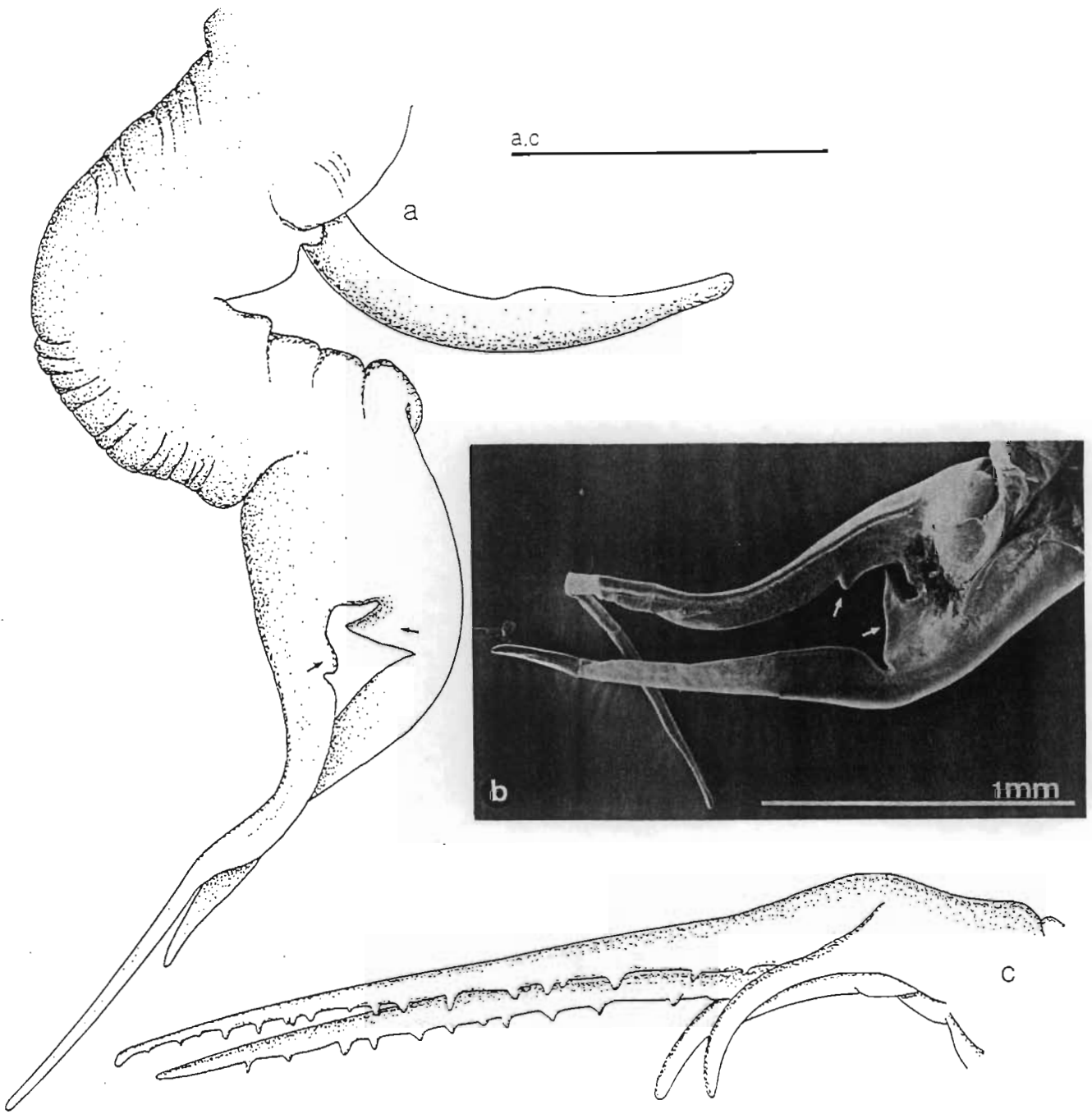


Fig. 4. *S. bouvieri* (male); a: lateral view of left antenna; b: medial view of hand region of right antenna; c: lateral view of frontal appendage.

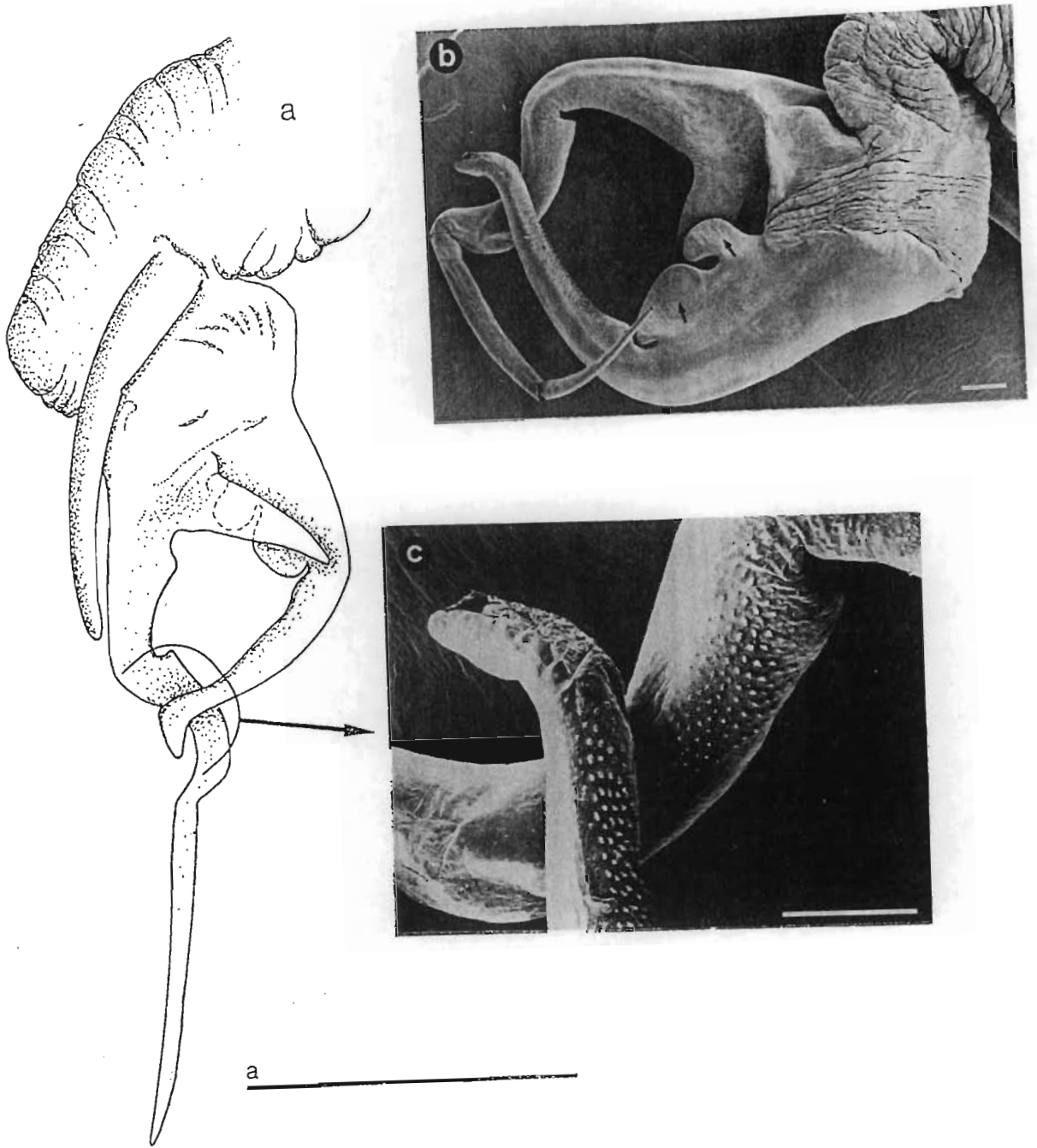


Fig. 5. *S. (P.) lamellifer* (male); a: lateral view of left antenna; b: medial view of hand region of right antenna; c: detail of spinules on finger and ventral region of thumb.

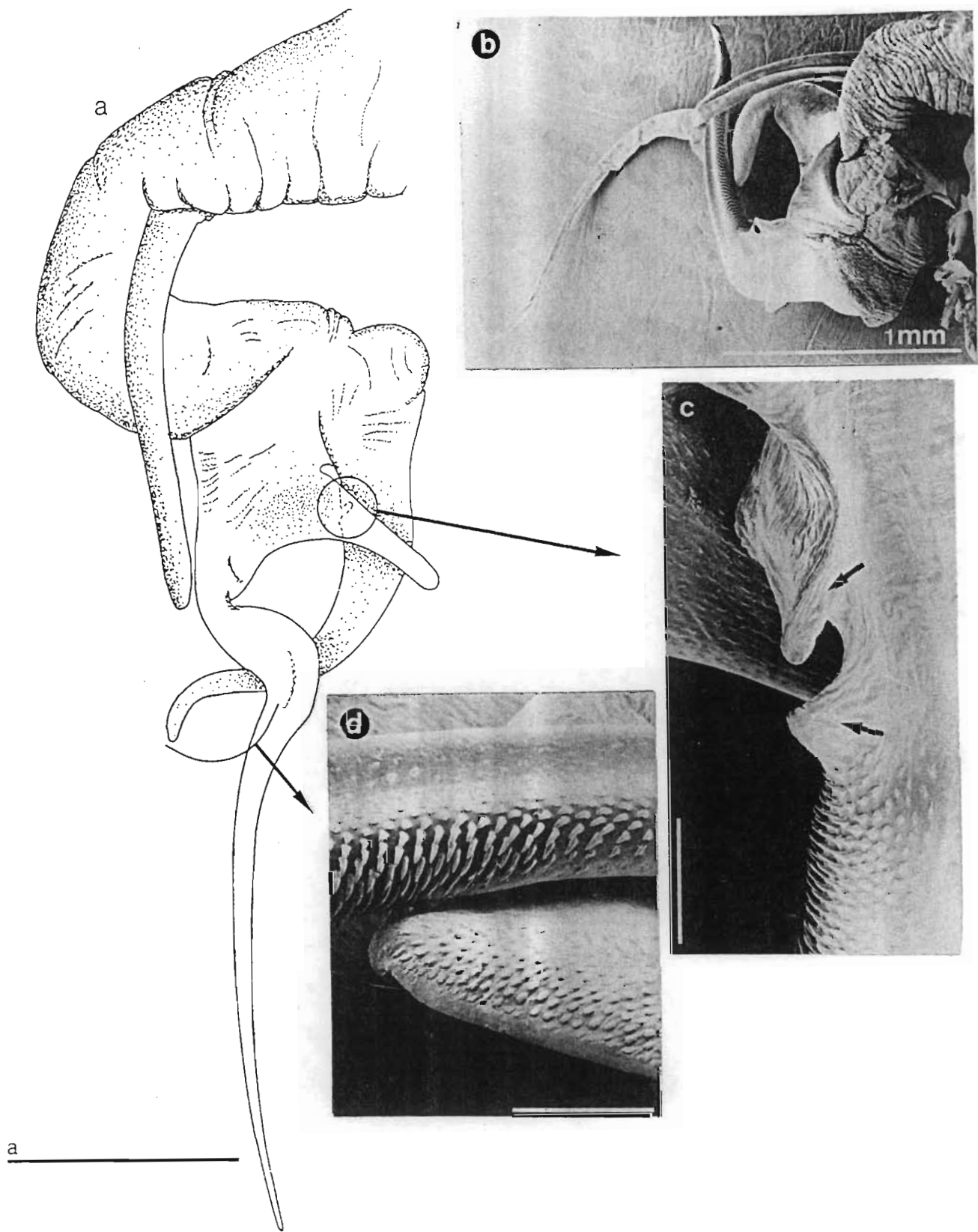


Fig. 6. *S. (P.) sudanicus* (male); a: lateral view of left antenna; b: medial view of right antenna; c: detail of teeth on dorsal margin of finger (medial view); d: detail of spinules on dorsal margin of finger and ventral region of thumb.

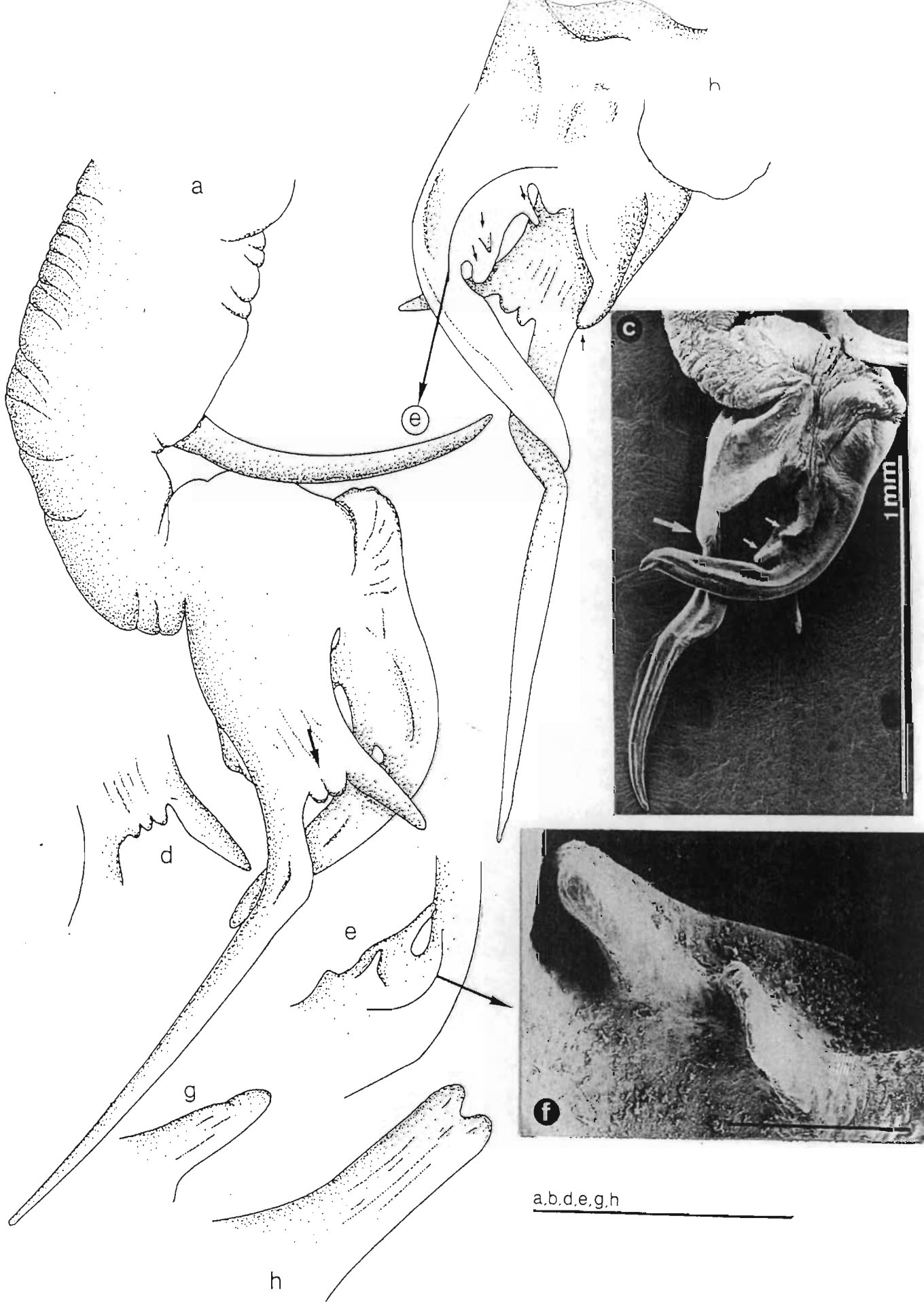


Fig. 7. *S. vitreus* (male); a: lateral view of left antenna; b: medial view of hand region of left antenna; c: medial view of hand region of right antenna; d: teeth separating anterior region of thumb and spur (AML specimens); e: medial view of teeth on dorsal margin of finger (ZMHUB specimen); f: medial view of finger showing variation in teeth on dorsal margin; g: frontal appendage (ZMHUB specimens); h: frontal appendage (AML specimens).

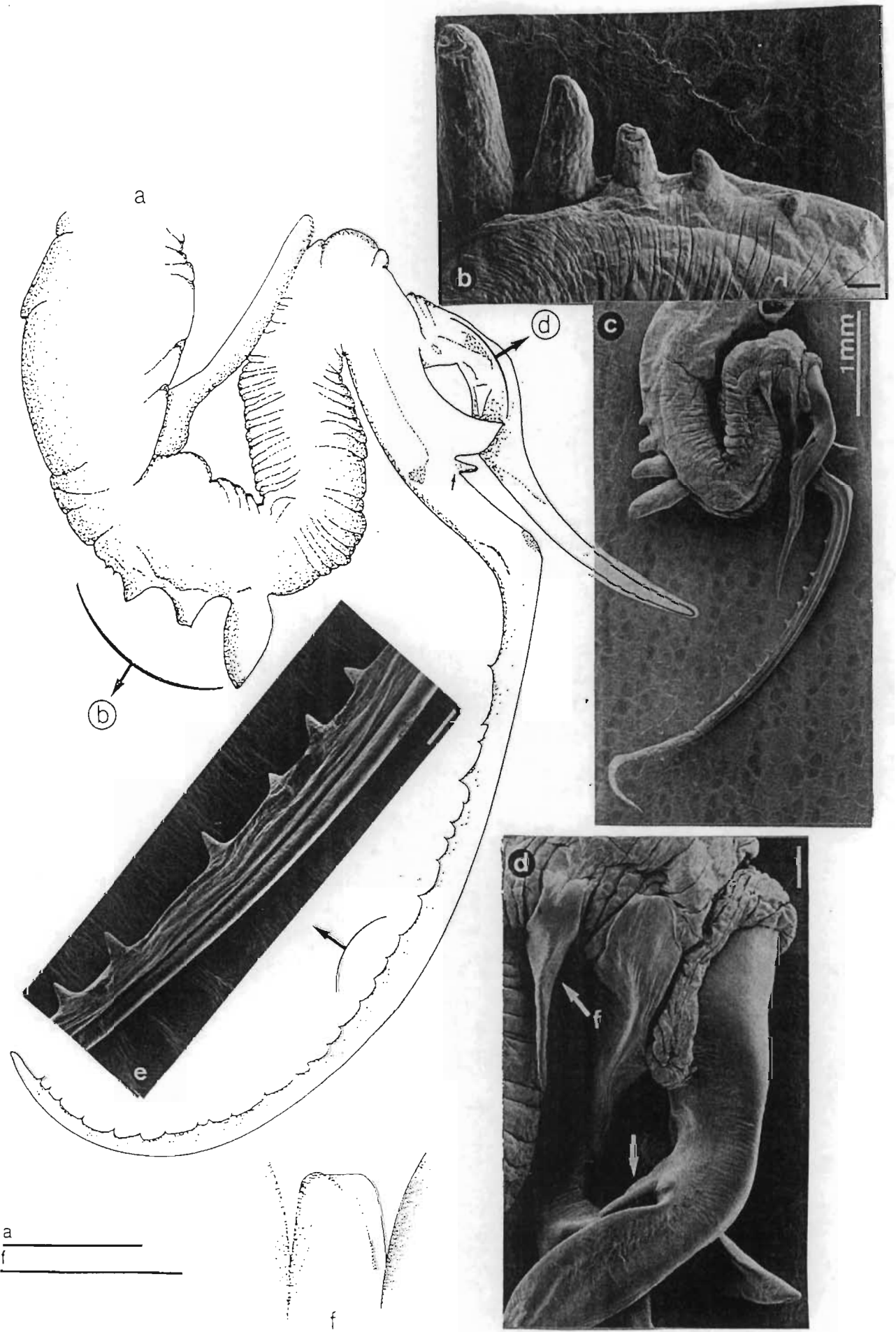


Fig. 8. *S. rubricaudatus* (male); a: lateral view of left antenna; b: dorsal surface of S-shaped antennal process with detail of processes; c: medial view of right antenna; d: medial view of right hand region; e: detail of spination of thumb; f: frontal appendage. f = membranous flap.

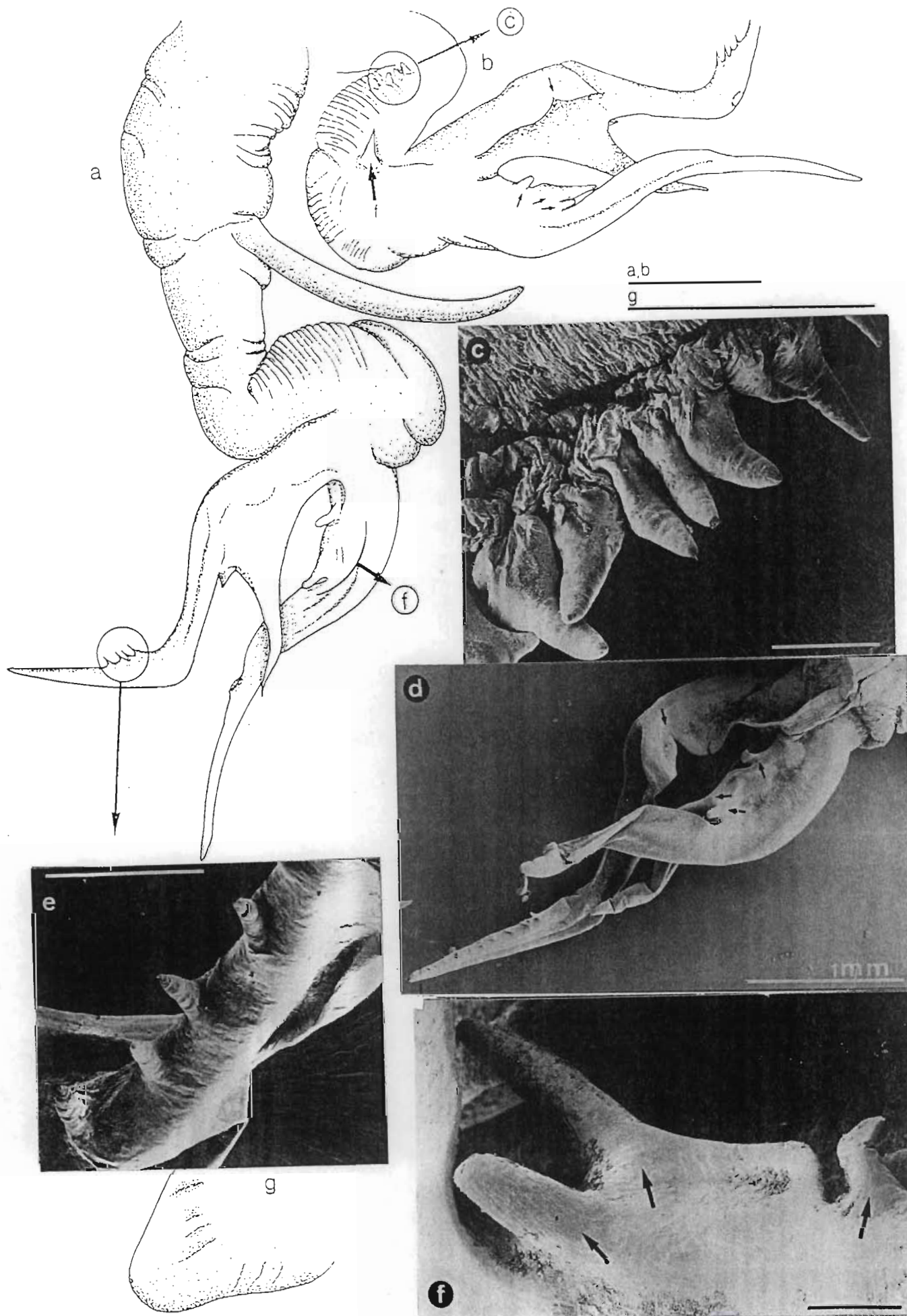


Fig. 9. *S. torvicornis* (male); a: lateral view of left antenna; b: medial view of left antenna; c: medial view of processes on S-shaped antennal process; d: medial view of right hand region; e: detail of spines on thumb; f: medial view of teeth on dorsal margin of finger; g: frontal appendage. f =

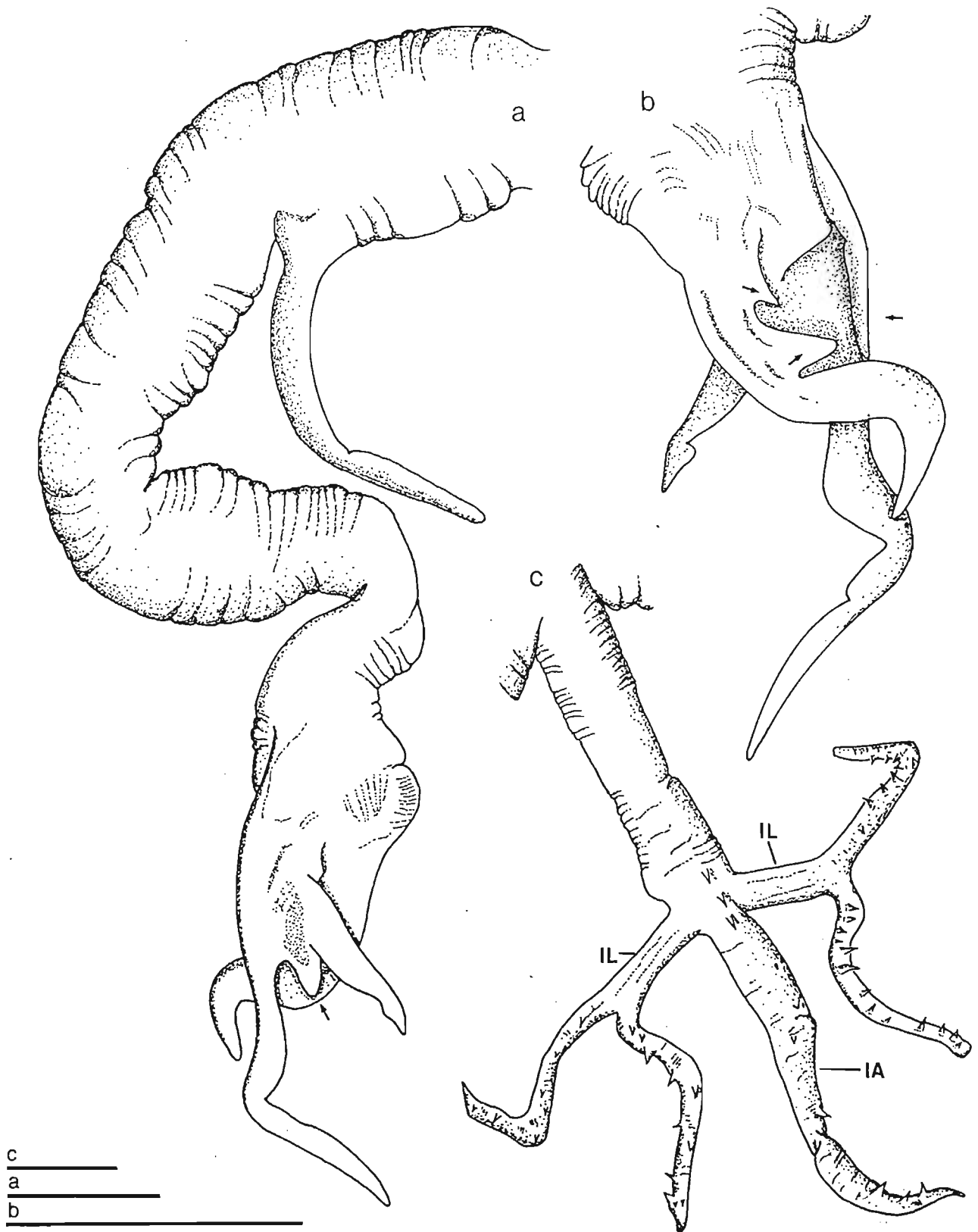


Fig. 10. *S. neumanni* (male); a: lateral view of left antenna; b: medial view of left hand region; c: dorsal view of frontal appendage. 1L = lateral branches of frontal appendage; 1A = anterior branch on trunk of frontal appendage (after BELK & PEREIRA (1982)).

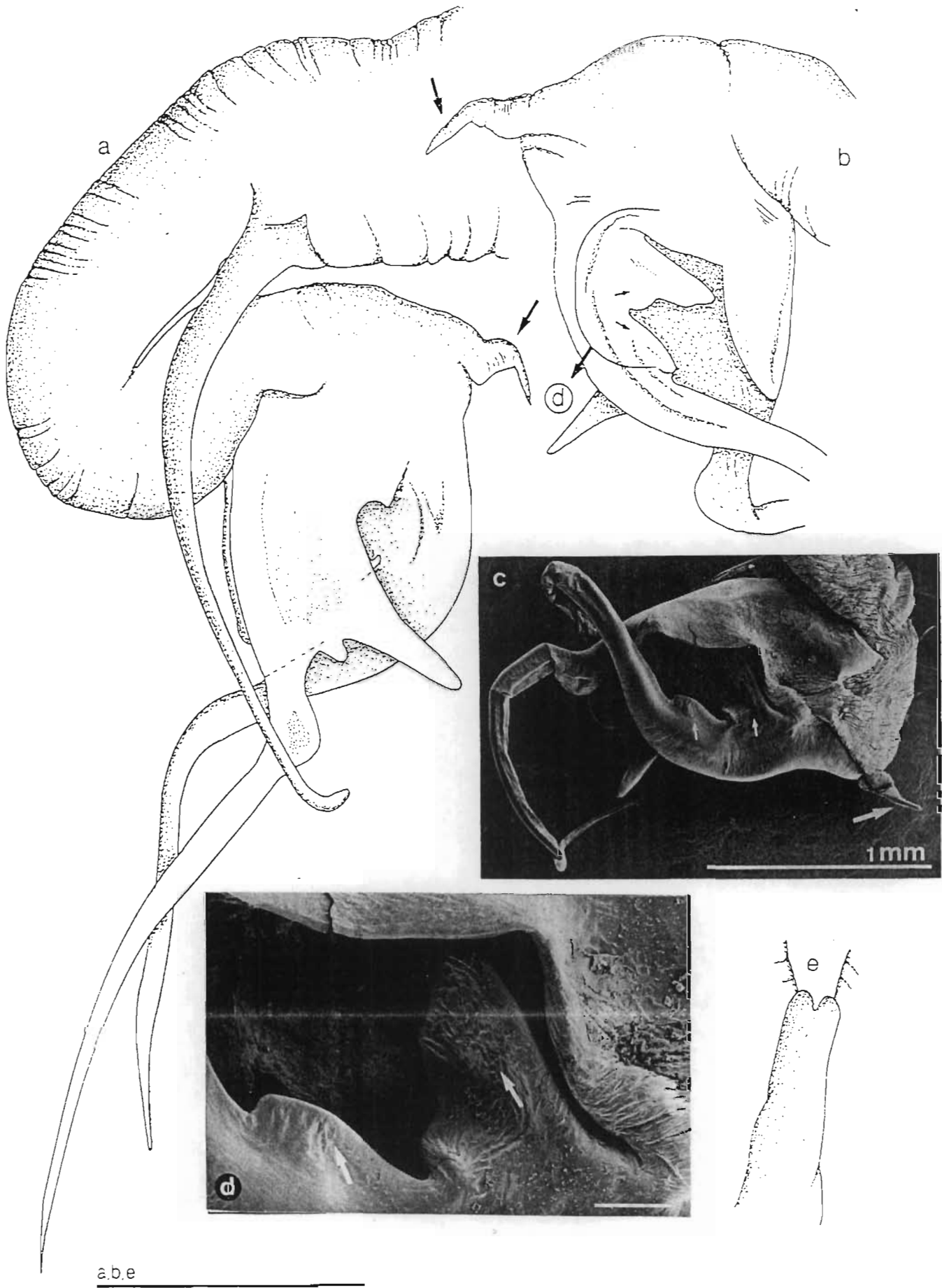


Fig. 11. *S. distinctus* (male); a: lateral view of left antenna of male; b: medial view of left hand region; c: medial view of right hand region; d: medial view of teeth on dorsal margin of finger; e: frontal appendage.

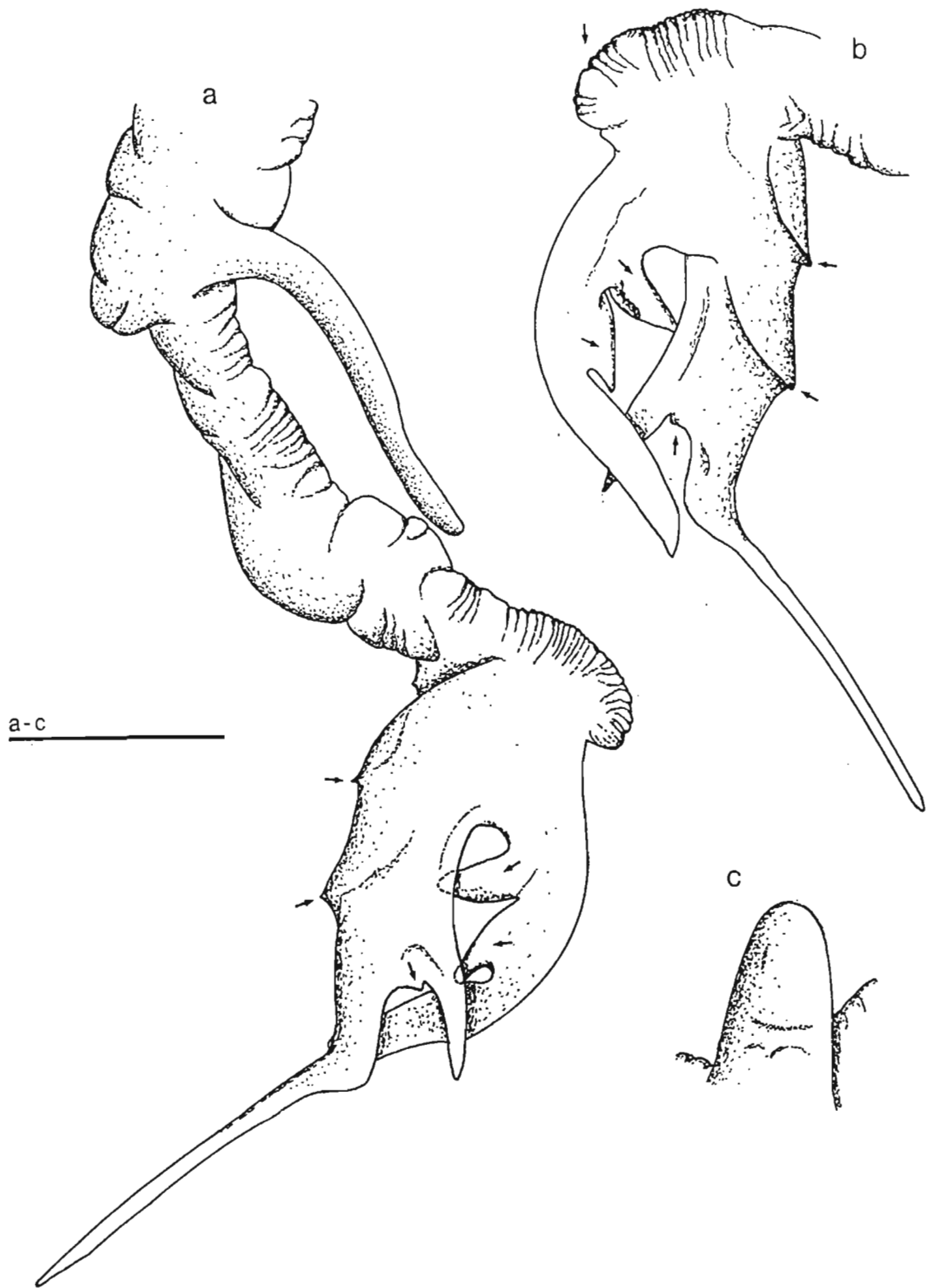


Fig. 12. *S. spinosus* (male); a: lateral view of left antenna; b: medial view of left hand region; c: frontal appendage.

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CHAPTER 2.5

ADDITIONAL RECORDS OF *Streptocephalus* (CRUSTACEA: BRANCHIOPODA: ANOSTRACA) IN SOUTHERN AFRICA, WITH THE DESCRIPTION OF A NEW SPECIES FROM ZIMBABWE

ABSTRACT

Additional specimen and locality data for 13 *Streptocephalus* species from southern Africa are presented. New distribution records from the eastern and north-eastern Transvaal, the northern Cape, Karoo, Zimbabwe and Zambia are included. A new species, similar in antennal morphology to *S. bourquinii* is described from Zimbabwe. A specimen which resembles *S. gracilis*, but which exhibits various antennal differences is illustrated and discussed. The coexistence of five *Streptocephalus* species, as well as other crustaceans in a pool in a dry river bed in the northern Cape, is unusual in a number of ways, and may have resulted from recent flooding in the area.

INTRODUCTION

During the period 1990-1992 the *Streptocephalus* of Africa were reviewed in some detail in a two part publication (Hamer, Brendonck, Appleton & Coomans in press a; Hamer, Brendonck, Coomans & Appleton in press b). A total of five new species were also described from southern Africa (Hamer & Appleton 1993; Hamer & Brendonck 1993). Subsequent to the submission of these manuscripts, a number of temporary pools in southern Africa were sampled specifically to collect anostracans. In addition, material from a survey of various waterbodies in the eastern Cape and Karoo, which was collected in 1989 and 1993 specifically for a study of the ostracod fauna of southern Africa by Dr K. Martens, was made available by the Albany Museum. These collections have revealed a number of previously unrecorded localities for various *Streptocephalus* species as well as a new species of the genus. A specimen which closely resembles *S. gracilis* Sars, but which exhibits differences in antennal morphology to this species was also collected. In order to keep the information on the anostracans of southern Africa in this thesis as up to date as possible, specimen details, locality co-ordinates and habitat data are provided for 13 *Streptocephalus* species, a description and illustrations of the taxonomically important features of the new species from Zimbabwe are presented, and the aberrant *S. gracilis* is illustrated and commented on.

MATERIALS AND METHODS

All collection, preservation, illustration and measurement techniques and specifications are as for those described in Hamer *et al.* (in press a, b) and Hamer & Appleton (1993). Material is either from the Albany Museum (AM), Grahamstown, the National Museum of Zimbabwe, Bulawayo (NMZ) or part of the author's collection which has been catalogued into the AM collection, where it will be deposited at the end of this study.

In order to avoid duplication, the new localities for those species which were presented in Hamer *et al.* (in press a) have been added to the maps in that manuscript. The localities for the species described in Hamer & Appleton (1993) and Hamer & Brendonck (1993) are illustrated, together with the new records, in figures 2 and 3 since no maps were included with the original descriptions.

RESULTS

The following data are arranged according to the order in which the species are presented in Hamer *et al.* (in press a), followed by the species described in Hamer & Appleton (1993) and finally, Hamer & Brendonck (1993).

Streptocephalus purcelli Sars, 1898b

AM LEN 130C, 1 male (18,6 mm); collected from N Cape, Grootvloer pan, 98 km S Kenhardt (30°06'24''S/20°36'15''E), a pool (4 X 5 m; 30-40 cm deep) in a dry river bed, by M. Hamer, 19 December 1992. AM LEN 230A, 23 males (23,7 ± 1,8 mm), 7 females (17,5 - 22,8 mm); collected from Namaqualand, 10 km S Niewoudtville (31°26'S/19°09'E), roadside pan 40 X 10 m, 30 cm deep, by O. Wirminghaus, 18 September 1993. AM LEN 231A, 8 males (19,4 - 22,3 mm); collected from Namaqualand, 12 km S Niewoudtville (31°26'S/19°09'E), pool 10 X 3 m, 30 cm deep, by O. Wirminghaus, 18 September 1993.

Comments

Streptocephalus purcelli had previously only been recorded from the winter rainfall region of the western Cape, in particular, Cape Town and northwards along the west coast. The last two localities fall into this area but the first is the most inland record for this species (Chp. 2.1, Fig. 2), as well as the only record from a summer rainfall habitat.

Streptocephalus dregei Sars, 1899

AM LEN 14, 1 male (26,0 mm); collected from E Cape, Grahamstown Golf Course (33°17'40''S/26°30'02''E), temporary ditch next to 9th green near clubhouse, ± 50 cm deep, by K. Martens, F. de Moor & H. Barber, 28 November 1989. AM LEN 20, 3 males (19,8; 25,0; 26,3 mm); collected from E Cape, Thomas Baines Nature Reserve, large flooded pool (50 X 50 m) on Rhino Ridge (33°23'42''S/26°30'10''E), by K. Martens, F. de Moor & H. Barber, 30 November 1989. AM LEN 29, 6 males (23,0 - 25,8 mm), 8 females 22,0-26,1 mm); collected from E Cape, 41 km from Bedford on Cradock road (32°27'30''S/25°47'50''E), small (10 X 5 m) pool in dried up dam off road to Dassiedeur, by K. Martens & H. Barber, 8 December 1989. AM LEN 34, 4 males (20,0 - 21,4 mm), 2

females (18,5; 19,9 mm); collected from E Cape, 17 km from Bedford (32°37'30''S/25°56'00''E), deep pool with little marginal vegetation and hard shale bottom, by K. Martens & H. Barber, 8 December 1989.

Comments

Streptocephalus dregei has only been recorded from the eastern Cape and appears to be the most common species in this region (Chp. 2.1, Fig. 2).

Streptocephalus cirratus Daday, 1908

AM LEN 315, 2 males (20,0; 20,6 mm), 2 females (19,0; 19,8 mm); collected from Karoo, \pm 8 km from Richmond (31°29'24''S/23°59'53''E), shallow, inundated area along road, by K. Martens, 6 April 1993.

Comments

Only five previous records exist for *S. cirratus* and the locality presented here is the second in the Karoo as well as the most southern locality (Chp. 2.1, Fig. 2).

Streptocephalus cafer (Lovén, 1847)

AM LEN 26, many specimens, most immature and in poor condition; collected from E Cape, 54 km from Bedford on the road to Cradock (32°19'S/25°44'E), muddy farm dam, by K. Martens & H. Barber, 8 December 1989. AM LEN 130C, 8 males (13,5 - 16,8 mm), 9 females (15,2 - 19,5 mm); collected from N Cape, Grootvloer Pan, 98 km S Kenhardt (30°06'24''S/20°36'15''E), pool (4 X 5 m, 30-40 cm deep) in dry river bed, by M. Hamer, 19 December 1992. AM LEN 311, many specimens, 20 males measured (13,9 \pm 0,8 mm), 18 females measured (12,6 \pm 0,9 mm); collected from road between Graaff-Reinet and Murraysburg, 1 km after entrance to Valley of Desolation (32°12'51''S/24°29'49''E), pool (5 X 15 m, 30 cm deep) along road, by K. Martens, 6 April 1993. AM LEN 322, 9 males (15,8 - 17,0 mm); collected from Karoo, road (R401) to Hofmeyer at 25km from R32 (31°41'30''S/25°29'35''E), natural pan \pm 7 m diameter, 30 cm deep, by K. Martens, 7 April 1993.

Comments

This is the most widely distributed species in southern Africa. The eastern Cape records are the first from this region and represent the most southern localities for *S. cafer* (Chp. 2.1, Fig. 2).

Streptocephalus indistinctus Barnard, 1924

AM LEN 99C, 3 males (9,3, 10,0; 10,3 mm), 2 females (9,5; 10,0 mm); collected from Kruger National Park, Pumbe Picket fence pool (24°10'S/31°55'E), by M. Hamer, 27 October 1990. AM LEN 134A, 8 males (15,0 - 17,3 mm), 2 females (13,8; 14,8 mm); collected from N Transvaal, Mopane (22°36'S/29°53'E), by O. Wirminghaus, 31 December 1992. AM LEN 135A, 1 male (12,4 mm), 3 females (11,3; 13,1; 13,5 mm); collected from Zimbabwe, 22 km N Beit Bridge on Masvingo road (22°08'S/30°03'E), by O. Wirminghaus, 31 December 1992. AM LEN 137A, large number of specimens, 21 males measured (13,6 ± 1,3 mm), 20 females measured (13,8 ± 1,1 mm); collected from Zimbabwe, 33 km S Bubi River on Beit Bridge road (21°45'S/30°28'E), by O. Wirminghaus, 31 December 1992.

Comments

These records represent the most eastern localities for *S. indistinctus*, which had previously only been collected from northern Namibia, western Zimbabwe and the Transvaal/Botswana border (Chp. 2.1, Fig. 3).

Streptocephalus ovamboensis Barnard, 1924

AM LEN 129A, large number of males, 20 measured (15,5 ± 0,7 mm), 13 females (15,0 ± 0,5 mm); collected from Tankwa Karoo, Gannakuil Farm (32°06'S/19°42'E), by M. Hamer, 4 January 1993. AM LEN 130B, 7 males (18,5 - 19,5 mm), 5 females (16,2 - 19,2 mm); collected from N Cape, Grootvloer Pan, 98 km S Kenhardt (30°06'24''S/20°36'15''E), pool (4 X 5 m, 30-40 cm deep) in dried river bed, by M. Hamer, 19 December 1992. AM LEN 232A, 8 males (22,5 - 25,0 mm), 6 females (24,0 - 24,5 mm); collected from Karoo, 98 km N Beaufort West along N1 (31°53'S/23°04'E), shallow farm dam (15 X 30 m), by O. Wirminghaus, 11 September 1993. AM LEN 304, 21 males (17,2 ± 0,9 mm), 16 females (17,2 ± 1,2 mm); collected from Karoo, road to Graaff-Reinet, ± 5 km from Pearston

(32°33'54''S/25°05'23''E), water catchment pond, by K. Martens, 5 April 1993. AM LEN 308, many specimens but most immature, 5 mature males measured (12,8 -14,3 mm), 4 mature females measured (14,0 - 15,0 mm); collected from Karoo, 6 km from turn off to Pearston (32°27'13''S/24°42'09''E), temporary dam, by K. Martens, 6 April 1993. AM LEN 316, large number of specimens, all in poor condition; collected from Karoo, 13 km from Richmond on road to Middelburg (31°23'35''S/24°03'40''E), large pan (50 X 50 m, > 1 m deep), by K. Martens, 7 April 1993.

Comments

Streptocephalus ovamboensis is the most common species in the arid southern Namibia, northern Cape and Karoo regions of southern Africa (Chp. 2.1, Fig. 3).

Streptocephalus gracilis Sars, 1898a

Fig. 1

AM LEN 130H, 1 male (18,1 mm); collected from N Cape, Grootvloer Pan, 98 km S Kenhardt (30°06'24''S/20°36'15''E), pool (4 X 5 m, 30-40 cm deep) in dried river bed, by M. Hamer, 19 December 1992.

Comments

This specimen shows a number of morphological features in common with *S. gracilis*, a species recorded only from Port Elizabeth and Cape Town (Chp. 2.1, Fig. 4) and of which little material has been collected. The two sets of specimens examined for Hamer *et al.* (in press a) exhibited differences in aspects of the male antennae and the Grootvloer specimen has a number of antennal features unique to it. The most obvious differences include the presence of various projections on the antennal process which are not present in either of the other sets of specimens. These projections take the form of numerous small, papilliform projections on the ventral surface of the proximal region of the median antennal process (Figs 1A-B) and a number of irregularly-sized and arranged projections on the folded part of the thumb of the antennal process (Fig. 1B). The frontal appendage of the recently-collected specimen is apically more deeply-indented than in the other specimens (Fig. 1C). Cercopod morphology (Fig. 1D) and the papillae on the abdomen are the same in all specimens examined.

Streptocephalus papillatus Sars, 1905

AM LEN 130A, 12 males ($19,6 \pm 0,5$ mm), 20 females ($20,1 \pm 1,1$ mm); collected from N Cape, Grootvloer Pan, 98 km S of Kenhardt ($30^{\circ}06'24''\text{S}/20^{\circ}36'15''\text{E}$), pool (4 X 5 m, 30-40 cm deep) in dried river bed, by M. Hamer, 19 December 1992.

Comments

This species was last collected in 1939 in the Karoo. *Streptocephalus papillatus* appears to be restricted to the arid Karoo and northern Cape regions of South Africa (Chp. 2.1, Fig. 4).

Streptocephalus zuluensis Brendonck & Hamer, 1992

AM LEN 136A, 7 males (14,4 - 17,5 mm), 8 females (13,8 - 14,8 mm); collected from Zimbabwe, 15 km S Bubi River on Beit Bridge road ($21^{\circ}42'\text{S}/30^{\circ}29'\text{E}$), by O. Wirminghaus, 31 December 1992.

Comments

This recently described species had only been collected from two pools on the Makatini Flats in north-eastern Natal. The Zimbabwe record illustrates that it has a wider distribution in the subtropical part of southern Africa than previously thought (Chp. 2.1, Fig. 4).

Streptocephalus trifidus Hartland-Rowe, 1968

AM LEN 138A, 1 male (10,6 mm), 5 females (12,5 - 14,8 mm); collected from Zimbabwe, 15 km S Chiru on Harare to Beit Bridge road ($19^{\circ}04'\text{S}/30^{\circ}55'\text{E}$), by O. Wirminghaus, 30 December 1992. AM LEN 143A, 1 male (9,4 mm), 3 females (10,5; 12,0; 12,3 mm); collected from Zambia, 21 km NE Monze on Lusaka road ($16^{\circ}16'\text{S}/27^{\circ}21'\text{E}$), by O. Wirminghaus, 20 December 1992.

Comments

Streptocephalus trifidus appears to be widespread in Zimbabwe, and the Zambian record (not indicated on Fig. 4 of Chp. 2.1) could indicate a distribution much further north

as well.

Streptocephalus bidentatus Hamer & Appleton, 1993

AM LEN 136B, many specimens, 20 males measured ($11,4 \pm 0,6$ mm), 20 females measured ($11,3 \pm 0,6$ mm); collected from Zimbabwe, 15 km S Bubi River, on Beit Bridge road ($21^{\circ}42'S/30^{\circ}29'E$), by O. Wirminghaus, 31 December 1992. AM LEN 137C, 2 males (8,3; 11,3 mm), 2 females (8,8; 9,4 mm); collected from Zimbabwe, 33 km S Bubi River on Beit Bridge road ($21^{\circ}45'S/30^{\circ}28'E$), by O. Wirminghaus, 31 December 1992.

Comments

This species had been recorded only from north-eastern Natal and Swaziland (Fig. 2). The new localities indicate that its range could extend further north into Mozambique (Fig. 2). The closely related species *S. vitreus*, which occurs in Chad, Tanzania, the Sudan and Kenya, has been recorded from Hwange (Wankie) Game Reserve in western Zimbabwe. The area between the *S. bidentatus* localities in southern Zimbabwe and those for *S. vitreus* in Hwange need to be sampled to determine whether specimens have a morphology intermediate between *S. bidentatus* and *S. vitreus* which could invalidate the former species.

Streptocephalus spinicaudatus Hamer & Appleton, 1993

AM ECR 149, 5 males (12,8 - 14,0 mm), 10 females ($13,4 \pm 0,5$ mm); collected from E Cape, pan near Glen Avis ($30^{\circ}47'37''S/28^{\circ}12'02''E$), diameter ± 20 m, shallow, vegetated, by K. Martens, 29 March 1993. AM ECR 192, 22 males ($22,9 \pm 0,8$ mm), 18 females ($21,6 \pm 0,5$ mm); collected from E Cape, Indwe/ Dordrecht road, ± 5 km outside Dordrecht ($31^{\circ}21'42''S/27^{\circ}06'06''E$), grassy and sedgy dam (5 X 15m), by K. Martens, 2 April 1993. AM ECR 193, 8 males (22,5 - 24,1 mm), 3 females (22,0; 22,5; 23,3 mm); collected from E Cape, ± 15 km from Queenstown on road from Dordrecht ($31^{\circ}49'46''S/26^{\circ}55'52''E$), shallow dam (50 X 50 m) with much vegetation, by K. Martens, 2 April 1993.

Comments

This species was described from Umtata in the Transkei. The new records indicate that

it is relatively common in the north-eastern Cape (Fig. 2) where temperatures are lower, and rainfall higher than in the southern region where *S. dregei*, a closely related species is found.

Streptocephalus namibiensis Hamer & Brendonck, 1993

AM LEN 131A, large number of specimens, 20 males measured ($14,0 \pm 0,8$ mm), 20 females measured ($13,1 \pm 0,8$ mm); collected from N Cape, Vaalbos Game Reserve, Graspan-Holpan area ($28^{\circ}47'S/24^{\circ}18'E$), large (50 X 40 m, 60 cm deep) pan with dense algae, by M. Hamer, 17 December 1992.

Comments

Streptocephalus namibiensis is distributed over a wide area; from northern Namibia and Botswana and into the southern Transvaal (Fig. 3). This is the only record of this species in the northern Cape, where the closely-related *S. proboscideus* is also found.

Streptocephalus wirminghausi n.sp.

Figs 4-5

Material

Holotype. AM LEN 141A, 1 male (12,6 mm); collected from NW Zimbabwe, Chirundu, turn off to sugar estate ($16^{\circ}02'S/28^{\circ}52'E$), by O. Wirminghaus, 29 December 1992.

Paratypes. AM LEN 141A, large number of specimens, 20 males measured ($12,4 \pm 1,2$ mm), 20 females measured ($12,8 \pm 1,0$ mm); same collection data as holotype specimen.

Other material examined. NMZ/Cr22, 1 male (10,5 mm), 1 female (13,1 mm); collected from NW Zimbabwe, ephemeral pools 4 km SW of Nyakaskanga Fly Gate ($16^{\circ}09'S/29^{\circ}08'E$), by Falcon College Expedition, 19 December 1984.

Differential diagnosis

These specimens resemble *S. bourquinii* Hamer & Appleton very closely in the morphology of the antennae. Both have simple antennal processes, a long, slender and geniculate anterior part of the thumb, and a curved, slender finger with a large, triangular tooth on the dorsal surface (Figs 4A, 5A-D). However, the tooth on the finger of *S. bourquinii*

is followed by a low, ridge-like tooth while this is absent in the Zimbabwe specimens (Figs 5B,D). In addition, the three irregular triangular processes present on the anterior margin of the antennal process just proximal to the hand region of *S. bourquinii* are absent in the Zimbabwe specimens and the tooth separating the anterior and posterior parts of the thumb is more prominent in the new species (Fig. 4A). The frontal appendage of the Zimbabwe specimens lacks the slight distal median indentation found in that of *S. bourquinii* (Fig. 4A). There is no difference in cercopod shape or setation (Fig. 4B). Egg shell sculpturing also differs slightly with the eggs of the Zimbabwe specimens having more distinct ridges separating depressions which are narrower and with a smoother surface than in *S. bourquinii* (Fig. 5E). The apex of the brood pouch in the new species reaches the last abdominal segment while in *S. bourquinii* it is only as long as the seventh segment.

Distribution

The new species has only been collected from the extreme western part of Zimbabwe.

Etymology

The Zimbabwe species is named after Mr. Olaf Wirminghaus, who collected not only the type material described here, but also a large amount of material from other areas during the course of this study.

Comments

The differences listed above are sufficient evidence that two separate species are involved; even small differences in the teeth on the finger usually indicate different species (Hamer & Appleton 1993).

DISCUSSION

The collection of five species of *Streptocephalus* species in a pool in a dry river bed in Grootvloer Pan is an unusual phenomenon since the occurrence of more than two anostracan species in a habitat has been found in only 1% of habitats in the United States, while single species have been found in 80% of the habitats (Donald 1983). In addition to the anostracan fauna, *Triops granarius* (Notostraca) and the conchostracan (Spinicaudata) genera *Leptestheria* and *Caenestheriella*, three calanoid copepod species and three *Daphnia* species were also

represented (Dr. N. Rayner pers. comm.). Such branchiopod diversity has only been approached in southern Africa in large pans in north-eastern Natal where there was marginal vegetation and a number of different types of microhabitat (Hamer & Appleton 1991). The Grootvloer pool lacked vegetation of any sort, and was, by comparison with the north-eastern Natal pans, very small. Thiéry (1991) found six anostracan species, two notostracans and two Spinicaudata in a pool on Chaouia plain in Morocco. He suggested the coexistence of this diverse fauna could have resulted from abiotic factors since the pool was located at the boundary between two climatic areas. A second reason for the unusually high number of species was given as the difference in life history characteristics, in particular the growth rates, maximum size and lifespan of the coexisting species, which allows them to utilise different resources in the pool. In the Grootvloer case, this may account for the survival of three branchiopod orders, but there was considerable overlap in size of the five streptocephalid species in the pool. In addition, in the Moroccan pool, the six anostracan species were distributed among at least four different genera. A possible explanation for the coexistence of five congeneric species in the Grootvloer Pan could be the floods in the area during February and March of 1988. The flood waters may have carried eggs or adult crustaceans from other areas in the northern Cape affected by the floods, into the river. Once the river subsided, a large number of species may have been trapped in a depression which has since become the ephemeral pool sampled. Subsequent to the 1988 floods, drought conditions have prevailed in the region, thus preventing the animals or their eggs from being washed downstream. This scenario, however, does not explain the presence of *S. purcelli*, previously only recorded from the west coast/ Namaqualand part of the Cape, in this pool which lies inland and upstream from these areas. The same is true for *S. gracilis*. The antennal morphology of the specimen identified as the latter species may be interpreted simply as intraspecific variation, or as representing an undescribed species. The presence, however, of the closely related *S. papillatus*, which has many papilliform processes on the antennae, in the same pool could, however, suggest that the *S. gracilis* specimen is a hybrid between these two species. Pre-mating reproductive isolation has been found to be unusual in the streptocephalids (Wiman 1979), and would be unlikely to evolve when two species do not occur sympatrically. In the unusual Grootvloer habitat, it is quite feasible to expect hybrids, particularly between closely-related species.

The collection and identification of specimens during the last four years illustrates that

in an area such as southern Africa, where temporary pools and their fauna have been neglected, there will be a need to constantly update distributional data and that new species as well as morphological variation in described species will be found. Unusual habitats and phenomena such as the fauna of the Grootvloer pool will also raise a number of interesting questions. This information, and continued study are important in the field of biogeography, in understanding speciation and dispersal processes and in the context of biodiversity conservation.

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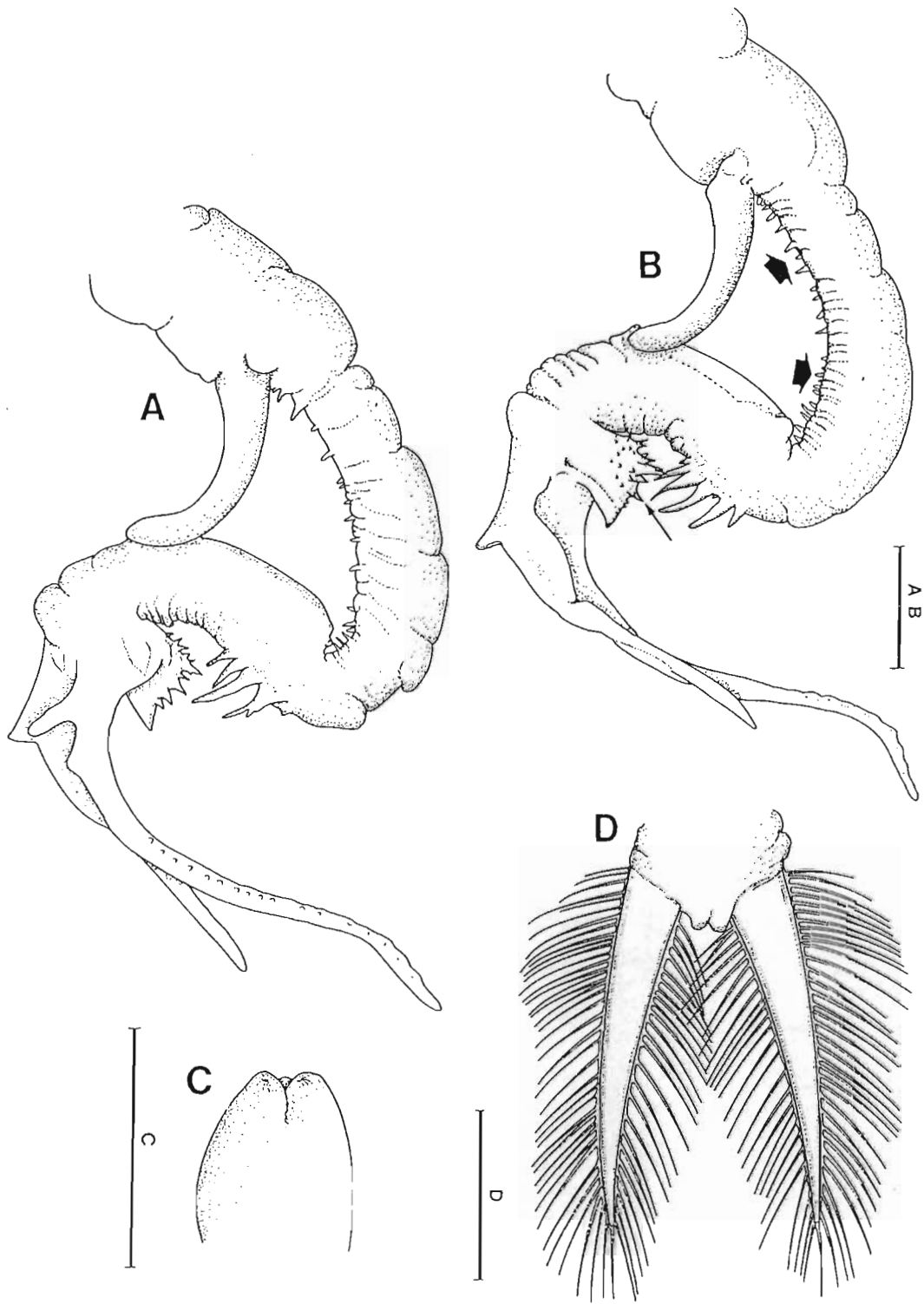


Figure 1. *Streptocephalus gracilis* (AM LEN 130H)

A = lateral view of second antenna. B = median view of second antenna, arrows indicate papillae not found in other *s.gracilis* specimens. C = frontal appendage. D = cercopods. Scale lines = 1,0mm.

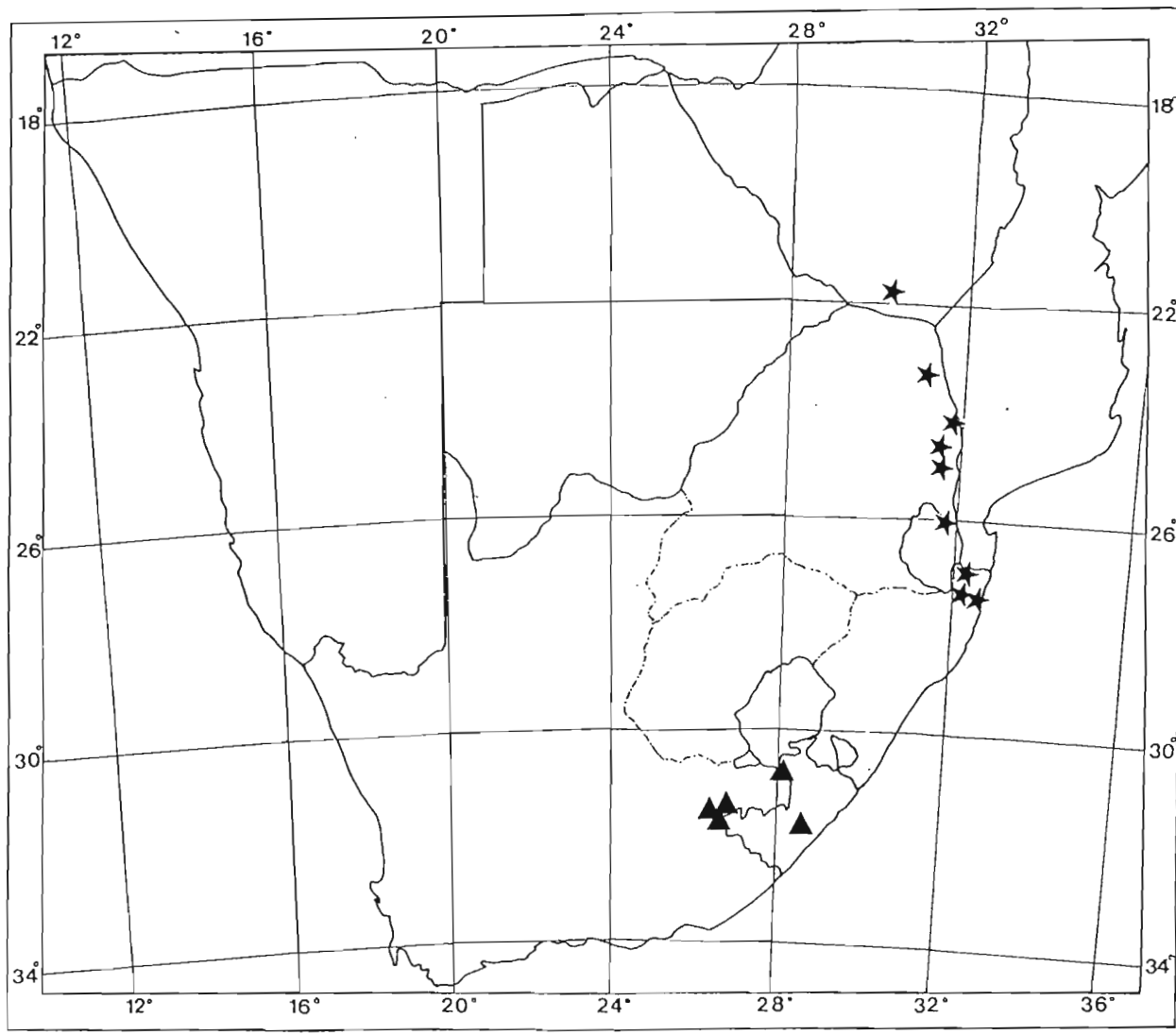


Figure 2. Map of southern Africa showing the distribution of ★ *S. spinicaudatus* and ▲ *S. bidentatus*.

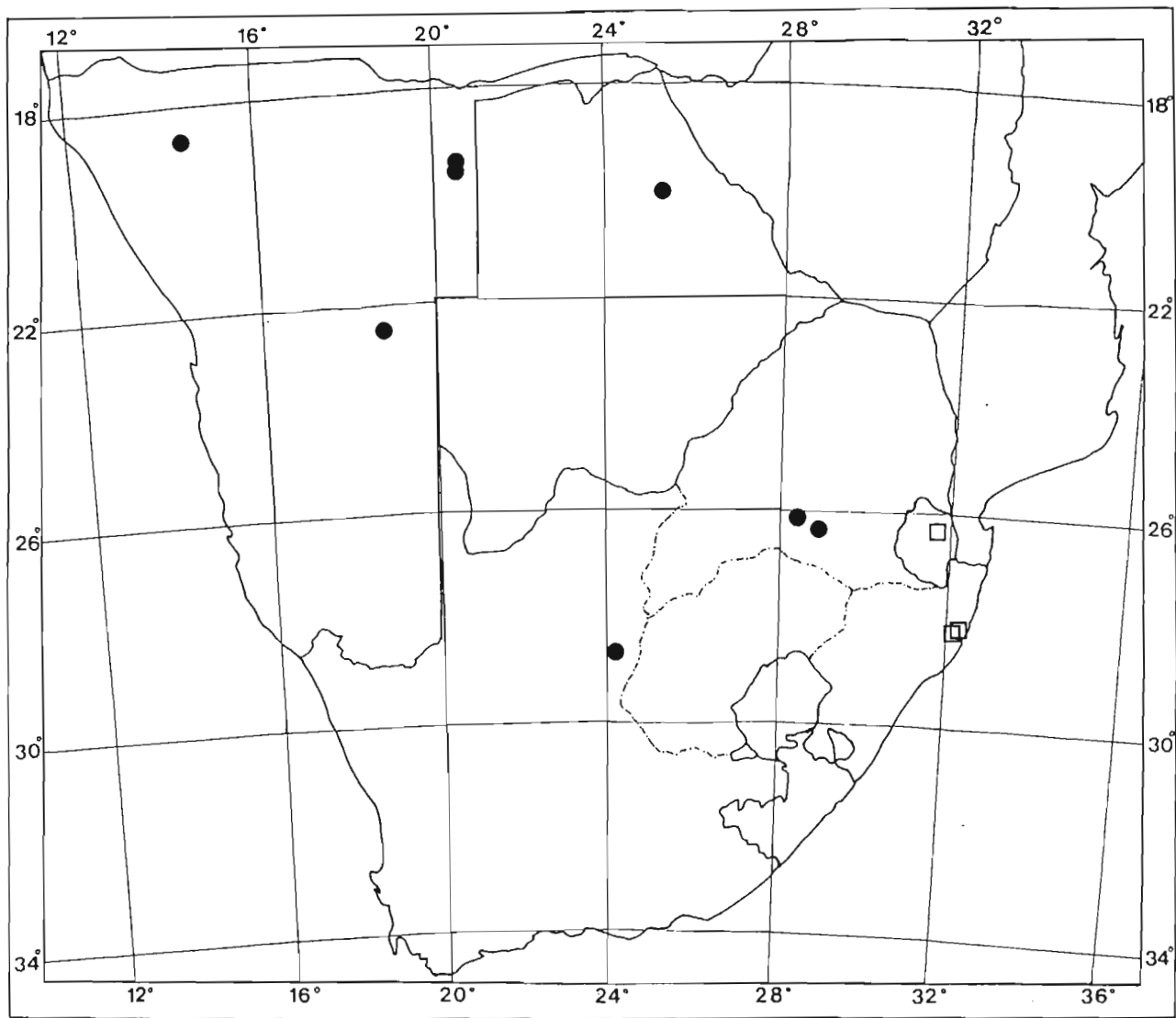


Figure 3. Map of southern africa showing the distribution of ● *S. namibiensis* and □ *S. bourquinii*.

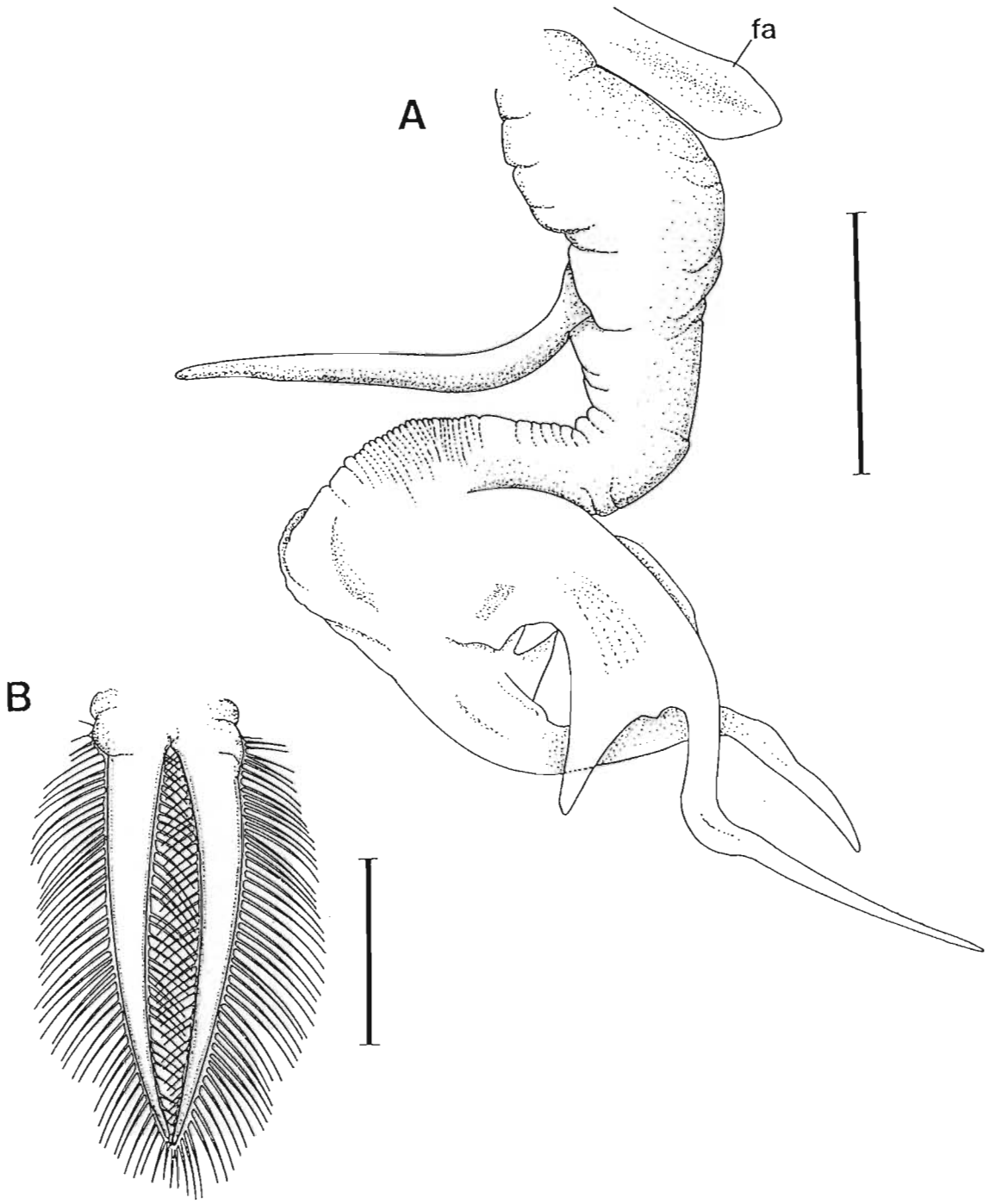


Figure 4. *Streptocephalus wirminghausi* n.sp.

A = lateral view of antenna and frontal appendage. B = cercopods. Scale lines = 1,0mm.

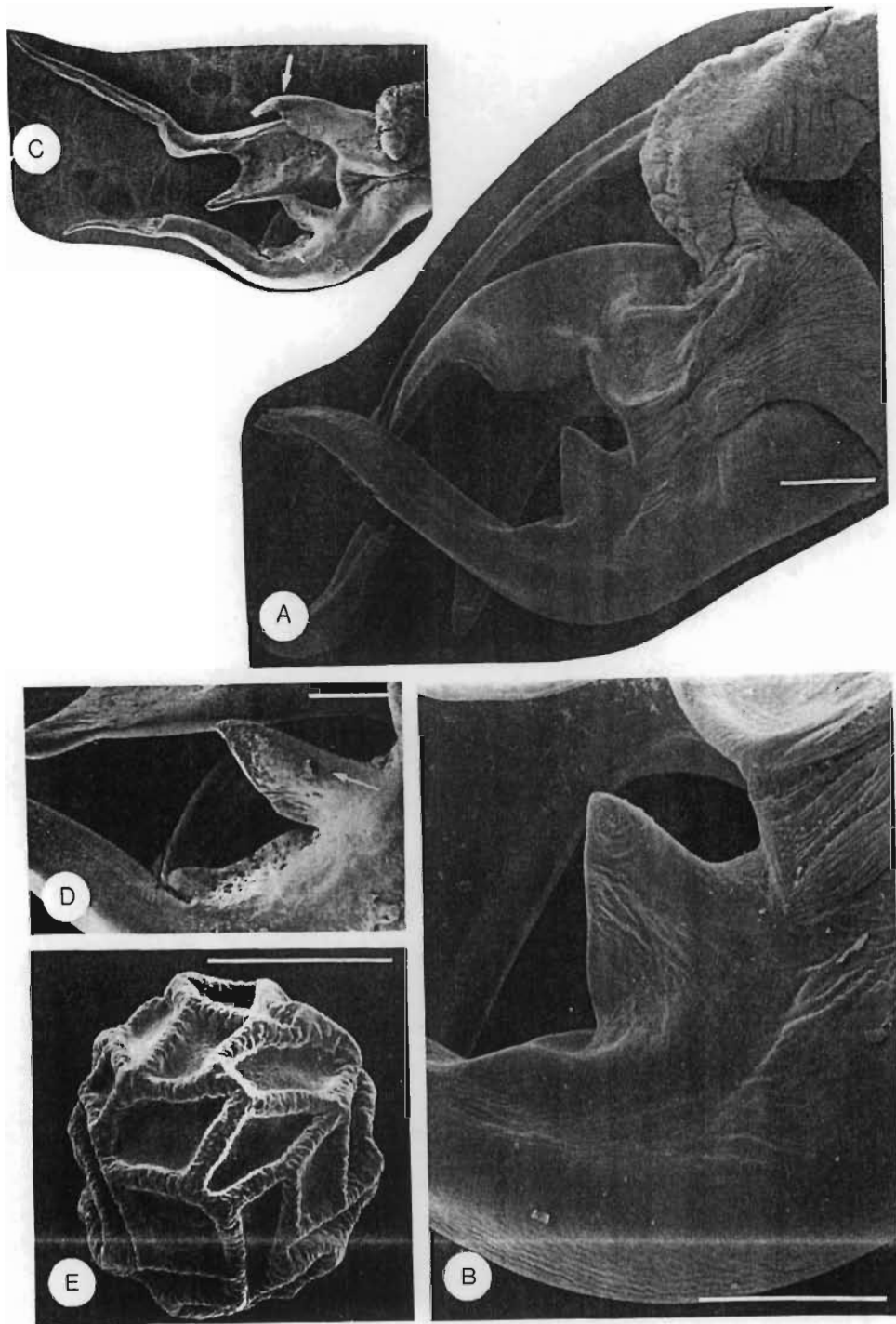


Figure 5. *Streptocephalus wirminghausi* n.sp. and *Streptocephalus bourquinii*.

A = median view of distal region of antennal process (*S. wirminghausi*); scale line = 100µm. B = detail of tooth on dorsal surface of finger (*S. wirminghausi*); scale line = 50µm. C = median view of distal region of antennal process (*S. bourquinii*). D = detail of tooth on dorsal surface of finger (*S. bourquinii*). E = cyst; scale line = 100µm.

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CHAPTER 3

A PRELIMINARY REPORT ON *Artemia* (BRANCHIOPODA: ANOSTRACA) IN SOUTHERN AFRICA

ABSTRACT

The genus *Artemia* has been recorded from very few localities in southern Africa. Bisexual populations were sampled from the coastal region of Port Elizabeth early this century and more recently, sexually reproductive specimens were collected from the Cape West coast. A sample which contains only females could indicate that a parthenogenetic population is present in Swakopmund, Namibia. Frontal knob morphology of the West coast specimens strongly resembles that of the type material of *A. salina* from Lynington, England which does not differ significantly from the Mediterranean and North African specimens. Populations from the latter regions have been designated *A. tunisiana*. The apparent absence of *Artemia* from many of the natural salt pans in southern Africa and the great similarity to *A. tunisiana* in frontal knob morphology could indicate the origin of the southern African populations in North Africa and/ or the Mediterranean. However, more data on the distribution of *Artemia* in southern Africa, as well as genetic and cross-breeding studies with populations from other regions are necessary before any conclusions can be drawn.

INTRODUCTION

The family Artemiidae includes a single genus, *Artemia* (Linder 1941) which is confined to hypersaline habitats between the latitudes 60°N and 40°S (Bănărescu 1990). A single species was described in 1755 and named *Cancer salinus* by Linneus in 1778 but renamed *Artemia salina* in 1819 by Leach. For many years it was accepted that a single, bisexual species existed. In 1840 a parthenogenetic population was discovered in France and during that century, variation within *A. salina* was observed which led to a number of different species being proposed. None of these, however, gained any long term recognition since much of the variation was a result of environmental influences. It was only in 1939, when reproductive isolation between two sexual populations was established (Kuenen 1939), that the idea of *A. salina* consisting of more than one species became accepted. During the 1960's (Gilchrist 1960; Bowen 1965; Halfer Cervini, Piccinelli, Prosdocimi & Baratellizambuni 1968) additional isolated populations were discovered. Barigozzi (1980) and Bowen, Davis, Fenster & Lindwall (1980) outlined the reorganisation of *A. salina* into a number of sibling species (species which are morphologically indistinguishable but which are isolated, either in terms of reproduction, or by the nature of their adaptations to a particular habitat). Five bisexual sibling species and *A. parthenogenetica* which encompassed all parthenogenetic populations were listed. The name *A. salina* was dismissed since it had been used to describe the type population from Lymington, England which had been extinct for almost two centuries and since the description had been found to apply to a number of species.

Browne & MacDonald (1982) stated that only sexual reproduction occurred in *Artemia* populations in the western hemisphere while in the Old World, parthenogenesis predominates, with 70% of the populations having this mode of reproduction. The most common species in the western hemisphere is *A. franciscana* Kellogg, 1906 while a second species, *A. monica* Verrill, 1869 occurs only in Mono Lake in California. The latter species is unable to survive in any other habitat because of the unique nature of the chemistry of Mono Lake. *Artemia persimilis* Piccinelli-Prosdocimi, 1968 is restricted to Hidalgo in Argentina and is isolated from the other species by having 44, rather than the usual 42, chromosomes (Browne 1993). Outside of the western hemisphere, sexual species of *Artemia* are represented by *A. tunisiana* Bowen-Sterling, 1978, which occurs in the Mediterranean and North Africa and by *A. urmiana* Günther, 1900, which has been described from Lake Urmia in Iran but may also occur in

central China and in some other Asian localities (Browne 1993). No sexual populations of the latter species have, however, been present in recent times in Lake Urmia (Mura, Del Caldo & Fanfani 1989a). *Artemia parthenogenetica* is widespread with localities in Spain, Italy, Yugoslavia, Bulgaria, Rumania, Russia, Turkey, Iraq, Israel, Morocco, India, Japan and China. It is believed (Geddes 1980) that both *A. parthenogenetica* and *A. franciscana* populations which are present in Australia were introduced by man.

Browne (1993) suggested that the parthenogenetic populations are monophyletic and arose from a bisexual population (probably *A. urmiana*) about 5,6 million years ago. At that same time the Mediterranean Sea was cut off from the Atlantic Ocean and dried up, leaving only shallow, saline lakes in which parthenogenetic reproduction would have been advantageous. Browne (1993) attributes the absence of parthenogenetic populations from the New World to the fact that the transition from sexual to asexual reproduction is a rare and complex phenomenon which either has not occurred in the New World or which has simply never become established in that area.

In spite of the more than 5000 publications and numerous books on *Artemia* (Browne 1992), very little information is available on this genus in the region of Africa south of the Sahara. Persoone & Sorgeloos (1980) listed several localities in Africa including Kenya (Elmenteita), Mozambique (Nhamaiane), South Africa (Coega Flats and Zwartkops) as well as Madagascar (Salins de Diego). However, they provided no information on whether the population is sexual, neither do they give the reference or contact from which their data were obtained. Browne (1993) reported a population of introduced *A. franciscana* in Kenya and this may be the same record as that mentioned above. Barnard (1929) reported *A. salina* var *Koppeniana* Fisher from salt pans at Port Elizabeth and Zwartkops (in the Port Elizabeth area) and a second variety (var *milhausenii*) (Fisher) from natural salt pans at Narugas and Kourop (Gordonia district of the northern Cape). Browne (1993) states that parthenogenetic populations are found from southern Africa and indicates the coastal region of Namibia as the locality on his map but the source of this record is also unknown.

Most evidence for the existence of distinct species within *Artemia* has been through isolation experiments and genetic data. Mura *et al* (1989a), however, examined the frontal knob morphology of four of the bisexual species to determine whether this could be used as

a taxonomic character. This structure is situated on the median surface of the basal joint of the male antenna. The taxonomic value of the frontal knob could be related to its function in reproduction. Wolfe (1980) stated that during mating and the normal clasping position, involving the male antennae, the frontal knobs are brought into close contact with the first genital segment of the female, where they are positioned into two depressions, the copulation cups, located along the lateral surfaces of the genital segment. Wolfe (1980) suggested that the spines on the frontal knob are probably modified for grasping. In addition to the spines, a series of sensory setae are also present on the anterior surface of the frontal knob. Mura *et al* (1989a) found a distinct difference in the shape and spinal arrangement in various sexual *Artemia* species. The Old World *A. tunisiana*, in particular, could be easily separated from the western hemisphere species. Mura *et al* (1989a), however, did state that the significance of these findings were unknown. In a later publication, Mura (1990) compared the frontal appendage morphology of specimens from the now extinct type locality of Lymington, England, with populations from four localities in Italy. All specimens were found to have very similarly-shaped frontal knobs, but some variation in the frequency of spines arranged in singles, doublets, triplets, quartets and quintets was evident. Mura (1990) did, however, conclude that the type specimens were the same as those from Italy, and those from North Africa in terms of frontal appendage morphology. She suggested that, at least the Italian populations, which had been investigated from a reproductive barrier, chromosome and DNA point of view and been found to conspecific, be referred to as *A. salina* rather than *A. tunisiana*.

As a result of the small amount of material collected during the course of this study and because of time and facility constraints, it was decided that only two aspects of the southern African *Artemia* be examined. The first of these is to determine and document the nature of reproduction of the populations sampled thus far. The second aspect is to illustrate the frontal knob morphology of a southern African population, to compare this with the findings of Mura *et al* (1989a), Mura, Fanfani & DelCaldo (1989b); and Mura (1990) and to attempt to identify the species present in the region on the basis of this characteristic. An abbreviated diagnosis for the genus and illustrations of the main features of the southern African representatives are also provided even though the former has been included in numerous other works and the latter do not differ significantly from other bisexual Old World *Artemia* populations.

MATERIAL AND METHODS

Artemia material was obtained on loan from the South African Museum (SAM), Cape Town, South Africa. Specimens from Namibia were collected by Dr. J. Day of the University of Cape Town and supplied for examination by Dr. D. Belk of Our Lady of the Lake University, San Antonio, Texas, USA.

Material collected during the course of this study will be deposited in the Albany Museum (AM), Grahamstown, South Africa and has been catalogued under AM LEN.

Drawings were done using a Wild M-5 dissecting or a Leitz Labor Lux 12 compound microscope and the appropriate drawing tube. Measurements were made under the dissecting microscope using a graticule at X6 magnification. Body length measurements were taken from the front of the head (excluding the antennae) to the tips of the cercopods (excluding the setae) and these are presented as the mean \pm standard deviation where more than ten specimens were available. Electron microscope preparation and procedures are as for the other anostracan families and the methods published in Hamer & Appleton (1993).

RESULTS

Family: Artemiidae Grochowski, 1896

Genus: *Artemia* Leach, 1819

Abbreviated diagnosis

Antennae of male somewhat fused basally by a narrow median plate. Median surface of basal joint with distinct, rounded frontal knob about halfway along its length. Terminal joint broad and flattened. No sharply defined seminal vesicles in the male, and penes project ventrally close together. Basal parts of penes thick proximally but tapering and with a pair of medio-ventral, spine-like outgrowths. Retractable apical parts without armature. Division between eighth segment and telson not always distinguishable. Cercopods broad, short and with long plumose setae along entire margin. Brood pouch of female short and broad with two lateral lobes and a pair of ventral spines.

Material examined with comments on reproductive mode

AM LEN 148A, 18 males ($8,2 \pm 0,9$ mm), 11 females ($8,4 \pm 0,8$ mm); collected from Cape, Yserfontein, Rooipan by M. Hamer, 16 July 1990. These specimens were collected from a clearly bisexual and abundant population inhabiting a large natural salt pan, approximately 1 km inland.

AM LEN 190A, 2 females (6,9; 5,1 mm) collected from Cape Agulhas region, Bredasdorp, Springfield commercial saltworks by M. Hamer, 19 July 1990. These two specimens were collected after much time spent sampling the pans which had been abandoned for a number of years and were thickly overgrown with algae. Neither of the specimens had a fully developed brood pouch. Because of the scarcity of specimens in the pans it is impossible to comment on the reproductive mode of the population.

JD P11, 12 females ($6,9 \pm 0,5$ mm), in poor condition, collected from Namibia, a pool on the roadside near Swakopmund, about 300 m from the sea by J. Day, date unknown. It is possible that this is a parthenogenetic population but more material needs to be collected before this can be validated.

All material housed in the SAM has dried out completely and for this reason, measurements were not made.

SAM-A6291 and SAM-A6292, these specimens are in the same vial and the following collection data are given: collected from Port Elizabeth, salt pan at north end of Port Elizabeth, January 1910; and Zoutpan of Zwartkops (also (Port Elizabeth) by Drege, 13 November 1909. These specimens are definitely *Artemia* and a number of males are present in the sample.

SAM-A7286, both males and females present, clearly *Artemia*; collected from Port Elizabeth, NE of Prince Alfred Lake by Drege, date unknown.

SAM-A7285, males and females present, collected from Mimosa by Drege, date unknown.

SAM-A7261, males and females collected from Cape, Gordonias district, Narugas and Kourop by K.H. Barnard in 1925. These specimens are in such poor condition that their identity as *Artemia* cannot be verified and may be inaccurate since the male antennae do appear smaller, in proportion to the body than the other dried *Artemia* examined. Barnard (1929) stated that he had picked the specimens out of dried mud and so they were in a poor, fragmentary condition when originally collected and examined. Natural salt pans are common in this area but attempts to hatch material out of dried sediment from here by both Barnard

and during the present study were unsuccessful.

Morphology of southern African specimens

The male and female antennae, male cercopods and penes and female brood pouch are illustrated in figures 2 and 3A. The spines on the median ventral surface of the penes and on the ventral surface of the brood pouch, mentioned by Linder (1941) are small and obscure in the Yserfontein (AM LEN 148A) specimens. The spines on the brood pouch were more obvious in the Swakopmund (JD P11) specimens.

Frontal knob morphology

Frontal knob of the Yserfontein (AM LEN 148A) specimens conical in dorsal view, almost kidney-shaped in median view. Sensory setae more numerous on dorso-median surface with spines concentrated on median and medio-ventral surface of frontal knob and few sensory setae scattered in this region. Spines arising from narrow depressions and arranged singly, or in twos, threes or fours with the frequency of these arrangements, compared with those of Mura (1990) for the type material from Lymington, England and Sfax from Tunisia shown in Table 1. Length of spines approximately 3,15 - 5,0 μ m.

Table 1: Frequency (expressed as a % of the total counted = 193) of spine groupings on the frontal knobs of *Artemia* from different localities

NO. SPINES/ GROUP	Yserfontein (S.Africa)	Lymington (England)	Sfax (Tunisia)
Quintets	0	1	0
Quartets	5	28	8
Triplets	34	35	22
Doublets	42	20	40
Singles	19	16	20

DISCUSSION

Of all the anostracans, *Artemia* is undoubtedly the best known and most well researched. This is a result of interest in the ability of the genus to tolerate extreme salinities, various interesting and unusual genetic characteristics such as polyploidy and automixis in some populations and because of their commercial value in salt works and in the field of aquaculture. In many countries they are harvested for use by aquarists as fish food and they also play a major role in clarifying water in salt works, thus allowing more rapid evaporation and increased extraction efficiency. In southern Africa, neither of these uses has been exploited even though there are a number of commercial salt pans and a relatively large tropical fish industry. Two commercial salt works which were sampled (one at Veldrift on the Cape West coast and one at Dealesville in the Orange Free State) did not contain any *Artemia* but those at Coega in Port Elizabeth are reported to support populations intermittently. In addition, apart from Barnard (1929), no other detailed published records or information on *Artemia* from southern Africa could be found. The reasons for this lack of information are uncertain but it may be a reflection of the restricted distribution of *Artemia* in southern Africa.

Perhaps surprisingly, brine shrimp are absent from the large, ephemeral salt pans such as Etosha in Namibia and Makgadikgadi in Botswana. The presence of large populations of other anostracans such as *Streptocephalus proboscideus* in the major parts of the pans which fill after heavy rains could indicate that the salinity is not sufficiently high to exclude competitors and predators, which are unusual in typical *Artemia* habitats and which they are unable to tolerate. Their absence from these and other natural salt pans may also indicate that *Artemia* populations are not endemic to the region and that they have been introduced by migratory waders through ingestion or in mud on their feet, a means of dispersal apparently common in this genus (Persoone & Sorgeloos 1980).

The similarity between the morphology of the frontal knobs of specimens from Yserfontein and those from the Mediterranean and North Africa also suggests some relationships between these populations. The general shape and spine arrangement of the frontal knob of the southern African specimens examined is the same as that illustrated by Mura *et al* (1989a) for *A. tunisiana*. The latter character is, however, variable and was illustrated as such by Mura *et al* (1989b) for five Italian populations. Of these, the southern

African specimens most strongly resemble the Sfax, Tunisia population in the frequency of variously grouped spines on the frontal knob, although the concentration of the spines on the median surface is somewhat different in the specimens. There are also strong similarities between the type specimens from Lymington, England and the spines on the frontal knobs of the southern African specimens (see Mura 1990). Further research has shown that the Italian populations illustrated in Mura *et al* (1989b) are conspecific, and Mura (1990) suggests that the frontal knob morphology reflects this as well. If the frontal knob does indicate taxonomic relationships, it is possible that the Yserfontein specimens also belong to *A. tunisiana*. It is also quite likely that the name *A. tunisiana* should be replaced by *A. salina* (Mura 1990).

In terms of reproduction, the southern African populations are unusual since most Old World *Artemia* reproduce parthenogenetically (Browne 1992, 1993). The Yserfontein and all the Port Elizabeth material represents bisexual populations. Browne (1992; 1993) suggested that the sexual species, for example, *A. tunisiana*, tolerate cold quite well and produce mostly drought-resistant eggs and so are well adapted to inland, ephemeral pools or lakes which are filled during the winter months. This is true for the Yserfontein habitat which lies in the winter rainfall region of the Cape as does Port Elizabeth. The specimens from the latter locality were, however, collected during the summer months. The parthenogenetic populations are often ovo-viparous and tolerate relatively high temperatures and are better suited to commercial saltworks because the populations there are maintained year-round. Unfortunately, the date which the specimens were collected in Namibia and the nature of the habitat are unknown, but this is a summer-rainfall area where temperatures would be expected to be high.

In all aspects of *Artemia* in southern Africa, more detailed studies using material from more localities and collected at different times of the year are necessary before any conclusions can be drawn. As the title suggests, this is only a preliminary report but it indicates that there is scope for a great deal more research on *Artemia* in southern Africa. It will only be possible to answer some of the issues raised here once genetic data are available for local populations, once cross-breeding experiments with sexual species from other regions have been performed and once a more detailed and accurate distribution pattern can be established. In view of the potential use in this region, and the large amount of interest in the brine shrimp in other areas, this research should be considered to have some relevance.

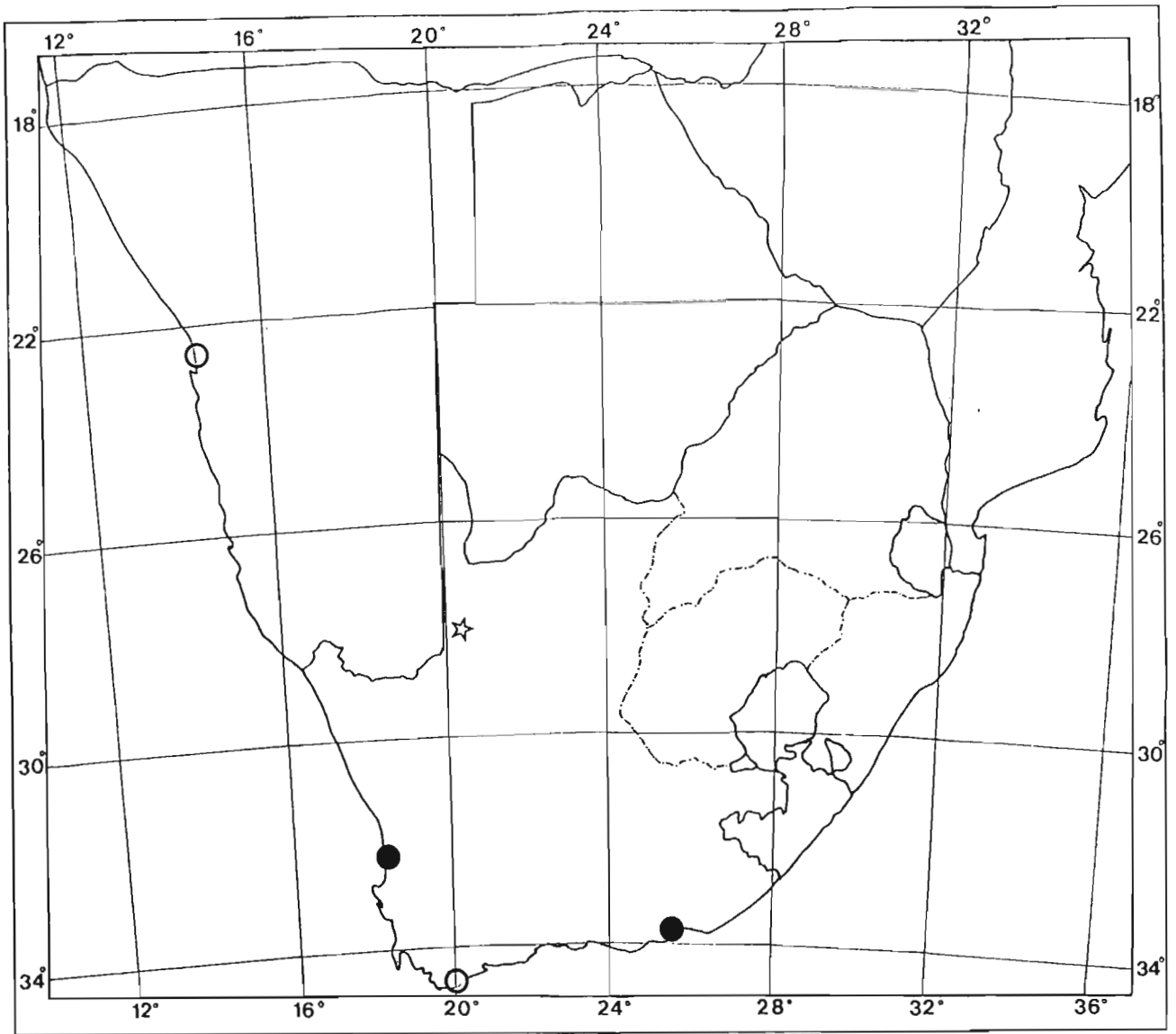


Figure 1: Map of southern Africa showing localities for *Artemia*.

○ possible parthenogenetic population/ female specimens only,

● bisexual populations, ☆ dubious population.

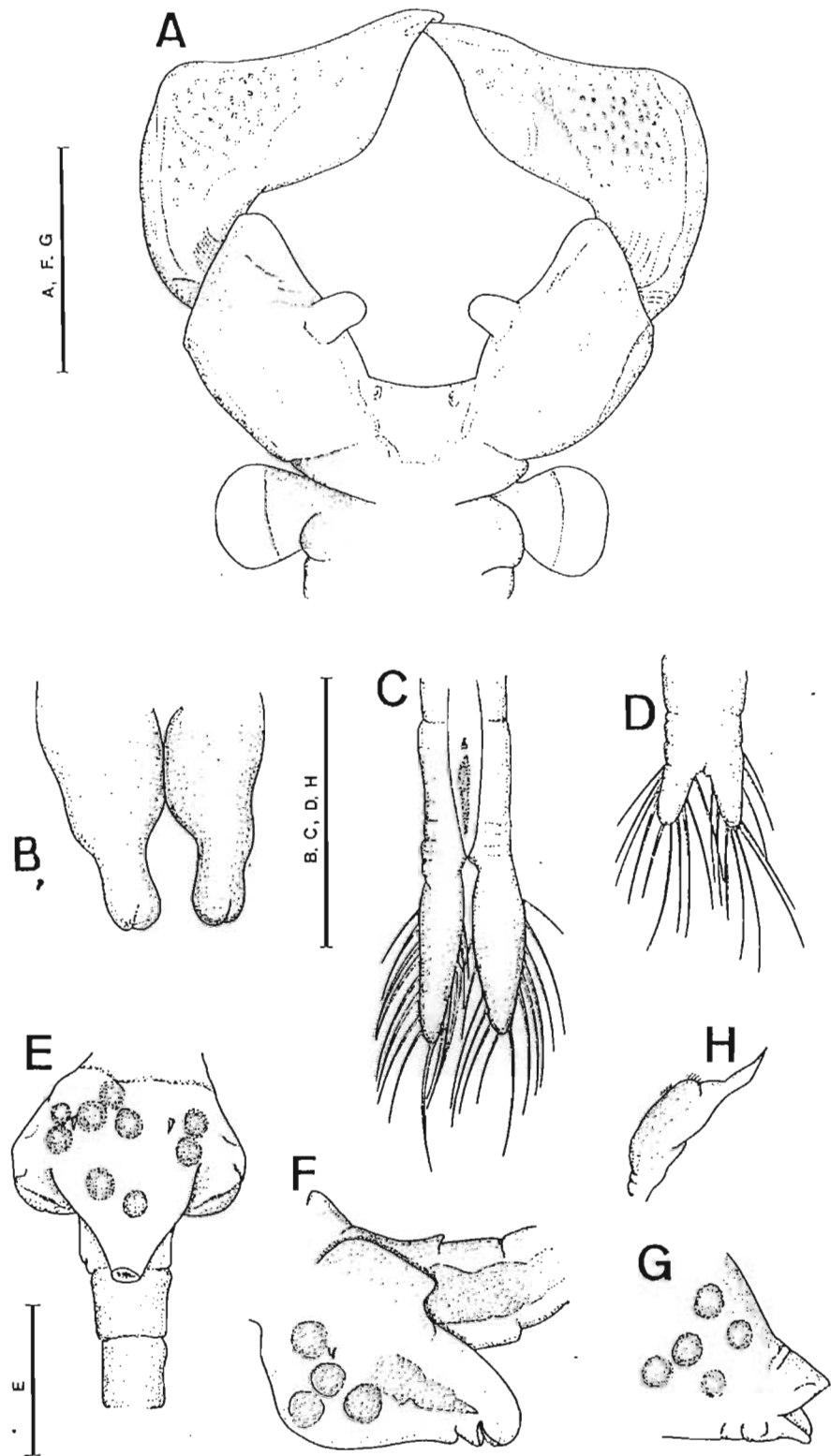


Figure 2: *Artemia salina*

A = dorsal surface of male antennae. B = ventral view of penes. C = cercopods of female, Yserfontein specimen. D = cercopods of Swakopmund specimen. E = ventral view of brood pouch of Swakopmund specimen. F = lateral view of brood pouch of Yserfontein female. G = detail of apical region of brood pouch of Yserfontein specimen. H = antenna of female from

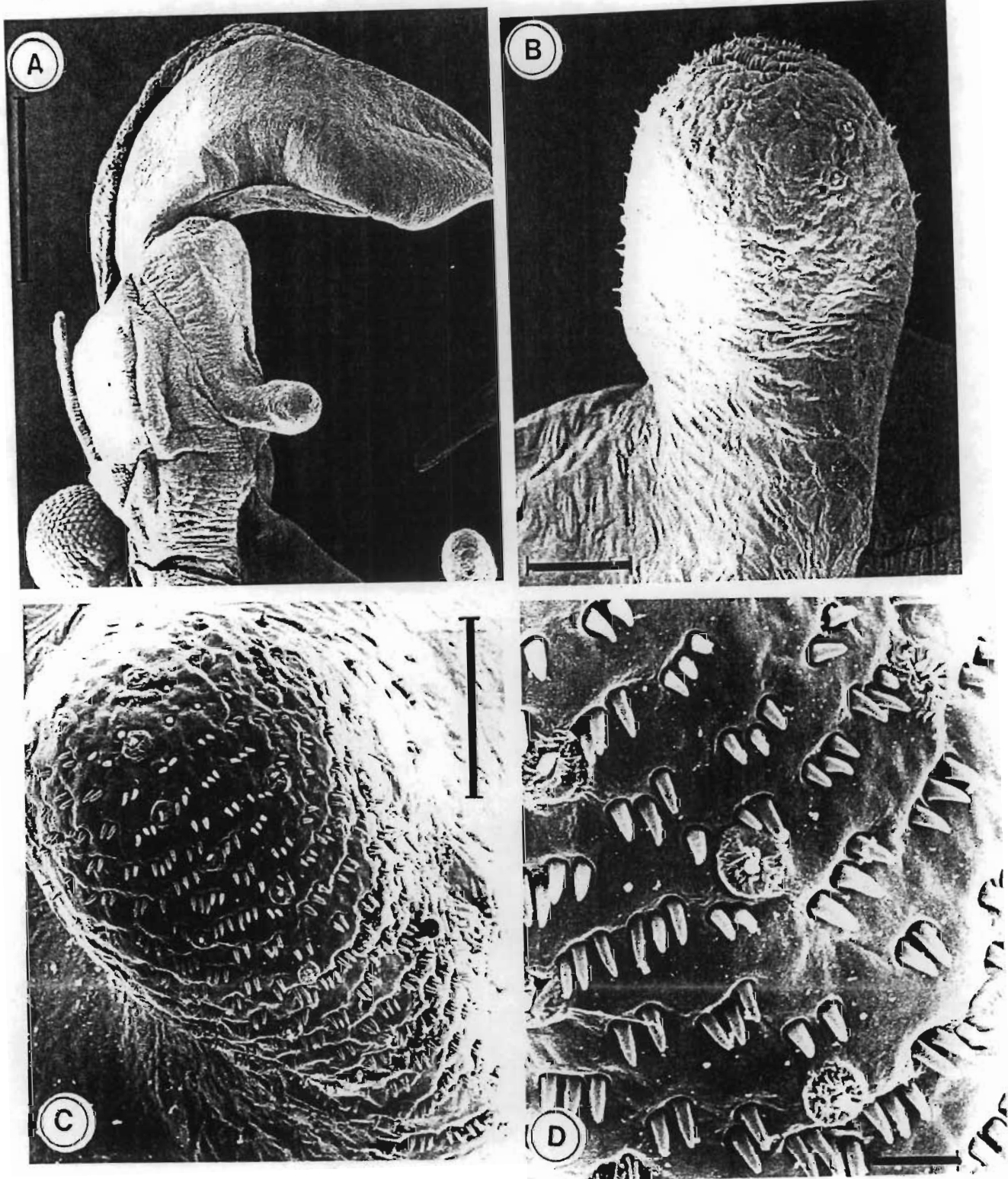


Figure 3: *Artemia salina*

A = dorsal view of left antenna of male; scale = 0,5 mm. B = dorsal surface of frontal knob of male antenna; scale = 50 μm . C = median ventral view of frontal knob; scale = 50 μm . D = detail of spines and their arrangement on the frontal knob. Arrows indicate sensory setae; scale = 10 μm .

GAZETEER

NAMIBIA

Swakopmund 22°36'S/14°31'E

SOUTH AFRICA

Cape Province:

Bredasdorp, Springfield saltworks 34°46'S/25°32'E

Gordonia district, Narugas and Kourop 28°09'S/20°05'E

Port Elizabeth: Coega saltworks 33°46'S/25°40'E

 Mimosa 33°25'S/25°49'E

 NE Prince Alfred Lake 33°S/25'E

 North End 33°S/25'E

 Zoutpan of Zwartkops 33°46'S/25°32'E

Veldrift 32°48'S/18°10'E

Yserfontein, Rooipan 33°19'37''S/18°09'40''E

Orange Free State:

Dealesville 28°40'S/25°47'E

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* indicates publication not seen.

CHAPTER 4

THE GENUS *Branchipodopsis* (CRUSTACEA, BRANCHIOPODA, ANOSTRACA) IN SOUTHERN AFRICA

ABSTRACT

The southern African species of *Branchipodopsis* are reviewed. Eleven previously known species are redescribed and an additional five new species (*B. barnardi*, *B. dayae*, *B. drakensbergensis*, *B. hutchinsoni* and *B. underbergensis*) are described. The male antennae (clypeus), cercopods, last abdominal segments and penes as well as extensions of the genital segments of the females of certain species are illustrated as are species distributions. The sixteen species have been divided into groups based on antennal morphology and a key, using the same character, is presented. Intraspecific variation in two widespread species, *B. tridens* and *B. wolffi*, is illustrated and discussed. The characters used in taxonomy of the genus *Branchipodopsis*, aspects of species diversity, habitats, dispersal and future research are commented on.

INTRODUCTION

The anostracan family Branchipodidae is represented in Africa, Asia, Australia and Europe and is characterised by having the basal joints of the antennae of the male fused to form a so-called 'clypeus'. In addition, according to Linder (1941), the genital segments of the male are negligibly swollen ventrally and there are no distinct seminal vesicles. The penes are close together, the basal parts rigid with proximal outgrowths and usually distal ones as well. The retractable parts of the penes are armed with longitudinal rows of spines. The female brood pouch is short and broad.

Initially, the family Branchipodidae Baird, 1852 included most of the known anostracan genera. Daday (1910) restricted the family to four genera which he split into two subfamilies, the Parartemiinae (which included the genus *Parartemia*) and the Branchipodinae (with three genera - *Branchipodopsis*, *Tanymastix* and *Branchipus*). This division was based on the number of abdominal segments (eight in Parartemiinae and nine in Branchipodinae) and whether the cercopods articulated with the telson (Branchipodinae) or not (Parartemiinae). The monotypic genus *Metabbranchipus* was later described by Masi (1925) and also included in the family Branchipodidae. Barnard (1929) and Linder (1941) disputed Daday's division. Linder (1941) pointed out that both groups have eight abdominal segments and a telson, although the anterior boundary is almost obscure in *Parartemia*, and that the cercopods of this genus are as articulated as in the other genera. In addition, Linder (1941) placed little taxonomic value on the number of abdominal segments as a character.

Linder (1941) provided a detailed synopsis of the family and stated that the degree to which the basal joints of the antennae are joined varies from almost complete in *Branchipus*, to the form where only the proximal halves are joined in those specimens of *B. hodgsoni* examined by him. He suggested, that in all of the Anostraca it is difficult to decide the degree to which the basal joints must be fused to be called a clypeus and this presents some problems in determining the limits of the family Branchipodidae. Subsequent to Linder's (1941) monograph, few taxonomic contributions, apart from single species descriptions, have been made to the family. Brtek (1972) described a new genus, *Tanymastigites*, from North Africa and divided the Branchipodidae into three subfamilies, the Branchipodinae (*Branchipodopsis*, *Branchipus* and *Parartemia*), the Tanymastiginae (*Tanymastix* and *Tanymastigites*) and a third which comprised a single genus, *Metabbranchipus*. An in depth review of the family and the characters uniting the genera

presently included in it is thus necessary. This is, unfortunately, beyond the scope of the present study which focuses on southern African anostracans. Only the genus *Branchipodopsis* is represented in the region and it has been neglected probably to an even greater extent than the other genera of the Branchipodidae.

Sars (1898) described the first *Branchipodopsis* species, *B. hodgsoni*, from Port Elizabeth, South Africa and established the genus but he did not provide a generic diagnosis. A species from Rio de Oro, Mauritania in North West Africa, *Branchipus abiadi* Brauer, 1877 was later transferred to the genus *Branchipodopsis* by Linder (1941). Sars (1901) described *Branchipodopsis affinis* from Central Asia and in 1910, in his monograph on the Anostraca, Daday described a further three species from southern Africa. In addition, he provided a general description of the genus. He used the median ventral process, a small outgrowth from the ventral, front edge of the clypeus, the presence of two flat outgrowths on either side of it, and two more lamelliform and short outgrowths near the terminal joints as diagnostic generic characters. Barnard (1929), however, in his review of the southern African phyllopods, suggested that the median ventral process is not always present; it may be present in some specimens of a species but not in others. Barnard (1929) provided illustrations, descriptions and locality data for those southern African species already described, as well as an additional seven new species of *Branchipodopsis* from the region.

In Linder's (1941) monograph he provided additional data on *Branchipodopsis*, including details of the second maxilla, the structure and setation of the thoracopods and the male genital segments and penes. He confirmed Barnard's (1929) comment on the median ventral process but suggested that it might be present in all specimens of a species but have broken off in some; the proximal part of this structure is very narrow and could break without leaving any trace of its presence on the clypeus. Linder (1941) considered the setiferous processes at the terminal joint the most unique characteristic of *Branchipodopsis*, since these are not present in any other anostracans.

Subsequent to the work of Linder (1941), the genus *Branchipodopsis* has been neglected. A number of articles have been published on the Asian species *B. acanthopenes* (Malhotra & Duda, 1970), *B. terpogossiani* Smirnov, 1936 and *B. affinis*, (Roén 1952; Hartland-Rowe 1968; Tiwari 1972; Battish 1983; Brtek, Forro & Ponyi 1984; Vechov 1988), but only two contributions have been made to the African representatives of the genus. Brehm (1958) illustrated, but did not name or provide detailed data of, one possible

new species and other specimens which he identified as *B. karroensis* Barnard, 1929. These specimens, however, cannot be located and his identification is probably inaccurate. Loffler (1968), described *B. candea*, a new species from Mt Elgon in Central Africa and provided data on *B. wolfi* Daday, 1910. Two recent publications (Hamer & Appleton 1991; Seaman, Kok, von Schlichting & Kruger 1991) provided brief ecological information on *B. wolfi* and *B. tridens* Daday, 1910 respectively.

In southern Africa, sporadic collecting of Anostraca over the last fifteen or so years and a more concentrated effort over the last four years has produced additional material of the genus *Branchipodopsis*. Examination of this has revealed the need to update Barnard's (1929) review in terms of distribution data, illustrations and descriptions, as well as to describe five new species. A key, based on the male clypeus is provided and a division of the genus into groups based on antennal morphology is attempted. Comments are made on the characters used for species identification and aspects of intraspecific variation, speciation, diversity, distribution and habitats are discussed.

MATERIALS AND METHODS

List of museums. The following abbreviations are used to indicate the museum collections included in this study: AM = Albany Museum, Grahamstown, South Africa; BMNH = British Museum of Natural History, London, England; HNHM = Hungarian Natural History Museum, Budapest, Hungary; MNHSI = Museum of Natural History of the Smithsonian Institution, Washington, U.S.A.; NM = Natal Museum, Pietermaritzburg, South Africa; SAM = South African Museum, Cape Town, South Africa; SMN = State Museum of Namibia, Windhoek, Namibia; TM = Transvaal Museum, Pretoria, South Africa; ZNM = Zimbabwe National Museum, Bulawayo, Zimbabwe.

Material catalogued under DB was collected by Dr. J.A. Day of the University of Cape Town and Dr. T. Rutherford of the University of Lesotho and was provided by Dr. Denton Belk of Our Lady of the Lake University, Texas, U.S.A. from his personal collection.

Collecting. Hand-held dip nets of varying sizes and with mesh of 0,5-2,0 mm were used to collect anostracans. Specimens were preserved in 70 per cent ethanol or 4 per cent formalin. Dried pool sediment was collected from a number of localities for later rehydration in the laboratory. Hatched anostracans were cultured until mature enough to be identified.

Illustrations. Drawings were made using a Wild M-5 dissecting microscope or a Leitz Labor Lux 12 compound microscope and drawing tube. The clypeus was dissected from those species for which sufficient material was available, cleaned and dehydrated in a graded ethanol series. Specimens were then critical point dried, mounted on stubs and coated with 20nm of gold for scanning electron microscope observation using a Hitachi S-570 at an accelerating voltage of 10 or 12kv. For some species, eggs were removed from the brood pouch of females, rinsed in distilled water, oven-dried at 50°C for 24 hours, coated and viewed.

Measurements. Specimens of suitable quality were measured using a dissecting microscope and graticule. All measurements are presented as total body length (mean \pm standard deviation where $n > 10$, or as a range of lengths where $n < 10$), from the front of the head (excluding the clypeus) to the tip of the cercopods (excluding the setae) for sexually mature specimens.

Terminology. The terminology used to describe the regions of the male clypeus is from Barnard (1929) and Linder (1941) and is illustrated in figure 1. Each half of the clypeus (c) consists of a broad, stout basal joint (bj) and a slender, inwardly curved terminal joint (tj). A lamelliform, setiferous process (lp) is present on the basal joint just proximal to the terminal joint. The basal process (bp) is a somewhat flattened process situated anteriorly/ antero-dorsally on the basal joint. The basal process may have adjacent, apical lobes; when bilobed these are termed the inner (il) and outer lobe (ol) and these are rounded or conical structures of varying widths. Tubercles (tu) are smaller, digitiform projections which may be present apically or dorsally on the basal process. A smaller, acute projection (pr) may also be present near the apex of the basal process. The median ventral process (mvp) is a small, usually spinose, rounded or oval process, situated on the ventral surface in an anterior, median position on the basal joint. This structure is not present in all species.

DESCRIPTIONS

Class Branchiopoda Latreille, 1817

Order Anostraca Sars, 1867

Family Branchipodidae Baird, 1852

Subfamily Branchipodinae Daday, 1910

Genus *Branchipodopsis* Sars, 1898

Branchipodopsis Sars, 1898: 26. Daday, 1910: 293. Barnard, 1929: 192. Linder, 1941: 228.

Eubranchinella Daday, 1910: 256.

Mongolobranchipus Dybowski, 1927.

Type species. Branchipodopsis hodgsoni Sars, 1898

Diagnosis

Males with basal joints of antennae fused to form a clypeus. Each basal joint broad with a basal process in an anterior, median position and a setiferous, lamelliform process distally. Terminal joint slender and curved inwards. A median ventral process may be present (Fig. 1). Basal part of penes with rounded projection on median margin about halfway along length. Apical, eversible part of penes with one longitudinal, and a second, less regular row or scattered arrangement of spines (Fig. 2A-D). Thoracopods with a single pre-epipodite (Fig. 2E). Brood pouch of female short and oval. Typical morphology of labrum and maxillae illustrated in figure 3.

Branchipodopsis barnardi sp. nov.

Figs 4-5

Material

Holotype. SAM-A40839, 1 male (13,9 mm); collected from rockpool (1,5 X 2 m), 15 cm deep, Sehlabatebe National Park area, Drakensberg, Natal/ Lesotho border by M. Hamer and O. Wirminghaus, 23 April 1993.

Paratypes. SAM-A40840, 23 males (14,8 \pm 1,0 mm), 44 females (15,5 \pm 1,5 mm); same collection data as holotype specimen.

Other material examined. SAM-A40841, 1 male (14,6 mm), 2 females (15,0; 15,3 mm); collected from type locality by O. Wirminghaus and H. Adie, 11 April 1993.

Description of male

Clypeus. Basal process long and slender. Apical region with digitiform inner lobe and short, flat outer lobe (Figs 4A, 5A-B). Reticulate patterning on dorsal, proximal surface of basal process (Fig. 5C). Lamelliform process long, prominent and elliptical in shape with long, sparse setae (Fig. 4A). Terminal joint slender, distal third weakly curved inwards and apex blunt (Figs 4A, 5A). Median ventral process absent.

Cercopods. Moderate length (ratio to body length about 0,2:1). Proximally stout, tapering distally and with outer margins weakly convex (Fig. 4B). Short to medium length setae on outer margins, replaced by three spines distally. Inner margins with small patch of sparse setae proximally, followed by 12-15 evenly-spaced spines (Fig. 4B).

Abdominal spines. Pair of short, stout and blunt spines present on ventral surface of last abdominal segment (Fig 4C).

Penes. Basal part short and stout, with proximal region bulbous and with indistinct rounded projection on inner margin (Fig. 4D).

Description of female

Thoracic segments. Last thoracic segment with pair of obvious, rounded and bulbous extensions dorsally (Fig. 4E).

Antenna. Apical point on antenna almost half length of antenna (Fig. 4F).

Egg morphology

Surface of egg with irregularly-shaped, 5-sided depressions separated by high, rounded ridges (Fig. 5D).

Differential diagnosis

Branchipodopsis barnardi is easily distinguished from all other described species of the genus by the large elliptical lamelliform process, the slender terminal joint and the long, digitiform and distally bilobed shape of the basal process.

Distribution

Branchipodopsis barnardi has, to date, only been collected from rockpools in the high altitude (2000 m) Drakensberg region, on the border of Sehlabatebe National Park in Lesotho and the Bushman's Nek area of Natal (Fig. 39).

Remarks

Branchipodopsis barnardi does share certain characters with *B. drepane* Barnard, 1929. Both species have slender bilobed basal processes, with a smaller outer lobe and the terminal joint is smooth and weakly curved. For these reasons, *B. barnardi* and *B. drepane* have been included in the same group (Table 1).

The colour of live specimens varied according to the pool from which they were collected. One population (used for DNA extraction) was a pale orange-red colour before preservation, while the type specimens were a pale aqua blue. The labral area, and a thin

stripe along the gut region was red in all specimens. There was also some degree of intrapopulation variation in the shape of the apex of the basal process as illustrated (Fig. 4G-I).

Etymology

Branchipodopsis barnardi is named for the late Dr. K. H. Barnard, of the South African Museum who was the author of the first review of the southern African "Phyllopoda" in 1929 and who collected a large number of specimens currently housed in that institution.

Branchipodopsis browni Barnard, 1924

Figs 6-7

Branchipodopsis browni Barnard, 1924: 217, pl. 26 (fig. 4); 1929: 198, fig. 5a.

Material

Syntypes. SAM-A6705, large number of specimens, 24 males measured (12.0 ± 0.7 mm), 26 females measured (13.3 ± 0.6 mm); collected from Kalkfontein South, Great Namaqualand, Namibia by J.S. Brown, date unknown.

Other material examined. SAM-A7600, 7 males (13,1 - 15,6 mm), 4 females (17,5 - 20,0 mm); collected from Williston, Cape Province in 1939, collector unknown. AM LEN 79B, 6 males (11,8 - 13,0 mm), 7 females (13,1 - 14,8 mm); collected from a large (20 X 30 m), shallow (20 - 35 cm) turbid pool, sparsely vegetated with grass, 10 km S of Carnavon on the road to Loxton, Karoo, Cape Province by M. Hamer, 16 February 1990. AM LEN 164A, 3 males (6,6; 8,0; 8,1 mm), 1 females (6,9 mm); hatched from dried sediment collected 8 km NE of Fraserburg, Karoo, Cape Province, by M. Hamer, 6 January 1993. AM 614/93, 1 male (14,2 mm), 1 female (16,5 mm), collected from inundated area along road, 8 km from Richmond by K. Martens, 6 April 1993.

Redescription of adult male

Clypeus. Basal process conical proximally, apically inflated and bluntly rounded, with a series of short denticles on apex (Figs 6A, 7A-C). A distal, anteriorly-curved, and pointed projection on inner margin of basal process (Figs 7B-C). One or two small, acute projections dorso-medianly near apex of basal process (Figs 7B-C). Lamelliform process very large (as long as basal process) and oval (Fig. 6A). Terminal joint slender, long, smooth and curved inwards with apex slightly inflated and blunt (Fig. 6A). Median ventral process large (approximately half length of basal process), oval and spinose (Figs 7A, 8A).

Cercopods. About one-fifth the length of body, margins straight, with long, plumose setae along outer margins and proximal two thirds of inner margins. Distal third of inner margins with 6-8 widely-spaced, long spines (Fig. 6B).

Abdominal spines. Two small ventral spines on last abdominal segment (Fig. 6C).

Penes. Median projection bluntly rounded and prominent. Distal region of basal part with small but distinct peg-like projection on outer margin (Fig. 6D).

Remarks

Barnard (1924) stated that *B. browni* closely resembles *B. hodgsoni* but that the presence of abdominal spines in the former species separates them. The arrangement of the basal process and associated projections is, however, quite distinct in these two species. *Branchipodopsis browni* shares an apical projection on the basal process, the absence of distinct lobes and distinctly-bent terminal joints with *B. wolffi* and these two species were grouped in Table 1.

Variation in the size of the dorso-median projection of the basal process and the apical denticles is illustrated in figures 7A and B.

Distribution

Branchipodopsis browni has only been reported from the above five localities which fall into the arid southern Namibia and Karoo regions (Fig. 38).

Branchipodopsis dayae sp. nov.

Figs 8-9

Material

Holotype. SAM-A40842, 1 male (17,3 mm); collected Eland's Bay, Cape Province by J. Lighton, 23 November 1980.

Paratypes. SAM-A40843, 2 males (15,3; 16,9 mm), 2 females (12,8; 14,4 mm); collection data as for holotype.

Other material examined. SAM-A40849, 1 male, in poor condition; hatched in laboratory from sediment collected from dry depression on roadside, Koppieskraal Pan, approximately 36 km from Namibian border on R31, Cape Province, by M. Hamer, 22 December 1992.

Description of male

Clypeus. Basal process broad and apically bilobed. Outer lobe rounded, inner more conical, with small acute projection apically on median margin (Figs 8A, 9A-B).

Lamelliform process small and round (Fig. 8A). Terminal joint weakly curved inwards, distal region foot-shaped (Figs 8A, 9A, C). Median ventral process small, round and with short, blunt spines (Fig. 9D).

Cercopods. Moderate length (ratio to body length approximately 0,25:1), outer margins weakly convex and with short setae along almost entire length except distal region where these replaced by 3-5 widely-spaced, short spines (Fig. 8B). Proximal fifth of inner margins with short setae and remainder of length with 12 short spines. (Fig. 8B).

Abdominal spines. A pair of blunt spines present on ventral surface of last abdominal segment.

Penes. Basal part stout, with distinct conical projection on inner margin proximally and indistinct peg-like projection distally on lateral margin (Fig. 8C-D).

Differential diagnosis

The distal region of the terminal joint and the shape of the two lobes of the basal process of *B. dayae* are unique to this species. *Branchipodopsis drepane* also has characteristic terminal joint apices but these are hook-shaped rather than foot-shaped. This species also shares the small, rounded lamelliform processes with *B. dayae* but the basal processes of the two species are clearly different. The basal process morphology of *B. dayae* resembles that of *B. karroensis* Barnard, 1929 and these two species have been included in the same species group (Table 1).

Distribution

Branchipodopsis dayae has been collected from Eland's Bay on the Cape West coast and from the Gordonia region between Namibia and Botswana (Fig. 40). It is possible that this species also occurs in other waterbodies in the area between these two localities.

Etymology

Branchipodopsis dayae is named after Dr. J.A. Day of the University of Cape Town who has contributed to the knowledge of temporary waterbodies in southern Africa. She also collected numerous Anostraca and kindly made her collection, including the type specimens of this species, available for study.

Branchipodopsis drakensbergensis sp. nov.

Figs 10-13

Material

Holotype. SAM-A40834, adult male (12,5 mm); collected from small (40 X 50 cm)

rockpool in boulder, 15 cm deep, Loteni Nature Reserve, Drakensberg mountains, Natal by M. Hamer, 6 January 1992.

Paratypes. SAM-A40835, 14 males ($12,6 \pm 0,5$ mm), 5 females (11,9 - 12,8 mm); same collection data as holotype specimen.

Other material examined. SAM-A40836, 17 males ($11,1 \pm 0,5$ mm), 34 females ($10,4 \pm 0,5$ mm); collected from small pool (30 X 40 cm) in boulder, 10 cm deep, Loteni Nature Reserve, Drakensberg, Natal by M. Hamer, 6 January 1992. AM LEN 158A, 7 males (7,5 - 10,5 mm), 5 females (9,0 - 18,1 mm); collected in rockpool on top of Prentjiesberg, Farm Montana, Ugie, Cape Province, by R. McC. Pott, 4 April 1991. AM LEN 159A, 12 males (2 with damaged cercopods, remainder 13,1 - 13,9 mm), 4 females (12,3 - 14,0 mm); locality as for AM LEN 158A; collected by R. McC. Pott, 22 January 1992. SAM-A11593, 4 males (9,4 - 12,0 mm), 5 females (10,0 - 11,3 mm); collected from Giant's Castle, Drakensberg, Natal, by Ewer, 1951. AM REA 77E, 12 males ($8,9 \pm 0,6$ mm), 26 females ($9,1 \pm 0,8$ mm); collected from temporary vlei at Witkoppies, Benoni, Transvaal by P.A. Reavell, 31 April 1971.

Description of male

Clypeus. Basal process slender, distally bilobed, with inner lobe twice as long as outer, both apically narrow and rounded (Figs 10A, 11A-B). Inner lobe with 1/2 small projections medianly on apex (Fig. 12A-C). Large spinous projection proximally on dorsal surface of basal process (Figs. 10B-C; 11A-C), half to two thirds length of basal process and with apical denticles or scales (Fig. 13A-C). Median ventral process prominent, ovate and with long spines distally (Figs 10A, 11B). Lamelliform process ovate, with long setae (Figs 10A, 11C). Terminal joint strongly curved inwards with rounded apices (Fig. 10A).

Cercopods. Average length (ratio to body length approximately 0,25:1). Outer margins strongly convex, with setae along entire length. Patch of setae on proximal fifth of inner margins, followed by 17 - 19 evenly-spaced spines. (Fig. 10D).

Abdominal spines. A pair of prominent spines on last abdominal segment.

Penes. Basal part long, with distinct, round projection about halfway along inner margin (Fig. 10E).

Egg morphology

Eggs with deeply crumpled appearance created by irregular, narrow depressions separated by high ridges (Fig. 13D). Surface of eggs roughened with numerous small lumps.

Differential diagnosis

Branchipodopsis drakensbergensis resembles *B. tridens* in the presence of a dorsal projection on the basal process and the bilobed basal process. However, the prominent median ventral process, absent or vestigial in *B. tridens* and the distinctly slender basal process as opposed to the broad shape of these structures in *B. tridens* separate the two species. As a result of this similarity, the Giant's Castle specimens (SAM-A11595) were previously labelled as *B. tridens* in the SAM collection.

Distribution

Branchipodopsis drakensbergensis occurs in high altitude rockpools in the southern and central Drakensberg mountains. The single Transvaal locality could indicate a wider distribution for this species as well as a wider habitat range (Fig. 39).

Remarks

There is some variation in clypeus morphology between populations from different localities. For example, the Loteni specimens have a flattened, spatulate process on the apex of the inner lobe of the basal process as opposed to the pointed one in the Benoni and Ugie specimens (Fig. 12A-C) and there is a slight difference in the shape of the basal process and spinous projection (Fig. 10B-C). The latter projection has long extensions apically in the Loteni specimens (Fig. 13A) while these are flattened and scale-like in the Benoni specimens (Fig. 13C) and somewhat intermediate in the Ugie specimens (Fig. 13B). In addition, the cercopods of the Benoni specimens have fewer (9) spines on the inner margin than those specimens from the Drakensberg. These differences could indicate two distinct species but in the light of the large amount of interpopulation variation in other widespread species of the genus, and because of the overall similarity in clypeus shape, a single species has been described.

In terms of relationships to other species of the genus, the spinous projection could indicate a relationship between *B. drakensbergensis* and *B. tridens* and the two species have been placed in the same species group. The spinous projection could, however, be a homoplasious character in the two species.

Etymology

Branchipodopsis drakensbergensis is named after the mountain range from which most of the material was collected.

Branchipodopsis drepane Barnard, 1929

Fig. 14

Branchipodopsis drepane Barnard, 1929: 199, figs 5e-f.

Material

Holotype. SAM-A7259, 1 male (12,4 mm), distal part of right terminal joint damaged; collected from Great Fish River, near Gibeon, Namibia by R.W. Tucker, date unknown.

Other material examined. BMNH 1932.2.25.41, 1 male (12,3 mm); same locality and collection data as type specimen.

Redescription of adult male

Clypeus. Basal process long and slender with distinct indentation about halfway along lateral margin. Distally, basal process with a smaller outer lobe and a higher and larger, rounded inner lobe (Fig. 14A). Lamelliform process small, slender and oval (Fig. 14A). Terminal joint weakly curved inwards, with hook-shaped, acute apex (Fig. 14A). Median ventral process obovate, apically flat and with surface covered by small spines (Fig. 14B).

Cercopods. Ratio to body length approximately 0,26:1, slender, and with outer margins only slightly convex. Outer margins and proximal half of inner margins with plumose setae. Distally, inner margins with 6 large, widely-spaced spines (Fig. 14C).

Abdominal spines. Last abdominal segment with two stout, blunt spines on ventral surface.

Penes. Proximal region of basal part with obscure bulge on lateral surface, followed by small rounded projection on median margin (Fig. 14D).

Distribution

Branchipodopsis drepane has only been collected from the type locality in southern Namibia (Fig. 38).

Branchipodopsis hodgsoni Sars, 1898

Figs 15-16

Branchipodopsis hodgsoni Sars, 1898: 26, pl. 3 (figs 1-9). Daday, 1910: 301, fig. 51. Barnard, 1929: 194, figs 5k-l.

Branchipodopsis braueri Pesta, 1921: 94.

Material

Syntypes. SAM-A1488, 1 male (11,6 mm), 1 female with damaged abdomen and cercopods; hatched from dried sediment collected from Port Elizabeth, Cape Province by J.V. Hodgson, May 1897.

Other material examined. SAM-A6721, 14 males ($14,0 \pm 1,3$ mm), 4 females (10,5 - 16,5 mm); collected Ashton, Cape Province; collector unknown, 27 August 1910. SAM-A13631, 1 male (11,9 mm), 5 females (8,8 - 14,4 mm); collected from freshwater pool, Kenton-on-Sea, Cape Province by R.A. Jubbs, April 1963. AM 107A, 1 male with right half of clypeus damaged (9,2 mm), 1 female (10,4 mm); same collection data as SAM-A13631. HNHM I/A-76, 1 male (11,8 mm), 1 female (8,3 mm); data as for syntypes. AM LEN 149A, 7 males (6,3 - 12,6 mm); collected from a shallow (5-10 cm), clear stretch of water with sparse, dead vegetation on side of main road from Bredasdorp to Struisbaai, Cape Province by M. Hamer, 17 July 1990.

Redescription of adult male

Clypeus. Basal process with broad, double-lobed base; second lobe slightly ventrally positioned to first (Figs 15A-C, 16A). Narrow, medianly-directed apex with two small, pointed tubercles (Figs 15A, 16A). Lamelliform process oval and slender (Fig. 15A). Terminal joint strongly curved, with distinct bend and blunt apex (Fig. 15A). Median ventral process large, oval and with blunt spines (Fig. 16B).

Cercopods. Moderate length (ratio to total body length approximately 0,24:1). Outer margins convex with short plumose setae along entire length. Proximal two-fifths of inner margins with plumose setae, followed by 8-10 acute, evenly-spaced spines (Fig. 15D).

Abdominal spines. Last abdominal segment without ventral spines.

Penes: Basal part with large, rounded projection on median margin and small, but distinct peg-like projection distally on lateral margin (Fig. 15E).

Distribution

Branchipodopsis hodgsoni appears to be concentrated in the south-east coastal region of South Africa, from Kenton-on-Sea in the north to Bredasdorp in the south. The locality of Ashton in the western Cape is the furthest inland (Fig. 38).

Remarks

Branchipodopsis hodgsoni is quite distinct from the other species of the genus in that the basal process has a bilobed appearance, with one lobe ventral to the other. This

double-lobed arrangement is not always as evident as illustrated but this is usually a result of the preservation of the specimens. The two small apical tubercles on the dorsal lobe are also unique to *B. hodgsoni*.

Branchipodopsis hutchinsoni sp. nov.

Figs 17-18

Material

Holotype. SAM-A40844, 1 male (12,3 mm); collected from heavily vegetated roadside ditch (30 X 1 m), 20-30 cm deep, 30km along dirt road from Hutchinson to Richmond, Karoo, Cape Province by M. Hamer, 16 February 1990.

Paratypes. SAM-A40845, 18 males (12,0 \pm 0,7 mm), 32 females (11,4 \pm 0,8 mm); collection data as for holotype.

Description of male

Clypeus. Basal process broad, apically bilobed, lobes subequal, rounded/ conical with inner lobe slightly more conical than outer (Figs 17A, 18A-B). Inner lobe with small, acute process on median, apical surface (Fig. 18B). A medianly directed, conical tubercle on dorsal surface at base of inner lobe (Fig. 18A-C). Lamelliform process obovate, with setulose, scalloped margin (Fig. 17A). Terminal joint with distinct inward bend, apically blunt and broad (Fig. 17A). Median ventral process prominent, ovate and with short spines (Fig. 17A).

Cercopods. Moderate length (ratio to body length approximately 0,25:1), outer margins strongly convex with medium length setae along four-fifths of length, distal fifth with 3-6 short spines. Inner margins with patch of setae on proximal quarter, followed by 12-16 strong spines (Fig. 17B).

Abdominal spines. A small, blunt spine present medianly at the base of each cercopod. A pair of rounded processes present ventrally on penultimate segment (Fig. 17C).

Penes. Basal part slender with small rounded projection proximally on median margin and a narrow, peg-like projection apically on lateral margin (Fig. 17D).

Egg morphology

Surface of egg with mildly crumpled appearance created by 3 to 5-sided depressions separated by broad ridges with sharp crests (Fig. 18D).

Differential diagnosis

Branchipodopsis hutchinsoni, *B. karroensis*, *B. dayae* and *B. natalensis* Barnard, 1929 all have broad, bilobed basal processes with both lobes of approximately equal size. The inner lobe of both *B. karroensis* and *B. dayae* also has the small, apical projection but neither has a dorsal tubercle such as that of *B. hutchinsoni* and *B. natalensis*. The latter two species can be separated by the rounder shape of the basal processes, the strongly curved cercopods and the scalloped lamelliform processes of *B. hutchinsoni*.

Distribution

Branchipodopsis hutchinsoni has, to date, only been collected from the type locality in the Karoo (Fig. 39).

Etymology

Branchipodopsis hutchinsoni is named in honour of the limnologist, Prof. Evelyn Hutchinson in memory of his contributions to the knowledge of freshwater habitats.

Branchipodopsis kalaharensis Daday, 1910

Figs 19-20

Branchipodopsis kalaharensis Daday, 1910: 296, fig. 49. Barnard, 1929: 194, fig. 5j; 1935: 487.

Material

Syntypes. 2 males and 2 females housed in the Senkenberg Museum. Collected from the Kalahari by D. Schultze, date unknown (Daday 1910).

Material examined. SAM-A11594, 2 males, 1 with damaged cercopods (other 11,2 mm), 6 females (10,0 - 13,5 mm); collected from Kanke Pan (90 miles W of Molepole), Botswana by the Vernay-Lang Kalahari Expedition, 19 March 1930. TM VLKE No. 94, 8 males (10,0 - 14,0 mm); same collection data as SAM-A11594. TM VLKE No. 460a, 8 males (10,6 - 12,8 mm); collected from Sunnyside, Botswana by the VLKE, 20 April 1930.

Redescription of adult male

Clypeus. Basal process broad, apically bilobed with a narrow conical inner lobe and an outer, less prominent but similarly-shaped lobe (Figs 19A, 20A-B). Lamelliform process narrow and oval (Fig. 19A). Terminal joint strongly curved inwards and with distinct bend (Figs 19A, 20A). Median ventral process absent or obscure.

Cercopods. Long (ratio to body length approximately 0,3:1), with proximal two

thirds of outer margins convex and with plumose setae of moderate length. Distal third of outer margins with 8-10 widely spaced, spiniform setae. Proximal quarter of inner margins with plumose setae, followed by approximately 15 regularly-spaced, strong spines (Fig. 19B).

Abdominal spines. Last abdominal segment without ventral spines.

Penes. Basal part with large rounded projection on proximal region of median margin and obscure, blunt projection on apex of lateral margin (Fig. 19C).

Remarks

Daday (1910) attributed *B. kalaharensis* to Wolf, who initially examined the type material. The description by Wolf was, however, never published (Forró & Brtek 1984).

Daday (1910) suggested that because of the simple structure of the basal process of this species, the other species of the genus are derived from it. Of the five species which had been described at that stage, Daday named the Indian species *B. affinis* as the closest relative of *B. kalaharensis*. In southern Africa there are a number of species which have bilobed basal processes but the lobes in these species are much rounder than in *B. kalaharensis*. It is, however, quite possible that the simple bilobed shape of the basal process of *B. kalaharensis* does represent the ancestral form for species such as *B. dayae*, *B. hutchinsoni*, *B. karroensis* and *B. natalensis* and these species have been grouped in Table 1.

Distribution

Branchipodopsis kalaharensis has, to date, only been collected from central Botswana (Fig. 38).

Branchipodopsis kaokoensis Barnard, 1929

Fig. 21

Branchipodopsis kaokoensis Barnard, 1929: 200, fig. 5q.

Material

Barnard (1929) stated that the type material was housed in the SAM but this could not be located. A single male and female specimen are, however, in the BMNH and since Barnard (1929) stated that only one male and four females were in his sample, presumably these represent his original specimens. Barnard (1929) gave the length as 13 mm but his measurements did not include cercopods and this could account for the different measurement presented here, or he could have presented an average length for all five

specimens. Details for these specimens are as follows:

BMNH.2.25.42-45, 1 male with left half of clypeus removed (21,0 mm), 1 female (13,5 mm); collected from Choabendus (115 miles NW of Outjo), Kaokoveld, Namibia, collected by K.H. Barnard, date unknown.

Redescription of adult male

Clypeus. Basal process broad, apically trilobed with inner lobe digitiform, the outer lobe similarly-shaped but more acute and the median lobe the largest and apically flattened. A long, conical, spiniform projection present dorsally at proximal region of basal process (Fig. 21A). Lamelliform process narrow and ovate. Terminal joint stout, curved inwards and apically deeply bifid. A short, spiniform projection on dorsal surface approximately midway along terminal joint, followed by a larger, triangular projection ventro-laterally just proximal to apex (Fig. 21A). Median ventral process absent.

Cercopods. Moderate length (ratio to body length approximately 0,26:1), slender and with outer margins slightly convex. Outer margins with moderately long plumose setae along about half of length, followed by 5-6 small, sharp spines. Inner margins with plumose setae along proximal quarter of length, followed by 15 prominent spines (Fig. 21B).

Abdominal spines. Last abdominal segment with two large, broad spines on ventral surface (Fig. 21C).

Penes. Basal part short and broad without distinct median projections (Fig. 21D).

Remarks

The penes of the single specimen examined could be shrunken by the preservative since they look different to those of other species of the genus.

Barnard (1929) remarked on the similarity between *B. kaokoensis* and *B. tridens* but stated that no *B. tridens* specimens had any hint of development of projections on the terminal joint of the clypeus. The two species are, however, obviously related and have been included in the same species group (Table 1).

Distribution

Branchipodopsis kaokoensis has only been recorded from the type locality in Namibia (Fig. 38).

Branchipodopsis karroensis Barnard, 1929

Fig. 22

Branchipodopsis karroensis Barnard, 1929: 198, figs 5m-n.

Material

Syntypes. SAM-A5919, 2 males (9,8 mm; 12,0 mm), 5 females (9,5 - 12,3 mm); collected from Hoogeveld, SW of Beaufort West, Cape Province by S.H. Haughton, date unknown.

Other material examined. BMNH 1932.2.25.36-40, 1 male (10,0 mm), 1 female (11,3 mm); data as for syntypes.

Redescription of adult male

Clypeus. Basal process broad. Apex with two rounded lobes and a small acute process on the median margin of the inner lobe (Fig. 22A). Lamelliform process oval (Fig. 22A). Terminal joint curved inwards with slight inflation just proximal to blunt apex (Fig. 22A). Median ventral process with broad base and narrower distal region (Fig. 22A).

Cercopods: Long (ratio to body length approximately 0,30:1). Outer margins weakly convex, and with setae along almost entire length. Distal region with three spines. Proximal half of inner margins with widely-spaced, short setae followed by 8-9 spines (Fig. 22B).

Abdominal spines. Ventral surface of last abdominal segment with two short but strong spines.

Penes. Basal part with distinct, rounded projection proximally on median margin and prominent peg-like projection apically on lateral margin (Fig. 22C).

Description of female

Antenna. Apical pointed process long (half the length of antenna) (Fig. 22D).

Distribution

Branchipodopsis karroensis has only been recorded from the type locality in the Karoo (Fig. 38).

Remarks

Brehm (1958) identified specimens from Blouberg in the Transvaal as *B. karroensis* but from his illustrations of the clypeus, two distinct tubercles are visible on the basal process which invalidates this record. These specimens probably belong to *B. wolffi*.

The penes of *B. karroensis* have been illustrated in the everted position. The apical part does, however, appear shorter than in other species and it is possible that it is not

fully everted, but with the limited number of specimens available, the structure cannot be verified.

Branchipodopsis natalensis Barnard, 1929

Figs 23-24

Branchipodopsis natalensis Barnard, 1929: 196, fig. 50.

Material

Syntypes. NM 1384, 1 male (5 mm), 2 females (no measurements); collected from Natal, half mile from Van Reenen (border of Orange Free State and Natal) (Barnard 1929). These specimens, apparently housed in the Natal Museum, Pietermaritzburg, could not be found in the institute's collections.

Material examined. SAM-40846, 10 males ($12,5 \pm 0,8$ mm), 1 female (12,3 mm); collected from a small depression in a boulder, Bushman's Nek/ Sehlabatebe Game Reserve area, Drakensberg, Natal, by M. Hamer and O. Wirminghaus on 23 April 1993. SAM-A40847, 4 males (9,4 - 9,8 mm); collected from a small rockpool, Sehlabatebe Game Reserve area, Drakensberg, Lesotho by M. Hamer and O. Wirminghaus, 24 April 1993. DB 818, 3 males (9,3; 10,8; 11,4 mm), 2 females (both 12,3 mm); collected from Sehlabatebe Game Reserve, Lesotho by T. Rutherford, 1985.

Redescription of adult male

Clypeus. Basal process apically bilobed with the inner lobe narrow and with a minute apical projection. Outer lobe rounded. A conical tubercle present on dorsal surface near base of inner lobe (Figs 23A, 24A-B). Lamelliform process small and oval. Terminal joint curved inwards and with rounded apex. Median ventral process narrow and ovate.

Cercopods. Moderate length (approximate ratio to body length 0,2:1). Outer margins convex with plumose setae along entire length. Inner margins with sparse setae along proximal two thirds; these replaced by 4-5 short spines on distal third (Fig. 23B).

Abdominal spines. Ventral surface of last abdominal segment with pair of small spines (Fig. 23C).

Penes. Proximal region of median margin with small, angular projection (Fig. 23D).

Description of female

Thoracic segments. Last thoracic segment with slightly laterally and posteriorly extended surface (Fig. 23E).

Remarks

It is impossible to confirm the identification of the Sehlabatebe material without the type specimens of *B. natalensis*. However, since both sets of specimens come from high altitude pools, and there is a resemblance between the new material and Barnard's (1929) illustration and description of *B. natalensis*, it is possible that a single species is represented.

Some of the specimens had distinctly rounded apices of the terminal joints, with the anterior, ventral surface expanded into a peg-like projection (Fig. 24A). There is, however, some intraspecific variation in this character and since it was not described by Barnard (1929), it has been excluded from the above species description.

Branchipodopsis scambus Barnard, 1929

Figs 25-26

Branchipodopsis scambus Barnard, 1929: 199, fig. 5p.

Material

Type material. Barnard (1929) stated that the type specimens were collected in the Cape, Grahamstown and were deposited in the Albany Museum. These have not been located.

Material examined. BMNH.1972.1.27.31-33, 1 male (12,8 mm), 1 female (15,2 mm); locality and date unknown, collected by K.G. McKenzie. AM LEN 18, 2 males (10,2; 11,8 mm), 1 female (15,0 mm); collected from flat, flooded grassland along Grahamstown/Cradock road; by F. de Moor, K. Martens and H. Barber, 28 November 1989. AM LEN 19, 1 male (10,1 mm), same collection data as AM LEN 18.

Redescription of adult male

Clypeus. Basal process slender, spiniform and apically acute (Figs 25A, 26A-B). Lamelliform process large and bluntly oval (Figs 25A, 26A). Terminal joint weakly curved, slender and smooth with rounded apex (Fig. 25A). Median ventral process oval and with longer spines apically (Fig. 25A).

Cercopods. Short (ratio to body length approximately 0,11:1), straight and with plumose setae along entire length of both inner and outer margins, excluding distal quarter of inner margins which have 4 spines and apices which have 2 spines (Fig. 25B).

Abdominal spines. Pair of spines on ventral surface of last abdominal segment.

Penes. Basal part short and with small projection halfway along median margin (Fig. 25C).

Remarks

Barnard (1929) made no comment on the cercopods of *B. scambus* but those of the specimens examined are unusual for the genus in terms of length and the small number of spines on the inner margins. In this, and in the simple shape of the basal processes, *B. scambus* could be considered as a primitive form of *Branchipodopsis*.

Distribution

Only the type locality of Grahamstown and the locality along the Grahamstown/Cradock road in the eastern Cape are known (Fig. 38).

Branchipodopsis simplex Barnard, 1924

Fig. 27

Branchipodopsis simplex Barnard, 1924: 217, pl. 26 (figs 2-3); 1929: 196, fig. 5b-c.

Material

Syntypes. SAM-A6006, 3 males (7,0; 8,0; 8,1 mm) collected from Eunda (about 100 miles WNW Ondangua), Ovamboland, Namibia by K.H. Barnard, date unknown.

Other material examined. BMNH 1932.2.25.11-15, 1 male (7,0 mm), 1 female (8,3 mm); collected from Ovamboland, Namibia; collector and date unknown.

Redescription of adult male

Clypeus. Basal process with inflated proximal region, apically narrower and rounded (Fig. 27A). Dorsal keel present along length of basal process (Fig. 27B). Lamelliform process small and rounded (Fig. 27A). Terminal joint with distinct bend, distal to which posterior margin inflated. Apex of terminal joint blunt (Fig. 27A). Median ventral process absent.

Cercopods. Moderate length (ratio to body length approximately 0,25:1) with outer margins weakly convex (Fig. 27C). Short setae on proximal part of inner margins and along length of outer margins. Distal two-thirds of inner margins with approximately 10 evenly-spaced spines (Fig. 27C).

Abdominal spines. Spines on ventral surface of last segment absent.

Penes. Proximal region of basal part with median margin bulbous and with rounded projection about halfway along length (Fig. 27D).

Remarks

The keel of the basal processes is difficult to see, particularly in such small

specimens, and is only obvious in lateral view (Fig. 27B). This character is autapomorphic and *S. simplex* has not been grouped with other species (Table 1).

Distribution

Branchipodopsis simplex has only been collected from the type locality in Namibia (Fig. 38).

Branchipodopsis tridens Daday, 1910

Figs 28-31

Branchipodopsis tridens Daday, 1910: 308, fig. 53. Barnard, 1924: 217; 1929: 197, fig. 5d; 1935: 487. Linder, 1941: 228, fig. 30b.

Material

Type material. Consists of two males and two females and is housed in the Senkenberg Museum. Type specimens collected from the Kalahari, by D. Schultze, date unknown (Daday 1910).

Material examined. SAM-A5980, 1 male (12,1 mm), 1 female (11,8 mm); collected from Papkuil, near Kimberley, Cape Province by Miss Wilman, date unknown. SAM-A7255, 1 male with cercopods missing; collected from Bak River, Cape Province by K.H. Barnard, 1925. SAM-A6290, 1 male, poor condition; collected from between Keimoes and Upington, Cape Province, 1909, collector unknown. SAM-A7257, specimens dehydrated, collected from Outjo, Kaokoveld, Namibia by K.H. Barnard, 1926. SAM-A7256, specimens in poor condition, collected from Narugas siding, Cape Province by K.H. Barnard, 1925. SAM-A7258, 2 males in poor condition collected from Kamanyab, Kaokoveld, Namibia by K.H. Barnard, 1926. SAM-A7267, 3 males (12,5; 12,6 mm; 1 with cercopods broken), 5 females (10,4 - 12,3 mm); collected from Cauas Okawa, Kaokoveld, Namibia by K.H. Barnard, March 1926. SAM-A5922, 1 male (19,0 mm); collected from Great Fish River, near Gibeon, Namibia by R.W. Tucker, January 1916. SAM-A7599, 1 male (cercopods removed), 12 females (poor condition); collected from Amadap Valley, Little Namaqualand, Cape province by Dendy, 1938. SMN 51291, 8 males (6,5 - 7,9 mm), 10 females (5,4 - 7,4 mm); collected from small pool in a rock kaross, Etosha Park, Namibia by E. Griffen, 7 October 1986. SMN 51197, large number of specimens, 25 males measured ($9,0 \pm 0,6$ mm), 22 females measured ($8,3 \pm 0,6$ mm); collected from large shallow rock pool at the base of a rock hill (Bakenkop), Namib Naukluft Park, Namibia by B.D. Collahan, 17 March 1986. SMN 51334, 1 male with broken abdomen; collected from Charl Marais Dam (Sukses Dam), Etosha Park, Namibia by M. & P. Lindeque, 26 January 1988. TM VLKE

No.443, large number of specimens, 33 males measured ($10,6 \pm 1,2$ mm), 25 females measured ($10,8 \pm 1,2$ mm); collected from Gori Pan (possibly Goru, Kangara), Botswana by the VLKE, 20 April 1930. HNHM I/A 78, 3 males (9,1; 9,2; 10,2 mm), 2 females (8,7; 10,2 mm); collected from Kalahari, Botswana, collector and date unknown. AM LEN 150A, large number of specimens, many immature, 14 males measured ($9,8 \pm 3,0$ mm), 20 females measured ($8,8 \pm 0,8$ mm); collected from Leeubron, Etosha Park, Namibia by A. Bowland, November 1985. AM LEN 156A, 1 male (11,5 mm); hatched from sediment (5 February 1993) collected from rockpool on top of Moonrock, Augrabies Falls National Park, Cape Province by M. Hamer, 19 December 1992. AM LEN 163A, 6 males (8,1 - 11,8 mm), 2 females (9,3; 10,9 mm); hatched from sediment (2 April 1993) collected from dry pool, 40 km S of Kalahari Gemsbok Park, Cape Province by M. Hamer, 24 December 1992. SAM-A40840, 7 males (10,6 - 14,4 mm); hatched from sediment collected from granite rock cavity, 10 km NE of Gobabeb, Kuiseb River bed, by J.A. Day, 24 June 1981. SAM-A40841, 2 males (15,6; 16,3 mm); hatched from sediment collected from Amichab, 140km W of Rheboth, Namibia by J.A. Day, 5 July 1981. SAM-A40842, 1 male (14,0 mm); locality data as for SAM-A40841, hatched from sediment collected by J.A. Day, 24 June 1981. DB 765, 1 male, 1 female (both poor condition); collected from series of pools at Blutkoppie on granite outcrop, Namib Desert, Namibia by J.A. Day, 27 March 1982. DB 767, 1 male (18,8 mm), 5 females (10,9 - 13,8 mm); hatched from sediment collected from Gemsbokwater, 18km N of Ganab, Namib Desert, Namibia by J.A. Day, 14 May 1980. DB 768, 1 male, 1 female (both poor condition); hatched from sediment collected from 4km NNW of Zebra Pan, Namib Naukluft Park, Namib Desert, Namibia by J.A. Day 2/12 May 1980.

Branchipodopsis cf. *tridens* Namibia. DB 761, 2 males (12,1; 12,5 mm); hatched from sediment collected from large gravel pool in desert plain near Heinrichsberg, Namib Desert, Namibia by J.A. Day, 5 July 1981. DB 763, 4 males (10,0 - 11,0 mm); collected from Mirabib, 2 sinkholes in granite inselberg, Namib Desert, Namibia by J.A. Day, 26 March 1982. DB 764, 9 males (13,1 - 15,8 mm), 25 females ($12,6 \pm 0,8$ mm); hatched from sediment collected from Gemsbokwater, series of pools in granite desert floor, Namib Desert, Namibia by J.A. Day, April 1978.

Branchipodopsis cf. *tridens* N Transvaal/ Zimbabwe. AM LEN 151A, 4 males (2 poor condition, others 6,9; 7,9 mm); collected from pool on rocky outcrop near Umzingwani River, Benfer Estates, Zimbabwe by O. Wirminghaus, 8 July 1988. AM LEN 134B, 1 male (13,4 mm), 1 female (12,3 mm); collected from Mopane, 35km S Beit Bridge, Transvaal by O. Wirminghaus, 31 December 1992.

Redescription of adult male

Clypeus. Basal process broad, distally with a large, angular inner lobe and a short, conical outer lobe. Inner lobe usually apically flat or slightly convexly rounded (Figs 28A, 29A-D) and with scale-like patterning on apex (Fig. 30A-C). Median margin of basal process usually with a distinct indentation at base of inner lobe (Fig. 29A-D). Large conical/digitiform projection present proximally on dorsal surface of each basal process (Figs 28A, 29A-D). Lamelliform process narrow and ovate (Fig. 29A-D). Terminal joint with distinct bend, and strongly curved inwards, usually apically indented or bifid (Fig. 28A). Median ventral process small and minutely setulose but in most cases absent.

Cercopods. Moderate length (ratio to body length approximately 0,25:1). Outer margins convex with short, plumose setae along three quarters of length, distal quarter with 4-6 spines. Proximal third of inner margins with sparse, moderate length setae, followed by 12-16 sharp spines (Fig. 28B).

Abdominal spines. Pair of spines on last abdominal segment usually prominent (Fig. 28C).

Penes. Basal part broad, with distinct rounded projection proximally on median margin (Fig. 28D).

Remarks

A large amount of variation is evident in the clypeus of *B. tridens* from different localities. In some cases the variation may be attributed to the specimens not being fully mature or a result of poorly preserved material. The HNHM specimens are, presumably, part of the type material. The clypeus of even these three specimens shows variability in terms of the median margin indentation, shape of the inner lobe (Fig. 28E, H) and apex of the terminal joint and this is probably size-related. Most of the specimens from the other localities are, however, fully developed and in fair condition but they still exhibit a certain amount of interpopulation variation in the shape of the lobes of the basal process, their relative lengths, the proportion of the dorsal, conical projection to that of the basal process and in the shape of the apex of the terminal joint. The indentation in the median margin of the basal process is also variable in extent. In some specimens it is so pronounced as to form a narrow third lobe while other specimens have a completely straight median margin. There are a number of sets of specimens with the median margin in a state intermediate between these two extremes. An attempt to divide the large number of specimens into morphological groups, based mainly on proportions of inner and outer lobes and dorsal process, failed because of a large amount of overlap of characters. Further comment on this intraspecific variation is made in the discussion section.

Certain of the Namib Desert specimens (DB 761, 762, 763, 764) do, however, have characters which allow them to be distinguished from the other *B. tridens* material. These specimens have a distinct, short and broad spinous projection just proximal to the bend in the terminal joint (Figs 29B, 30D). This structure is absent in all other *B. tridens* specimens examined and from both Daday (1910) and Barnard's (1929) descriptions and illustrations. In addition, these specimens have a deep indentation in the median margin of the basal process, such that a narrow third lobe is formed (Fig. 32B, D) and the dorsal projection is broad and blunt as opposed to the conical and apically narrow process of other specimens. These differences could indicate that this material represents a species or population intermediate between *B. tridens* and *B. kaokoensis*.

The Zimbabwe and Mopane specimens show the greatest difference from Daday's (1910) figures and specimens and are easily distinguished from the remainder of the *B. tridens* material. The inner lobe is broadly hook-shaped with a convex median margin and the apex of the terminal joint is tapered and narrow (Fig. 31A-B). For this reason, and because identical specimens have been collected from two localities, it is quite possible that they represent a closely related, but separate species from *B. tridens*. However, no material has been collected from the area between Namibia and northern Transvaal/southern Zimbabwe and the possibility of intermediate forms exists.

Until such time as collecting over greater areas of southern Africa has been done and further research into sexual isolation and molecular biology has been undertaken, it seems prudent to simply describe the variation observed without drawing any conclusions.

Distribution

Branchipodopsis tridens is widely distributed in the arid western region of southern Africa. A large number of records from northern Namibia exist, and this species has also been collected from the southern part of that country as well as the north-western Cape (Fig. 39). The Zimbabwe specimens represent the most eastern record for the species and *B. tridens* has also been collected from Bloemfontein in the central region of South Africa (Seaman *et al.* 1991).

Branchipodopsis underbergensis sp. nov.

Figs 32-33

Material

Holotype. SAM-A40837, 1 male (14,4 mm); collected from rockpool on Bamboo mountain, near Underberg, Drakensberg, Natal by T. Clarke & N. Crouch, December 1993.

Paratypes. SAM-A40838, 15 males (14,3 \pm 0,6 mm), 8 females (12,0 - 15,0 mm);

same collection data as holotype specimen.

Other material examined. SAM-A40848, 24 males ($10,7 \pm 0,6$ mm), 29 females ($10,1 \pm 0,7$ mm); collected from Underberg, Drakensberg, Natal, collector and date unknown (specimens were previously in the teaching collection of the Zoology Department, University of Natal, Pietermaritzburg).

Description of male

Clypeus. Basal process positioned low on basal joint (apex not reaching past anterior median margin of basal joints) on inflated base, slender and digitiform (Figs 32A, 33A-B). Prominent short and conical projection on proximal, dorsal surface of basal process (Figs 32A-B; 33A-B). Apical region of basal process and projection patterned by series of rounded ridges and depressions (Fig. 33C). Median ventral process ovate and spinous with blunt apex (Figs 32A, 33A). Lamelliform process very large and round-ovate (Figs 32A, 33A). Terminal joint curved inwards and with inflated apex (Figs 32A, 33A).

Cercopods. Long (ratio to body length approximately 0,35:1). Outer margins proximally convex, distal halves slightly concave and with short, spinous setae along entire length. Small patch of setae proximally on inner margins followed by about 14 short spines (Fig. 32C).

Abdominal spines. Pair of small spines on ventral surface of last abdominal segment (Fig. 32D).

Penes. Basal part short, with moderate-sized, rounded projection on median margin (Fig. 32E).

Description of female

Pair of small pouches on dorsal surface of penultimate thoracic segment and lateral surfaces of last thoracic segment extended outwards (Fig. 32G).

Egg morphology

Egg surface with irregular, 4-5 sided depressions, separated by narrow, sharp ridges (Fig. 33D).

Differential diagnosis

Superficially, *B. underbergensis* resembles *B. drakensbergensis*. This is largely because of the proximal projection of the basal process and the slender shape of the basal process. However, the fact that the basal process of the former species is single as opposed to bilobed in the latter, suggests two distinct species. Further differences include

the very large lamelliform process in *B. underbergensis* and the small basal process positioned low on the basal segment of the clypeus of this species. The median ventral process also differs in shape, as do the cercopods. In addition, the females of *B. drakensbergensis* lack the thoracic pouches (Fig. 10F) which are distinct in *B. underbergensis* females.

Distribution

Branchipodopsis underbergensis has only been collected the foothills of the Natal Drakensberg in the Underberg area (Fig. 38).

Remarks

As a result of the general similarity between the basal processes of *B. drakensbergensis* and *B. underbergensis*, these two species were linked in Table 1. However, *B. underbergensis* does have a number of characteristics which could indicate that it does not belong in the same species group as *B. drakensbergensis*, *B. tridens* and *B. kaokoensis*. For example, the proximal, dorsal process on the basal process of *B. underbergensis* could be homologous to the dorsal lobe of the basal process of *B. hodgsoni* rather than the process in the *B. tridens* group. The low position of the basal process in *B. underbergensis* and in *B. hodgsoni* could provide further evidence for the relationship between these two species.

Etymology

Branchipodopsis underbergensis is named after the type locality of Underberg.

Branchipodopsis wolffi Daday, 1910

Figs 34-37

Branchipodopsis wolffi Daday, 1910: 304, fig. 52; 1913: 4. Barnard, 1924: 217; 1929: 197, fig. 5g.

Material

Type material. Collected in the Kalahari and housed in the Senkenberg Museum. No further information available.

Material examined. SAM-A7268, 1 male (11,9 mm), 1 female (10,3 mm); collected from Altmark, Outjo district, Namibia by K.H. Barnard, January 1926. SAM-A6004, 18 males ($6,5 \pm 0,5$ mm), 15 females ($6,5 \pm 0,4$ mm); collected from Onganjera, Ovamboland, Namibia by K.H. Barnard, 1926. SAM-A5920, 5 males (11,9 - 15,6 mm);

collected from Beaufort West, Karoo, Cape Province by W.F. Purcell, 24 September 1905. SAM-A7253, 20 males ($6,3 \pm 0,6$ mm), 11 females ($5,8 \pm 0,5$ mm); collected from Kamanyab, Kaokoveld, Namibia by K.H. Barnard, 1926. SAM-A7273, 8 males (10,0 - 12,0 mm), 9 females (10,0 - 11,5 mm); collected SE of Choabendus, Kaokoveld, Namibia by K.H. Barnard, January 1926. SAM-A5921, 19 males ($12,8 \pm 1,5$ mm), 13 females ($12,1 \pm 0,9$ mm); collected from Great Fish River, near Gibeon, Namibia by R.W. Tucker, January 1916. SAM-A4248, large number of specimens, 23 males measured ($7,8 \pm 0,8$ mm), 15 females measured ($7,9 \pm 0,8$ mm); collected from Kimberley, Cape Province by J.H. Power, 1917. SAM-A7254, 9 males (12,8 - 14,8 mm), 1 female (15,0 mm); collected from Kimberley, Cape Province by J.H. Powers, 1917. SAM-A6005, 5 males (8,5 - 10,5 mm), 21 females ($8,6 \pm 0,7$ mm); collected from Waterberg, Namibia by R.W. Tucker, 1920. SMN 51217, 5 males (8,0 - 9,1 mm), 6 females (7,8 - 8,8 mm); collected from rainpool near Otjituuo, Hereroland West, Namibia by B.A. Curtis, 28 April 1987. HNHM I/A-77, 1 male (8,9 mm), 1 female (8,2 mm); collected from Kalahari, Botswana, collector and date unknown. AM LEN 99B, 4 males (14,8 - 15,3 mm), 8 females (9,5 - 11,3 mm); collected from Pumbe Pan, Kruger National Park, Transvaal by M. Hamer, 28 October 1990. AM LEN 154A, 3 males (8,1; 9,6; 10,0 mm), 5 females (8,9 - 9,5 mm); collected from Nylsvlei Nature Reserve, Transvaal by C. Pitzke-Widdig & T. Widdig, February 1990. DB 668: 1 male (12,5 mm), 5 females (10,0 - 13,0 mm); collected from Machoarane Mountain, about 2km S of Morija (Moraija), Lesotho by T.C. Rutherford, 8 November 1985. DB 667, 1 male (abdomen removed), 2 females (10,1; 12,8 mm); collected from Brakfontein, 17km S of Mochales Hoek, Lesotho by T.C. Rutherford, 12 December 1985. DB 669, 8 males (8,1 - 13,9 mm), 7 females (11,3 - 12,8 mm); collected from Leloaleng near Quting, Lesotho by T.C. Rutherford, 13 December 1985. DB 817, 3 males (14,0; 16,4; 17,0 mm), 3 females (13,0; 13,9; 15,6 mm); collected from Outward Bound, Leribe, Lesotho by T.C. Rutherford, 4 January 1986.

Branchipodopsis cf. *wolffi*. AM LEN 69B, 3 males (8,5; 8,8; 9,0 mm), 2 females (8,0; 9,8 mm); collected from Mala Mala Game Reserve, Transvaal by W.A. Taylor, 25 June 1989. AM LEN 155A, 3 males (9,9; 11,1; 11,3 mm); cultured from dried sediment (February 1990) collected from Mala Mala Game Reserve, Kirkmans Kamp area, Transvaal by M. Hamer, September 1989. AM LEN 120A, 7 males (7,8 - 10,0 mm), 2 females (6,8; 9,5 mm); collected from region S of Skukuza, Kruger National Park, Transvaal by A. & J. Bowland, 14 October 1990. AM LEN 121A, 15 males ($9,8 \pm 0,6$ mm), 22 females ($8,7 \pm 0,5$ mm); same collection data as AM LEN 120A.

NMZ/Cr 29, 1 male (damaged), 3 females (damaged); collected from Matopos, Zimbabwe in December 1964, collector unknown. NMZ/Cr 6, 9 males (15,0 - 20,6 mm), 14 females

(17,9 ± 2,0 mm); collected from Matopos, Zimbabwe by A.N. Smith, December 1981. USNM 184629, 3 males (9,0; 9,3; 9,4 mm), 2 females (8,1; 8,6 mm); collected from Bulawayo, Zimbabwe by D.H. Eccles & W.G. Moore, 10 February 1955. USNM 102318, 3 males (8,8; 9,0; 10,6 mm), 1 female (9,5 mm); collected from pools at isoyds of the tomb of Cecil John Rhodes, 25 miles SSW of Bulawayo, Zimbabwe by D.H. Eccles, 10 February 1955.

Redescription of adult male

Clypeus. Basal process wide with single large, conical or triangular inner lobe and two apical tubercles (Figs 34A, 35A-D). Lateral tubercle digitiform/ conical and positioned slightly ventrally (Fig. 36A-D). Median tubercle usually similar in size and shape to outer tubercle and situated dorsally at base of inner lobe (Figs 36A-D; 37B-C, F). A small, flattened projection often present on median apex of inner lobe (Figs. 36A, C; 37D, F). Lamelliform process small and round or oval (Figs 34A, 35A-D). Terminal joint curved inwards with apex varying from flattened (Fig. 35B) to slightly indented (Fig. 35D). Median ventral process very small to large and prominent, usually oval and with surface covered by short spines (Fig. 35A-D).

Cercopods. Average length (ratio to body length approximately 0,27:1). Outer margins weakly convex and with plumose setae of moderate length but these replaced by 2-4 short spines distally. Proximal third of inner margins with plumose setae followed by 10-16 spines of unequal size (Fig. 34B).

Abdominal spines. Last abdominal segment with two strong ventral spines (Fig. 34C).

Penes. Basal part slender, with proximal rounded projection on median margin. Peg-like projection near apex on lateral margin (Fig. 34D-E).

Remarks

Much variation is evident in the clypeus of *B. wolfi* from different localities. This was observed and commented on by Barnard (1929). Variation is most obvious in the following features of the clypeus: the apex of the terminal joint, the shape of the tubercles and the inner lobe, the presence and shape of a projection on the inner lobe, the relative lengths of the tubercles, the position and size of the median tubercle and the shape of the median margin of the basal process.

The HNHM specimen is most likely from the type material as it is from Daday's collection and from the type locality. In this specimen the tubercles and inner lobe are rather short and rounded and all of similar shape. A small apical projection is present on

the inner lobe. The median margin has an inflation just proximal to the base of the inner lobe. Most of the other specimens show some variation on this basic arrangement. The median tubercle of the Lesotho specimens is small and lies in the same plane as the inner lobe and the apical process is very prominent and rounded (Fig. 36A). In the Altmark specimen the inner lobe is roughly triangular and lacks the apical projection (Fig. 36D). The Kruger Park (Pumbe) specimens have an angular median margin and a very broad inner lobe (Fig. 36B). It is, however, the Zimbabwean and southern Kruger Park specimens that show the greatest morphological divergence from the *B. wolfi* 'types'. The median tubercle is small and triangular and is situated about halfway along the length of the inner lobe (Fig. 37B, F). These specimens could be regarded as a separate species but have been included with *B. wolfi* here because there is a series of intermediate basal process morphologies between these and the other, more typical representatives. For example, the Mala Mala specimens have a larger median tubercle than the other two sets of specimens, those from the Kruger Park have a slightly smaller tubercle, and the Zimbabwe specimens have an even smaller one. These specimens therefore form a series from a prominent to a small median tubercle and yet all three sets share a very similar basal process shape. The specimens from Nylsvlei represent a basal process morphology intermediate between the Kruger Park, Mala Mala and Zimbabwe specimens and other, more typical, *B. wolfi* specimens and this makes it impossible to divide, with any confidence, these specimens into separate species or subspecies at this stage.

The structure of the basal process of *B. wolfi* can be interpreted in a number of different ways and this further complicates any attempt to identify species or subspecies, and to determine relationships with other species of the genus. It is uncertain whether the median tubercle illustrated in Figure 36B and D is homologous to that illustrated in Figures 36A and 37 B and F. In addition, the inner lobe could be interpreted as a third tubercle and the lateral tubercle could represent a second lobe.

Distribution

As Barnard (1929) stated, *B. wolfi* is the most widely distributed species of *Branchipodopsis*. This species occurs in arid northern and southern Namibia, the northern Cape and Karoo, in the sub-tropical eastern Transvaal and Zimbabwe and in the high-altitude, mountainous habitats of eastern Lesotho (Fig. 40). *Branchipodopsis wolfi* was also collected from Umfolozi Game Reserve in north-eastern Natal but these specimens had dried out and they were not listed under specimens examined. An additional set of specimens from pools outside Gaborone was examined and identified as *B. wolfi* for Dr M. Cantrell, formerly of the University of Botswana. Barnard (1929) referred to the presence

of *B. wolfi* in Kenya but illustrations or specimens from there have not been seen and so this locality cannot be verified. However, a set of specimens in the BMNH from "40km north of Soroti in the Eastern province of Uganda" were examined and their identification as *B. wolfi* confirmed in terms of the features of the species as presented here. This record may indicate a wider distribution of *B. wolfi* than for the other southern African *Branchipodopsis* species.

KEY TO THE SOUTHERN AFRICAN SPECIES OF THE GENUS *BRANCHIPODOPSIS*
(using features of the male clypeus)

1a. Basal process distinctly bilobed apically, lobes of similar height and positioned adjacent to each other 2

1b. Basal process either unlobed (with a single lobe), or if bilobed, lobes of distinctly different heights or not positioned adjacent to each other 5

2a. Basal process with tubercle on median dorsal surface and smaller projection on median margin of inner lobe 3

2b. Basal process with small projection on median surface of inner lobe only 4

3a. Basal process lobes equal in size and shape, apex of terminal joint blunt, lamelliform processes broadly oval, with scalloped margin

B. hutchinsoni sp. nov. (Figs 17-18)

3b. Inner lobe of basal process narrower than outer, apex of terminal joint peg-like or rounded, lamelliform processes narrow oval with smooth margin

B. natalensis Barnard, 1929 (Figs 23-24)

4a. Inner lobe of basal process more conical than rounded, lamelliform process small, distal region of terminal joint foot-shaped *B. dayae* sp. nov. (Figs 8-9)

4b. Both lobes of basal process rounded, lamelliform process distinct, distal region of terminal joint with slight inflation and with blunt tip

B. karroensis Barnard, 1929 (Fig. 22)

- 5a. Basal process with large, spine-like or conical projection proximally on dorsal surface 6
- 5b. Basal process without proximal spine-like or conical projection 9
- 6a. Basal process with three distinct lobes, inner and outer lobes similar in size and smaller than median lobe *B. kaokoensis* Barnard, 1929 (Fig. 21)
- 6b. Basal process with only one or two distinct lobes 7
- 7 a. Basal process with one or two lobes, narrower than high, median ventral process prominent 8
- 7b. Basal process wider than high, median ventral process vestigial or absent
B. tridens Daday, 1910 (Figs 28-31)
- 8a. Basal process bilobed and almost as high as division between basal and terminal joints, lamelliform process smaller than basal process
B. drakensbergensis sp. nov. (Figs 10-13)
- 8b. Basal process with single lobe and lower than anterior median margin of basal joint, lamelliform process very large (larger than basal process)
B. underbergensis sp. nov. (Figs 32-33)
- 9a. Basal process single or bilobed, if bilobed, lobes of distinctly different heights, dorsal or apical projections or tubercles absent 13
- 9b. Basal process with single lobe, dorsal or apical tubercles or projections present 10
- 10a. Basal process with inflated base, rounded apex and with keel-like structure dorsally
B. simplex Barnard, 1924 (Fig. 27)
- 10b. Basal process without keel-like structure dorsally, but with one or more tubercles or projections near apex 11
- 11a. Basal process with two digitiform or conical tubercles apically, projecting beyond anterior margin of basal process, lamelliform processes small or moderate-sized 12

11b. Basal process with without apical tubercles projecting beyond anterior margin, lamelliform processes enlarged *B. browni* Barnard, 1924 (Figs 6-7)

12a. Two tubercles present, second positioned ventrally to first, distinct inner lobe absent *B. hodgsoni* Sars, 1898 (Figs 15-16)

12b. Two tubercles present, one median and one ventro-lateral, large inner lobe present *B. wolfi* Daday, 1910 (Figs 34-37)

13a. Basal process with single lobe of spiniform shape *B. scambus* Barnard, 1929 (Figs 25-26)

13b. Basal process bilobed, outer lobe distinctly shorter than inner lobe 14

14a. Width of basal process greater than or equal to height, terminal joint stout and strongly inwardly curved with distinct bend

B. kalaharensis Daday, 1910 (Figs 19-20)

14b. Basal process longer than wide, terminal joint slender, weakly curved and without distinct bend 15

15a. Terminal joint distally hook-shaped, median ventral process present

B. drepane Barnard, 1929 (Fig. 14)

15b. Terminal joint distally smooth and straight, median ventral process absent

B. barnardi sp. nov. (Figs 4-5)

Table 1. Tentative division of the southern African species of the genus *Branchipodopsis* into species groups based on male antennal morphology.

1. Basal process slender, bilobed, with outer lobe considerably shorter than inner lobe. Terminal joint without distinct bend.
2. Basal process not lobed, dorsal, median tubercle present near apex, small projection present near apex.
3. Basal process with two, similar-sized lobes.
4. Basal process with two lobes, one positioned dorsally to other.
5. Basal process simple, slender, without projections or lobes, terminal joint smooth.
6. Basal process with dorsal keel, without lobes.
7. Prominent projection on dorsal surface of basal process.

Group	1	2	3	4	5	6	7
Species	<i>B. barnardi</i> <i>B. drepane</i>	<i>B. browni</i> <i>B. wolfi</i>	<i>B. dayae</i> <i>B. hutchinsoni</i> <i>B. B. kalaharensis</i> <i>B. karroensis</i> <i>B. natalensis</i>	<i>B. hodgsoni</i>	<i>B. scambus</i>	<i>B. simplex</i>	<i>B. drakensbergensis</i> <i>B. kaokoensis</i> <i>B. tridens</i> <i>B. underbergensis</i>

DISCUSSION

Of the approximately 21 known species of *Branchipodopsis*, 16, including the five new species described here, occur in southern Africa and 15 of these are apparently restricted to this region. There is little morphological variety among the three Asian *Branchipodopsis* species and it has even been suggested that they may belong to a single species (Hartland-Rowe 1968; Brtek *et al.* 1984). The status and morphology of the two remaining *Branchipodopsis* species, namely *B. abiadi* from Mauritania in West Africa and *B. candea* from central Africa is uncertain since these specimens are unavailable, and either

the descriptions are inadequate, or, in the case of the latter species, the original description cannot be located.

Taxonomic characters

The antennae of the male, as in most other anostracan genera, is the character of greatest taxonomic value within *Branchipodopsis*. The male anostracans use the enlarged, and two-jointed antennae to clasp the female during mating. Belk (1991) found that within the Anostraca, mating depends on female choice, with males attempting to mate completely unselectively. The female does not, however, always successfully recognize conspecific males by the structure of the antenna or by body armature or cercopod structure. This statement was based on Wiman's (1979) findings that hybridization occurred between North American species of *Streptocephalus* both in the laboratory, and, under sympatric conditions, in the field. Selection, therefore, is not for antihybridisation mechanisms. Belk (1991) suggested that the antennae, because of their function in mating, are ideal candidates for runaway sexual selection by female choice and their 'elaborate structure should be viewed as arbitrary additions to the complexity of structures providing tactile clues'. Speciation in anostracans appears to be the result of the slow accumulation of genetic differences in allopatric populations (Wiman 1979).

In contrast to the streptocephalids where the male cercopod setation, frontal appendage, abdominal armature and external egg morphology are frequently species-specific, these characters either vary little between species of *Branchipodopsis* or they are largely absent. Authors such as Linder (1941) emphasized the structure of the penes as taxonomic characters at the family and genus levels, but between species, these do not differ to any extent. There is some interspecific variation in the prominence of the rounded projection on the median margin of the penes in *Branchipodopsis* species examined but this is difficult to quantify and is often dependent on the preservation method or condition of the specimens. The peg-like projection at the apex of the proximal part of the penes is very obvious in some species, while in others, only a blunt, obscure projection is present. In other species, no distal, lateral projection of any kind is visible. In certain cases, preservation state is responsible for the variation but this structure is quite clearly absent in certain species. Unfortunately, these structures do not appear to reflect relationships between species. Within *Branchipodopsis* there is little interspecific variation in cercopod shape or setation; the number of spines on the inner margin does vary to some extent between species but there is a significant amount of overlap as well as intraspecific variation. External egg morphology is also of limited value for the same reasons (personal

observations). Body armature such as that seen in certain *Streptocephalus* species is absent in *Branchipodopsis* with the exception of the two spines on the ventral surface of the last abdominal segment. Again, however, this character does not appear to reflect species relationships since it is often present in species with very different antennal morphologies, and since these spines are present in approximately half the described species, they cannot be used for species identification. A character not mentioned by other authors but used in this review is the presence, position and shape of pouches proximal to the genital segments of the females of some species. The significance of these structures is uncertain but since they only occur in high altitude species (*B. barnardi*; *B. underbergensis* and *B. natalensis*), they may be of physiological importance. Until such time as these structures are proved otherwise, however, they can provide a useful additional character in separating species with similar basal process morphology such as *B. hutchinsoni* and *B. natalensis*, and *B. drakensbergensis* and *B. underbergensis*.

Division of species into groups

An attempt was made to divide the southern African species of *Branchipodopsis* into species groups. This was recently done for the African streptocephalids (Hamer, Brendonck, Coomans & Appleton in press a,b) as a step towards understanding relationships between species and in examining the biogeography of the genus *Streptocephalus*. For the southern African *Branchipodopsis* species, the form of the clypeus, and in particular, the basal processes, was used for this division. The groupings resulting must be seen as tentative since inadequate data on the morphology, ontogeny and evolution of the genus and family are available. For example, it is almost impossible to determine, with any degree of confidence, homologous structures and incidences of homoplasy. A limited number of characters, and in certain species, specimens, which can be used is a further limitation to such a division, as is the large amount of intraspecific variation in some species. For these reasons, cladistic analyses were not attempted here.

Intraspecific variation

The large amount of variation observed in the basal processes of *B. wolffi* and *B. tridens* presented a major problem in this study. Specimens from some localities exhibited a considerable degree of diversion from the original description and the type material in terms of antennal, and particularly basal process, morphology. However, other sets of specimens had basal process morphologies intermediate between these and the original material. An attempt was made to group populations of *B. tridens* and *B. wolffi* with the most similar basal process structure morphometrically but this produced a large degree of

overlap and no distinct clusters, which may have suggested different species, were evident. For these reasons the variation was simply described and/or illustrated. In the case of *B. wolfi*, antennal variation was evident in almost every population and it was impossible to illustrate all of this. Similar intraspecific variation was also observed in the Asian species *B. affinis* and was illustrated by Brtek *et al.* (1984). In the case of these three species, more advanced taxonomic methods, most important of which will certainly be molecular techniques, are necessary to determine the relevance of this variation. At this stage, however, lack of sufficient quantities of material of all representative populations presents the major obstruction to such a study.

Distribution and ecology

An in depth discussion of the biogeography of *Branchipodopsis* will be published elsewhere and only a brief comment will be made here about distribution and habitats. The majority of *Branchipodopsis* specimens were collected from small waterbodies such as roadside ditches, shallow rainpools and small rockpools where conditions would be expected to be extreme. Observations under both laboratory and field conditions have revealed that a number of *Branchipodopsis* species (*B. tridens*, *B. wolfi*, *B. dayae* and *B. browni*) grow very rapidly and reach sexual maturity four to six days after hatching. Their life span is only two to four weeks. This contracted life history allows members of the genus to exploit habitats not available to the other main group of southern African anostracans, the streptocephalids which generally have a slower, longer life history. Species of the genus *Streptocephalus* have never been collected from high- altitude rockpools, thus allowing *Branchipodopsis* to dominate such habitats. Belk (1991) found a similar situation with *S. texanus* and *Branchinecta packardi* in central Texas. In temporary pools in southern Africa where *Streptocephalus* occurs, *Branchipodopsis* species are found in low numbers and complete their life history before the streptocephalids reach maturity, they occupy a different niche, or they are absent. This may imply a reduced competitive ability for the genus. Further evidence for this is the rarity of the presence of more than one species in a single habitat. Barnard (1929) reported that two male *B. drepane* were found among a sample of *B. tridens* and *B. wolfi* but this is the only known case of multispecies existence. This could be a result of the restricted resources in habitats such as montane rockpools; but the forces separating species such as *B. barnardi* and *B. natalensis*, which inhabit the same type of rockpools in the Drakensberg in an area of less than five km², are not known. Perhaps, as has been suggested (Wiman 1979; Williams 1985; Brendonck Thiéry & Coomans 1990) branchiopods are adapted to resisting, rather than promoting, dispersal which may be a rare occurrence.

Williams & Busby (1991) suggested that only in episodically-filled temporary pools could one expect to find widespread and easily-dispersed species. The reason for this is that the irregularity of filling of such habitats does not allow the evolution of local adaptations and subsequent speciation. Many *Branchipodopsis* habitats, however, because of their small size, are likely to undergo a number of wet and dry phases during a single rainy season. As a result, many *Branchipodopsis* generations could be expected to hatch as opposed to a single generation in large pools which remain full for the duration of the rainy season or those which only fill every decade or less often. This would allow relatively rapid differentiation and could account for the large amount of intraspecific variation in such species as *B. wolfi* and *B. tridens*.

Conclusions

Southern Africa has the greatest diversity of *Branchipodopsis* species. This may be, as suggested by Banarescu (1990), a result of the genus having a Gondwanaland origin, or the result of a wide adaptive radiation having occurred in response to the habitat diversity present in southern Africa. However, of the 16 species now described, six species (*B. drepane*; *B. kaokoensis*; *B. karroensis*; *B. natalensis*; *B. dayae* and *B. simplex*) are known only from a single collection (the type material) consisting of fewer than five male specimens. For an additional species (*B. hutchinsoni*) only the type material has been collected although this is in larger quantities than for the former species. Most species appear to have restricted distributions and it is possible that some of the species which were last collected early this century have become extinct. Further collecting will certainly reveal a number of undescribed species as will research into intraspecific variation using molecular techniques to examine mitochondrial DNA. The distribution of species also needs to be reassessed as previously unexplored areas such as the northern and western Transvaal, Zimbabwe, Botswana and Mozambique are sampled. Detailed investigation of species relationships, and of the position of the genus within the Branchiopodidae needs to be undertaken to answer the taxonomic questions raised here.

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GAZETEER

Southern African *Branchipodopsis*

BOTSWANA

Gaberone	24°42'S 25°54'E
Gori (Goru?) Pan	18°S 22°E
Kalahari	20°S 24°E
Kanke Pan, 90 miles W of Molepole	24°24'S 25°32'E
Sunnyside	21°40'S 22°03'E

LESOTHO

Brakfontein, 17km S Mohale's Hoek	30°14'S 27°23'E
Leloaleng, near Quting	30°24'S 27°42'E
Machoarane Mountain, ± 2km S Morija (Moraija)	29°38'S 27°33'E
Outward Bound, Leribe	28°58'S 28°09'E
Sehlabatebe National Park	29°50'26''S 29°06'52''E

NAMIBIA

Amichab, 140km E Rheboth	23°13'S 15°32'E
Etosha Park	18°S 14°E
Etosha Park, Charl Marais (Sukses) Dam	19°00'32''S 15°26'46''E
Etosha Park, Leeubron	19°03'48''S 15°48'54''E
Great Fish River, near Gibeon	25°13'S 17°42'E
Great Namaqualand, Kalkfontein South (Karasburg)	28°01'S 18°45'E
Hereroland West, near Otjituuo	19°39'S 18°34'E
Kaokoveld, Choabendus, 115 miles NW of Outjo	19°50'S 15°41'E
Kaokoveld, Cauas Okawa	19°30'S 15°05'E
Kaokoveld, Kamanyab	19°40'S 14°50'E
Kaokoveld, Outjo	20°06'S 16°09'E
Kaokoveld, Outjo district, Altmark	20°06'S 16°09'E
Namib desert, Blutkoppie	22°48'S 15°22'E
Namib desert, Gemsbokwater, 18km N Ganab	22°56'S 15°37'E
Namib desert, 10km NE Gobabeb, Kuiseb River bed	23°37'S 15°05'E

Namib desert, near Heinrichsberg	23°14'S 15°34'E
Namib desert, Mirabib	23°26'S 15°18'E
Namib Naukluft Park, base of Bakenkop	23°11'S 15°34'E
Namib Naukluft Park, 4km NNW Zebra Pan	23°31'S 15°28'E
Ovamboland, Eunda, ± 100 miles WNW of Ondangua	17°31'S 14°39'E
Ovamboland, Onganjera	17°54'S 15°04'E
Waterberg	20°32'S 17°08'E

SOUTH AFRICA

Cape Province

Amadap Valley	25°14'S 18°43'E
Ashton	33°49'S 20°03'E
Augrabies Falls, Moonrock	28°35'S 20°19'E
Bak River	28°31'S 17°15'E
Bredasdorp, road to Struisbaai	34°35'S 20°00'E
Carnavon, 10km S	31°10'S 22°08'E
Eland's Bay	32°18'S 18°19'E
Fraserburg, 8km NE	31°52'S 21°58'E
Gordonia, between Keimoes and Upington	28°30'S 21°14'E
Grahamstown	33°17'S 26°31'E
Grahamstown to Cradock road	33°16'40''S 26°29'05''E
Kalahari Gemsbok Park, 40km S	26°10'S 20°38'E
Karoo, Beaufort West	32°22'S 22°35'E
Karoo, Carnavon, 10km S on road to Loxton	31°10'S 22°08'E
Karoo, Fraserburg, 8km NE	31°52'S 21°58'E
Karoo, Hoogevelde, SW Beaufort West	33°10'S 21°46'E
Karoo, Hutchinson, 30km S on road to Richmond	31°30'S 23°29'E
Karoo, Williston	31°20'S 20°50'E
Kenton-on-sea	33°41'S 26°40'E
Kimberley	28°45'S 24°45'E
Koppieskraal Pan	26°56'26''S 20°18'47''E
Narugas siding	28°08'24''S 20°18'47''E
Papkuil, near Kimberley	30°12'S 18°21'E
Port Elizabeth	34°S 25°E
Ugie, Prentjiesberg	31°09'09''S 28°07'48''E

Williston 31°20'S 20°50'E

Natal

Drakensberg, Giant's Castle 29°16'S 29°30'E

Drakensberg, Loteni Nature Reserve 29°26'21''S 29°32'48''E

Bushman's Nek/ Sehlabatebe Game Reserve border 19°50'S 29°06'E

Drakensberg, Underberg 29°02'S 29°30'E

Drakensberg, Underberg, Bamboo mountain 29°43'S 29°20'E

Umfolozi Game Reserve 28°17'S 31°49'E

Orange Free State

Bloemfontein 29°07'S 26°14'E

Van Reenen, 1/2 miles from 28°21'S 29°22'E

Transvaal

Benoni, Witkoppies 26°11'S 28°16'E

Kruger National Park, Pumbe Pan 24°10'S 31°55'E

Mala Mala Game Reserve 24°45'S 31°30'E

Mopane, 35km S Beit Bridge 22°36'S 29°52'E

Nylsvlei Nature Reserve 24°39'S 28°42'E

ZIMBABWE

Benfer Estates, near Umzingwani River 22°12'S 29°56'E

Bulawayo 20°11'S 28°35'E

Bulawayo, 25km SSW, tomb of Rhodes 20°30'00''S 28°31'11''E

Matopos 20°33'S 28°20'E

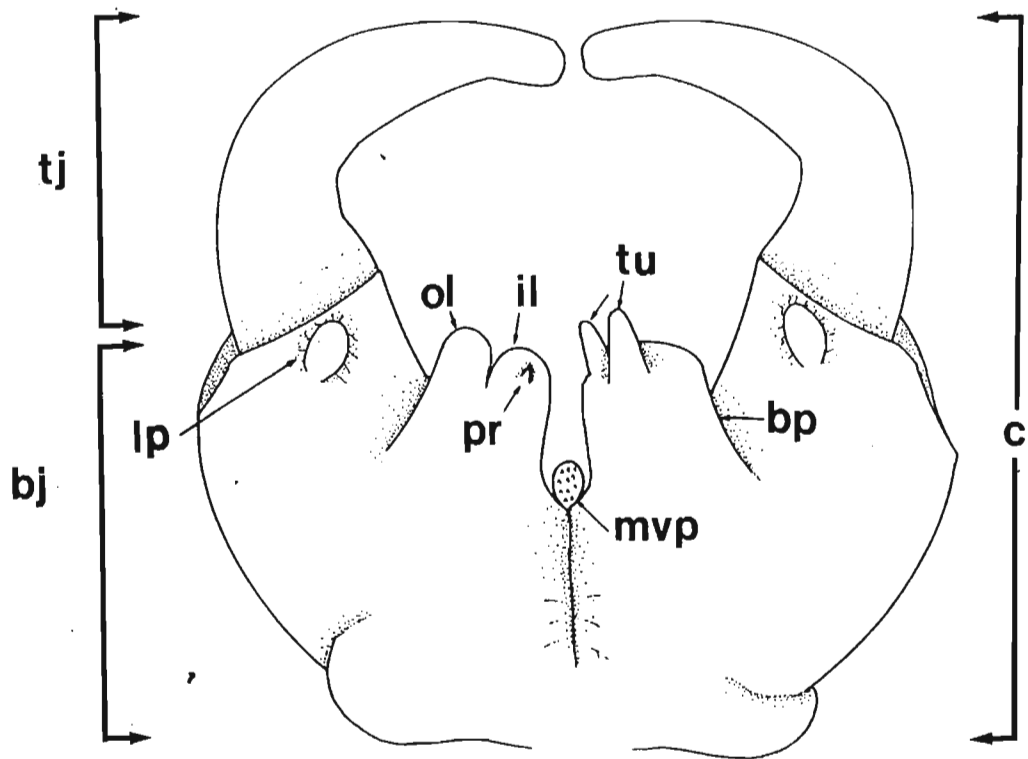


Figure 1: Diagram of idealised male antennae (clypeus) illustrating terminology used in text and figures. tj = terminal joint; bj = basal joint; bp = basal process; lp = lamelliform process; il = inner lobe; ol = outer lobe;.mvp = median ventral process; pr = projection; tu = tubercle.

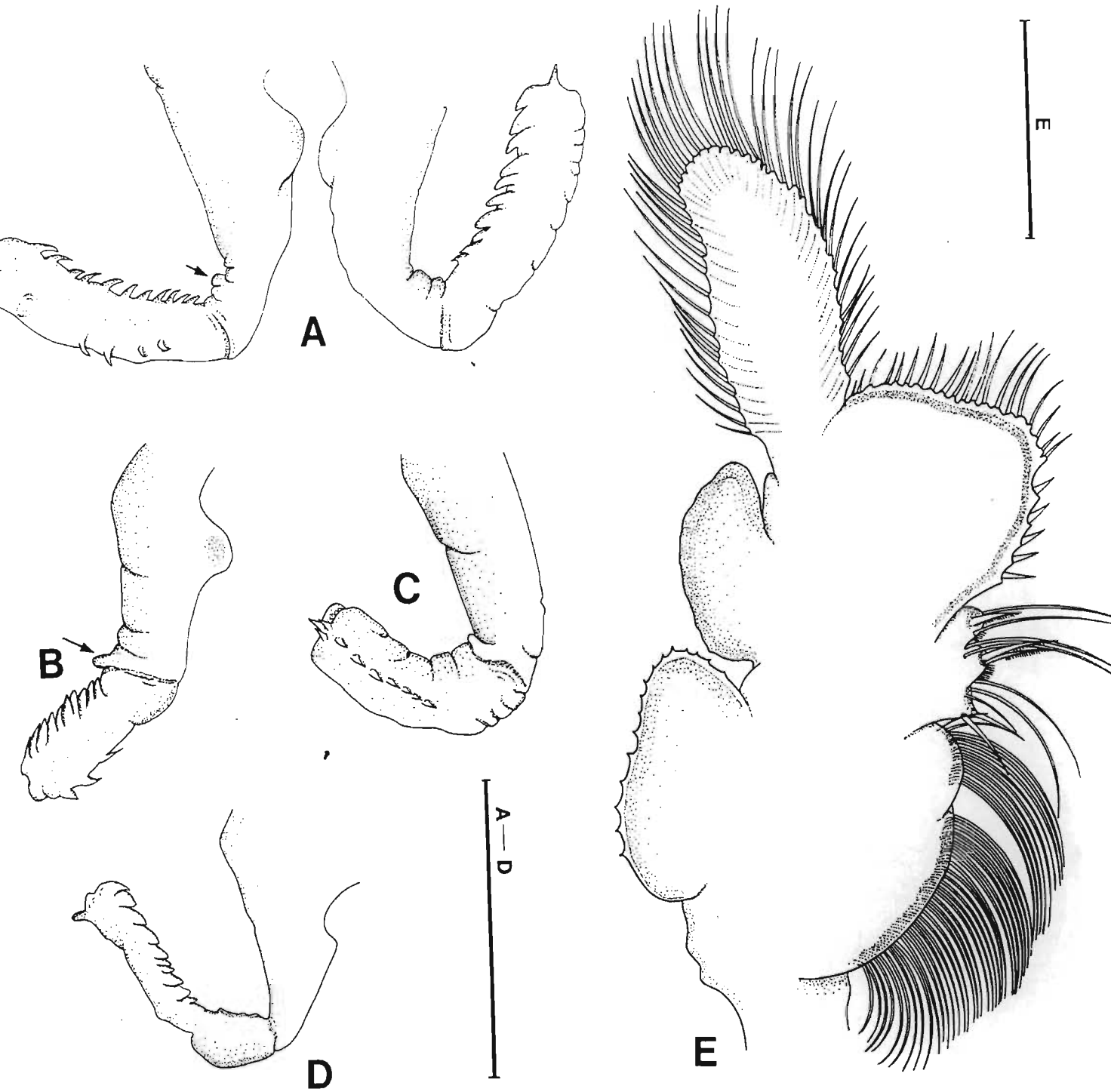


Figure 2: A = penes of *B. wolfi* (DB 817); Ai = ventral view of right penis; arrow indicates peg-like projection; Aii = dorsal view of right penis; 1 = row of regular spinous processes; 2 = irregular row of spinous processes. B = ventral view of right penis of *B. wolfi* (NMZ/Cr 6); arrow indicates peg-like projection, mp = median rounded projection. C = lateral view of right penis of *B. wolfi* (NMZ/Cr 6); a = apical eversible part; b = basal part. D = ventral view of right penis of *B. natalensis* (DB 818). Scale A-D = 1 mm. E = right thoracopod 4 of *B. tridens* (AM LEN 150A); Scale E = 0,5 mm.

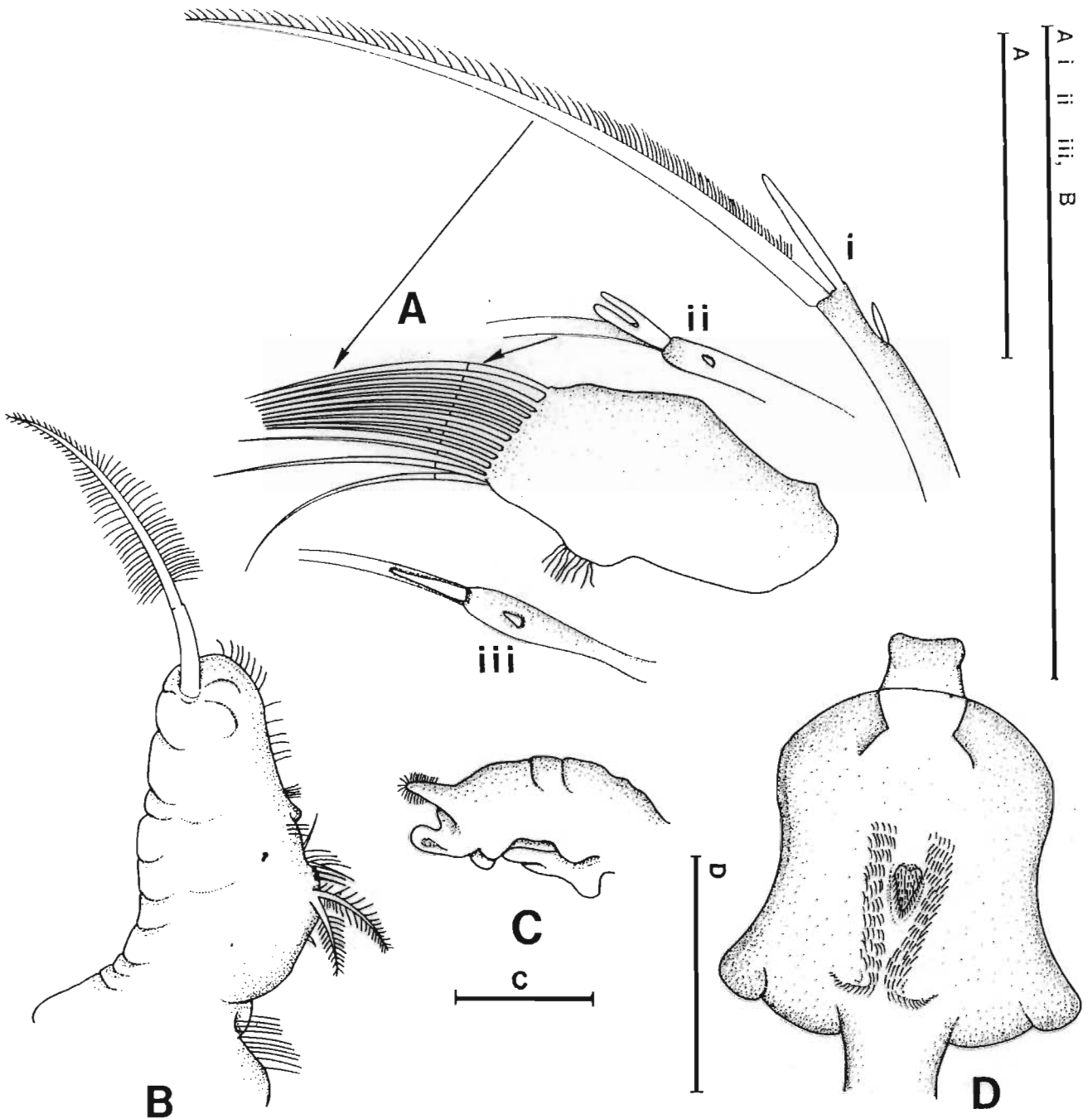


Figure 3: Mouthparts of male *Branchipodopsis barnardi* sp. nov.

A = maxilla I, scale = 0,1 mm; i, ii, iii = detail of setae on maxilla I, scale = 0,05 mm;

B = maxilla II, scale = 0,05 mm; C = lateral view of labrum, scale = 0,5 mm; D = left dorsal view of labrum, scale = 0,1 mm.

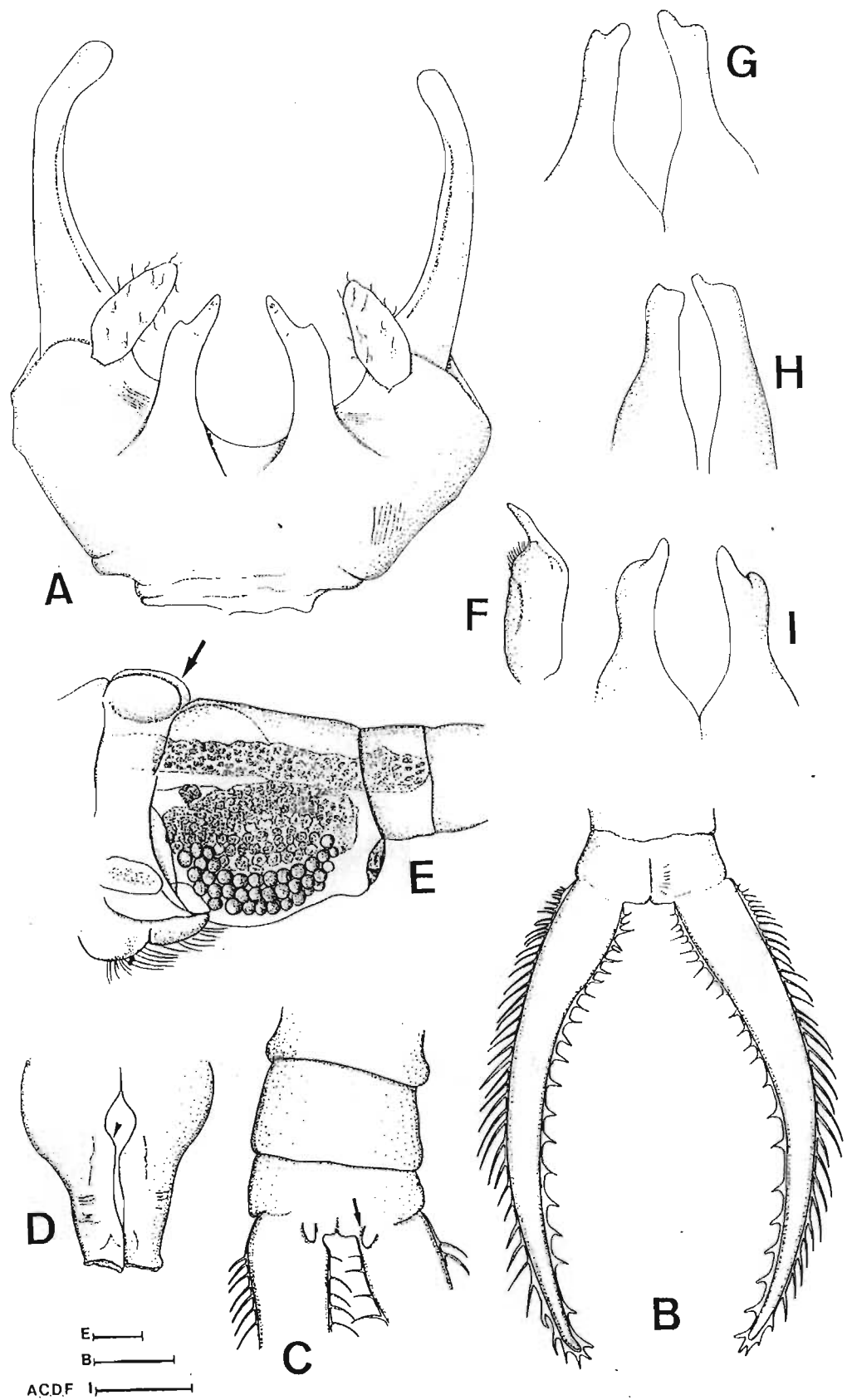


Figure 4: *Branchipodopsis barnardi* sp. nov. (SAM-A40840)

A = clypeus; B = dorsal view of cercopods of male; C = ventral view of posterior region of abdomen, arrow indicates spine; D = ventral view of basal part of penes, arrow indicates median projection; E = lateral view of genital segments of female showing brood pouch and bulbous processes (indicated by arrow); F = dorsal view of female antenna; G-I = basal processes of three specimens illustrating intra-population variation in shape of apical region. Scale = 0,5 mm.

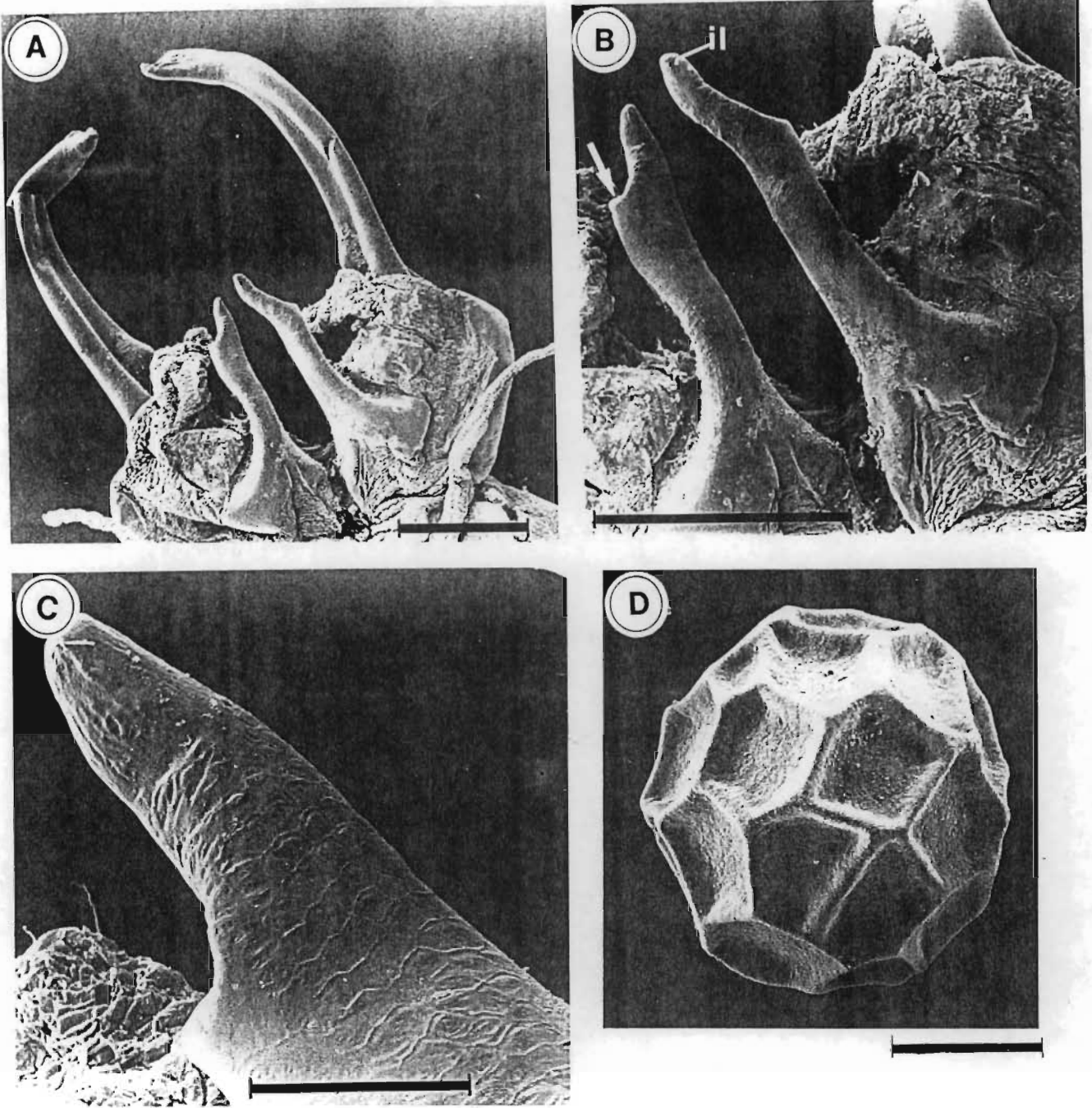


Figure 5: *Branchipodopsis barnardi* sp. nov. (SAM-A40840)

A = dorsal view of clypeus; scale = 0,5 mm; B = basal processes; il = inner lobe, arrow indicates position of outer lobe, scale = 0,5 mm; C = apical region of left basal process showing reticulate patterning; scale = 100 μ m; D = egg; scale = 100 μ m.

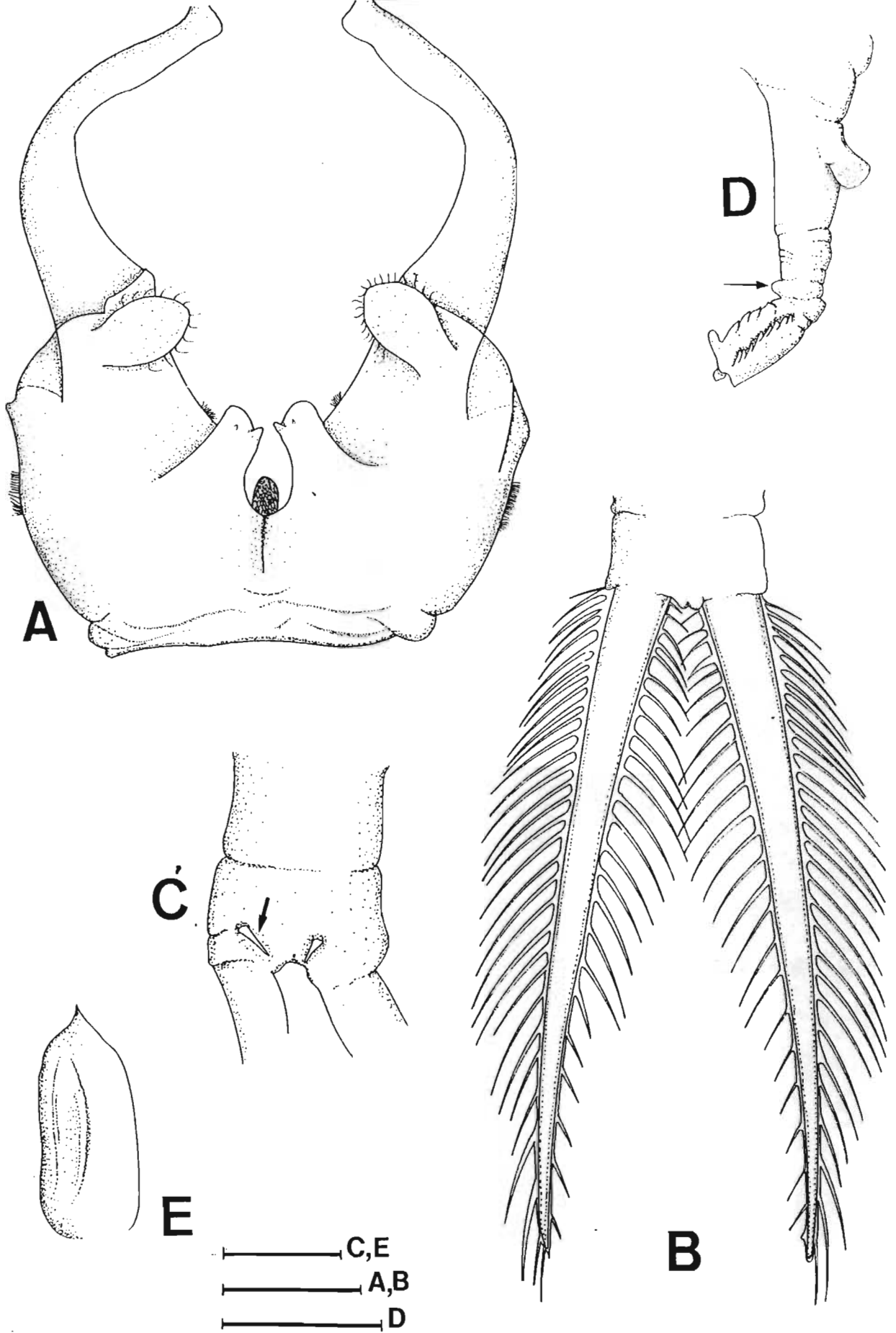


Figure 6: *Branchipodopsis browni*

A = dorsal view of clypeus (AM LEN 79B); B = cercopods of male (AM LEN 79B); C = ventral view of last abdominal segment of male (SAM-A6705); arrow indicates spine; D = ventral view of right penis with apical region extended (SAM-A6705), arrow indicates peg-like projection; E = female antenna (SAM-A6705). Scale bars: C, E = 50 μm; A, B = 100 μm; D = 50 μm.

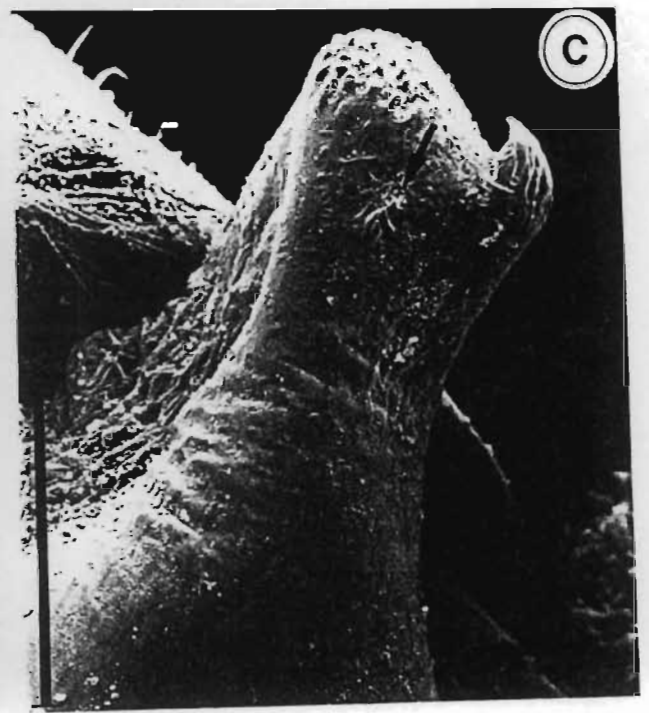
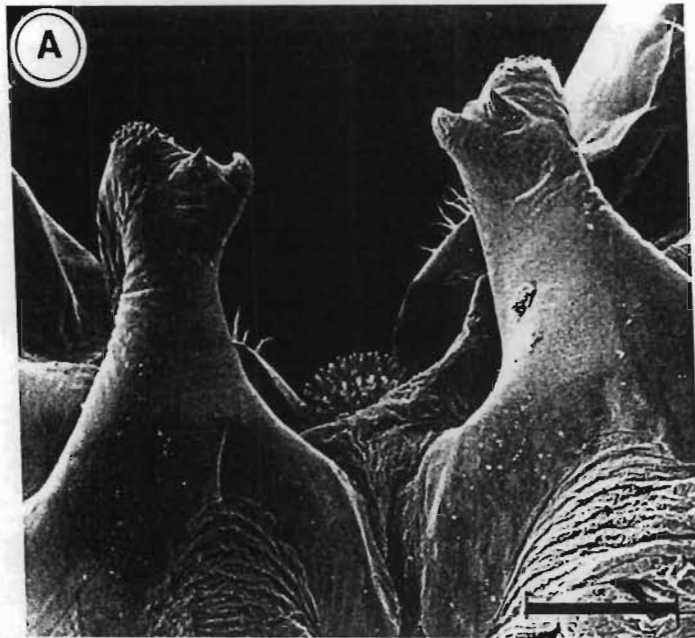


Figure 7: *Branchipodopsis browni*

A = basal processes and median ventral process of AM LEN 164A specimen; scale = 150 μm ; B = detail of apex of left basal process; arrow indicates median, dorsal projection; scale = 50 μm ; C = detail of left basal process of AM LEN 79B specimen; arrow indicates small median, dorsal projection; scale = 100 μm .

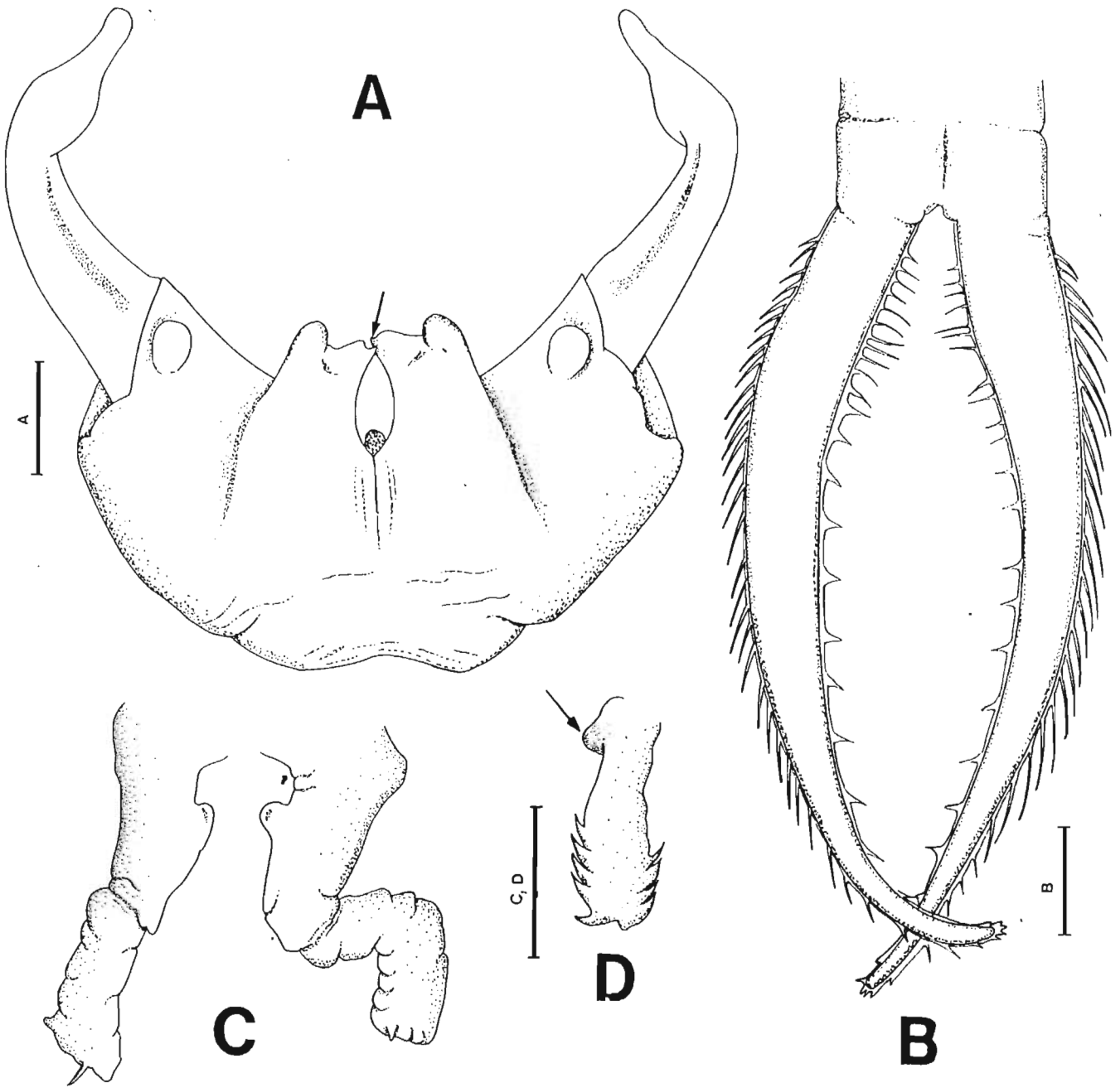


Figure 8: *Branchipodopsis dayae* sp. nov. (SAM-A40843)

A = dorsal view of clypeus; arrow indicates small projection on apical, median margin of basal process; B = cercopods of male; C = ventral view of basal part of penes; D = median view of apical, everted part of penes, arrow indicates blunt, peg-like projection. Scale = 0,5 mm.

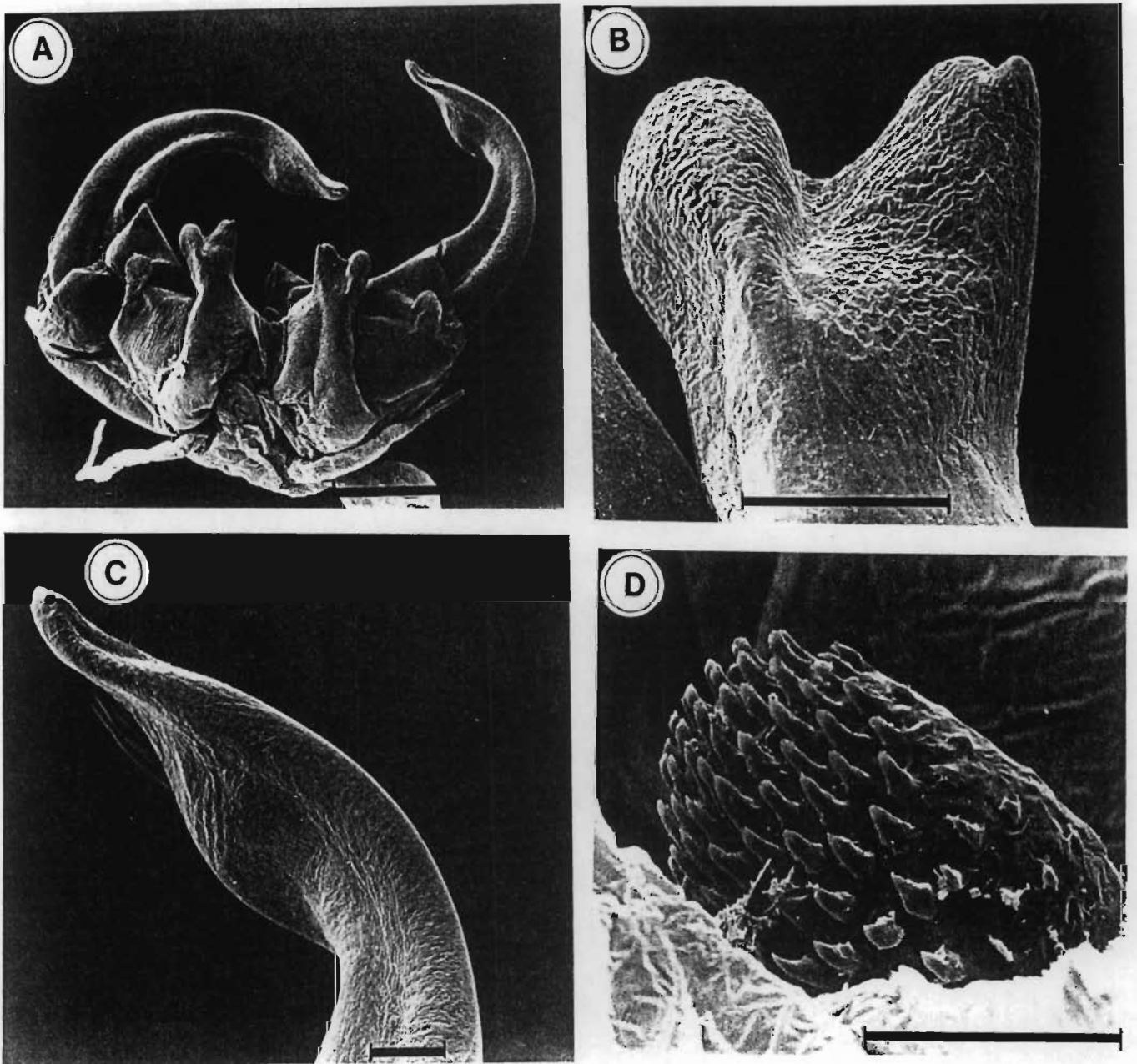


Figure 9: *Branchipodopsis dayae* sp. nov. (SAM-A40843)

A = dorsal view of clypeus; scale = 0,5 mm; B = apical region of left basal process; scale = 100 μ m; C = distal region of terminal joint; scale = 100 μ m; D = dorsal view of median ventral process; scale = 50 μ m.

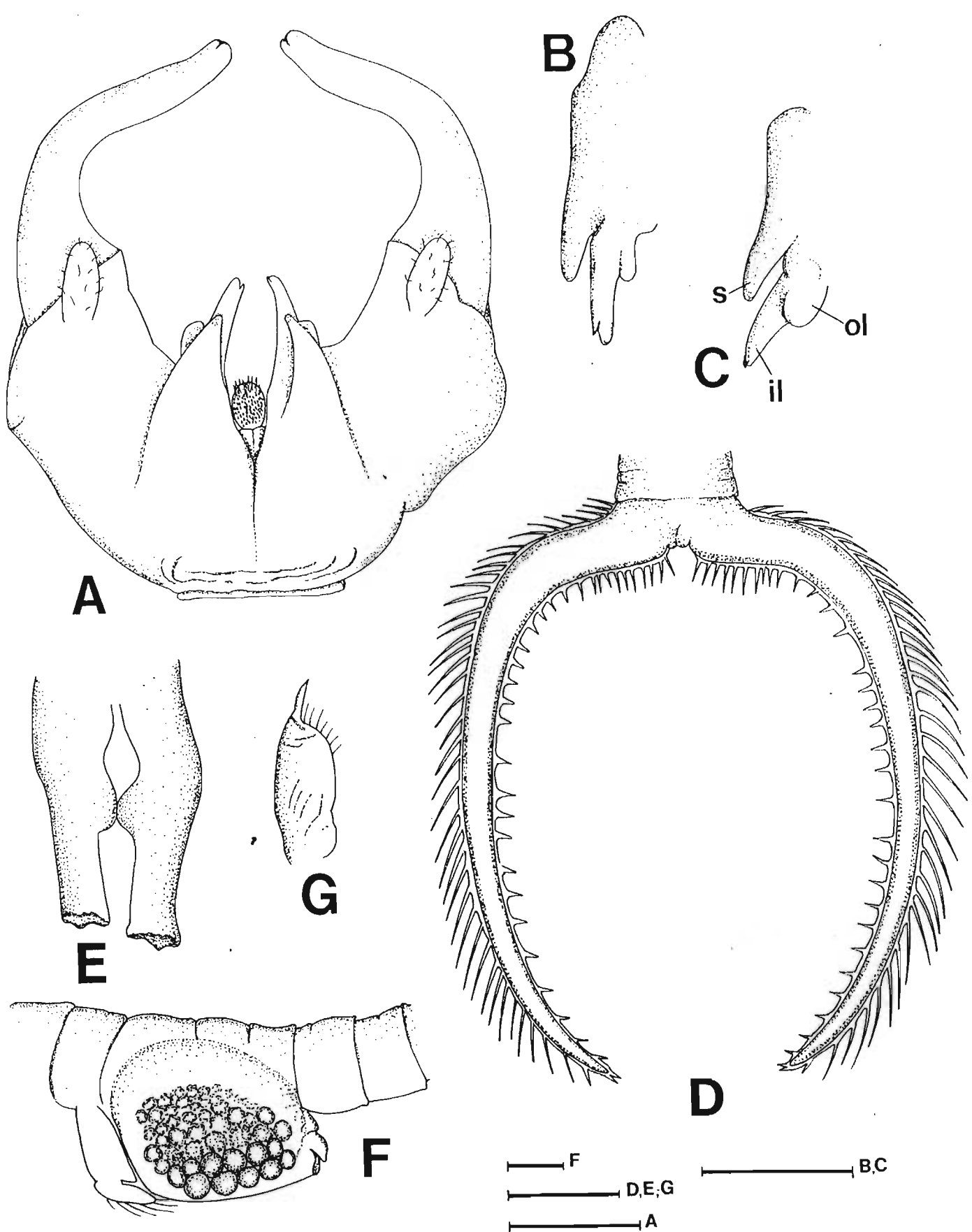


Figure 10: *Branchipodopsis drakensbergensis* sp. nov.

A = dorsal view of clypeus (SAM-A40835); B = lateral view of basal process of Loteni specimens (SAM-A40835); C = lateral view of basal process of Ugie specimen (AM LEN 159A), il = inner lobe, o = outer lobe, s = spinous projection; D = cercopods of male (SAM-A11593); E = ventral view of basal part of penes (SAM-A40835); F = lateral view of genital segments of female (AM LEN 159A) showing brood pouch; G = female genital segment (AM LEN 159A).

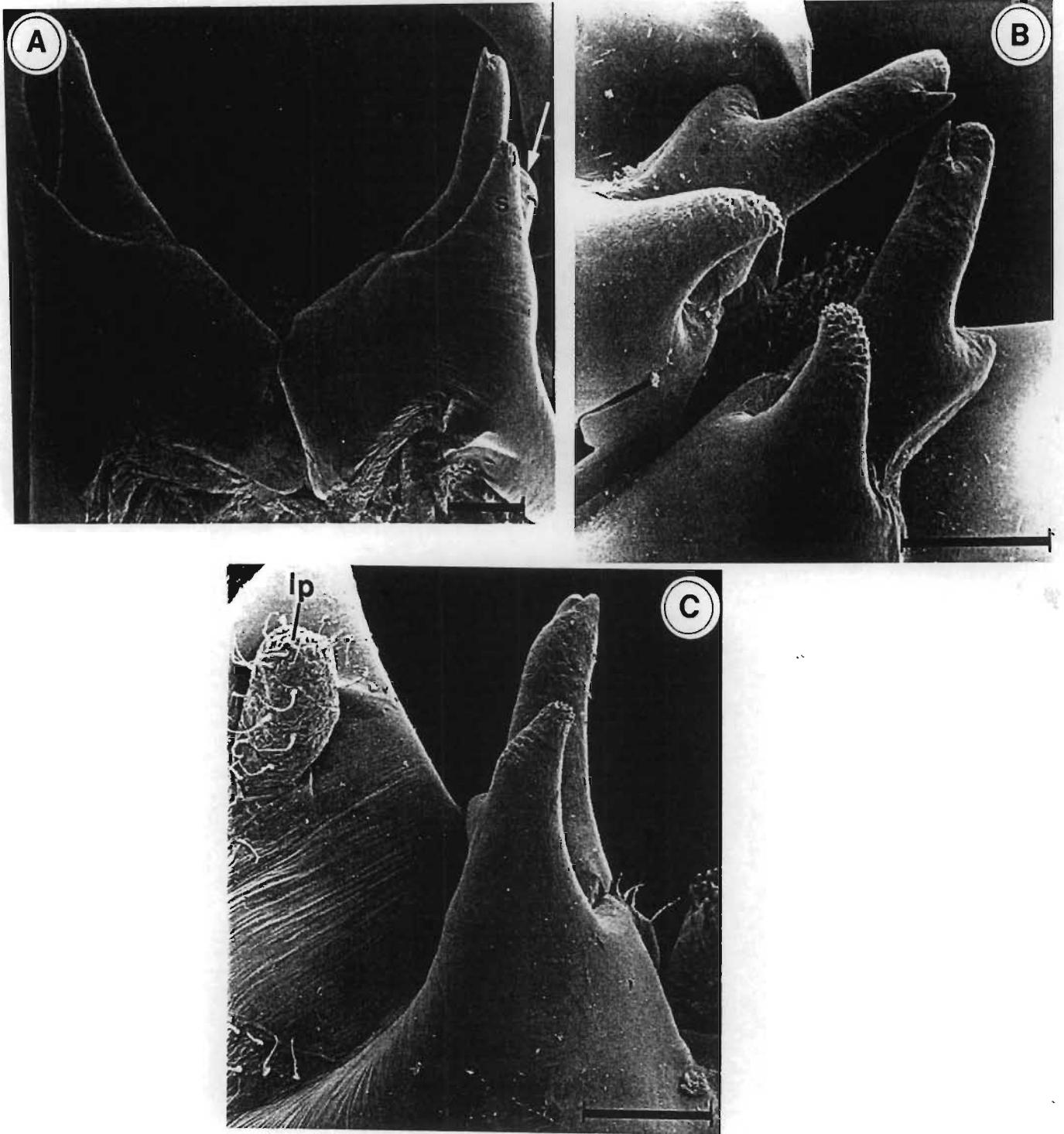


Figure 11: *Branchipodopsis drakensbergensis* sp. nov.

A = dorsal view of basal processes of clypeus, Loteni specimen (SAM-A40835); outer lobe of left basal process not visible, arrow indicates outer lobe of right basal process, s = spinous projection; B = basal processes of Ugie specimen (AM LEN 159A); arrow indicates median ventral process; C = left basal process of Benoni specimens (AM REA 77A); lp = lamelliform process. Scale = 100 μ m.

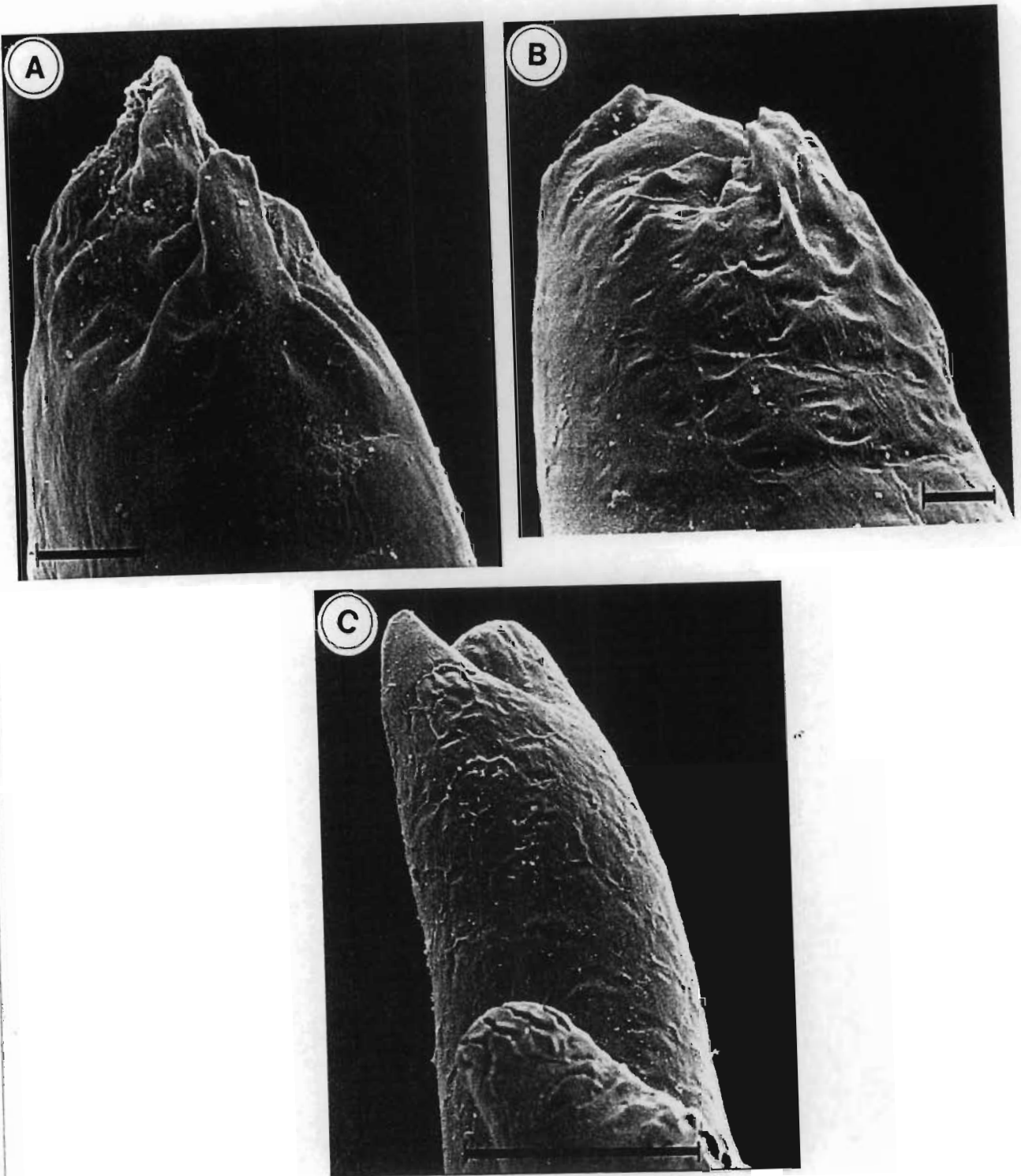


Figure 12: *Branchipodopsis drakensbergensis* sp. nov.

A = detail of apex of inner lobe of basal process, Loteni specimen (SAM- A40835); scale = 10 μm ; B = detail of apex of inner lobe of basal process, Ugie specimen (AM LEN 159A); scale = 10 μm ; C = detail of apex of inner lobe of basal process, Benoni specimen (AM REA 77A); scale = 50 μm .

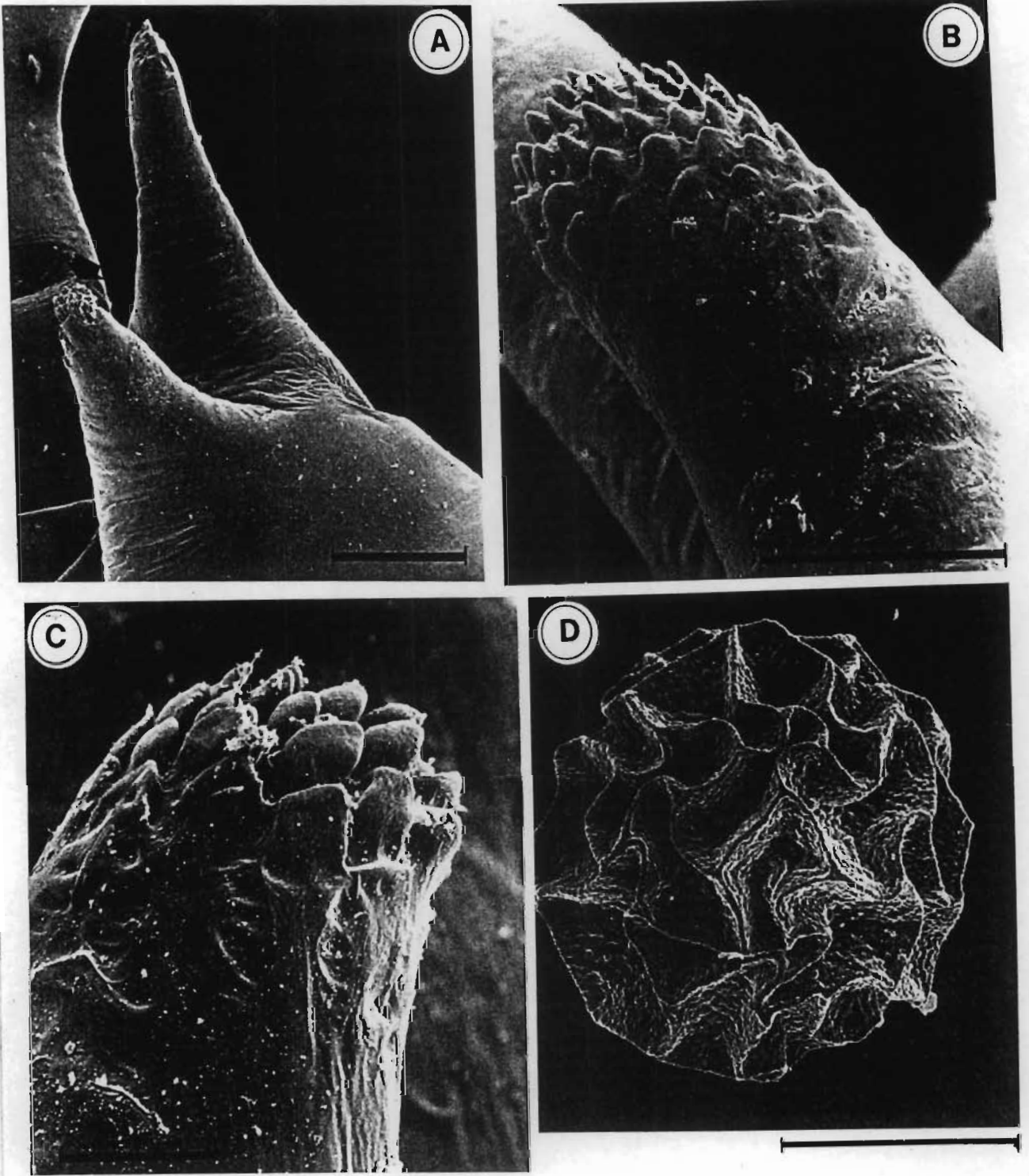


Figure 13: *Branchipodopsis drakensbergensis* sp. nov.

A=basal process, illustrating apex of spinous process (indicated by arrow), Loteni specimen (SAM-A40835); scale = 100 μ m; B=detail of apex of spinous process, Ugie specimen (AM LEN 159A); scale = 50 μ m; C=detail of apex of spinous process, Benoni specimen (AM REA 77A); scale = 10 μ m; D=egg; scale = 100 μ m.

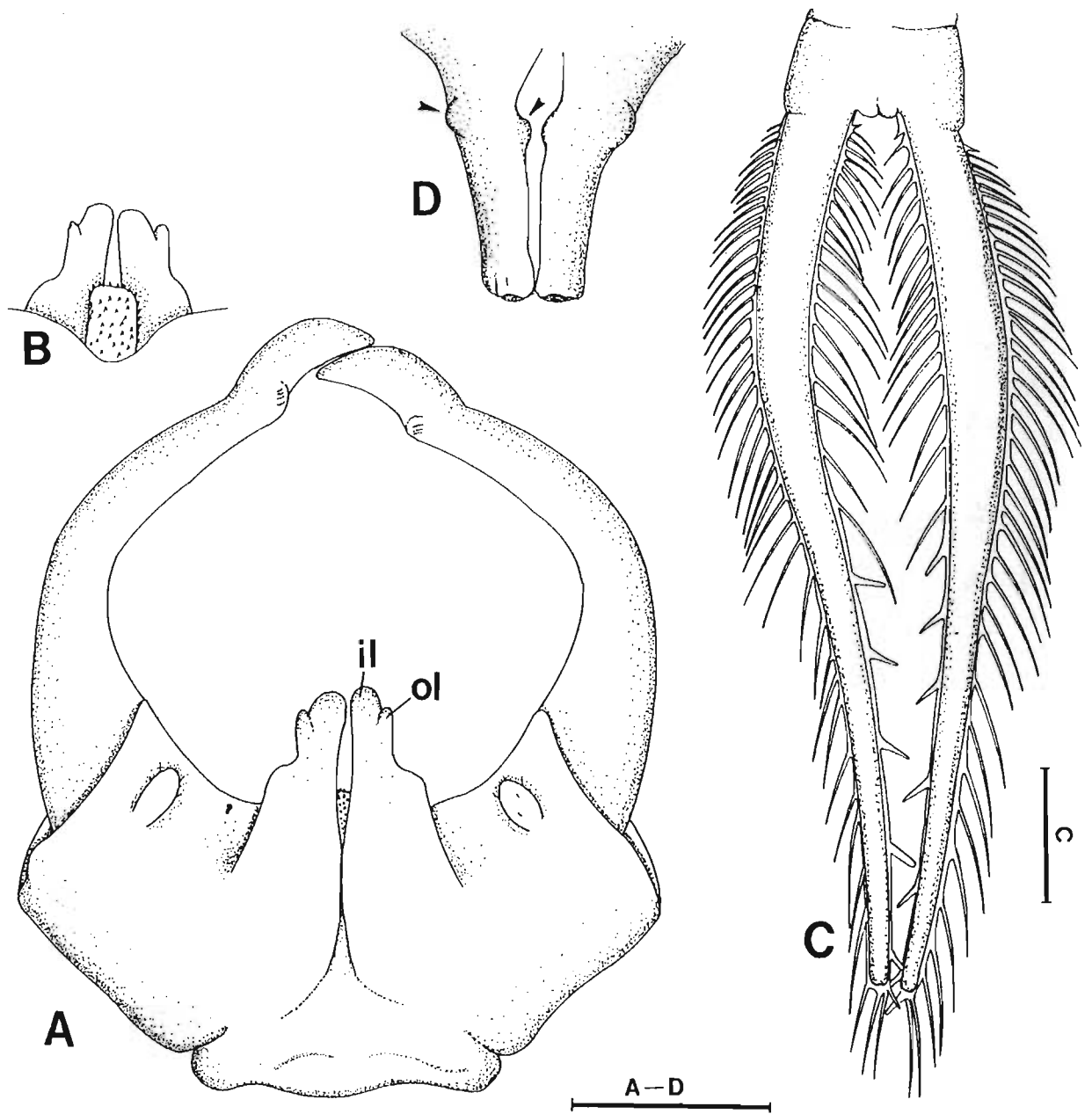


Figure 14: *Branchipodopsis drepane* (BMNH. 1932.2.25.41)

A = dorsal view of clypeus; il = inner lobe, ol = outer lobe; B = ventral view of basal processes and median ventral process; C = cercopods of male; D = ventral view of basal part of penes, arrow indicates lateral, proximal projection. Scale = 0,5 mm.

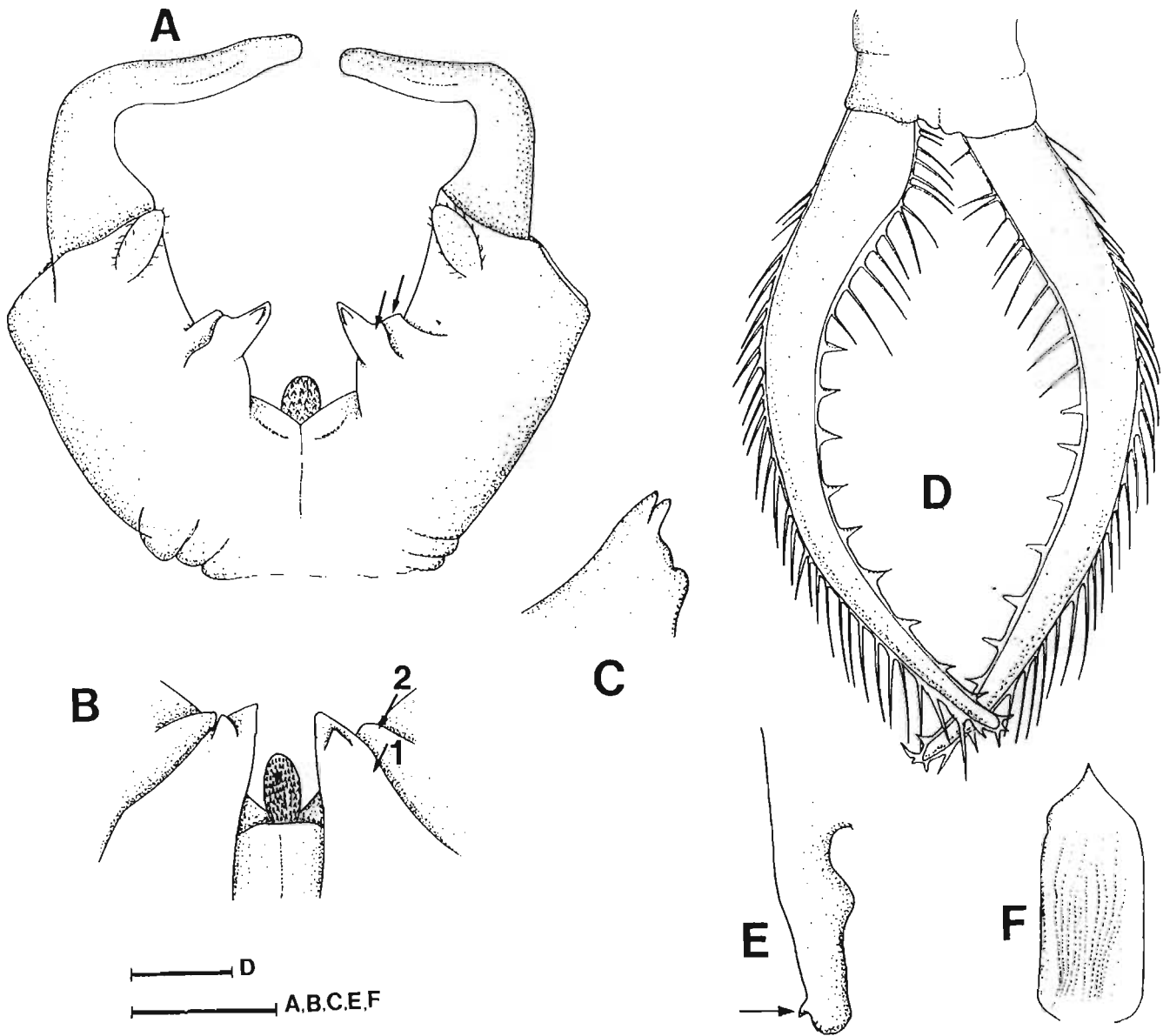


Figure 15: *Branchipodopsis hodgsoni*

A = dorsal view of clypeus (HNHM I/A-76), arrows indicate dorsal and ventral lobes of basal process; B = basal processes and median ventral process of AM LEN 149A specimen, 1 = dorsal lobe, 2 = ventral lobe; C = lateral view of basal process (AM LEN 149A); D = cercopods of male (SAM-A6721); E = ventral view of basal part of right penis (AM LEN 149A), arrow indicates peg-like process; F = female antenna (SAM-A6721). Scale = 0,5 mm.

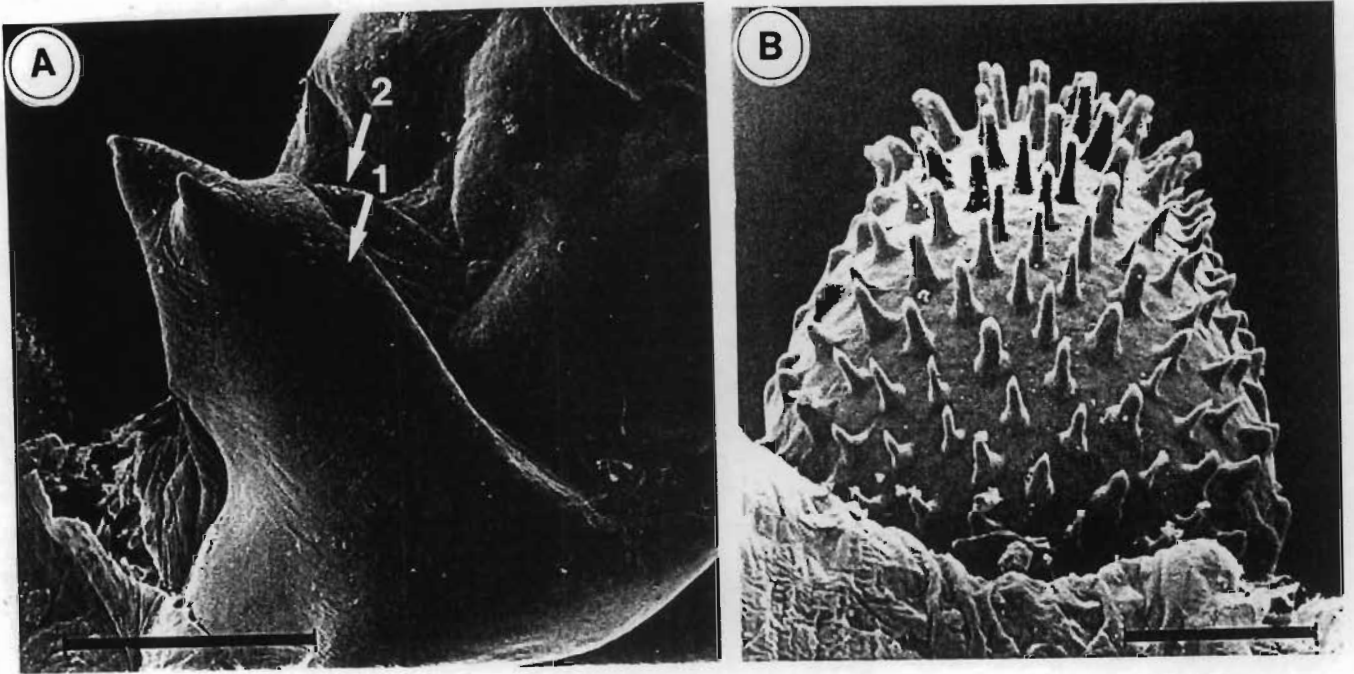


Figure 16: *Branchipodopsis hodgsoni* (AM LEN 149A)

A = right basal process; 2 lobes indicated by arrows, 1 = dorsal lobe, 2 = ventral lobe; scale = $50\mu\text{m}$; B = dorsal view of median ventral process; scale = $25\mu\text{m}$.

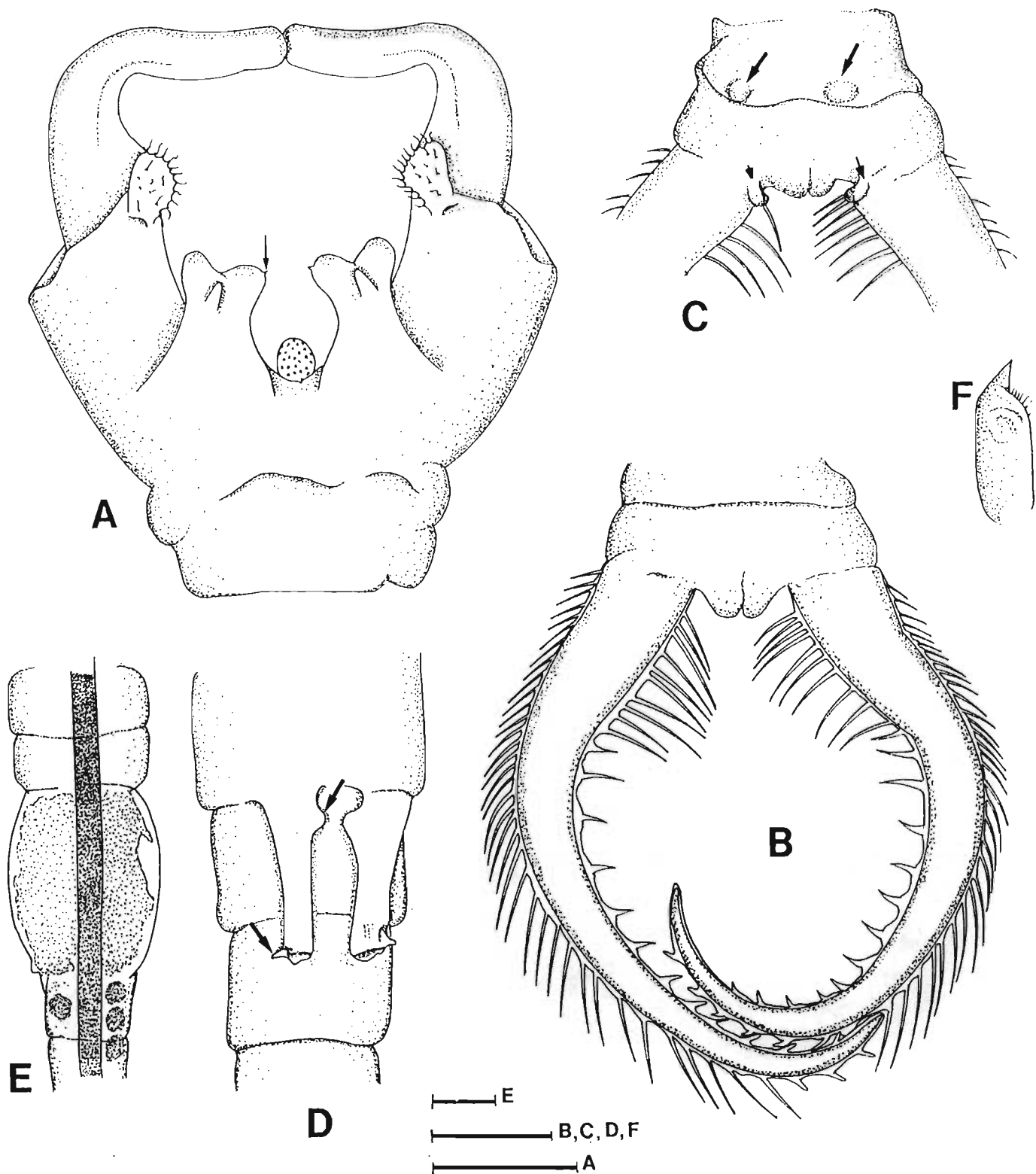


Figure 17: *Branchipodopsis hutchinsoni* sp. nov. (SAM-A40845)

A = dorsal view of clypeus, arrow indicates small projection on apex of inner lobe; B = cercopods of male; C = ventral view of posterior region of abdomen showing rounded projections on penultimate segment (indicated by large arrows) and blunt spinous processes (indicated by small arrows); D = ventral view of genital region of male showing basal parts of penes, arrow indicates peg-like projection; E = dorsal view of genital segments of female showing absence of outgrowths in this region; F = female antenna

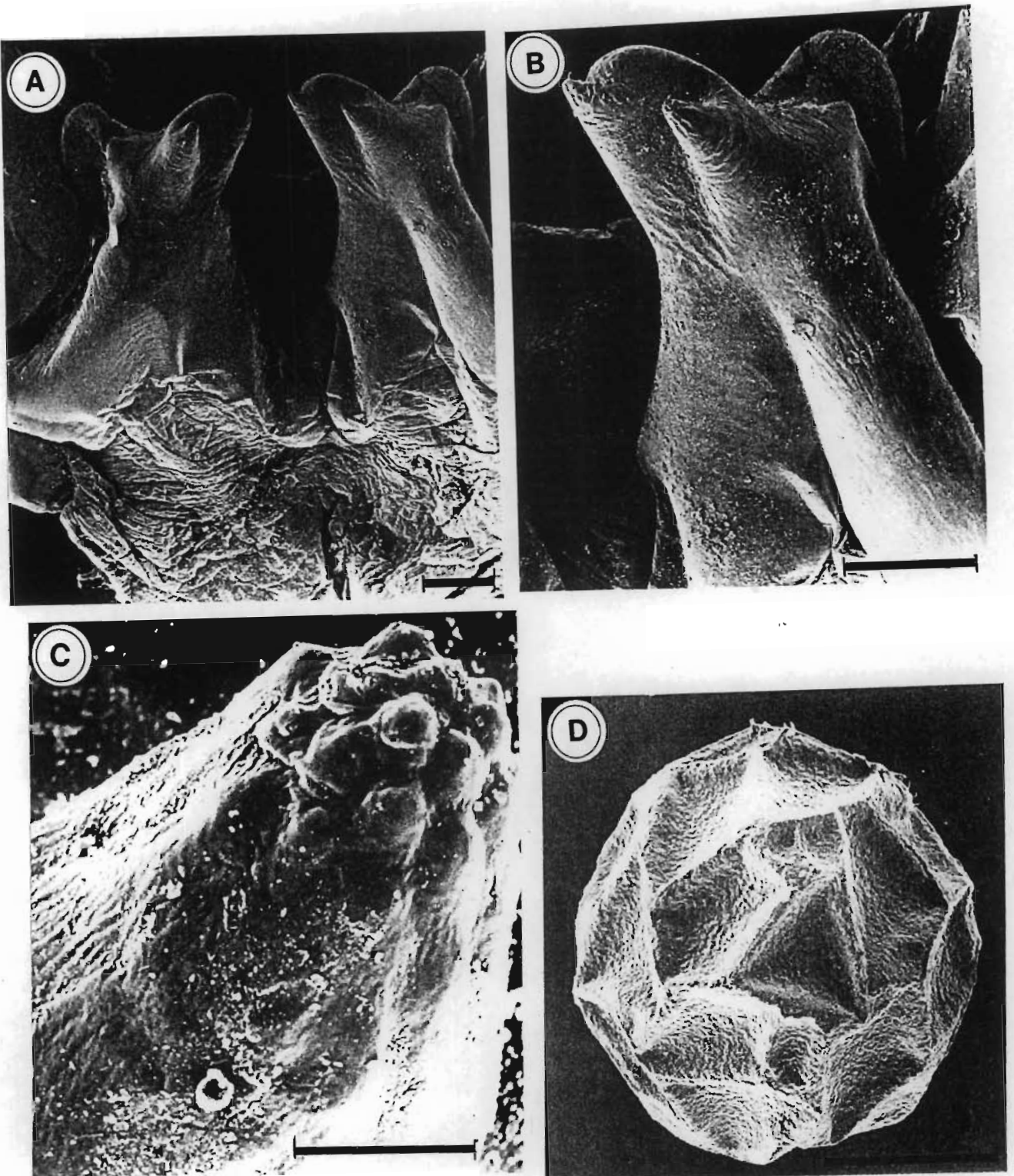


Figure 18: *Branchipodopsis hutchinsoni* sp. nov. (SAM-A40845)

A = dorsal view of basal processes of clypeus; scale = 100 μm ; B = detail of right basal process; scale = 100 μm ; C = detail of apex of median, dorsal projection on basal process; scale = 10 μm ; D = egg; scale = 100 μm .

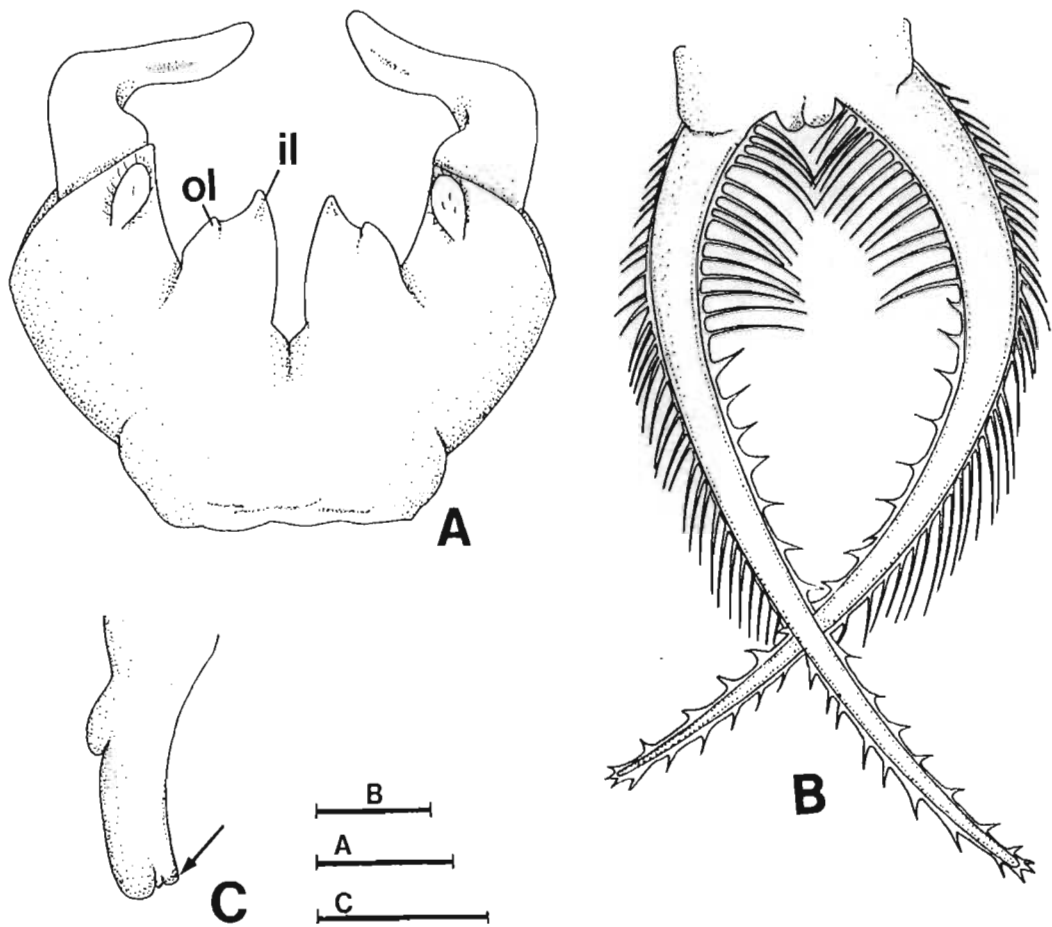


Figure 19: *Branchipodopsis kalaharensis* (TM VLKE No. 94)

A = dorsal view of clypeus; il = inner lobe, ol = outer lobe; B = cercopods of male; C = ventral view of basal part of left penis, arrow indicates blunt, apical projection. Scale = 0,5 mm.

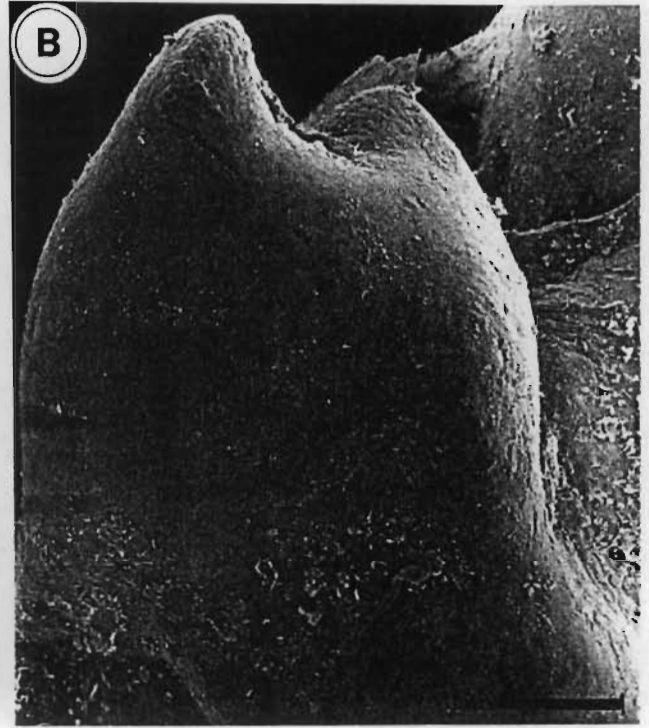
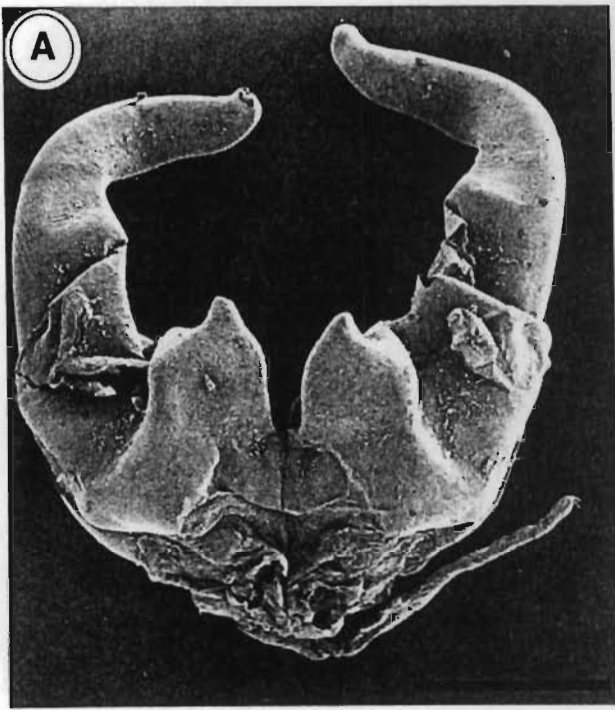


Figure 20: *Branchipodopsis kalaharensis* (TM VLKE No. 94)

A = dorsal view of clypeus; scale = 0,5 mm; B = detail of right basal process; scale = 100 μm .

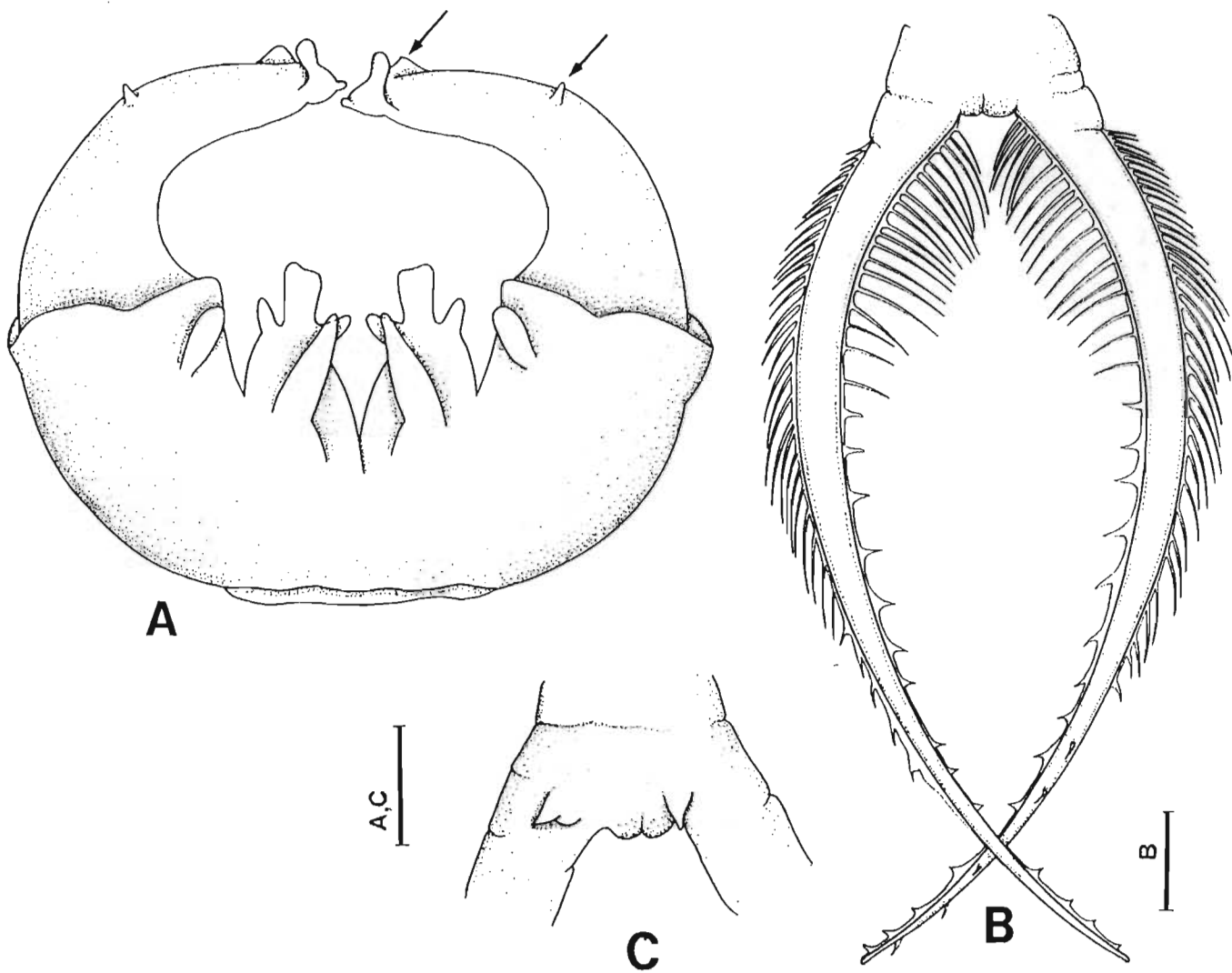


Figure 21: *Branchipodopsis kaokoensis* (BMNH 1932.2.25.42-45)

A = dorsal view of clypeus, arrows indicate projections on terminal joint; B = cercopods of male; C = ventral view of last abdominal segment of male. Scale = 0,5 mm.

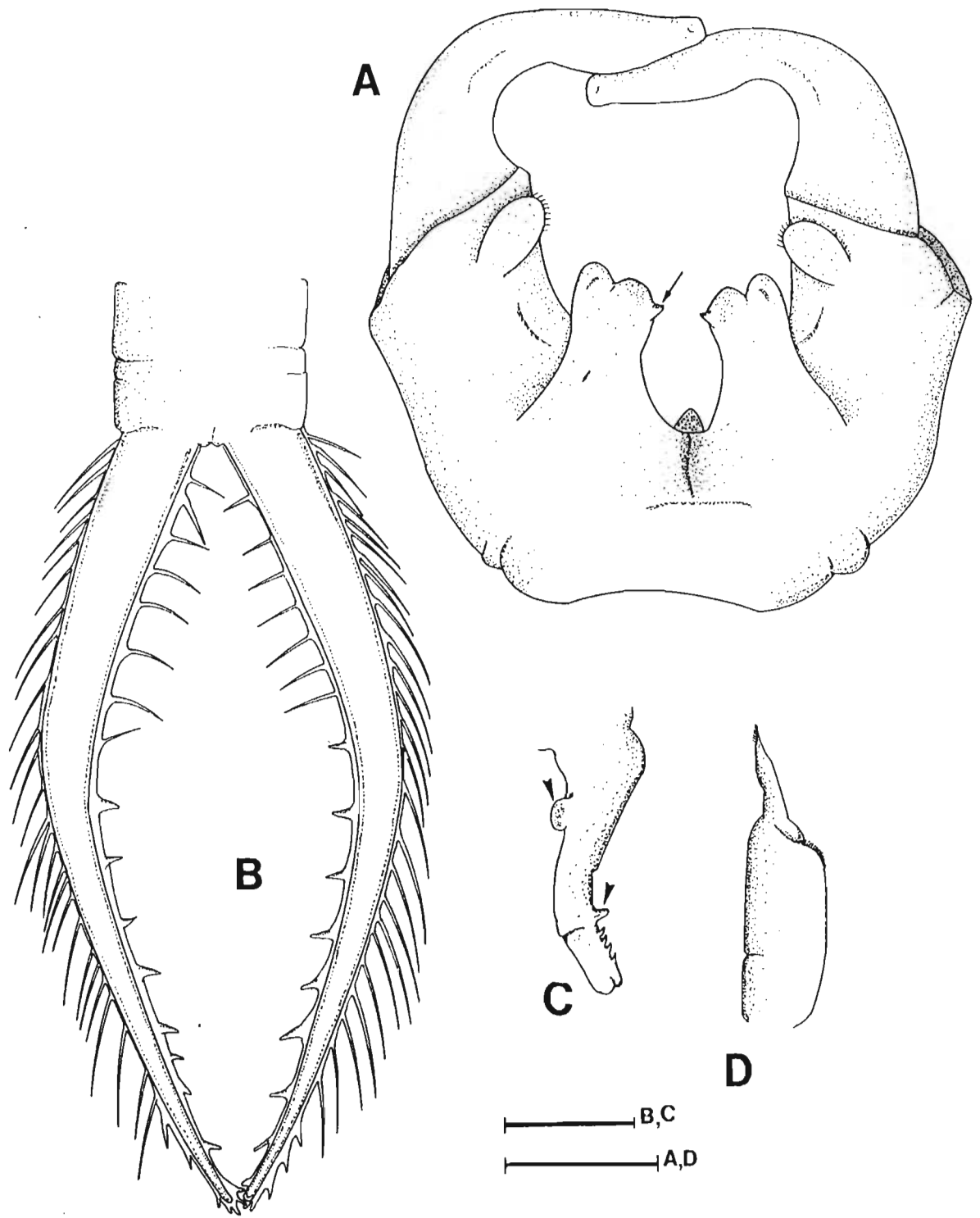


Figure 22: *Branchipodopsis karroensis*

A = dorsal view of clypeus (SAM-A5919), arrow indicates projection on median margin of inner lobe; B = cercopods of male (BMNH. 1932.2.25.36-40); C = left penis with apical region partially extended (SAM-A5919), arrow indicates peg-like projection; D = female antenna (SAM-A5919). Scale = 0,5 mm.

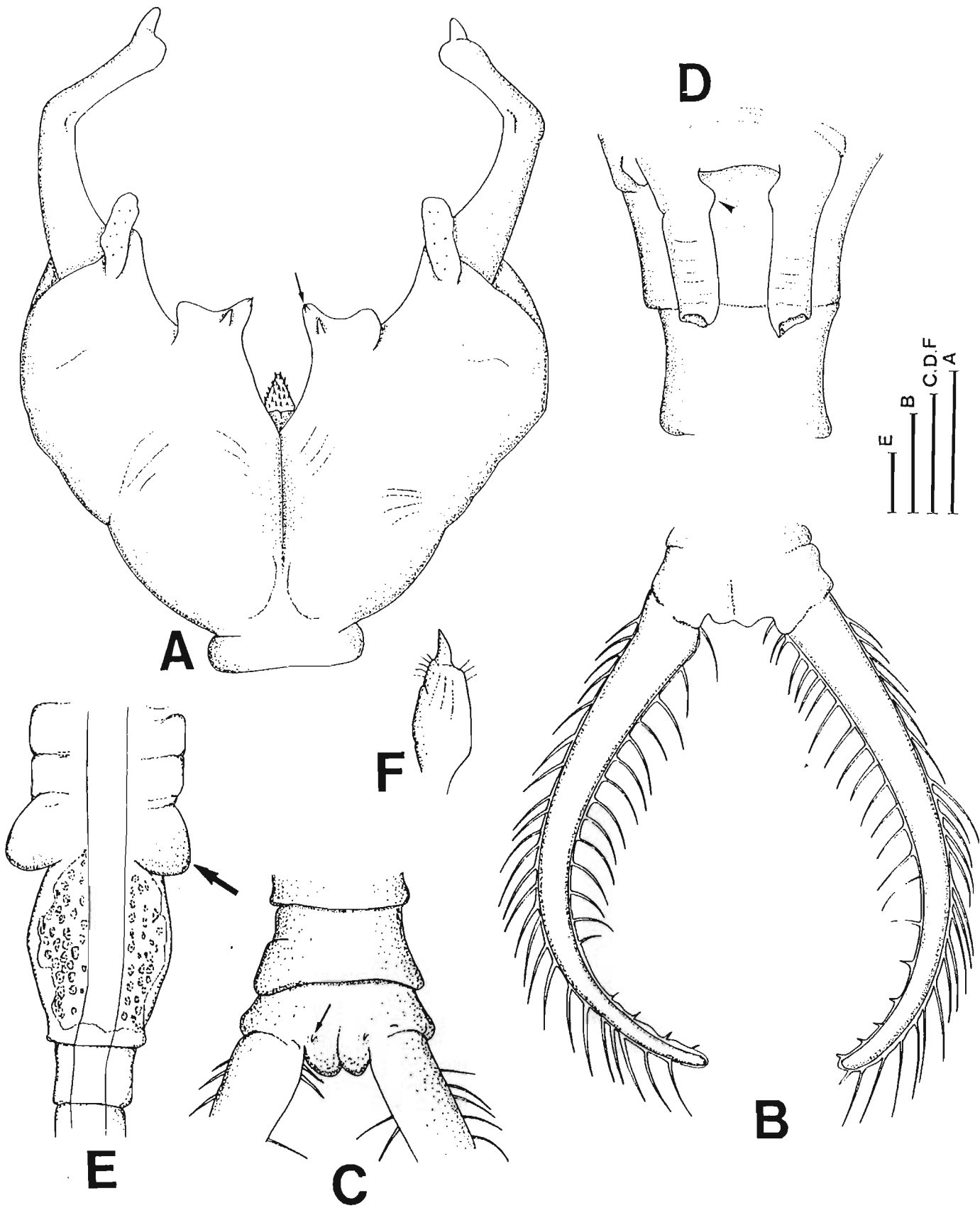


Figure 23: *Branchipodopsis natalensis* (SAM-A40847)

A = dorsal view of clypeus, arrow indicates small projection on inner lobe; B = cercopods of male; C = ventral view of last abdominal segments of male, arrow indicates small spinous processes; D = ventral view of male genital segments showing basal part of penes, arrow indicates median rounded projection; E = dorsal view of genital segments of female showing lateral extensions of last thoracic segment (indicated by arrow); F = female antenna. Scale = 0.5 mm.

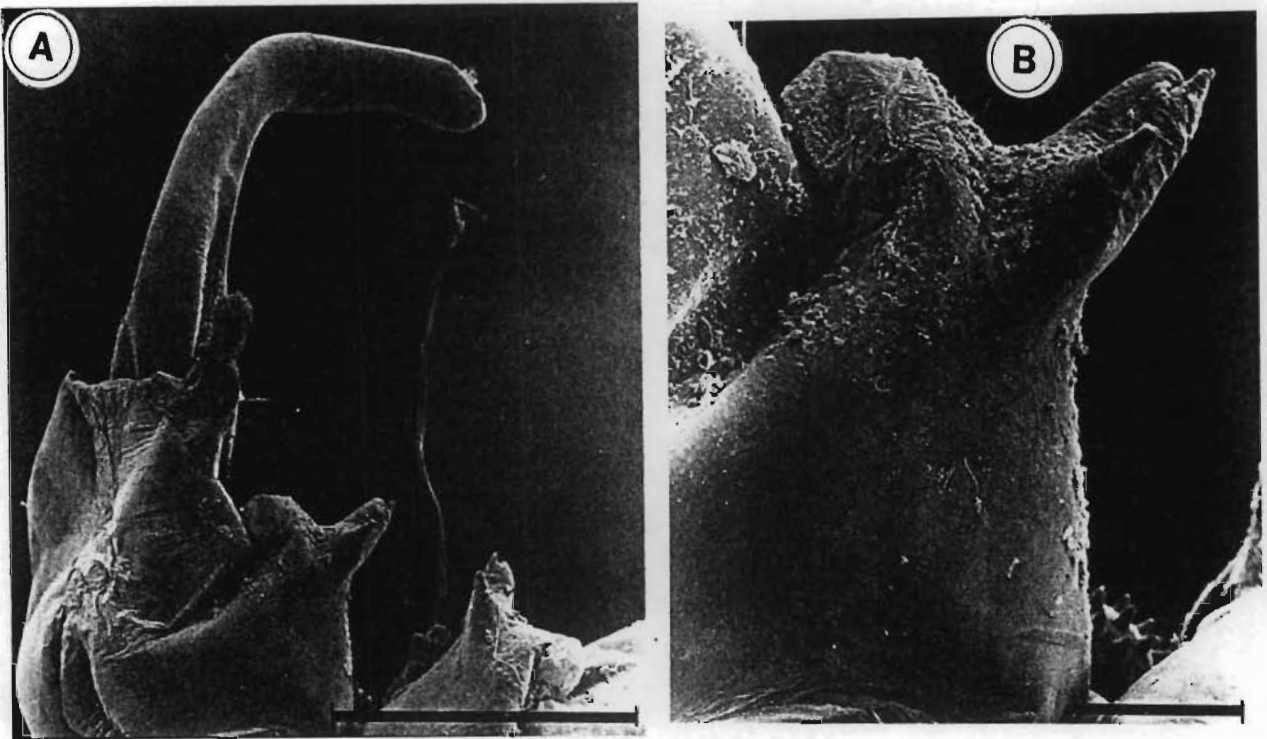


Figure 24: *Branchipodopsis natalensis* (SAM-A40847)

A = dorsal view of left half of clypeus; scale = 0,5 mm; B = detail of apical region of left basal process; scale = 100 μ m.

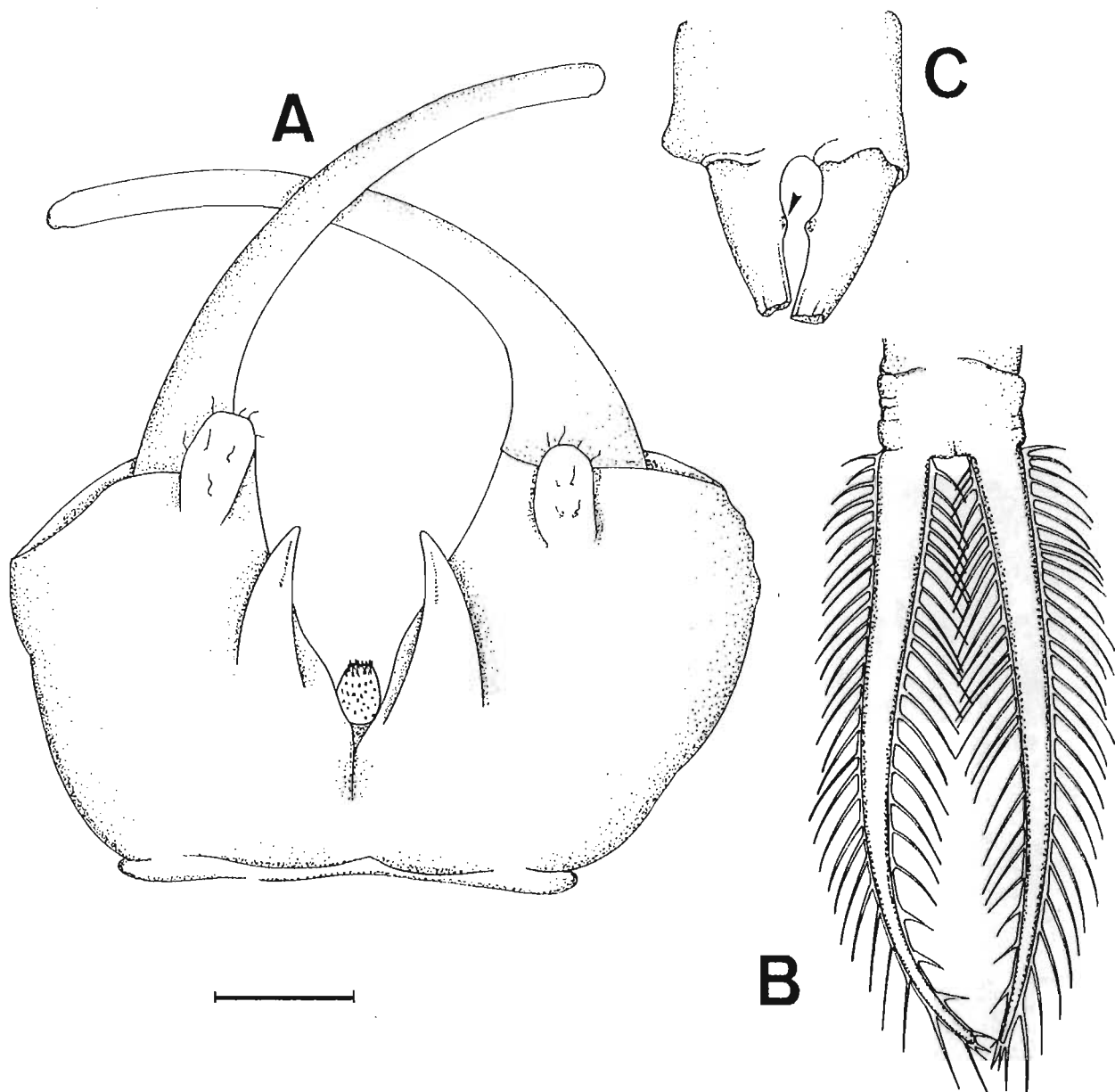


Figure 25: *Branchipodopsis scambus*

A = dorsal view of clypeus (BMNH. 1972.1.27.31-33); B = cercopods of male (AM LEN 18); C = ventral view of basal part of penes (AM LEN 18), arrow indicates small rounded median projection. Scale = 0,5 mm.

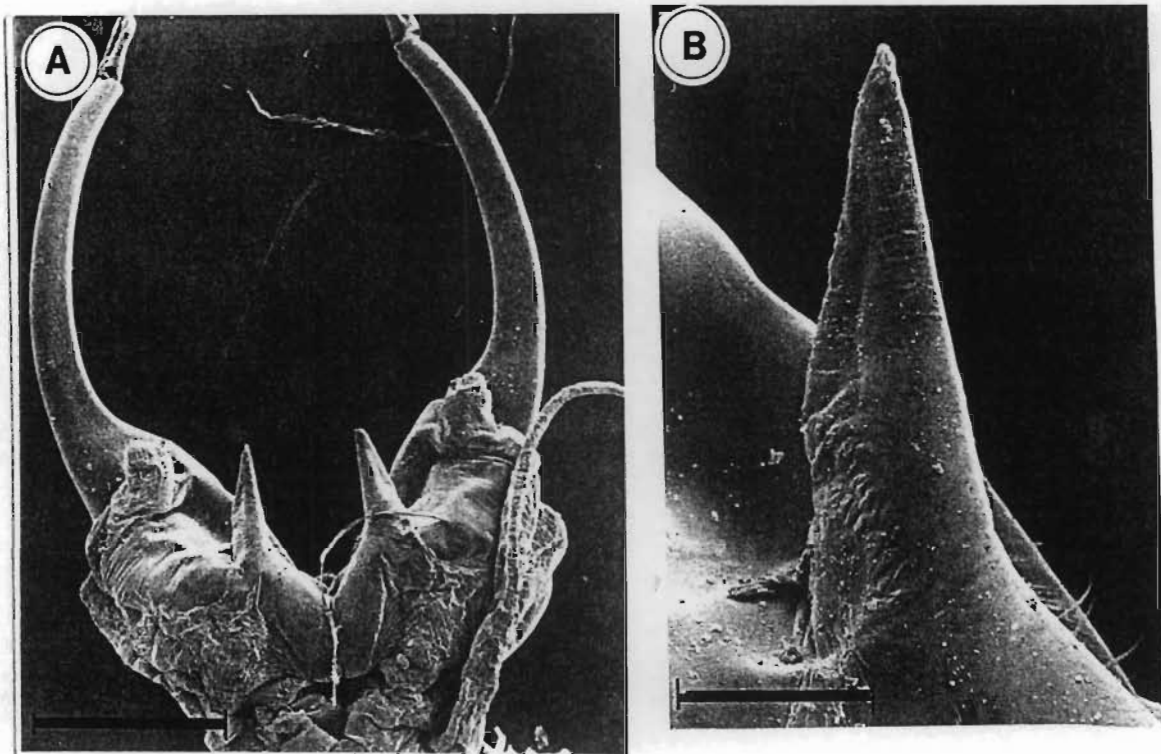


Figure 26: *Branchipodopsis scambus* (AM LEN 18)

A = dorsal view of clypeus; scale = 0,5 mm; B = detail of left basal process; scale = 100 μ m.

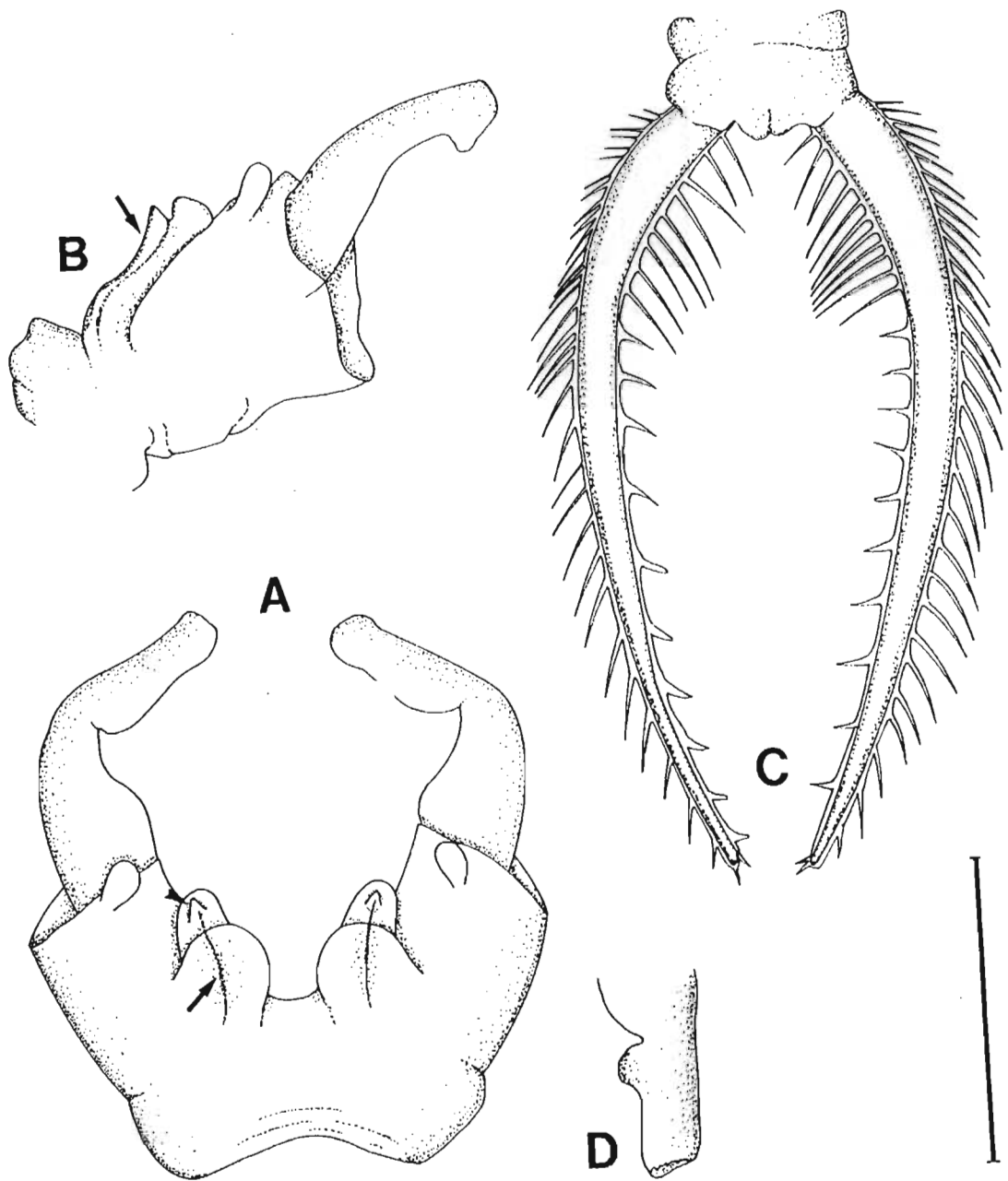
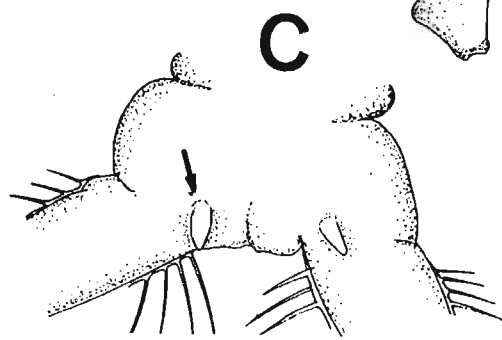
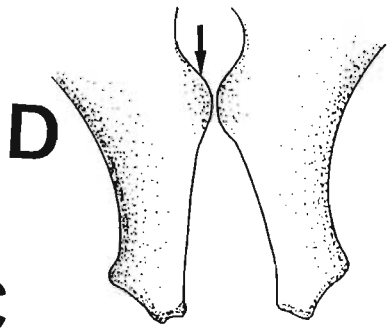
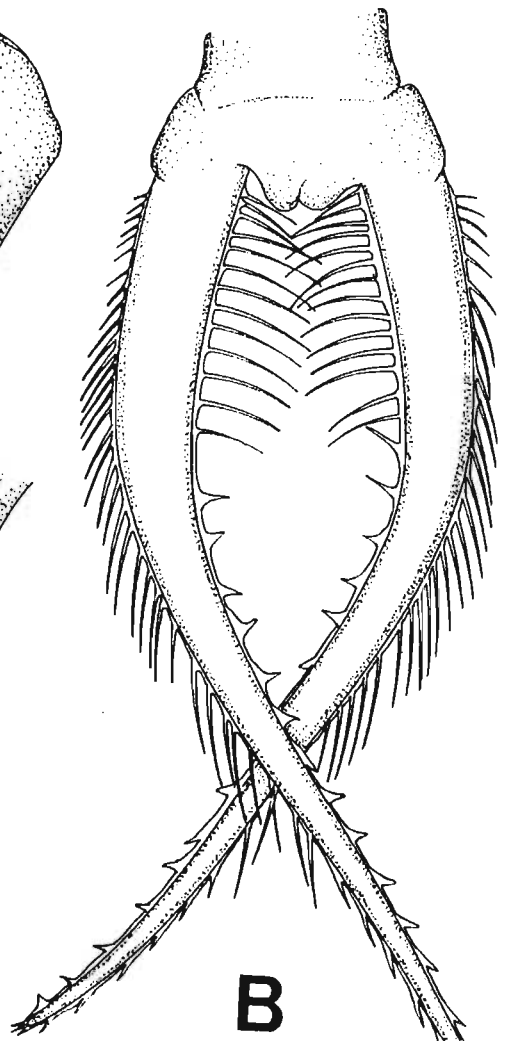
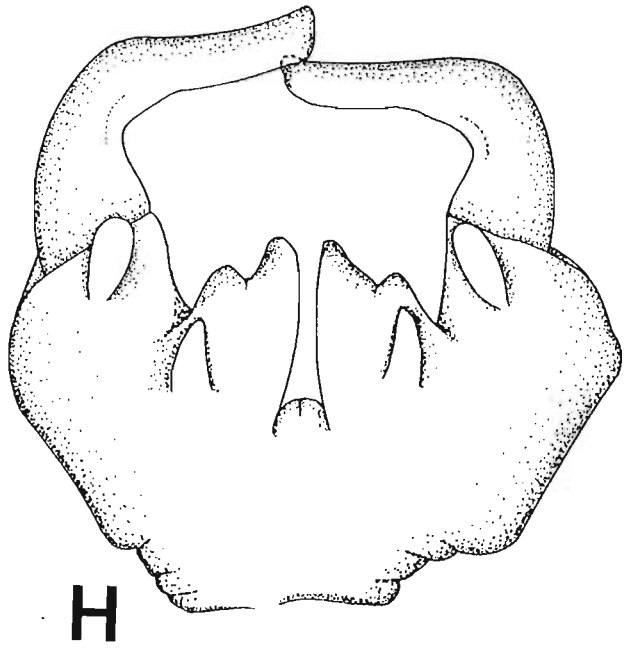
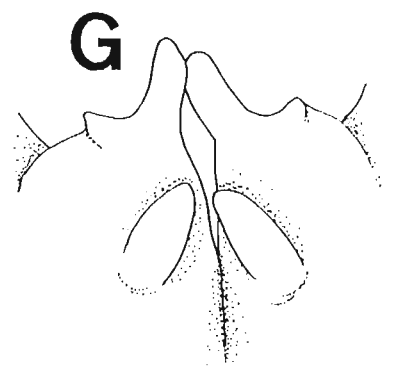
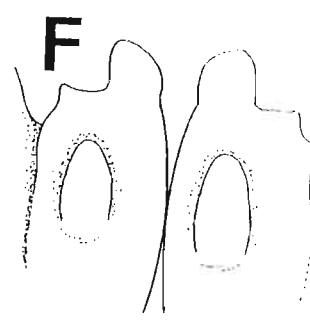
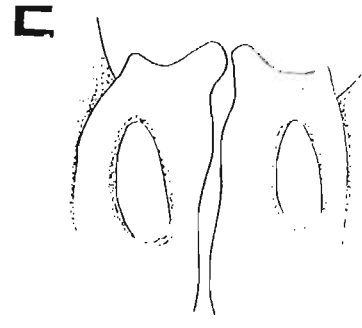
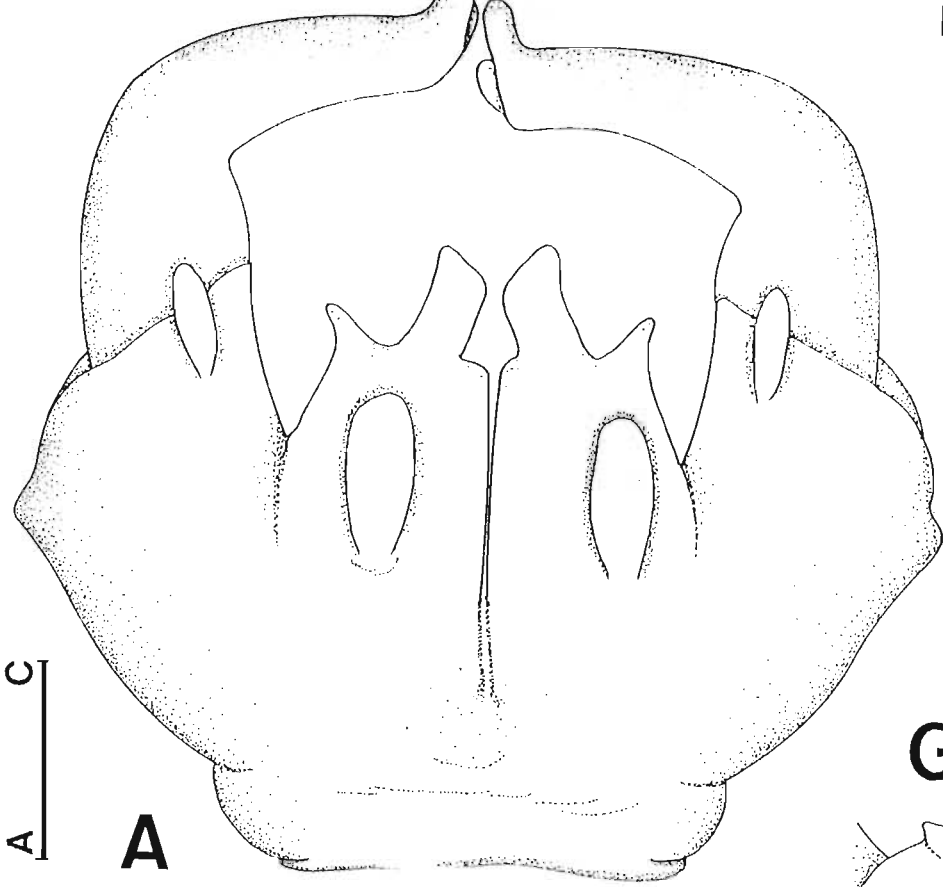


Figure 27: *Branchipodopsis simplex* (SAM-A6006)

A = dorsal view of clypeus, large arrow indicates dorsal keel, small arrow indicates apex of keel; B = lateral view of clypeus, arrow indicates keel; C = cercopods of male; D = ventral view of basal part of left penis. Scale = 0,5 mm.



E, F, G, H

B

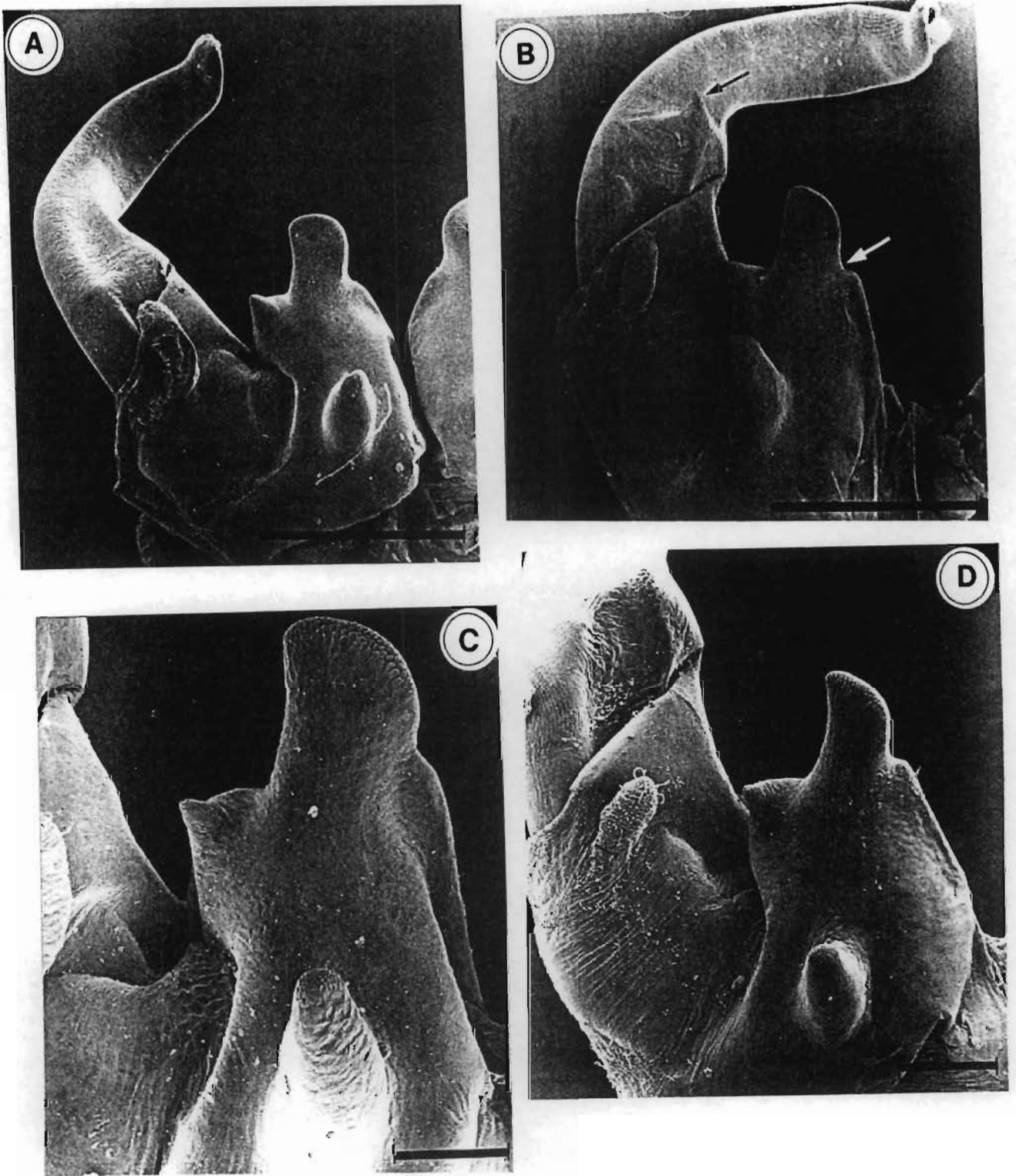


Figure 29: *Branchipodopsis tridens*

A = dorsal view of left half of clypeus (AM LEN 163A; outside Kalahari Gemsbok Park), scale = 0,5 mm; B = dorsal view of left half of clypeus (DB 764; Gemsbokwater); white arrow indicates indentation in median margin, black arrow indicates projection on terminal joint, scale = 0,5 mm; C = detail of left basal process (AM LEN 163A); scale = 100 μ m; D = detail of left basal process (DB 764); scale = 100 μ m.

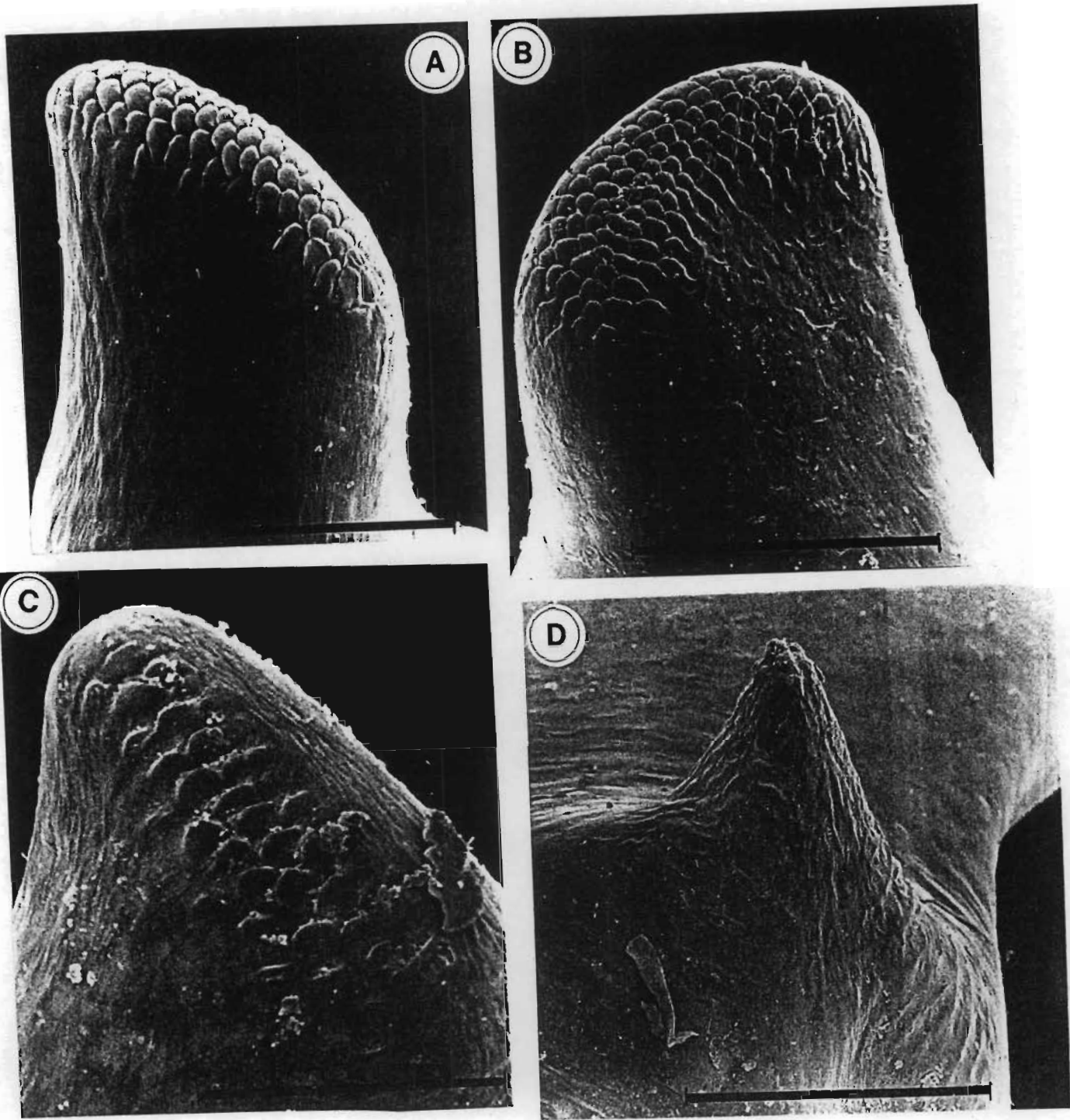


Figure 30: *Branchipodopsis tridens*

A = detail of apex of inner lobe of left basal process (Namib Naukluft, SMN 51197),
 B = detail of apex of inner lobe of right basal process (AM LEN 163A), C = detail of apex
 of inner lobe, left basal process of Goru Pan specimen (TM VLKE No. 443); D = projection
 on terminal joint of Gemsbokwater specimen (DB 764). Scale = 50 μ m.

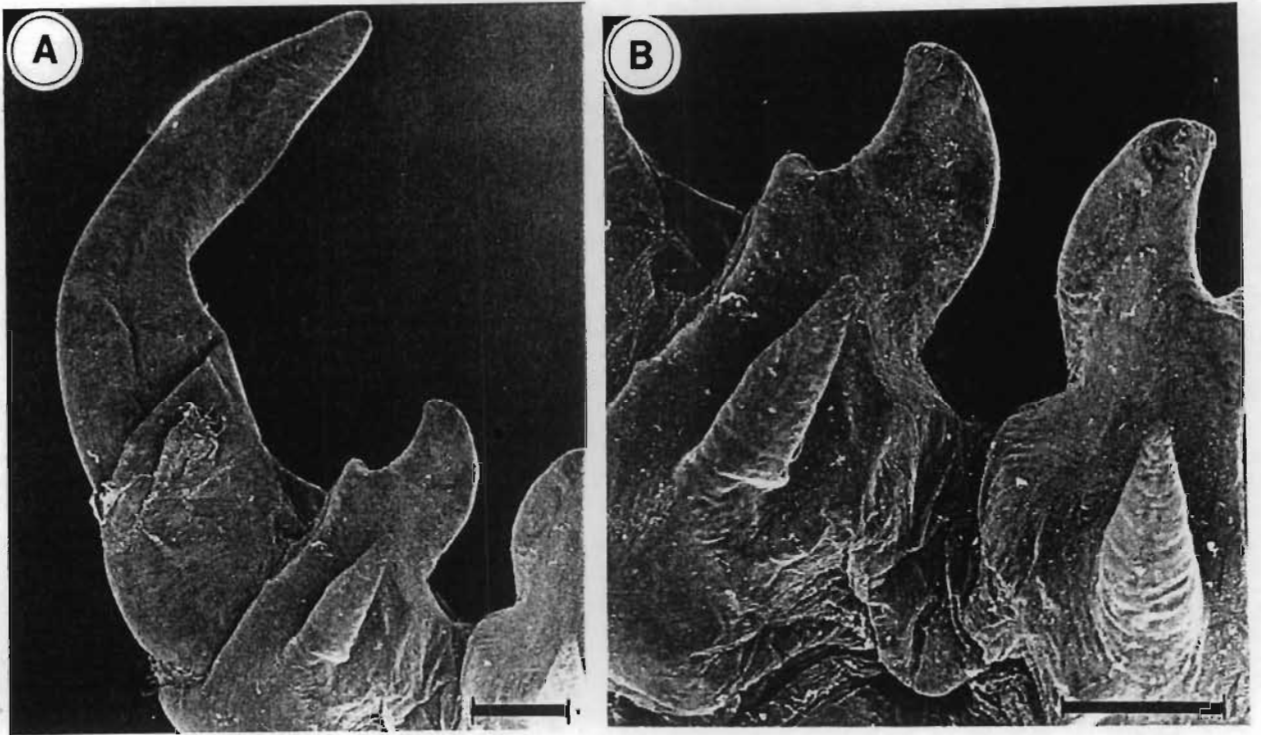


Figure 31: *Branchipodopsis cf tridens* (AM LEN 151A)

A = dorsal view of left haft of clypeus, Zimbabwe specimens; B = detail of basal processes.

Scale = 100 μ m.

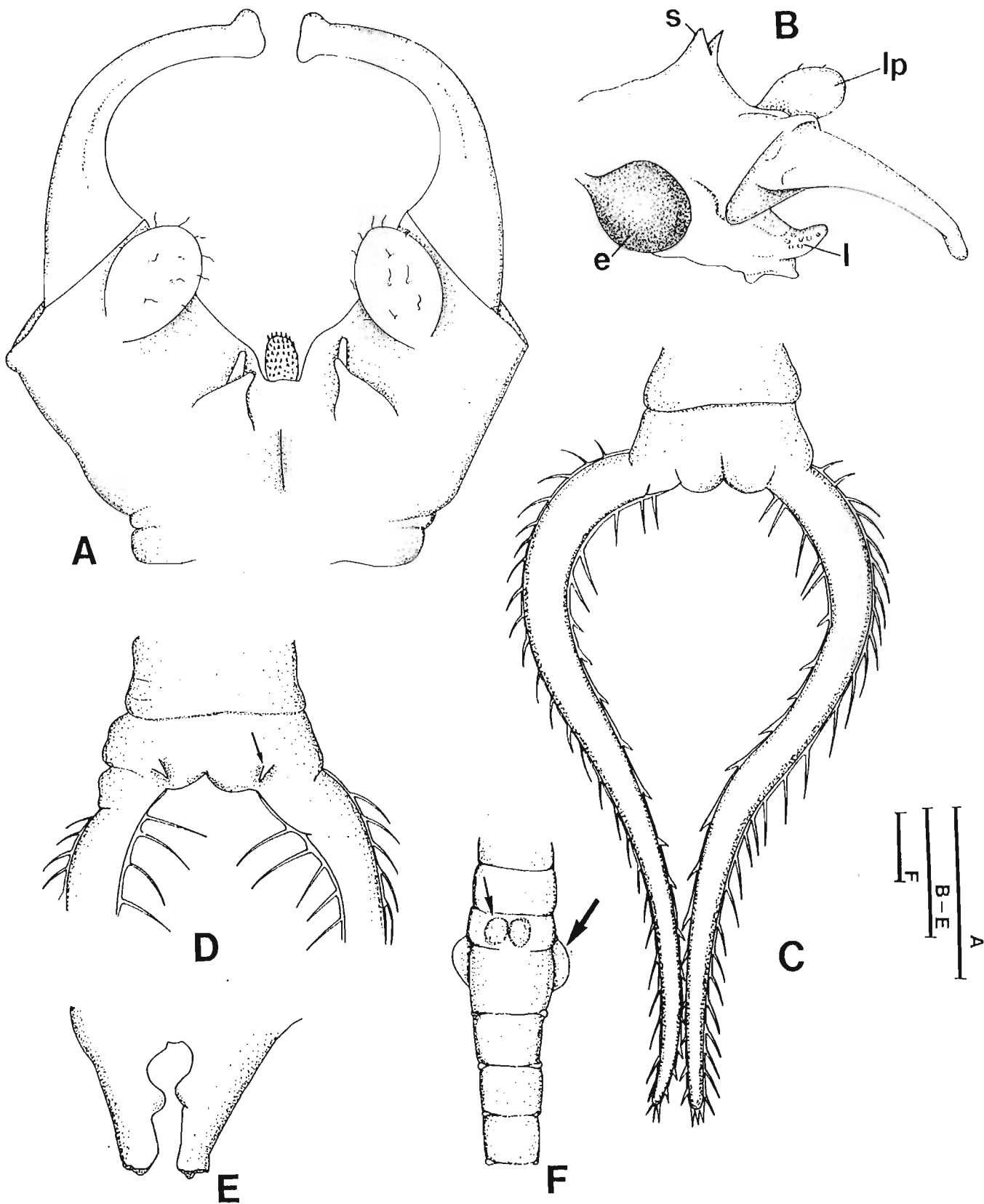


Figure 32: *Branchipodopsis underbergensis* sp. nov. (SAM-A40839)

A = dorsal view of clypeus; B = lateral view of clypeus, e = eye; s = spinous projection of basal process; lp = lamelliform process; l = labrum; C = cercopods of male; D = ventral view of last abdominal segments of male, arrow indicates spinous projections; E = ventral view of basal part of penes; G = dorsal view of genital segment of female, small arrow indicates dorsal extensions, large arrow indicates posterior, lateral extensions.

Scale = 0,5 mm.

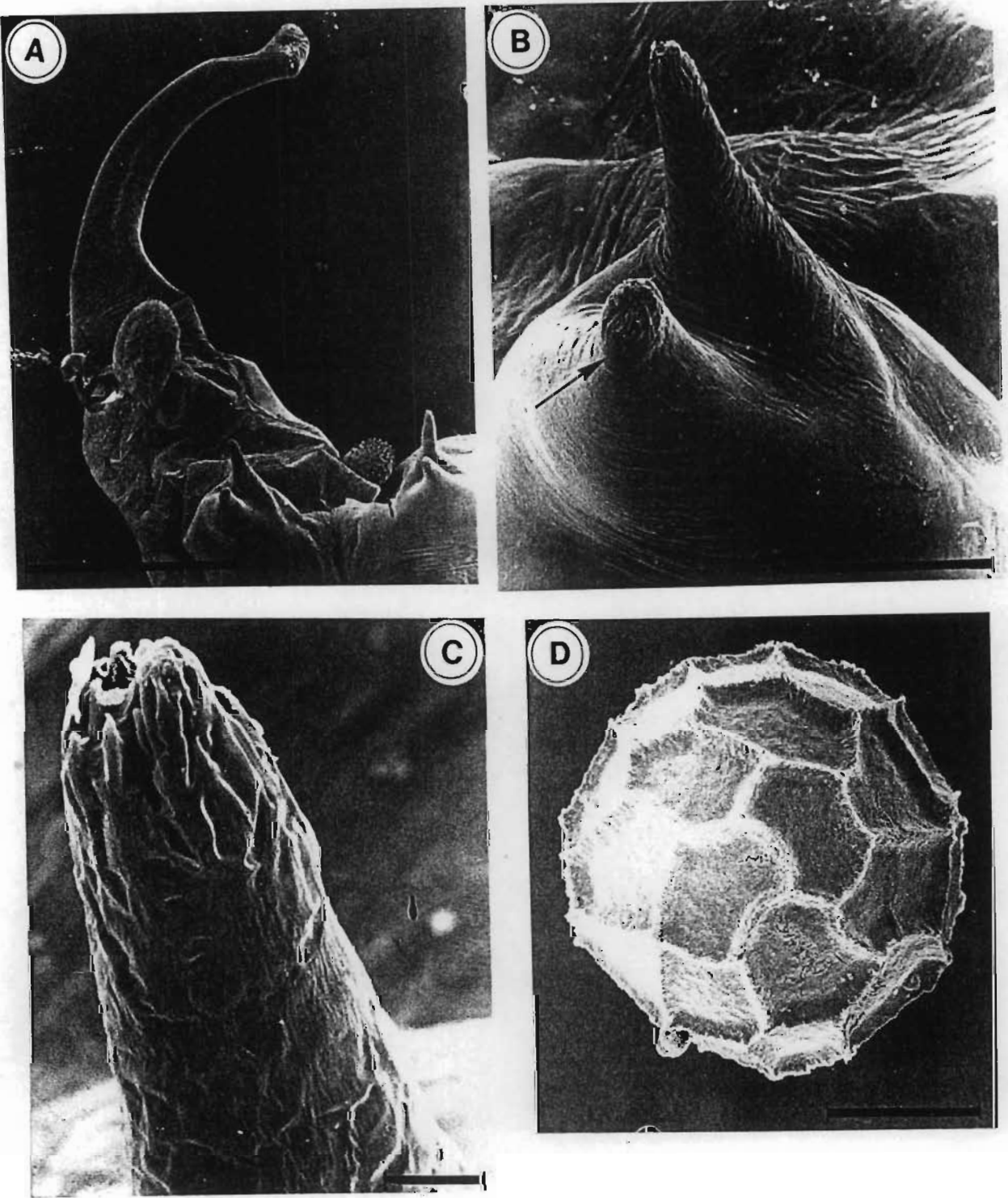


Figure 33: *Branchipodopsis underbergensis* sp. nov. (SAM-A40839)

A = dorsal view of left part of clypeus; scale = 0,5 mm; B = detail of left basal process, arrow indicates spinous projection; scale = 100 μ m; C = detail of apical region of basal process lobe; scale = 10 μ m; D = egg; scale = 100 μ m.

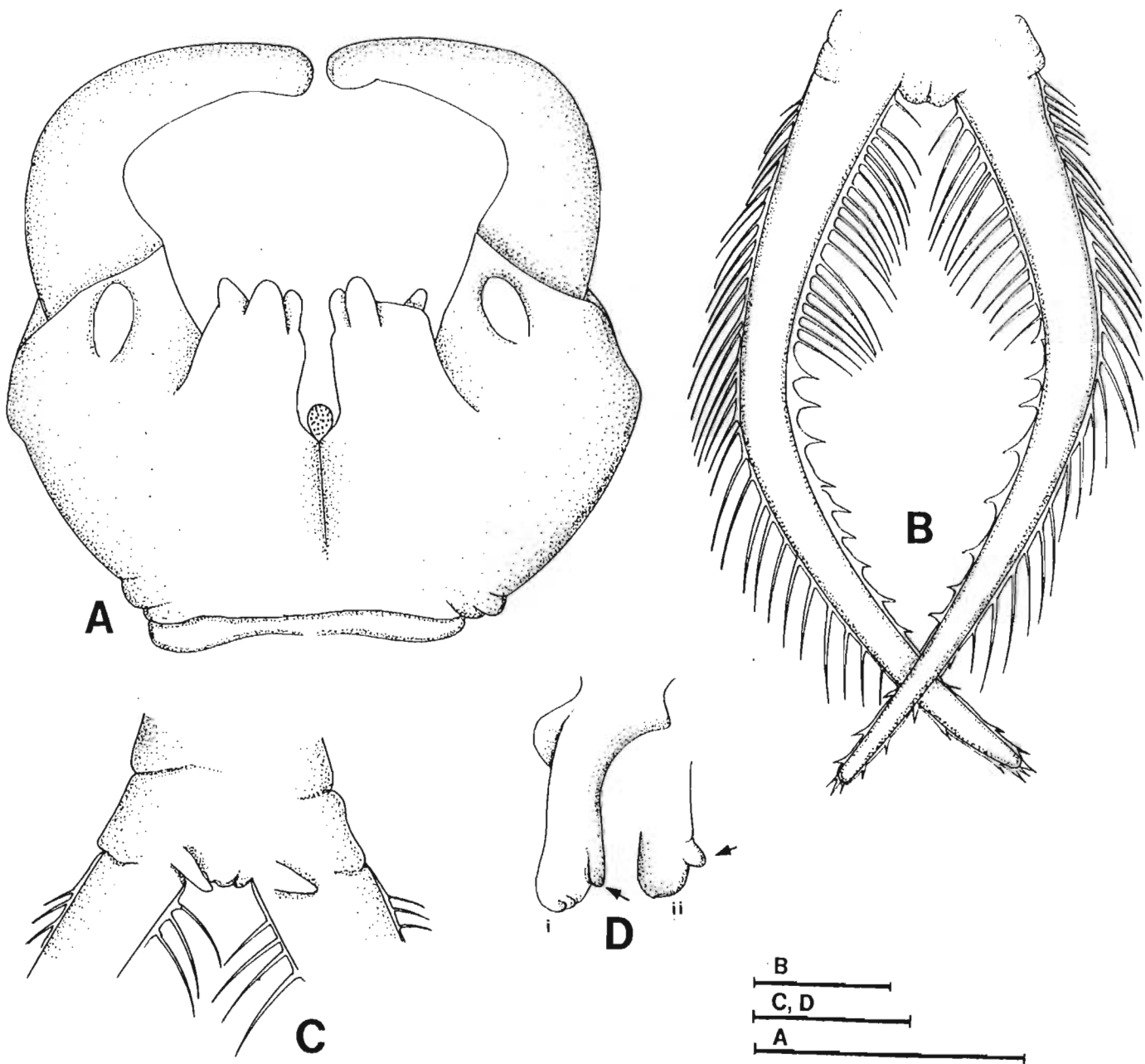


Figure 34: *Branchipodopsis wolfi*

A=dorsal view of clypeus of specimen HNHM I/A-77Z from Daday's collection; B=cercopods of male (AM LEN 99B); C=ventral view of last abdominal segments of male (AM LEN 99B) showing spinous processes; Di=dorsal view of basal part of right penis (SAM-A5921), arrow indicates blunt projection; Dii=ventral view of apex of basal part of right penis (SAM-A5921), arrow indicates blunt projection on lateral surface. Scale = 0,5 mm.

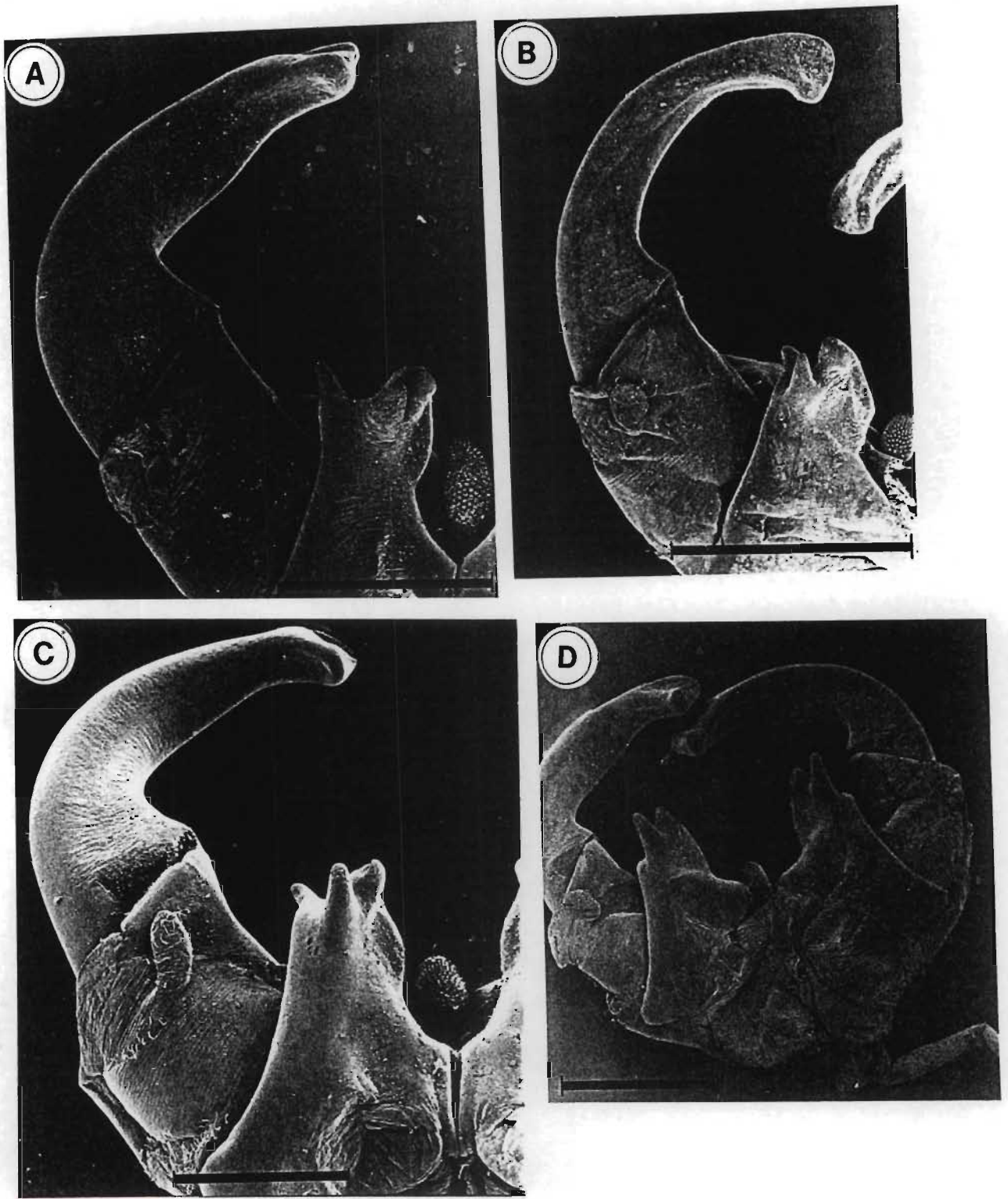


Figure 35: *Branchipodopsis wolfi*

A = left half of clypeus, Lesotho (DB 669) specimen; B = left half of clypeus of KNP, Pumbe (AM LEN 99B) specimen; C = left half of clypeus of Great Fish River (SAM-A5921) specimen; D = clypeus of Altmark (SAM-A7268) specimen. Scale = 0,5 mm.

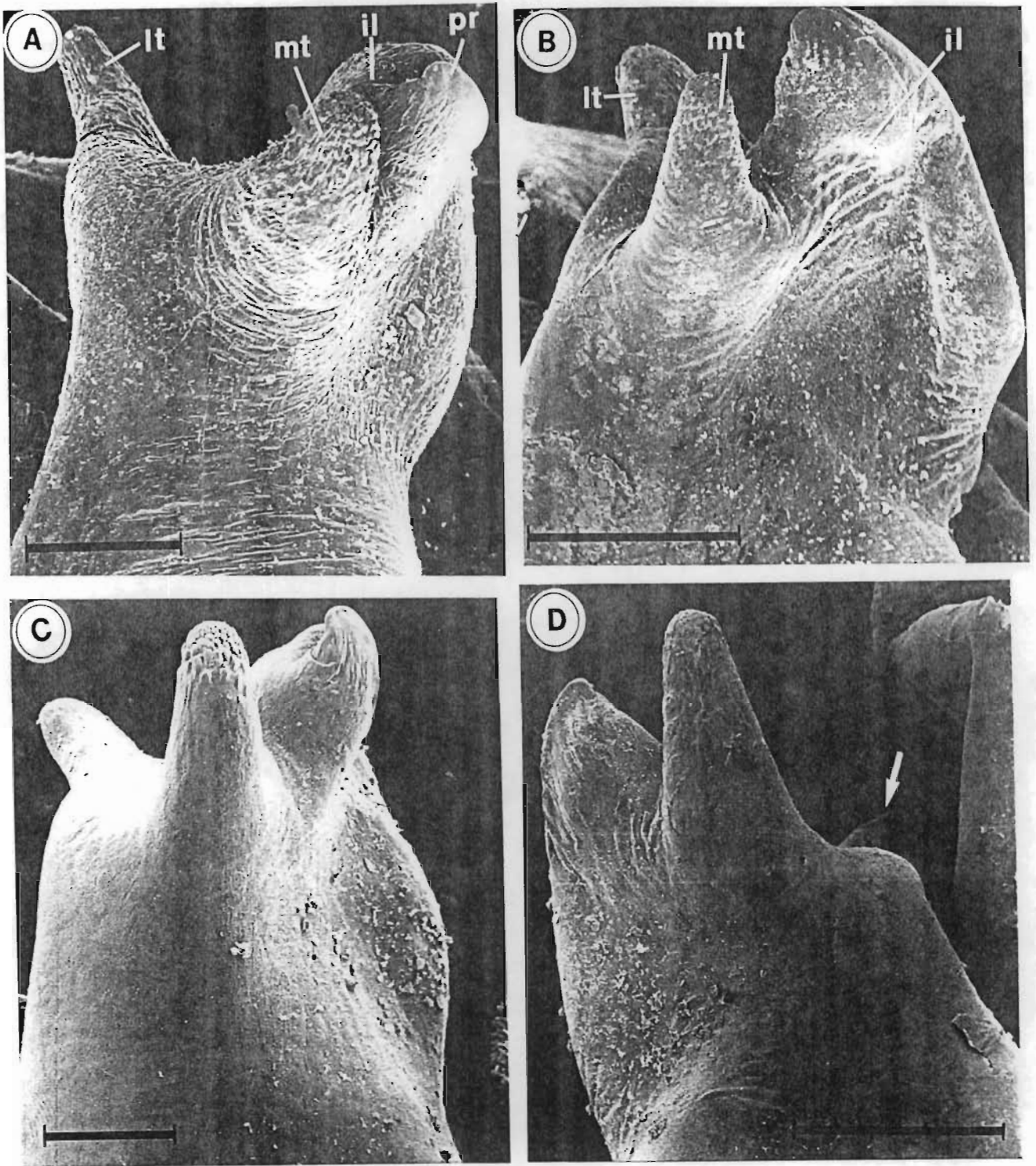
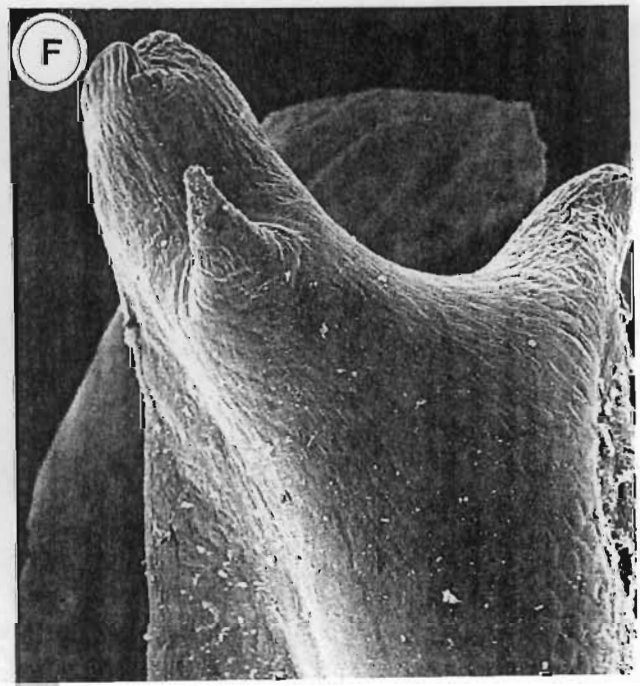
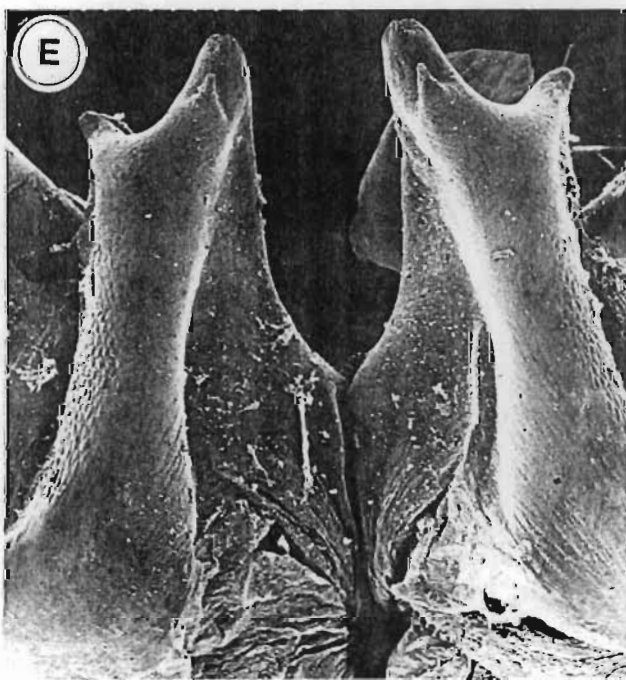
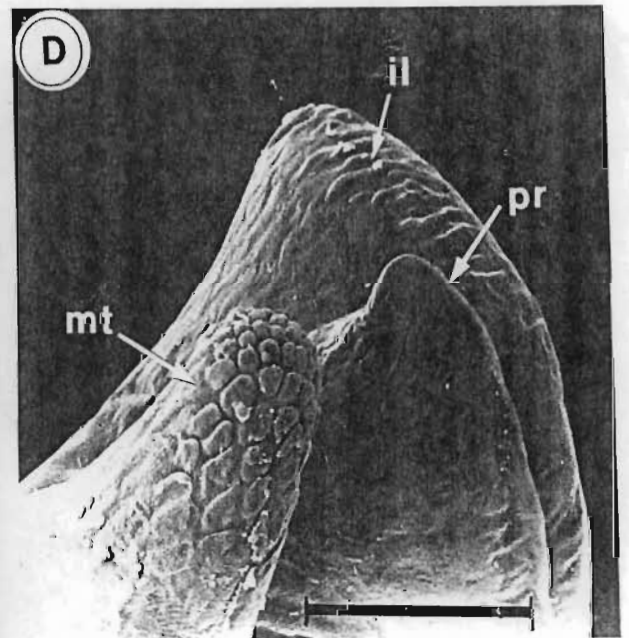
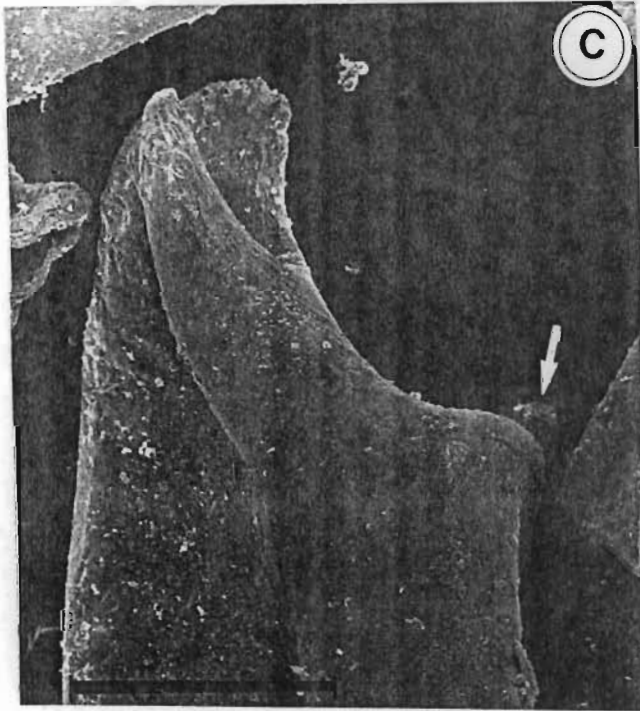
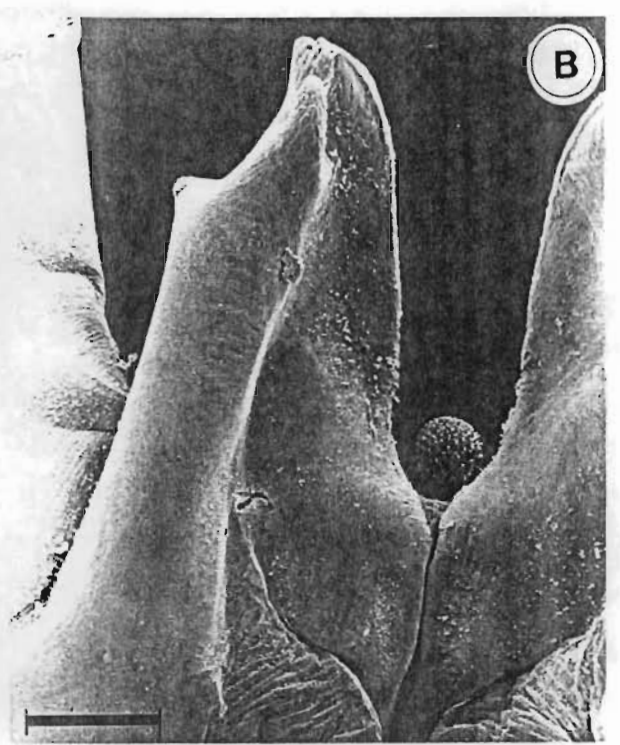
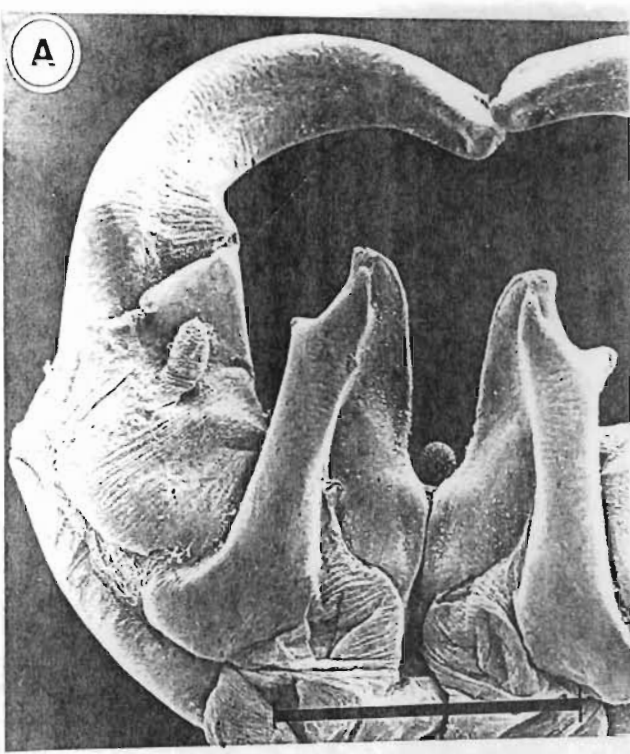


Figure 36: *Branchipodopsis wolfi*

A = detail of left basal process of DB 669 specimen; B = detail of left basal process of AM LEN 99B specimen; C = detail of left basal process of SAM-A5921 specimen; D = detail of right basal process of SAM-A7268 specimen (arrow indicates lateral tubercle). il = inner lobe, lt = lateral tubercle, mt = median tubercle, pr = projection on inner lobe. Scale = 100 μm .



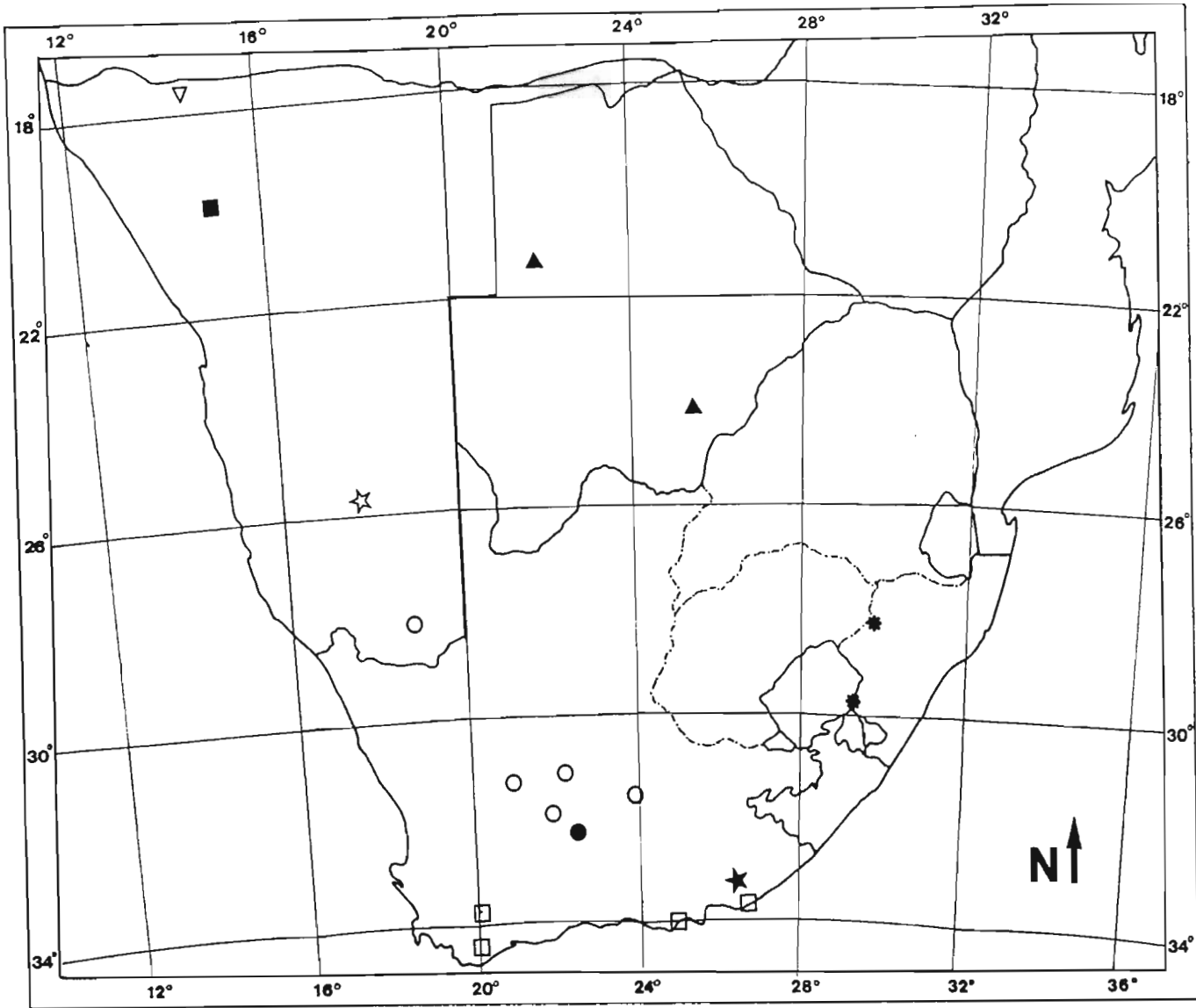


Figure 38: Map of southern Africa illustrating the distribution of
 ○ *B. browni*; ☆ *B. drepane*; □ *B. hodgsoni*; ▲ *B. kalaharensis*;
 ▽ *B. kaokoensis*; ● *B. karroensis*; ★ *B. natalensis*; ■ *B. simplex*;
 ★ *B. scambus*.

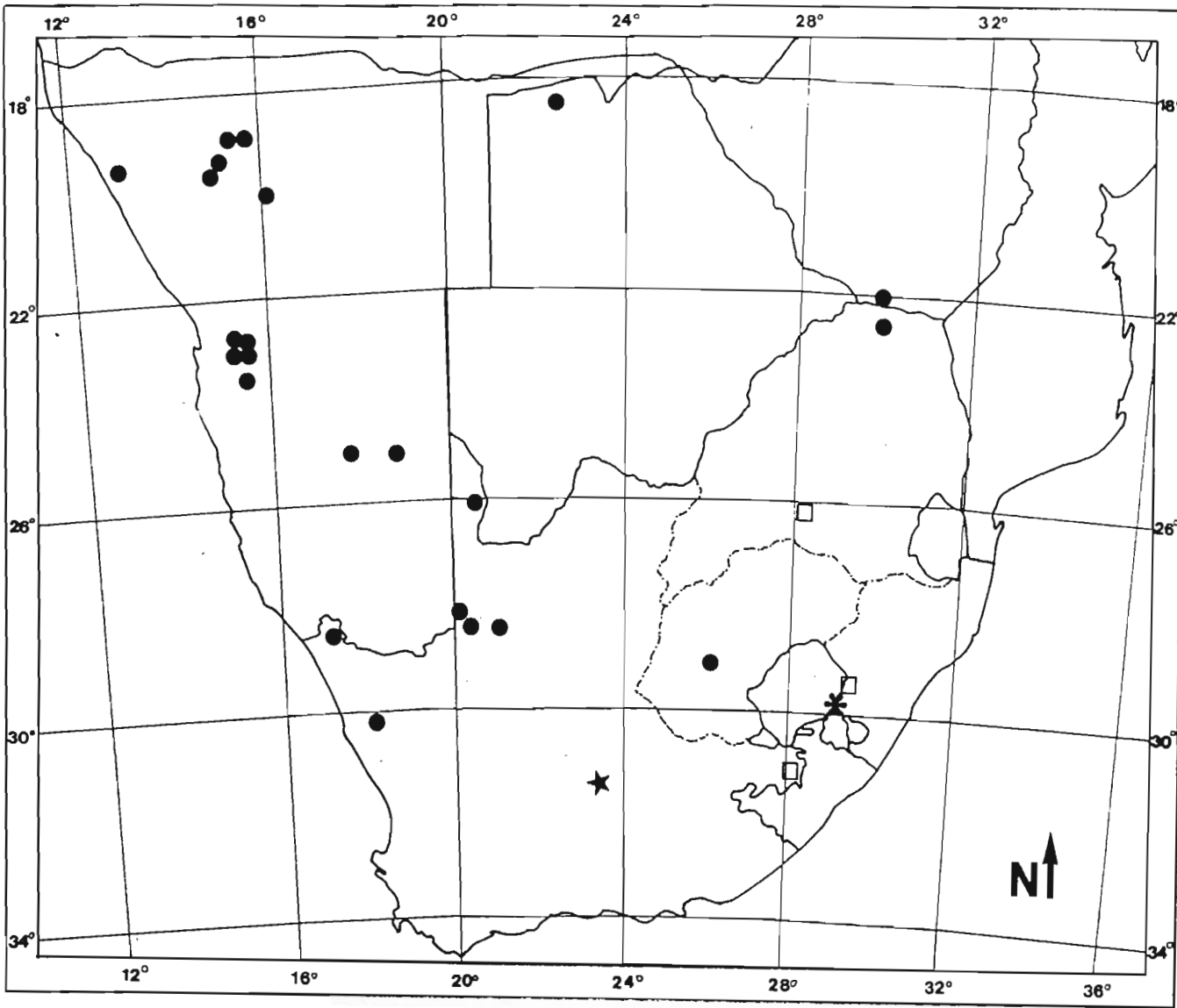


Figure 39: Map of southern Africa illustrating the distribution of
 ● *B. tridens*; ★ *B. hutchinsoni* sp. nov.; □ *B. drakensbergensis* sp. nov.;
 ✱ *B. barnardi*.

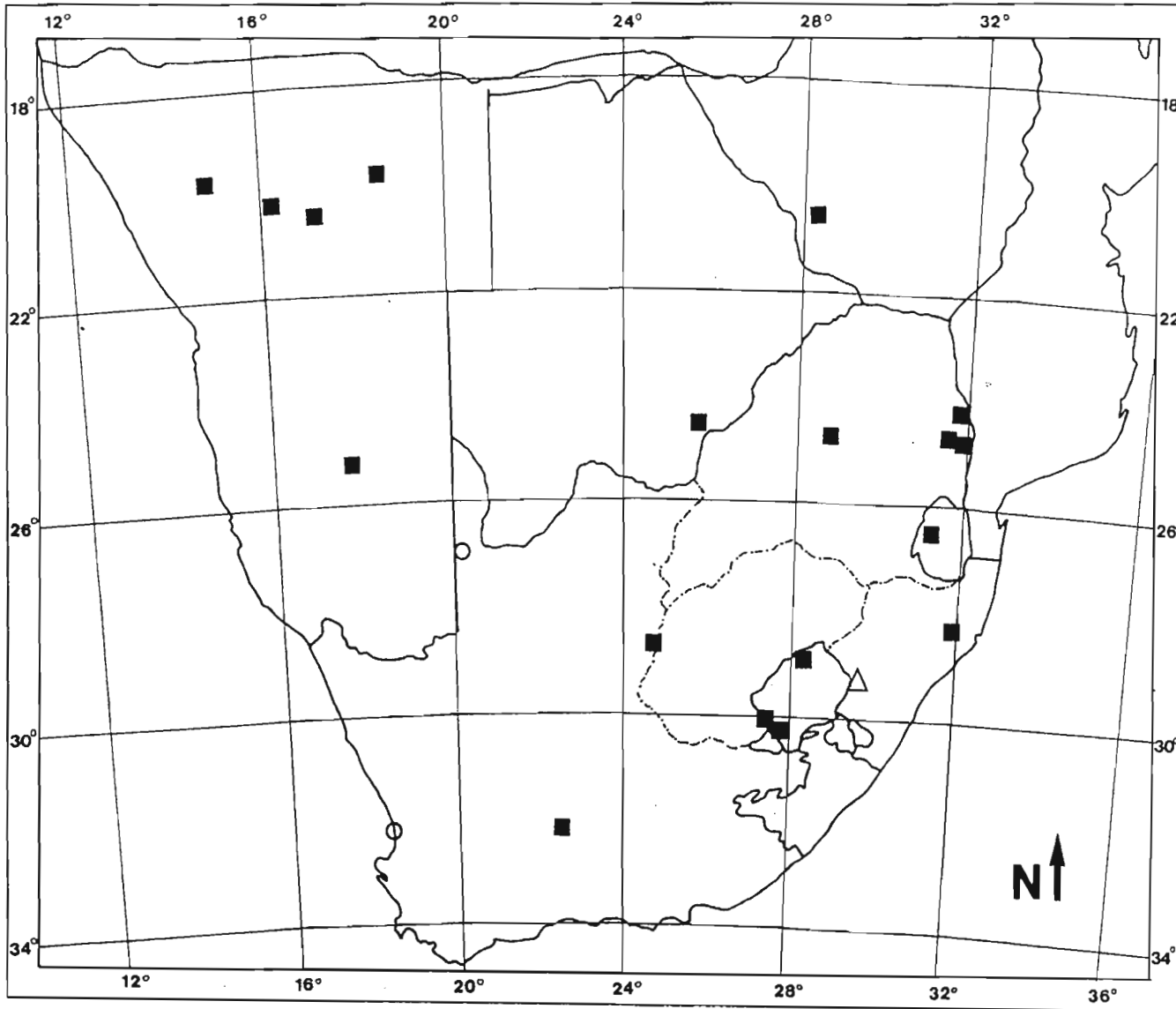


Figure 40: Map of southern Africa illustrating the distribution of
 ■ *B. wolffi*; △ *B. underbergensis* sp. nov.; ○ *B. dayae* sp. nov.

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CHAPTER 5

THREE NEW GENERA OF THE FAMILY BRANCHIPODIDAE (CRUSTACEA: ANOSTRACA) FROM SOUTHERN AFRICA

ABSTRACT

Three sets of specimens, one each from north-eastern Natal, the eastern Cape (Grahamstown), and Namibia (Namib desert) were identified as undescribed genera belonging to the family Branchipodidae. All three share a large, single median process on the anterior margin of the fused basal joints of the male antennae; not a feature found in any of the six known genera of the family. However, other taxonomically significant characters such as penis morphology and the shape of the terminal joint of the antennae indicate that the specimens are sufficiently distinct to represent three separate genera. Each of the genera appears to have a restricted distribution and to be limited to few habitats.

INTRODUCTION

The Anostraca are considered to be well known in terms of taxonomy at the family and generic levels (Bănărescu 1990; Dodson & Frey 1991). However, there are problems associated with the distinction of the family Branchipodidae as discussed by Linder (1941), and there is only a meagre amount of published data on the characteristics of this family. In the Thamnocephalidae, there are difficulties in distinguishing between two of the genera. In addition, a new subgenus has been proposed for *Streptocephalus* (Brendonck, Hamer & Thiéry 1992). These facts indicate that our knowledge at the level of genus and family is far from complete for all anostracans. The recent discovery of three sets of specimens from southern Africa, each morphologically distinct, which could not be allocated to any known genus, emphasized the need for further taxonomic research and revision within the Anostraca, particularly in those groups and geographic regions previously neglected.

The family Branchipodidae, to which the three sets of specimens have been allocated, currently includes six genera; only one of which, *Branchipodopsis*, has been recorded from southern Africa. *Tanymastigites* is the most recent addition to the family and also to the Anostraca, and was described in 1972 by Brtek. In this publication, comment was also made on the family Branchipodidae which was split into three subfamilies; the Branchipodinae (*Branchipodopsis*; *Branchipus* and *Parartemia*); the Tanymastiginae (*Tanymastix* and *Tanymastigites*) and a third subfamily which included only the little-known genus, *Metabbranchipus* from Somalia. However, a detailed analysis of the genera has still not been accomplished.

A relatively recent effort to sample temporary pools by a number of institutions and individuals in southern Africa has led to the collection of a large amount of anostracan material and many new distribution records. As a result of this effort, three sets of specimens identified as new genera were collected during the latter part of the last decade. The antennal process of these closely resembles that illustrated by Brehm (1958) for unidentified specimens collected during the Lund University Expedition to southern Africa. Unfortunately, the latter material could not be obtained for examination. For two of the genera (referred to as genus A and C), the material available is inadequate to publish the description of a new genus. For the third genus (genus B) the material was collected by a visiting Belgian scientist, Dr. Koen

Martens and the staff of the freshwater department of the Albany Museum, Grahamstown. A duplicate set of specimens was collected for Dr. Luc Brendonck of the Belgian Royal Institute of Natural History in Brussels. The specimens were recognised as representing an undescribed genus simultaneously in Belgium and in this study but by mutual agreement, Dr. Brendonck has prepared a manuscript entitled "*Rhinobrachipus martensi* n. genus, n. sp. with a discussion on the affinities within the Branchipodidae". The description of this material here is for the sake of completeness only and the interpretation of the material is a personal one. For the above reasons, the genera have not been named, and are referred to as genera A, B and C. In addition to describing and illustrating the taxonomically important features of the three genera, the relationships between each of them and between them and the other members of the family are discussed as is the significance of certain characters used at generic and familial levels. Brief comment is also made on the distribution of the three genera and possible evolutionary implications.

MATERIALS AND METHODS

Specimens of genus C were obtained on loan from the State Museum of Namibia (SMN) in Windhoek, Namibia and of genus B from the Albany Museum (AM), Grahamstown, South Africa. Specimens of genus A were collected by the author during the course of a M.Sc study and have been catalogued into the AM collection where they will eventually be deposited.

Material and methods used in the collection of material, preservation, drawings and scanning electron microscopy and measurement details are as for those presented for *Branchipodopsis*.

RESULTS

Taxonomic descriptions

Family Branchipodidae Baird, 1852

Abbreviated diagnosis

Basal joints of the antennae of the male fused and heavily sclerotised to form a "clypeus". Flattened outgrowths present on anterior margin of basal joints. Genital segments of male negligibly swollen ventrally and without distinct seminal vesicles. Penes close together, with basal parts rigid and with proximal and distal outgrowths. Apical part of penes armed with longitudinal rows of spines.

Genus A

Figs 1-2

Material

AM LEN 201A, 1 male (8,2 mm), 3 females (9,4; 10,5; 11,3 mm); collected from north-eastern Natal (Zululand), Mkuze Game Reserve, temporary pool near airstrip (27°36'/32°14'E) by M. Hamer, January 1988.

Description of adult male

Antennae. Basal joints fused along about two thirds of length to form a large, broad, angular and heavily sclerotised clypeus (ratio to body length 0,28:1) (Fig. 1A). A large, wide median process present on anterior margin of fused basal joints (Fig. 1A). Median process with a long, digitiform projection on each corner of distal edge and a second, shorter, blunter projection at the base of each of these (Fig. 1A). Margin of median process between two pairs of projections slightly convex. Terminal joints very long (more than twice the width of the fused basal joints), and bent inwards, lying in a crossed over position in front of the head. Median margin inflated about halfway along terminal joint. Distal part of terminal joint slender and tapering to an acute apex (Fig. 1A).

Penes. Basal region of penes broad, with infolding about halfway along inner margin and leaf-like projection proximally on dorsal surface (Fig. 1B). Apical region stout, with a number of irregular, short longitudinal rows of spines distally, and a few scattered spines at

tip (Fig. 1B). Genital segments swollen laterally and ventrally (Fig. 1C).

Abdomen. Short and broad (ratio to total body length 0,4:1) (Fig. 1C) with a slender, apically bifid process mid-ventrally on fourth abdominal segment (Fig. 1B).

Cercopods. Short (ratio to body length 0,12:1), broad and almost straight with plumose setae along entire margin (Fig. 1D).

Thoracopods. Single pre-epipodite with serrated margin and distinct notch. Epipodite with smooth margin. Exopodite with 7 spines on outer, proximal margin and longer than the broad and apically-flattened endopodite. Lateral margin of endopodite with 6 strong spines. Endites 3-5 with 2-2-1 anterior setae (Fig. 2).

Description of adult female

Brood pouch. Short (ratio to body length 0,25:1), broad and rounded (Fig. 1E).

Remarks

Specimens with the same morphology as those described above were collected from the shallow, vegetated region of a pool on the Makatini Flats (27°25'S/32°11'E) in north-eastern Natal (Fig. 3). Unfortunately, these specimens were destroyed. Recently the pool at Mkuze where this genus was collected was sampled again but no specimens were collected. Numerous attempts to hatch specimens from dried sediment have also proved unsuccessful. The habitat and life history pattern of genus A is described and discussed in some detail in Hamer & Appleton (1991a; b) where it was referred to as *Branchipodopsis* sp.

The fused basal joints of the antennae indicate that genus A belongs to the family Branchipodidae. However, the genital segments of the male and the penes are more developed than usual within the family. The single median anterior process on the basal joints is not seen in any of the other genera described to date.

Genus B

Figs 4-6

Material

AM LEN 13, 14 males, 2 with the clypeus removed ($10,8 \pm 0,7$ mm), 18 females ($11,3 \pm 0,9$ mm); collected from Cape, Thomas Baines Nature Reserve, temporary pool at Rhino Ridge (33°23'35''S/26°30'25''E) by K. Martens, F. de Moor and H. Barber, 27

November 1989. AM LEN 20, 1 male (13,3 mm); collected from temporary pool near AM LEN 13 locality (33°23'42''S/26°30'10''E) by K. Martens, F de Moor and H. Barber, 30 November 1989.

Description of adult male

Antennae. Basal joints fused along about two thirds of length and heavily sclerotised to form a clypeus (ratio to body length 0,22:1). A round, setulose process distally on dorso-median surface of each basal joint (Figs 4A, 5C). Large, rounded median process with a pair of flattened, bifid process attached proximally and ventro-laterally, projecting from anterior margin of basal joints (Fig. 4A). Terminal joint curved inwards with weak bend and with an inflation on outer margin proximal to, and at bend (Figs 4A, 5A). A triangular ridge, with a small, elevated depression at the apex present on dorso-median surface of terminal joint at bend (Figs 5A-B). Distal region of terminal joint tapering to an acute apex (Figs 4A, 5A).

Penes. Basal part broad, with prominent, slender and curved projection proximally on median surface. A rectangular, mound-like ridge with a low conical projection on each side present proximally on dorsal surface. Just distal to rectangular ridge, circular area of surface of penes with distinct reticulate patterning (Fig. 5E). A small, blunt spine situated distally on median margin (Figs 4B, 5E). Apical part of penes with two rows of longitudinally-arranged, small spines (Fig. 4B). Genital segments slightly swollen laterally and ventrally.

Abdomen. A pair of strong spines ventrally on the distal part of first eight abdominal segments (Figs 4C, 5D).

Cercopods. Moderate length (ratio to body length 0,16:1), weakly curved outwards and with plumose setae along entire margin (Fig. 4D).

Thoracopods. Pre-epipodite with serrated margin in legs 2-10 (Fig. 6A) but only a portion of anterior margin serrated in legs 1 and 11 (Figs 6B-C). Pre-epipodite reduced in last leg (Fig. 6B). Epipodite small and slender (Fig. 6A), with smooth margin, except for anterior region of last leg which is serrated (Fig. 6B). Exopodite elongated and longer than endopodite, particularly in last leg (Fig. 6B). Outer margin of exopodite with 6-8 spines and lateral margin of endopodite with 5-6 widely-spaced spines on legs 2-10 (Fig. 6A). Endopodite of last leg with setae replaced by strong spines along entire margin (Fig. 6B). Endites 3-5 with anterior setae numbering 2-2-1 except last leg where these arranged as 2-1-1.

Description of adult female

Brood pouch. Short and rounded (Fig. 4E).

Thorax. Dorsal surface of last two thoracic segments each with a pair of spines (Figs 4E-F).

Egg morphology

Eggs with a crumpled appearance, with deep four-sided depressions separated by narrow ridges (Fig. 5F).

Remarks

The heavily sclerotised clypeus and the form of the penes indicate that genus B is a member of the Branchipodidae. The abdominal spines are unusual for the family but do occur in a few species of other genera. As in genus A, the presence of a single, median process from the anterior surface of the basal joints is not a character of the other branchipodids. The rounded processes on the dorsal surface of the basal joints are similar to the lamelliform processes of *Branchipodopsis* but the position and form of these in the two genera is somewhat different.

Genus C

Figs 7-10

Material

SMN 51346, 19 males ($8,7 \pm 0,9$ mm), 19 females ($8,9 \pm 0,9$ mm); collected from Namibia, Kaukausib River, Red pond ($26^{\circ}52'S/15^{\circ}29'E$) by K. Roberts, 14 July 1986.

Description of adult male

Antennae. Basal joints fused along about half their length to form a clypeus (ratio to body length 0,13:1). Each basal joint with a row of setae along dorsal surface (Figs 7A, 8A). A prominent, medianly-directed digitiform process present at the distal margin of each basal joint (Figs 7A, 8A). A large, apically flat median process, with slightly extended corners on anterior margin of clypeus (Fig. 8B). Terminal joints weakly curved and tapering to a subacute apex (Fig. 7A).

Frontal appendage. Bifid frontal appendage, almost twice as long as antennae, attached proximally on fused basal joints. An irregular row of prominent spinous projections along

ventro-lateral surface, with these decreasing in size towards the tapered apex (Figs 7A, 8C).

Penes. Basal region with large, triangular extension proximally on median margin and small, blunt spine distally (Figs 7B, 8D-E). Apical part with single row of 3-5 large, tooth-like projections along lateral margin (Fig. 8E). Genital segments slightly ventrally swollen (Fig. 7C).

Cercopods. Short (ratio to body length 0,12:1), straight and with plumose setae along entire margin (Fig. 7D).

Thoracopods. Pre-epipodite of all legs with distinct notch and with smooth margin (Figs 9A-C). Exopodite oval and not much longer than endopodite (Fig. 9A). Endopodite of last pair of legs reduced (Fig. 9C). Anterior setae on endites 3-5 numbering 2-2-1 on all legs.

Description of adult female

Brood pouch. Proximally broad but distally narrow and elongated, the apex reaching the fifth abdominal segment (Fig. 7E).

Egg morphology

Eggs spherical, with surface covered by small, shallow circular depressions (Figs 10A-B).

Remarks

The frontal appendage attached proximally on the basal joints of the male is a character which genus C shares with *Branchipus*, *Tanymastix* and *Tanymastigites*, three genera of Branchipodidae. The frontal appendage of the latter two genera is longer than the antennae, and frequently ornamented while in *Branchipus*, it is about the same length as the antennae and is usually smooth. Structures similar to the pair of digitiform processes on the basal joints of genus C are also found in some species of these genera. However, the single median process on the anterior margin of the clypeus, the single row of long, dentate projections on the apical part of the penes and the simple, smooth terminal joints of the antennae are features of genus C not shared with *Branchipus*, *Tanymastix* or *Tanymastigites*. In addition, the egg morphology is quite distinct from that commonly found in the first two genera. It is quite possible that the specimens examined are not fully mature; the small size and the absence of eggs from the brood pouches of most females indicates a young population, and the eggs prepared for electron microscopy may not have completely developed shell

sculpturing. Immaturity may also account for the simple terminal joints of the male antennae but even in the largest of the males there was no hint of the development of projections or inflations on the terminal joint such as those seen in *Branchipus*, *Tanymastix* or *Tanymastigites*. The differences described above indicate that genus C represents a genus, which although closely related, is quite distinct from these three genera.

DISCUSSION

Genera A, B and C have been included in the family Branchipodidae mainly on the basis of the fused basal joints of the male antennae. The only other family which exhibits fusion to any comparable degree is the Thamnocephalidae but here the basal joints are not sclerotised any more than the remainder of the body. In addition, a number of other features of the Thamnocephalidae, in particular the fully retractible penes, clearly distinguish this family from the Branchipodidae. The single pre-epipodite, notched in two of the genera and the number of anterior setae on endites 3-5 of the thoracopods of genera A, B and C also indicate that they are members of the Branchipodidae although these characters are not exclusive to this family. The form of the penes is also consistent with that prescribed for the branchipodids; a proximal projection is present on the basal part, and in genus B and C, a second one is positioned distally. The rows of longitudinal spines on the apical part of the penes are also shared with the other genera of the family. However, in not all aspects of morphology are the three sets of specimens described here compatible with the diagnosis for the family. The most obvious difference is the presence of a single, large process on the anterior margin of the basal joints as opposed to the pair of dorsoventrally-flattened processes in this position in the other genera.

A wide variety of antennal processes is present on the basal joints of the genera of the Branchipodidae. Linder (1941) listed these, including the distal, lamelliform ones seen in *Branchipodopsis*, the more proximal paired ones which are common to five of the genera, a median spine in some *Parartemia* species and the club-shaped median ventral process in a number of *Branchipodopsis* species. The latter two median processes are, however, small and simple in these genera and it is difficult to imagine them developing to the extent seen in genera A, B and C but considering the elaboration of processes such as the frontal appendage in some genera, this is not impossible. No genera with a median process in any sort of

intermediate form between *Parartemia* and *Branchipodopsis* and genera A, B and C is known. Linder (1941) also stated that grouping genera into families based solely on the form of the antennae, and in particular, the antennal outgrowths, as was done by Daday (1910) results in assemblies of genera which share few or no other characters. He stated that within some families the genera exhibit quite diverse antennal morphologies, but share others which are often exclusive. It is, therefore feasible to include genera A, B and C in the family Branchipodidae even though their antennal outgrowth is a unique character. The embryological origin of the median antennal process needs to be established, as does that of the other basal processes of genera such as *Branchipodopsis* and *Parartemia* in order to establish possible homologies between these structures.

The single, large median antennal process is a feature which genera A, B and C share with the material illustrated by Brehm (1958). In the latter, the median antennal process is illustrated as being as long as the apices of the terminal joints, oval and with setae along the margin. A rounded process is present on each basal joint, and the terminal joints are simple and short. Unfortunately, the penes are not illustrated or described, but it is likely that these specimens, from "25 miles south of Middelburg in the Cape" (31°47'S/24°46'E), are related to genera A, B and C.

The three sets of specimens described here all share a single large median antennal process which could suggest a common ancestor but a number of other characteristics indicate that they are not congeneric. The overall shape of the median process is very different in the three genera, with the projections on that of genus A and B situated in different positions. The other processes on the basal joints are different in both form and position in genera B and C and are entirely absent in genus A. The terminal joints of the three genera are also significantly different. The presence of a well-developed frontal appendage in genus C clearly separates it from the other two genera. In genera such as *Streptocephalus* and *Branchinella*, not all species have an elaborate frontal appendage but in the Branchipodidae, in those genera (*Branchipus*, *Tanymastix* and *Tanymastigites*) in which this structure is found, it is a feature common to all members of the genus.

Linder (1941) based his division of the Anostraca into families largely on the form of the penes and genital segments and his classification has changed little in the ensuing years.

Generally, there is not much variation in this character between species, but at a generic and family level, differences are usually quite marked. The penes of genera A, B and C provide further evidence that they do not belong to the same genus. The large, curved spinous projections on the basal part of the penes of genus B as opposed to the broad, triangular extensions proximally in genus C distinguish these two sets of specimens. In addition, the single row of only 3-5 very large spines on the apical part of the penes of genus C is a feature which is unusual even within the Branchipodidae and is probably taxonomically important. The extremely well-developed penes of genus A, which lack a proximal outgrowth on the median margin such as that seen in the other two genera, but which have a leaf-like process dorsally and a simple infolding on the median margin instead, are also unusual within the Branchipodidae and could indicate that this genus is separate from the other two.

The relative proportions of body regions (genus A), body ornamentation (genera A and B), brood pouch shape (genus C), thoracopod shape and setation and egg morphology are characters which may be taxonomically significant here but the degree to which this is so is not clear. Egg morphology has received considerable attention as a taxonomic tool in recent years (Gilchrist 1978; Mura, Accordi & Rampini 1978; Mura 1985; Mura & Thiéry 1986; De Walsche, Munuswamy & Dumont 1991; Thiéry & Gase 1991) but unfortunately, it is only useful in some cases in identifying species and does not generally provide any clues as to phylogenetic relationships. However, in the family Branchipodidae the eggs do not appear to have the same degree of diversity within genera as in groups such as *Streptocephalus*. For example, the species of *Branchipus* all have a relatively uniform egg morphology (Mura 1986; Alonso & Jaume 1991) which is similar in shape and sculpturing to that seen in genus B and the eggs of *Tanymastix* are characteristically biconvex (Thiéry & Gase 1991). This may provide further evidence that genera A, B and C, with their diverse egg morphologies are indeed separate genera.

Bănărescu (1990) suggested an eastern Pangean origin for the ancestral Branchipodidae, with the Branchipodinae concentrated in the south (eastern Gondwanaland), the areas which later split into Australia and Indo-Africa, and the Tanymastiginae in the north which later became Europe. The discovery of three new genera of Branchipodidae in southern Africa provides further evidence for the origin of the family in eastern Pangea and more specifically, for the ancestral Branchipodinae, to which the three probably belong, in eastern

Gondwanaland.

The fact that only one species of each of the genera described here has been collected to date could indicate that, as a result of adaptations to a particular set of environmental conditions, they have not dispersed to other habitats and speciation has not occurred. Although a large number of pools in the areas surrounding the localities where genera A and B were collected were sampled, they appeared to be restricted to only two pools within a relatively small area which provides evidence for the above suggestion. Alternatively, genera A, B and C could represent relic species of a previously widespread form which, because of specific habitat or climatic requirements was unable to survive past changes. The distribution of the three genera could be interpreted as being indicative of this possibility. However, until the relationship between the three genera and between them and the other members of the Branchipodidae is known, through DNA and embryological investigations, the answers to questions such as this will remain purely speculative.

ACKNOWLEDGEMENTS

Dr. F de Moor and H. Barber of the Albany Museum are thanked for their hospitality and for making large amounts of material available for this study. Mrs B.J. White and Mrs P. Donnelly of the Electron Microscope Unit of the University of Natal, Pietermaritzburg assisted with the electron microscopy and micrographs.

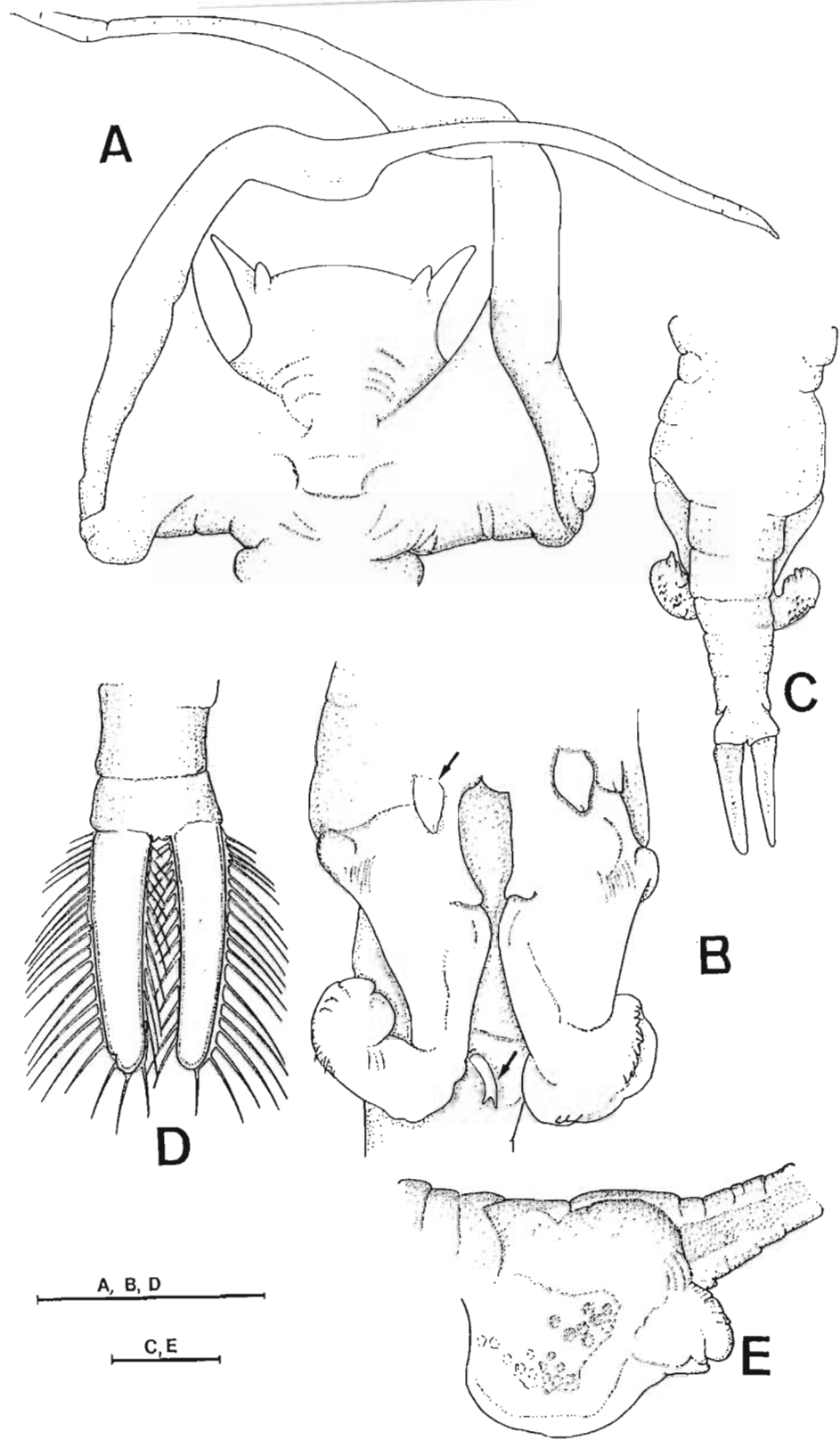


Figure 1. Genus A.

A = dorsal view of clypeus. B = ventral view of penes and abdominal process (indicated by arrow). C = dorsal view of genital segments and abdomen of male. D = cercopods of male. E = lateral view of brood pouch of female. Scale = 1 mm.



Figure 2. Genus A.

Thoracopod 5 of male. Arrow indicates notch in pre-epidite. Scale = 0,5 mm.

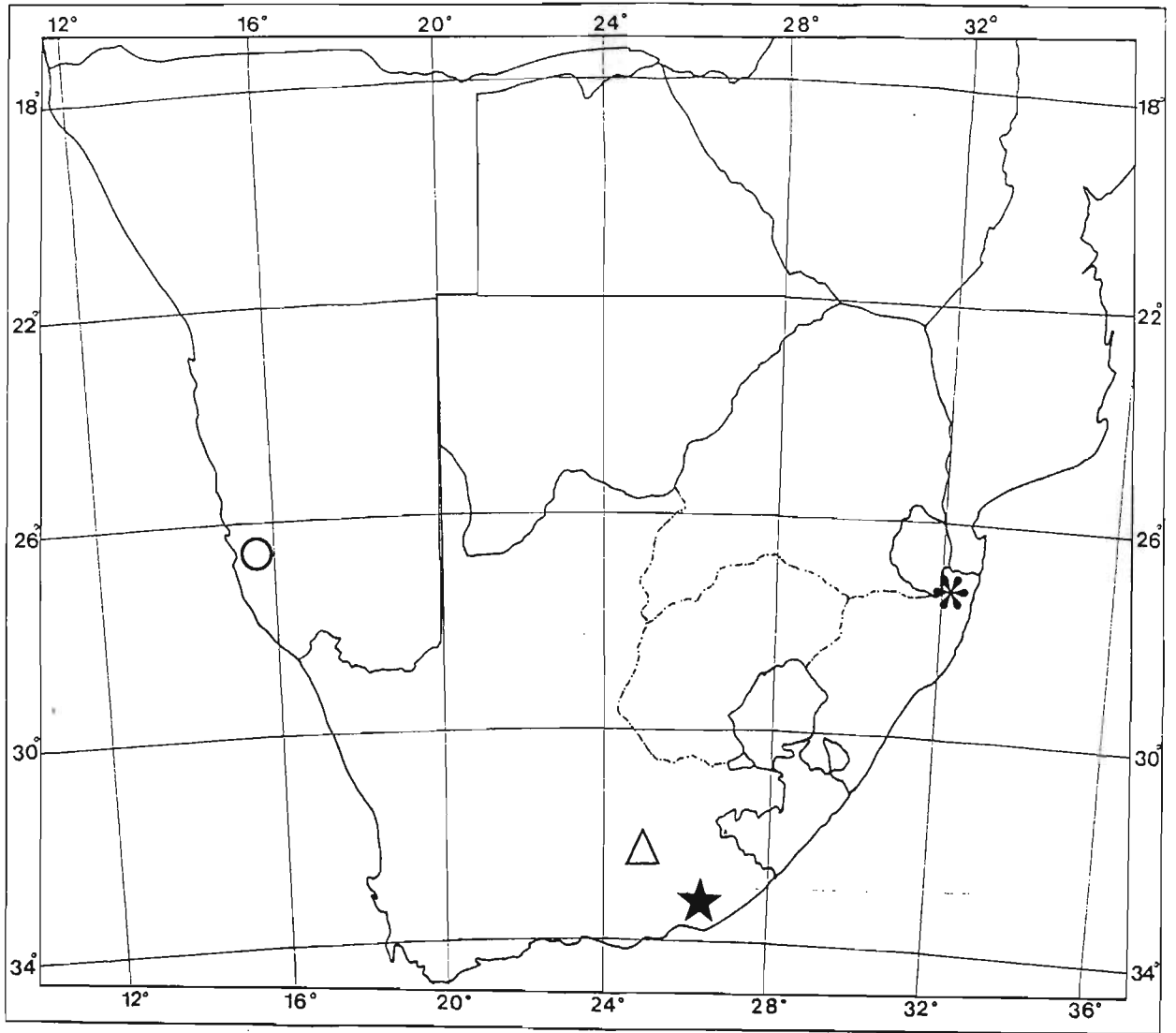


Figure 3. Map of southern Africa showing collection localities for * genus A, ★ B and ○ C and the material examined by Brehm (1958) △

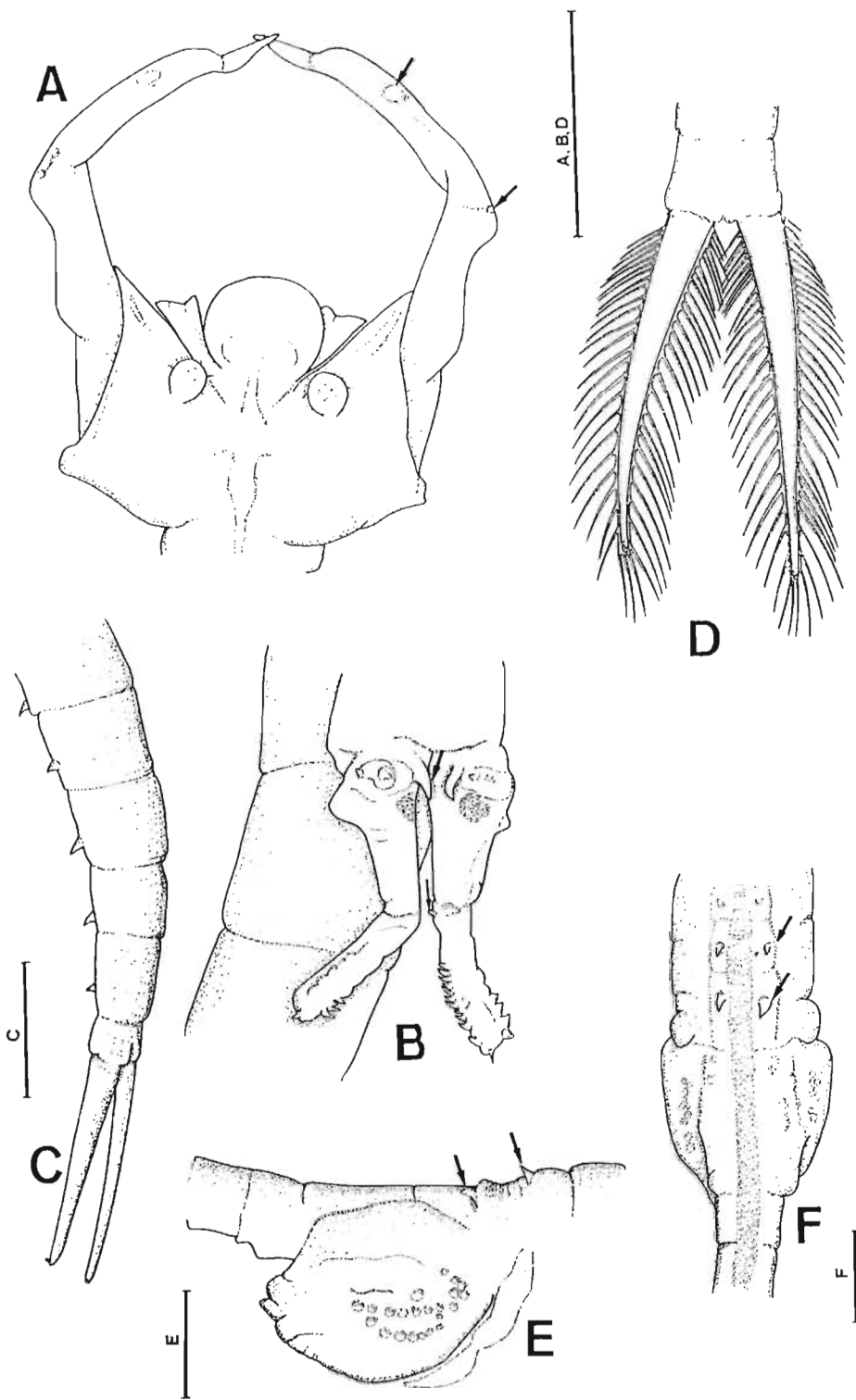
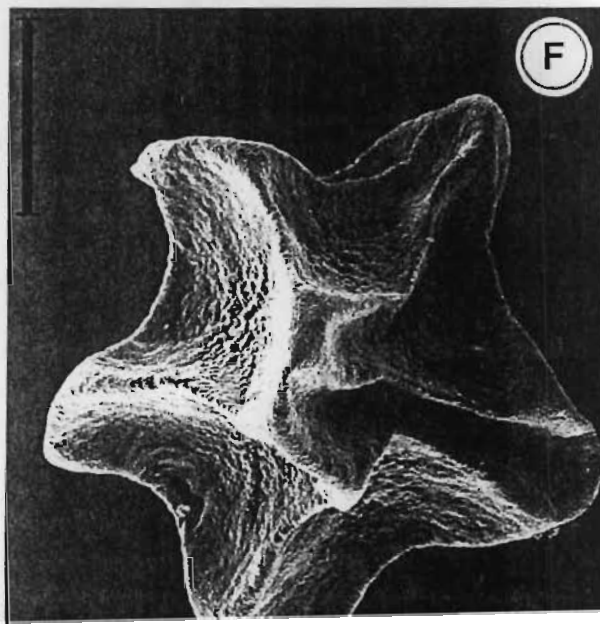
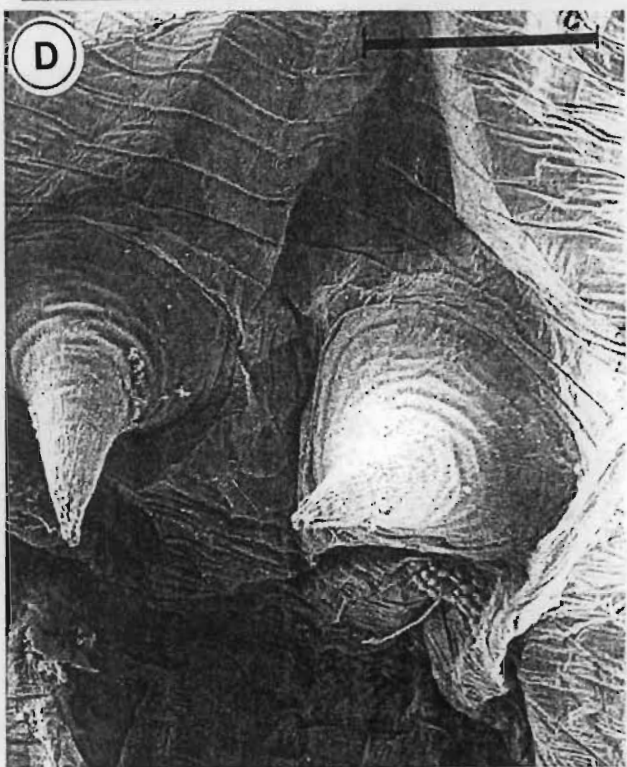
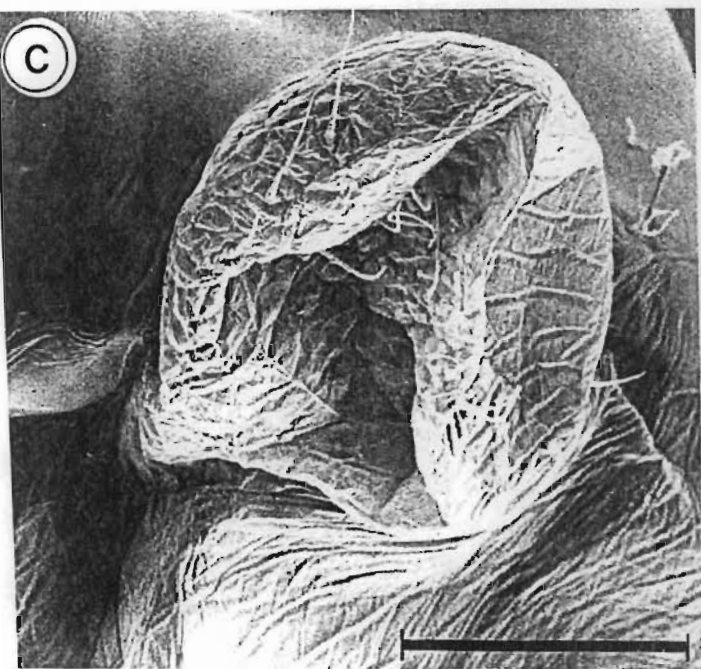
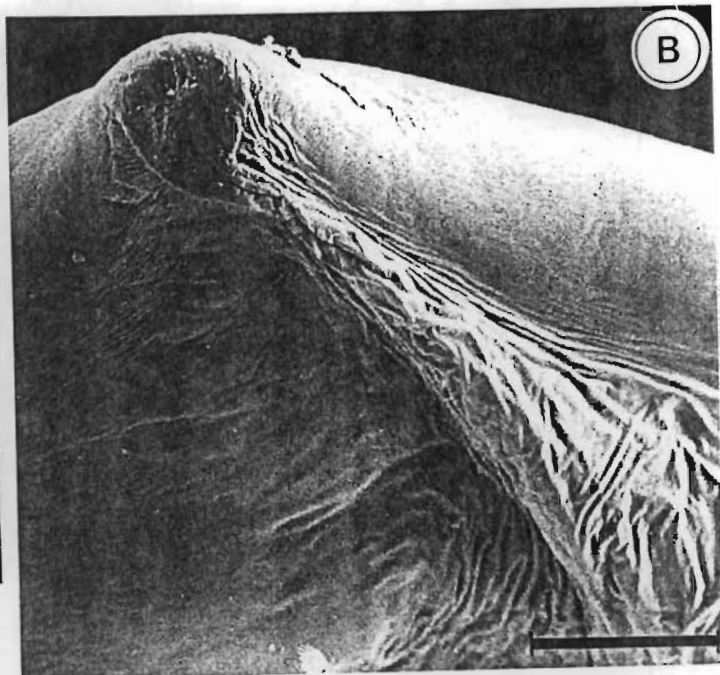
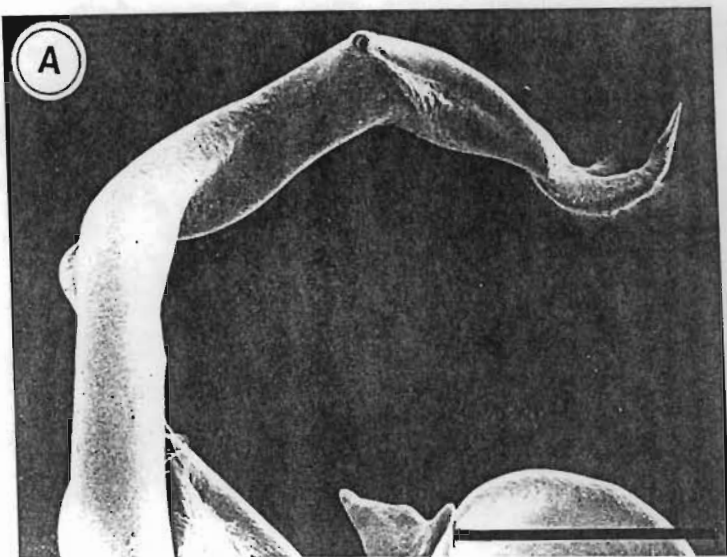


Figure 4. Genus B.

A = dorsal view of clypeus, arrows indicate projections on terminal joint. B = ventro-lateral view of penes, arrow indicates curved, proximal projection. C = lateral view of male abdomen, showing ventral spinous projections. D = male cercopods. E = lateral view of brood pouch and female genital segments, arrows indicate dorsal spines. F = Dorsal view of female genital segments, arrows indicate dorsal spines. Scale = 1,0 mm.



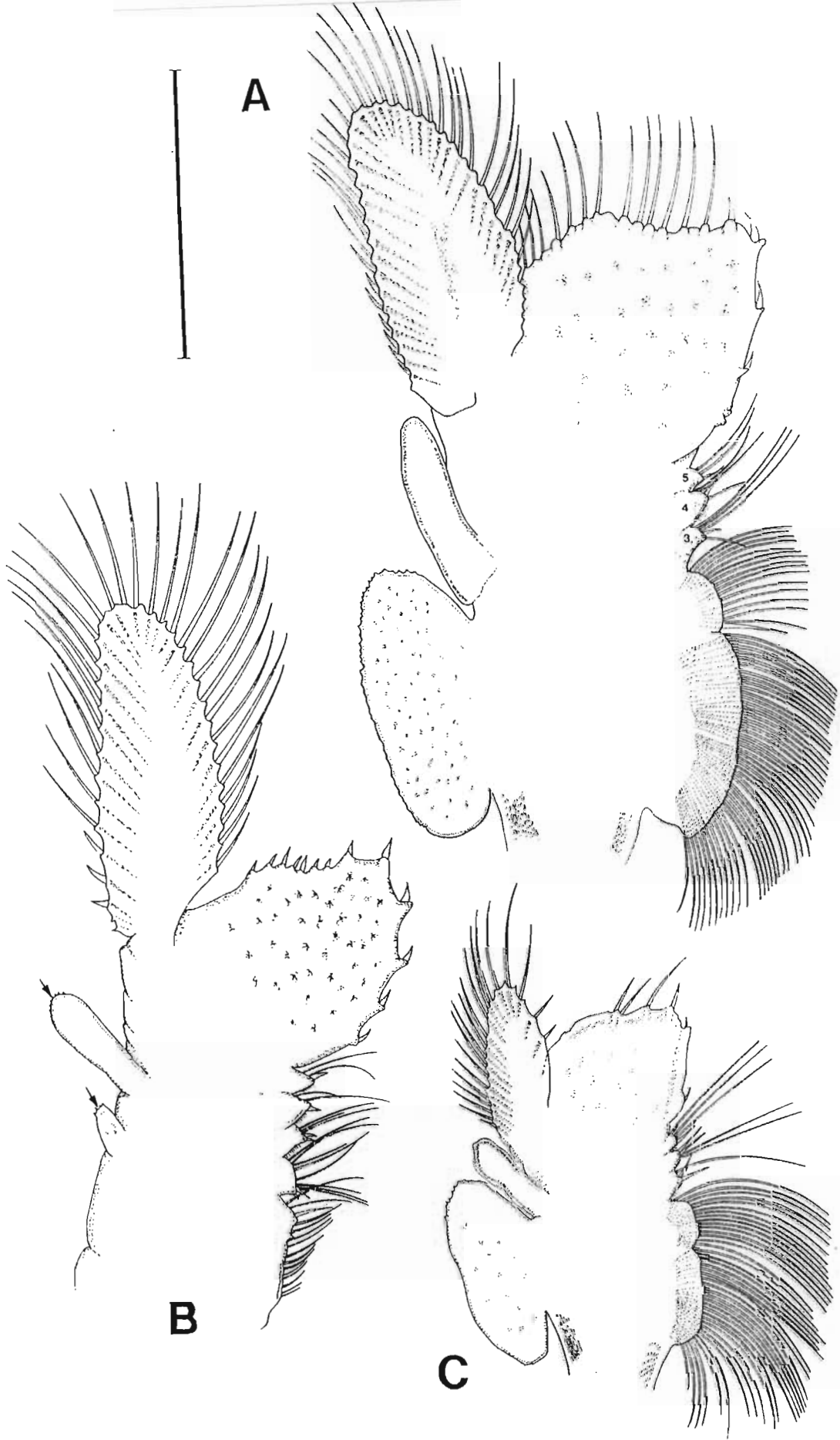


Figure 6. Genus B.

A = male thoracopod 5. B = thoracopod 11. C = thoracopod 1. Arrows indicate serration on margin of pre-epipodite and epipodite. Scale = 0,5 mm.

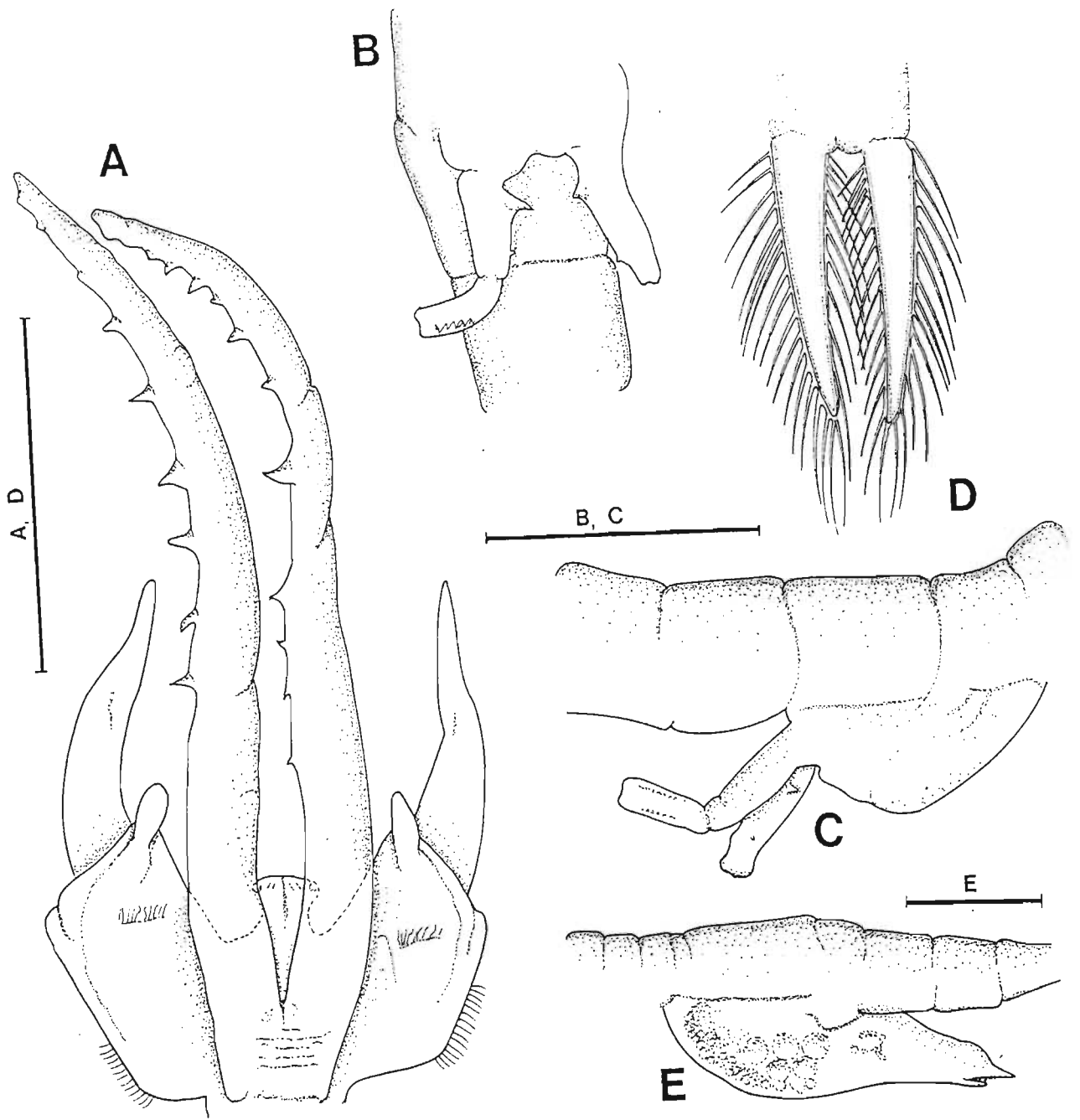
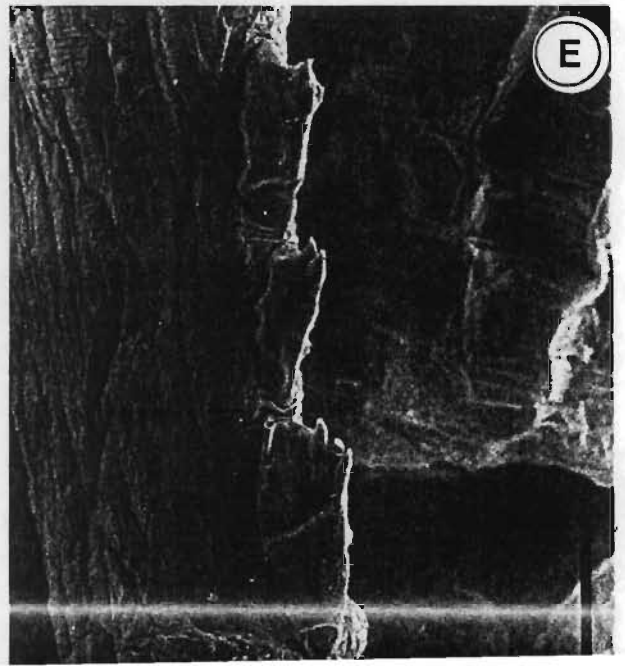
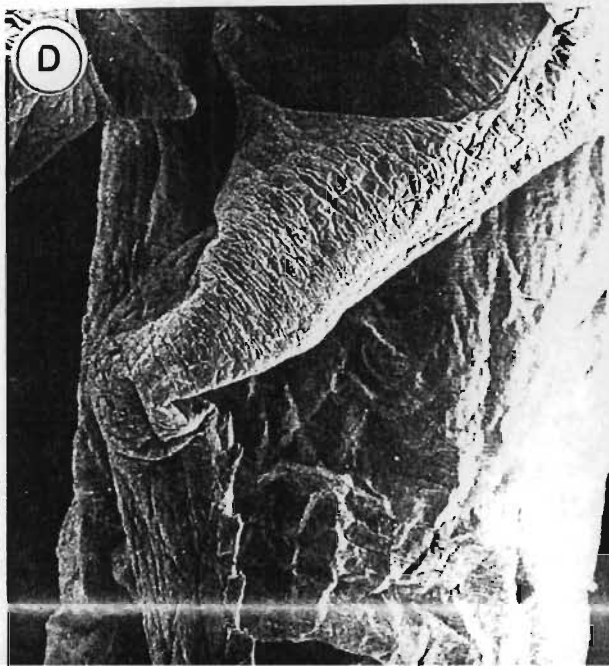
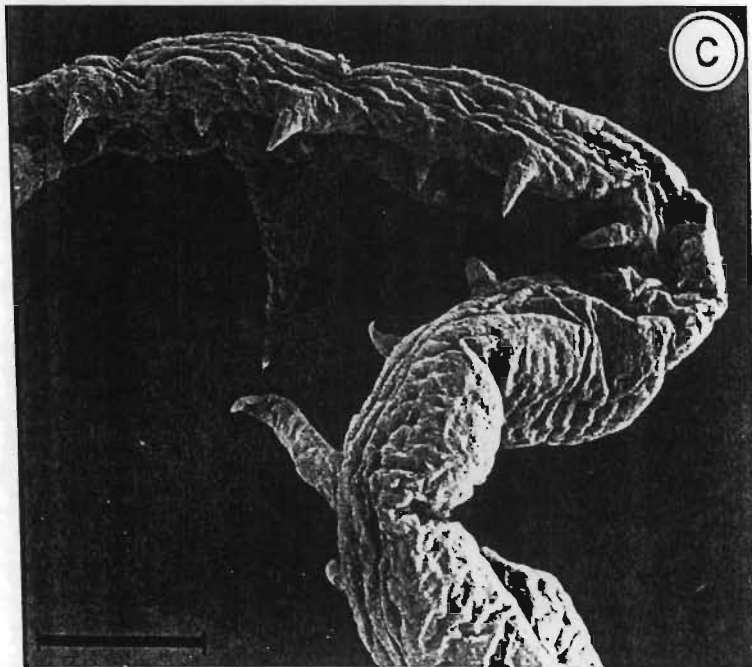
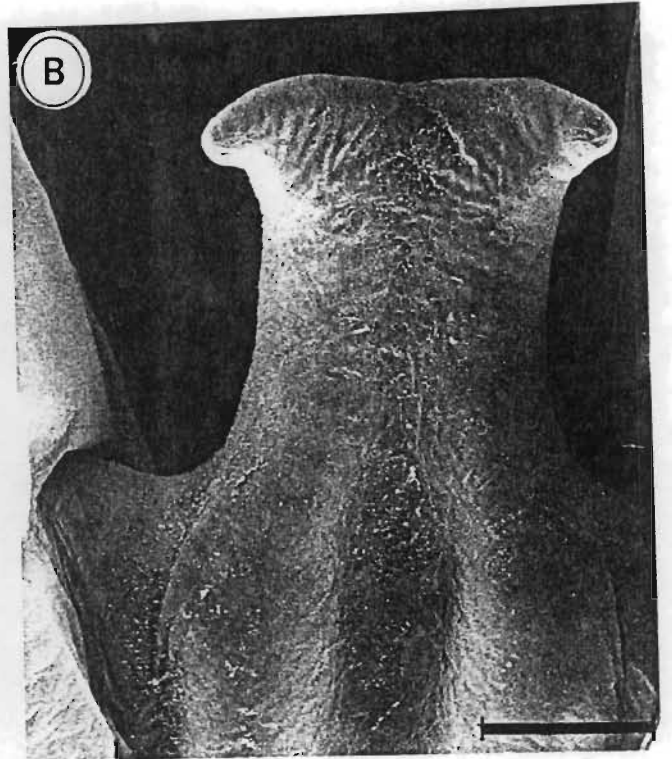
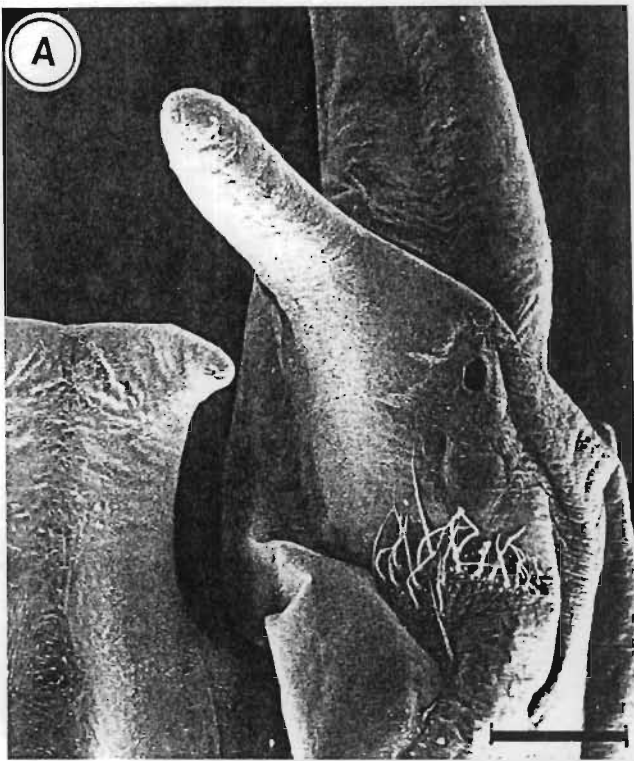


Figure 7. Genus C.

A = dorsal view of clypeus and frontal appendage. B = ventral view of penes. C = lateral view of genital segments and penes. D = male cercopods. E = lateral view of brood pouch of female.

Scale = 1,0 mm.



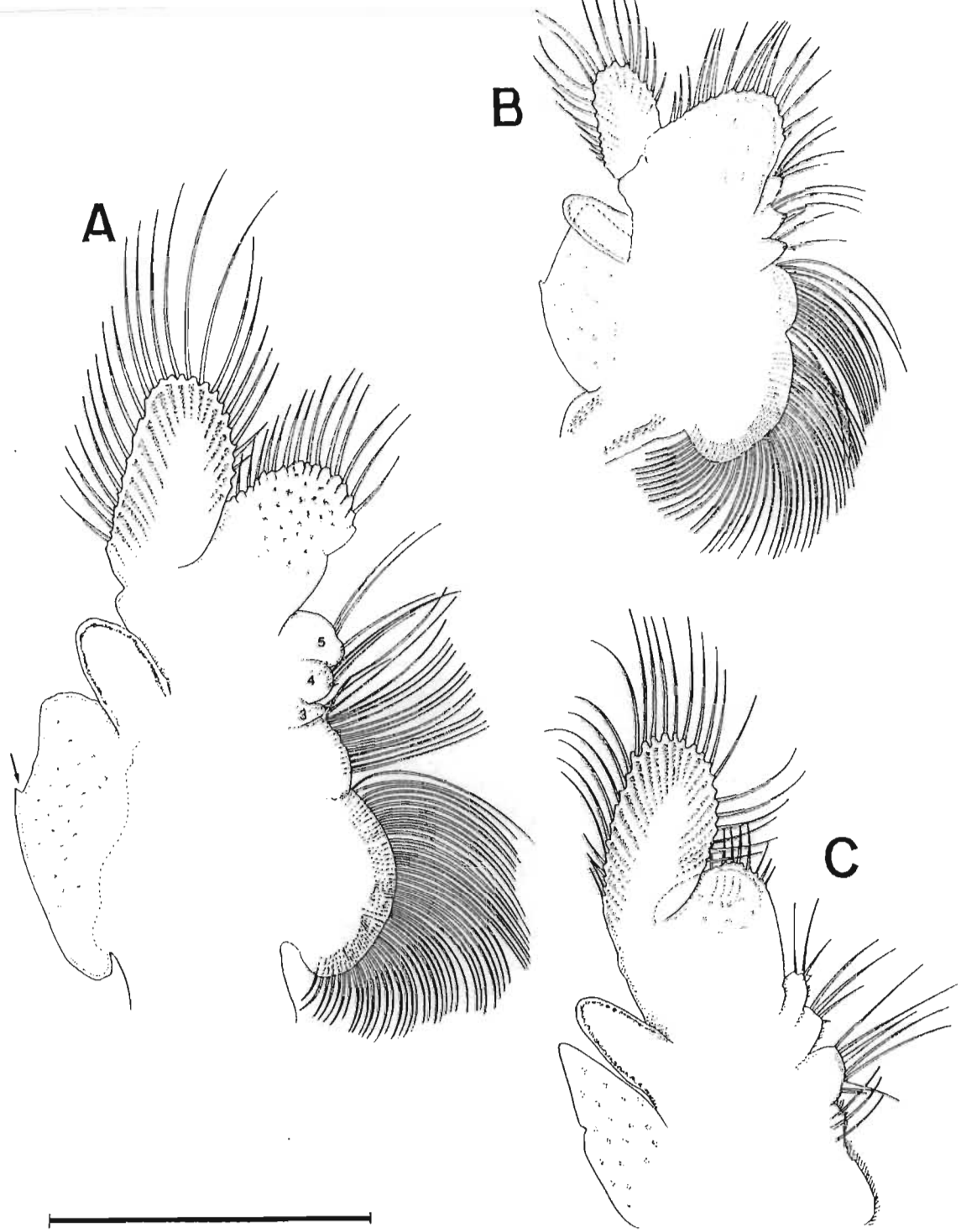


Figure 9. Genus C.

A = thoracopod 5, arrow indicates notch in pre-epipodite. B = thoracopod 1. C = thoracopod 11. Scale = 0,5 mm.

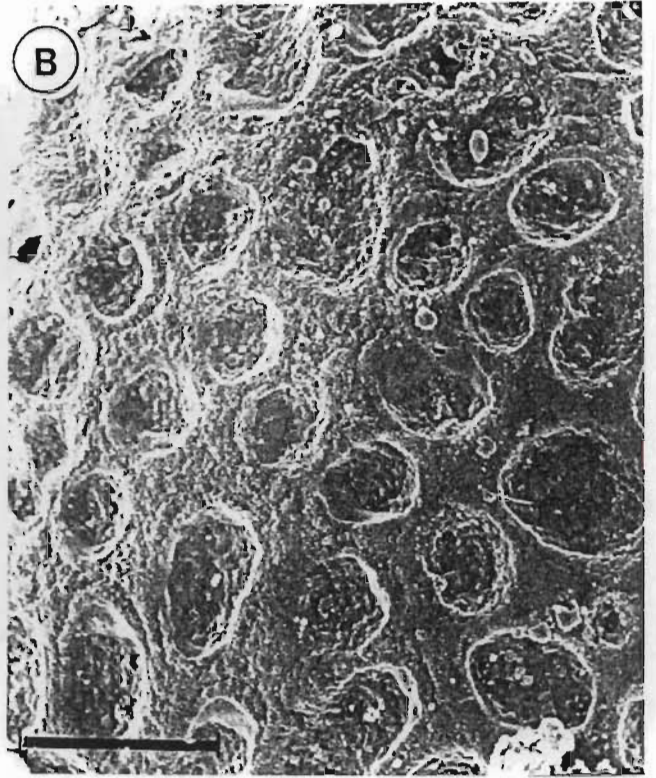
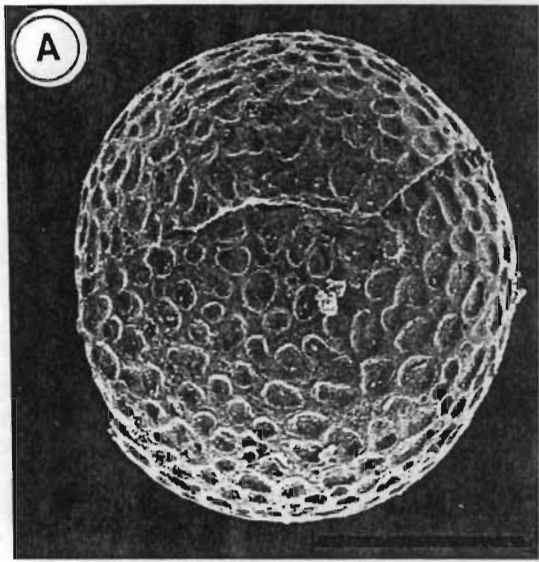


Figure 10. Genus C.

A = egg, scale = 100 μm . B = detail of egg shell, scale = 25 μm .

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CHAPTER 6

THE *Branchinella* (ANOSTRACA: THAMNOCEPHALIDAE) OF SOUTHERN AFRICA

ABSTRACT

The family Thamnocephalidae is represented in southern Africa by three species of the genus *Branchinella*, namely *B. spinosa*, *B. ornata* and *B. ondonguae*. Both the family and the genus are characterised mainly by the fused basal joints of the second antennae, which are no more sclerotised than the remainder of the body, the simple, curved terminal joints and, in most cases, a well developed, bifurcate frontal appendage. The frontal appendage is the most useful character in species identification and its elaborate structure is most likely related to its function in mate selection by females. The southern African *Branchinella* are not well represented in museum collections and appear to occur in low numbers in their natural habitats. In addition, all three species have been collected from only a few, isolated localities. This could be a result of a lack of collecting in large areas of southern Africa or because *Branchinella* eggs hatch infrequently.

INTRODUCTION

The family Thamnocephalidae is characterised by a two-jointed male antenna, which has the basal joints more-or-less fused proximally, no more sclerotised than the rest of the body, and a relatively simple terminal joint. In most species a frontal appendage, which ranges in size from very small to long and elaborate, is present on the antero-median surface of the basal joint. The frontal appendage is always bifurcate distally and is usually covered by small spines. The thoracopods have a single pre-epipodite and the endopodites of the first legs of the male differ considerably from those of the other legs. According to Linder (1941), the most important characters of the family are the vas deferens which makes a loop upwards in the first genital segment and the relatively soft, retractible basal parts of the penes. The male genital segments are only slightly swollen, without sharply defined seminal vesicles.

Initially, the three genera currently included in the family Thamnocephalidae, *Thamnocephalus*, *Dendrocephalus* and *Branchinella*, as well as the genus *Eubranchinella*, were included in the subfamily Branchinellinae belonging to the family Chirocephalidae (Daday 1910a). Linder (1941) however, found that the species for which *Eubranchinella* was described, belonged to *Branchipodopsis*. He decided that after the elimination of this genus the other three forms constituted a natural group which he presented as the family Thamnocephalidae. This family is quite distinct from the Chirocephalidae in the form of the male genital organs, the female ovisac, the unfused basal joints of the antennae of the male in the chirocephalids and the absence of a frontal appendage in this family. In addition, the thoracopods of the Chirocephalidae have either two distinct pre-epipodites, or a distinct notch if only one is present.

Within the Thamnocephalidae the three genera are distinguished by the presence of outgrowths or spines or a combination of these two on the lateral margin of the endopodite of the first male thoracopods in *Dendrocephalus* (Pereira & Belk 1987) and the modified, fin-like cercopods of *Thamnocephalus*. The presence of the family characters but the absence of the features of the other two genera distinguishes *Branchinella* (Linder 1941). The first two species are restricted to the Americas and only *Branchinella* occurs in Africa.

The genus *Branchinella* was first established to include two Australian species. In his

second publication in 1910 (1910b), Daday described the genus *Branchinellites* to include two species which were separated from *Branchinella* on the basis of distal outgrowths from the basal joints of the male second antennae. Barnard (1924) assigned the southern African species *B. ondonguae*, which he described, to this genus. However, subsequent to Daday's (1910b) work, a number of species with a range of outgrowths, from small to large, were described. Linder (1941) noted these intermediate forms and since this was the only character on which Daday (1910b) had based the establishment of his new genus, Linder (1941) considered *Branchinellites* as part of *Branchinella*. This synonymy is further supported by the form of the frontal appendage, the thoracopods, penes and the cercopods.

The genus *Branchinella* currently includes approximately 32 species, 18 of which are endemic to Australia (Geddes 1981), four occur in the United States (Belk & Sissom 1992), six in Asia and one species, *B. spinosa*, is found in the Palaearctic steppes, from the Aralo-Caspian area to eastern Europe, Spain and North Africa (Bănărescu 1990). *Branchinella chudeaui* (Daday) has been recorded from West Africa (Linder 1941) and two more species have been described from southern Africa. These two species, as well as *B. spinosa* (*Milne-Edwards*), which has been identified from Botswana during the course of this study, are reviewed in this text.

The three species of *Branchinella* which occur in southern Africa are relatively well known. Apart from the type descriptions, Linder (1941) discussed certain features of them in some detail. However, not all important morphological characters have been illustrated or described. Therefore, in this review, the male antennae, frontal appendages, relevant aspects of the thoracopods, penes and the female antennae are redescribed and illustrated where necessary and possible. Unfortunately, a paucity of material has not allowed electron microscopic investigation of the southern African species. The mouthparts, cercopod shape and setation and vas deferens are relatively consistent throughout the genus (Linder 1941) and these are therefore not illustrated for all species. A key, based on male antennae and frontal appendages, is provided for the three *Branchinella* species found in southern Africa. The southern African species are compared with species from other regions and with the three species groups erected by Geddes (1981) for the Australian *Branchinella*. Aspects of sexual selection, the significance of the frontal appendage and distribution and dispersal are discussed.

MATERIALS AND METHODS

Specimens of the *Branchinella* species from southern Africa were obtained on loan from the following institutions:

British Museum of Natural History (BMNH), London, England; Museum of Natural History of the Smithsonian Institution (MNHSI), Washington, U.S.A.; South African Museum (SAM), Cape Town, South Africa; State Museum of Namibia (SMN), Windhoek, Namibia.

No live material of the genus was collected during this study. A single male specimen was hatched from sediment collected from a dry pan in the Kruger National Park. Deionised water was used to hydrate the sediment and a bench lamp was used to provide additional light and heat to the water. The specimen was allowed to reach maturity and was collected after it died, when two weeks old. The specimen was preserved in 70% ethanol and has been catalogued into the National Freshwater Invertebrate Collection in the Albany Museum (AM), Grahamstown, South Africa where it will be deposited at the end of the study.

Drawings were made using either a Wild M-5 dissecting microscope or a Leitz Labor Lux 12 compound microscope and the appropriate drawing tube. Thoracopods which were dissected from specimens were permanently mounted in glycerine jelly on slides.

Specimens of suitable quality were measured under the dissecting microscope with a graticule at X6 magnification. Body length measurements were taken from the front of the head (excluding the antennae) to the tip of the cercopods, excluding the setae and these are presented as a range where there were more than three specimens. The second antennae of the male were measured from the proximal edge of the basal joints to the furthest point on the anterior margin of the terminal joints with these structures lying in front of the head but in their naturally-curved position. The frontal appendage was measured from its origin at the basal joints of the antennae, to the apex with this lying stretched out anteriorly.

RESULTS

Terminology

The male antenna consists of a broad basal joint which may have outgrowths of varying shape and size, referred to as antennal appendages, and a more slender, curved terminal joint. The terminology used to describe the frontal appendage, a structure which is present on the antero-median surface of the fused basal joints of the antennae, is from Belk & Pereira (1982). The proximal, fused region, or trunk has two arms branching off it and outgrowths or branches from the arms are given consecutive numbers, starting with the one most proximal to the trunk and proceeding distally. A letter (M = median, L = lateral, D = dorsal, V = ventral) is used in conjunction with the number to describe the position of the outgrowths on the arm. The letter A is used for anterior if the insertion is on the tip of the arm. The letters MD, DL and so on are used to describe outgrowths in a medio-dorsal or dorso-lateral position respectively. Pair or multiple outgrowths at the same point are listed, using the number only once, but listing the positions separated by a "/" to indicate "and".

Geddes (1981) suggested using the terms distal (or sixth) endite and exite for the portions of the thoracopods referred to as the endopodite and exopodite by Linder (1941) and most other anostracan workers. He suggested that the latter terms be restricted to crustaceans with truly biramous appendages. However, for the sake of uniformity and clarity throughout this anostracan review, the more established terms are used to describe the distal regions of the legs. Terminology used to describe remaining morphology is the same as that used for the streptocephalids and branchiopodids and is largely after Barnard (1929) and Linder (1941).

Taxonomic review

Family Thamnocephalidae Linder, 1941

Genus *Branchinella* Sayce, 1903

The following diagnosis is largely after Linder (1941) and Geddes (1981).

Basal joints of antennae fused to varying degrees in the male, but this area no more sclerotised than the rest of the body. Outgrowth from distal end of basal joint may be present,

often with ornamentation of spines, hairs or pads on basal joint. Terminal joint simple, curved and generally heavily sclerotised. Usually with frontal appendage which is bifurcated and often covered with spines or projections. Cercopods of both sexes similar, placed obliquely on telson and evenly setulose. Thoracopods with single pre-epipodite. Genital segments of male negligibly swollen and without distinct seminal vesicles. Vas deferens making a loop upwards in first genital segment. Penes proceed ventromedially, basal parts not rigid and generally with small median spine. Apical parts with spines, usually with some of these arranged in a longitudinal row and others scattered over the surface. Female brood pouch usually flask-shaped or oval. Antennae of females often fused basally.

Branchinella spinosa (Milne-Edwards)

Fig. 1

Branchipus spinosus Milne-Edwards, 1840: 367, figs 9-15. Baird, 1852: 20.
Branchinella spinosa Daday, 1910a: 261, fig. 37. *Branchinella media* Pesta, 1921: 90.
Branchinella spinosa Linder, 1941: 255. Cottarelli & Mura, 1983: 17, fig. 4. Thiéry, 1987: 154, fig. 92.

Material

Type material. Type locality is given as a saline lake in Odessa by Daday (1910a). Date of collection, collector and museum are unknown.

Material examined. BMNH 1958.10.2.4, 1 male (16,7 mm), 1 female (13,8 mm); collected from Botswana, Makgadikgadi salt pan by Rhodesian Schools Exploration Society's Makgadikgadi Expedition (RSESME), 4 May 1957, donated by D.H. Eccles. BMNH 1979.276-276, 2 males, 2 females (no measurements), collected from Libya, Zuara by C. Woods, 1979. BMNH 1985.283-286, 2 males (12,7; 13,7 mm), 2 females (12,0; 12,2 mm); collected from Botswana, Sua pan, 11km E of Nata by R. Hartland-Rowe, 4 May 1985. MNHSI 102321, 5 males (8,3 - 10,8 mm), 3 females (9,8; 10,6; 10,8 mm) all in poor condition; collected from Botswana, Makgadikgadi salt pan, in bed of Nata River by RSESME, 1 May 1957, donated by R.H. Eccles.

Redescription of adult male

Antennae. Basal joints of antennae fused for about half length, broad and without any processes or hairs but with distinct stippling on median surface lateral to frontal appendage.

Terminal joint tapered, smooth and curved inwards, apically subacute (Fig. 1A).

Frontal appendage. Short (\pm 16% antennal length), broad and often carried in a rolled up position. Bifurcate along most of length, with each arm tapering to a subacute apex (Fig. 1A).

Penes. Basal parts fully retractible, short and broad without median spine (Fig. 1B).

Abdomen. Ventral surface of abdomen with prominent, paired spines on each segment, these decreasing in size and progressively more medianly-positioned towards telson. Third abdominal segment with small, bifurcate spine in ventro-median position (Fig. 1B).

Thoracopods. All legs with 2:2:1 anterior setae on endites 3-5.

Redescription of adult female

Brood pouch. Short (ratio to body length 0,2:1) and oval shaped (Fig. 1C).

Antennae. Slender, oval with acute projection at apex. Proximally fused by narrow band (Fig. 1D).

Remarks

There is some variation in the length of the frontal appendage. Such variation appears to be common in the genus and Geddes (1981) stated that a reasonable amount of variation must be allowed for within species even amongst adult individuals.

Branchinella spinosa is quite distinct from the other members of the genus. Spines on the ventral surface of the abdomen are only found in this species and the North American *B. acacioidea* Belk & Sissom. The spines in the latter species are, however, restricted to the third and fourth abdominal segments. There is a similarity between the frontal appendages of *B. spinosa* and the Australian species *B. lyifera* Linder which also has a short, bifid frontal appendage but this is the only similarity between the two species. *Branchinella spinosa* cannot be assigned to any of Geddes' (1981) species groups.

Distribution

Branchinella spinosa has the most northerly distribution in the genus and has been collected in Europe (Spain, Italy) as well as Siberia, Rumania and Afghanistan. This species also occurs in North Africa (Algeria, Tunisia and Libya) (Thiéry 1987) and has been recorded from Makgadikgadi Pan and its surrounds in northern Botswana, southern Africa (Fig. 2).

Branchinella spinosa favours saline habitats and is frequently collected with the brine shrimp, *Artemia salina* (Mura & Hadjistephanou 1987; Thiéry 1987).

Branchinella ornata Daday, 1910

Figs 3-4

Daday, 1910a: 266, fig. 40. Barnard, 1929: 201, fig 6. Linder, 1941: 266, fig. 40.

Material

Type material. Housed in the Zoologisches Museum, Berlin (12571, 12572); collected in the Kalahari, "Pfanne van Kang", by D. Schultz, 1904 (Daday 1910a; Forró & Brtek 1984).

Material examined. BMNH 1957.6.12.1. 1 male (19,3 mm), 1 female (18,8 mm); collected from Botswana, Makgadikgadi salt pan by RSESME, 3 May 1957, donated by D.H. Eccles. MNSHI 102319, 7 males (14,4 - 18,8 mm), 4 females (14,4 - 15,6 mm); collected from Botswana, Makgadikgadi salt pan, by RSESME, donated by D.H. Eccles, 1955. SAM-A7297, 1 male, 1 female (pleisiotypes), specimens completely dehydrated; collected from Potchefstroom by G. Hutchinson, 1928. SMN 51237, 1 male (10,8 mm); collected from Namibia, Bushmanland, Gautscha Pan by B.A. Curtis, 17 March, 1988.

Redescription of adult male

Antennae. Basal joints joined proximally by frontal appendage and with large, leaf-shaped extension of distal, median surface (Figs 3A-B). Ventro-median surface with acute, triangular projection (Fig. 3C). Terminal joints slender and gently curved inwards (Fig. 3A) with fine, median striations.

Frontal appendage. Long (136% antennal length), unarmed trunk dividing into two arms about one to two thirds along frontal appendage length. Each arm with the following outgrowths: 1L; 2L/M; 3L/M; 4DM and 5AM/AL. Median branches with irregularly arranged, scattered and small papillae (Figs 3A-B). Apices of branches may have small spines (Fig. 3A).

Penes. A prominent, triangular process present ventrally, just proximal to the basal region of each penis (Fig. 3D). Basal region short and stout, with distinct, median, narrow process with many small spines (Fig. 3E).

Thoracopods. Exopodite and endopodite both broad (Figs 4A-B). Setae on endites 3-5 on first legs number 4:5:4 (Fig. 4A) but on all others 2:2:1 (Fig. 4B). Pre-epipodite with small notch on lateral margin (Figs 4A-B).

Redescription of adult female

Brood pouch. Flask-shaped, with narrow apex, which reaches the third abdominal segment (Fig. 4D).

Antennae. Broad, almost rectangular, with acute projection on anterior corner. Basally, two antennae joined by narrow band (Fig. 3F).

Remarks

Daday (1910a) attributed *Branchinella ornata* to Wolf who sent him the type specimens which he had described and named as *Branchinema ornata*. Wolf's description, however, was never published (Forró & Brtek 1984) and thus both Barnard (1929) and Linder (1941) credited Daday with this species.

In Daday's (1910a) description of this species, he suggested that the material examined by him was not fully developed and both Barnard (1929) and Linder (1941) agreed with this. The Makgadikgadi pan specimens have a frontal appendage arrangement similar to that illustrated in the type description. The arms of these specimens are not as long as those of the Namibian specimen (SMN 51237) and the branches of the arms in the Makgadikgadi specimens are also closer together. The Makgadikgadi female specimens have fully mature brood pouches containing eggs and specimens of both sexes are considerably larger than the Namibian specimen. The variation observed in these specimens and by Barnard (1929) and Linder (1941) may, therefore, not be maturity-related but rather an indication of genetic variation between populations. In terms of all other distinguishing characters of the species, the two sets of specimens are identical.

Branchinella ornata has a number of characters which are unique within the genus. For example, the triangular processes on the ventral surface proximal to the basal part of the penes and the leaf-like extensions of the basal joints of the antennae are not found in any other *Branchinella* species.

The single male Gautscha Pan specimen (SMN 51237) was identified from a large sample of *Streptocephalus proboscideus* Frauenfeld. No females, which could have been distinguished from the streptocephalids by the shape of the brood pouch, were present in the sample.

Distribution

Linder (1941) quoted the type locality as "Pfanne van Kang, South West Africa" but Daday (1910) had given the locality as the Kalahari. Since Kang is located in the Kalahari, Botswana this is accepted as the type locality and is indicated in figure 2.

Branchinella ornata has been collected from four disjointed localities; with one each in northern Namibia, northern Botswana, central Botswana and the western Transvaal, South Africa (Fig. 2). In addition, there are specimens in the BMNH (BMNH 1957.10.9.2) from Manyanya in Uganda, East Africa which are labelled as *B. ornata*. However, these specimens are immature since the female brood pouches are not developed and the single male specimen is only 7,2 mm in body length. The frontal appendage of this specimen is similar to that of the southern African *B. ornata* specimens but since it is not fully developed, its identification and thus the locality, cannot be verified.

Branchinella ondonguae Barnard 1924

Fig. 5

Branchinellites ondonguae Barnard, 1924: 216, pl 26 (1). Masi, 1925: 97. Barnard, 1929: 203, fig 7. *Branchinella ondonguae* Linder, 1941: 271.

Material

Type material. SAM-A6002, 8 males (specimens brittle, estimates of length: 17,5 - 22,5 mm), 8 females (specimens brittle, slightly smaller than males); collected from Namibia, Ovamboland, Ondongua by K.H. Barnard, 1921.

Other material examined. AM LEN 187A, 1 male (17,5 mm), hatched from dry sediment (February 1991) collected from a clay pan, Kruger National Park, south of Pafuri, Nyandu Flats by M. Hamer, 2 November 1990. BMNH 1932.2.25.49-53 (ex SAM, presumably from type material), 1 male (17,2 mm), 1 female (16,8 mm), collected from Namibia, Ovamboland, Ondongua by K.H. Barnard, 1921. SAM-A6003, 7 males, all in brittle, poor condition; collected from Namibia, Ovamboland, Ongka by K.H. Barnard, 1923. SAM-A6745, 1 male, 1 female, both in brittle, poor condition; collected from Somalia by Sav. Ptrizi, October 1923.

Redescription of adult male

Antennae. Basal joint broad, with four long, slender digitiform processes on median margin (Fig. 5A). Antennal appendage/ outgrowth on dorso-median surface of basal joint as long as terminal joint but carried in a rolled up position and with digitiform processes of varying length along margins (Fig. 5A). Lateral corner of basal joint produced to form a short, apically blunt projection (Fig. 5A). Terminal joint slender, with numerous fine ridges on median margin, apically slightly inflated and blunt (Fig. 5A).

Frontal appendage. Very long (about half length of body). Trunk with long, slender projections from ventro-lateral surfaces, these of unequal size and distribution. A prominent fold on dorsal surface about halfway along trunk. Trunk branches into two arms, each with latero-ventral projections on distal half and with two subequal length anterior branches (1A/A). These with numerous irregular projections, and tapered to a narrow apex (Fig. 5B).

Penes. Basal region with leaf-shaped, lateral extension of the genital segment and with proximal small, triangular projection medianly (Fig. 5C).

Thoracopods. First pair of thoracopods with anterior setae of endites 3-5 numbering 4:4:3 (Fig. 5F). Exopodite of first leg similar height to endopodite, but much longer and more slender in remainder of legs (Fig. 5E).

Redescription of adult female

Brood pouch. Flask-shaped, broad proximally with narrow apical region and reaching abdominal segment 7 or 8 in type specimens.

Antennules. Twice as long as antennae and slender.

Antennae. Oval, slender and with long, acute apical process.

Remarks

Branchinella ondonguae, has, according to Linder (1941), the longest frontal appendage in the Anostraca. The frontal appendage of the specimen measured (AM LEN 187A) was not as long as described by Barnard (1924) who stated that it was as long as the entire head and body in the type specimens. This could suggest some degree of intraspecific variation in *B. ondonguae* but unfortunately the type and other specimens in the SAM collection are not in a condition which allows them to be measured.

Branchinella ondonguae resembles the West African species, *B. chudeaui* which also

has an antennal outgrowth from the basal joint, a long frontal appendage with a deep dorsal fold along the trunk and two arms with irregular projections. However, the apical region of each arm has a large median outgrowth (1M) as well as the two anterior branches (2A/A) which are smaller than in *B. ondonguae*. In addition, the digitiform processes on the median margin of the basal joint in *B. ondonguae* are absent in *B. chudeaui* and the processes on the antennal outgrowth are of a more regular nature in the former species.

Other species which share the antennal outgrowths and long, elaborate frontal appendage with *B. ondonguae* are the Australian species *B. nicholli* Linder and *B. denticulata* Linder but these species have no other characters in terms of the thoracopods and penes in common with the southern African species or, for that matter, with each other and were assigned to different species groups by Geddes (1981). The Asian species *B. kugenumaensis* (Ishikawa) also has antennal outgrowths and an frontal appendage similar to that of *B. ondonguae* and was initially also included in Daday's (1910b) genus *Branchinellites*, along with the latter species and *B. chudeaui*.

Distribution

Branchinella ondonguae has been collected from two localities in northern Namibia (Ovamboland) and a single pool in the north-eastern region of the Kruger National Park (Fig. 2). The specimens in the SAM from Somalia are in very poor condition and their identity cannot be verified with any degree of confidence but considering the disjointed nature of the distribution of this, and the other *Branchinella* species found in southern Africa, it is possible that this locality is valid.

KEY TO THE SOUTHERN AFRICAN *Branchinella*

The following key is to adult male specimens only, and is based on the frontal appendage and antennal morphology.

- 1 a. Frontal appendage longer than total antennal length, with arms having apical or lateral branches 2
 - b. Frontal appendage shorter than total antennal length, without lateral branches but bifurcate for approximately half its length *Branchinella spinosa* (Fig. 2)

- 2 a. Basal joint of antenna with dorso-median leaf-like extensions, each arm of frontal appendage with 6 lateral/ median and 2 apical branches *Branchinella ornata* (Fig. 3)
 - b. Basal joint of antenna with slender outgrowth with numerous projections, each arm of frontal appendage without lateral branches and apical *Branchinella ondonguae* (Fig. 5)

DISCUSSION

The three *Branchinella* species found in southern Africa represent a small proportion of the anostracan fauna of the region and of the genus, which includes approximately 35 species. In addition, the southern African representatives have very restricted distributions, and populations appear to be small in contrast to other anostracans found here. However, in terms of dispersal and distribution, abundance, and in certain features of morphology, the southern African *Branchinella* illustrate some significant aspects of the Anostraca.

Bănărescu (1990), based on present distribution, suggested that the ancestral forms of the Thamnocephalidae occurred in Gondwanaland and that *Branchinella* extended its range from South and East Asia to North America, as well as to Siberia, west Asia and Europe. Those species endemic to Africa could, therefore, represent relict populations and species from pre-drift Gondwanaland since they do not show any strong affinities to the species from other regions.

Branchinella spinosa has the widest distribution of any anostracan species recorded from southern Africa. It is likely that this species has been introduced to the Makgadikgadi Pan area by migratory waders, some of which migrate from Siberia and parts of Europe to areas which include northern Botswana (Maclean 1984). There is evidence that branchiopods are eaten by waterfowl (Siegfried 1965) and that the eggs of anostracans are able to survive the passage through the digestive system of various birds (Horne 1966). The possibility of dispersal by birds for *B. spinosa*, is therefore, great but the chances of eggs, introduced from areas with vastly different climates, hatching, is less likely. This could either indicate that the southern African population originated in north Africa or the warmer parts of Europe, or that the eggs and larvae have a very wide temperature tolerance. Unfortunately, no studies on this aspect of *B. spinosa* have been undertaken. The reason for the restricted nature of the distribution of this species in southern Africa could be that this is a relatively recent introduction, or could be a result of a lack of collecting in the region.

The two other species of *Branchinella* in southern Africa also have restricted distributions, with neither species having been collected from more than four localities. However, the nature of their distribution, with records from widely separated points, could indicate that this is simply a result of a lack of sampling in the intervening areas. Most of Botswana and much of Zimbabwe have not been sampled. In addition, from the paucity of material in collections, it would appear that the southern African members of *Branchinella* do not occur in large numbers and it is also possible that they have very specific hatching requirements and do not hatch each time the waterbody is inundated. These factors could result in members of the genus being overlooked even in areas which have been sampled. The fact that only one specimen, in spite of repeated hydrations using large quantities of sediment, hatched from the Kruger National Park sediment, supports this idea. Geddes (1981) described a similar situation with the Australian *Branchinella*. Of the 19 species recorded, 13 were known only from the type locality, three were known from two localities and another two from three localities. Only one species had been collected frequently. In nine species three or fewer male specimens were available. Geddes (1981) attributed this lack of material largely to many areas of Australia not being sampled. He did, however, discuss the possibility of egg hatching requirements influencing the distribution of some species since Belk (1977) and Horne (1967) had both found this to be an important aspect of anostracan distribution. Obviously, at this stage it is impossible to draw any conclusions but a similar phenomenon

regarding the distribution and abundance of *Branchinella* appears to be operating in the southern African species and many of those found in Australia.

The taxonomic significance of the antennae of the males in the Anostraca is well documented. Within the Thamnocephalidae, the structure of the frontal appendage is probably of greater value in species identification. However, Geddes (1981) cautioned that this structure is a secondary sexual feature and that it is only useful in fully mature specimens. In addition, the frontal appendage does not always reflect taxonomic relationships since it is well developed in species which share very few other characters. Geddes (1981) used the setation of the anterior thoracopods, the shape of the endites and endopodites, the presence of swellings lateral to the penes and body size, in addition to frontal appendage development to divide the Australian species into three groups. Two of the southern African species have well-developed, complex frontal appendages in common with some of the Australian species but cannot be allocated to any of the species groups. The frontal appendage thus appears to have evolved an intricate structure in separate groups not only within *Branchinella*, but also within the family Thamnocephalidae and in some other families. Some members of the southern African Streptocephalidae, for instance, have an elaborate frontal appendage.

Linder (1941) explained that the frontal appendage appears to originate from outgrowths from the basal joints of the male second antennae. These may vary in size but during larval development the outgrowths migrate from the antennae to the head where they coalesce and form a common stem. The fact that the frontal appendage is frequently biramous at its apex is a result of its origin from two structures. The elaboration of this structure has, undoubtedly been driven by sexual selection. Belk (1984) found that antennal appendages, and suggested that the same applies to frontal appendages, were not used in clasping the female during mating, but are, rather, important in providing tactile cues in mate selection by females (Belk 1991). This probably accounts for the extreme development of these structures in several groups of anostracans. The antennal outgrowths, seen in *B. ondonguae*, and various other *Branchinella* species, most likely serve the same function and are subject to the same selection pressures.

Linder (1941) suggested that the Streptocephalidae and the Thamnocephalidae are closely related. He based this suggestion on the presence of antennal outgrowths from the

basal joint of the antennae in both families. In the Thamnocephalidae, these outgrowths are not present in all species, and they exhibit a wide range of sizes and shapes. Within the streptocephalids, the antennal outgrowth is large, and forms the median or s-shaped antennal process, essentially pushing the terminal joint, or lateral process to the side. The presence of the frontal appendage in both families could provide further evidence for the relationship.

In conclusion, the three species of *Branchinella* which have been recorded from southern Africa are relatively well known in terms of morphology. There do, however, remain unanswered questions relating to their status, the regularity with which they hatch and their abundance as well as their distribution not only in the southern parts, but in the whole of Africa.

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GAZETEER OF LOCALITIES FOR THE SOUTHERN AFRICAN *Branchinella*

BOTSWANA

Kang	23°48'S/23°08'E
Makgadikgadi Salt Pan	20°S/25°E
Makgadikgadi Salt Pan, in bed of Nata River	20°S/26°E
Sua Pan, 11km E of Nata	20°21'S/26°04'E

NAMIBIA

Bushmanland, Gautscha Pan	19°00'S/20°00'E
Ovamboland, Ondongua	17°55'S/16°00'E
Ovamboland, Ongka	17°35'S/15°50'E

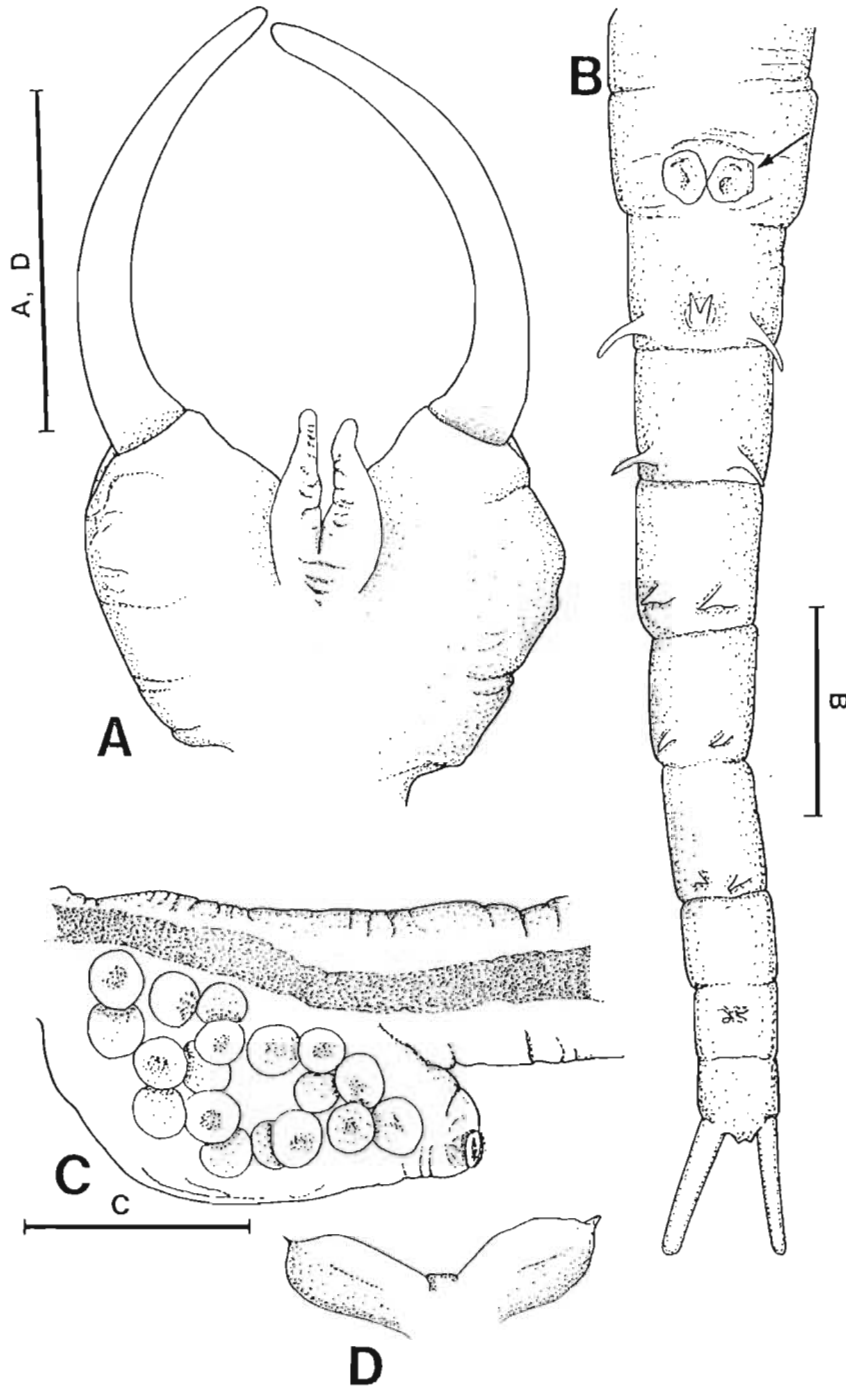


Figure 1. *Branchinella spinosa* (MNHSI 102321)

A=Dorsal view of antennae and frontal appendage. B=Ventral view of abdomen, arrow indicates retracted penes. C=Lateral view of brood pouch. D= Dorsal view of female antennae. Scale = 1,0 mm.

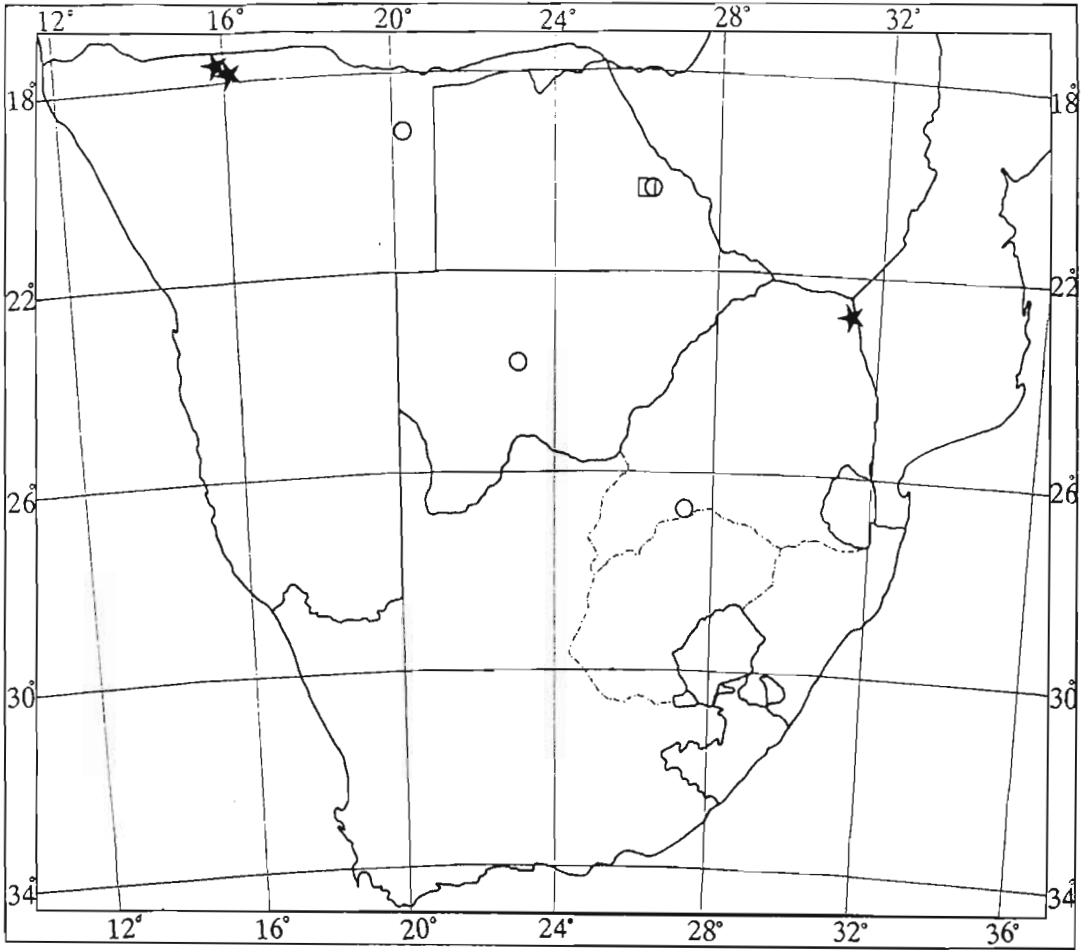


Figure 2. Map of Southern Africa showing the distribution of

□ *Branchinella spinosa*

○ *Branchinella ornata*, ★ *Branchinella ondonguae*

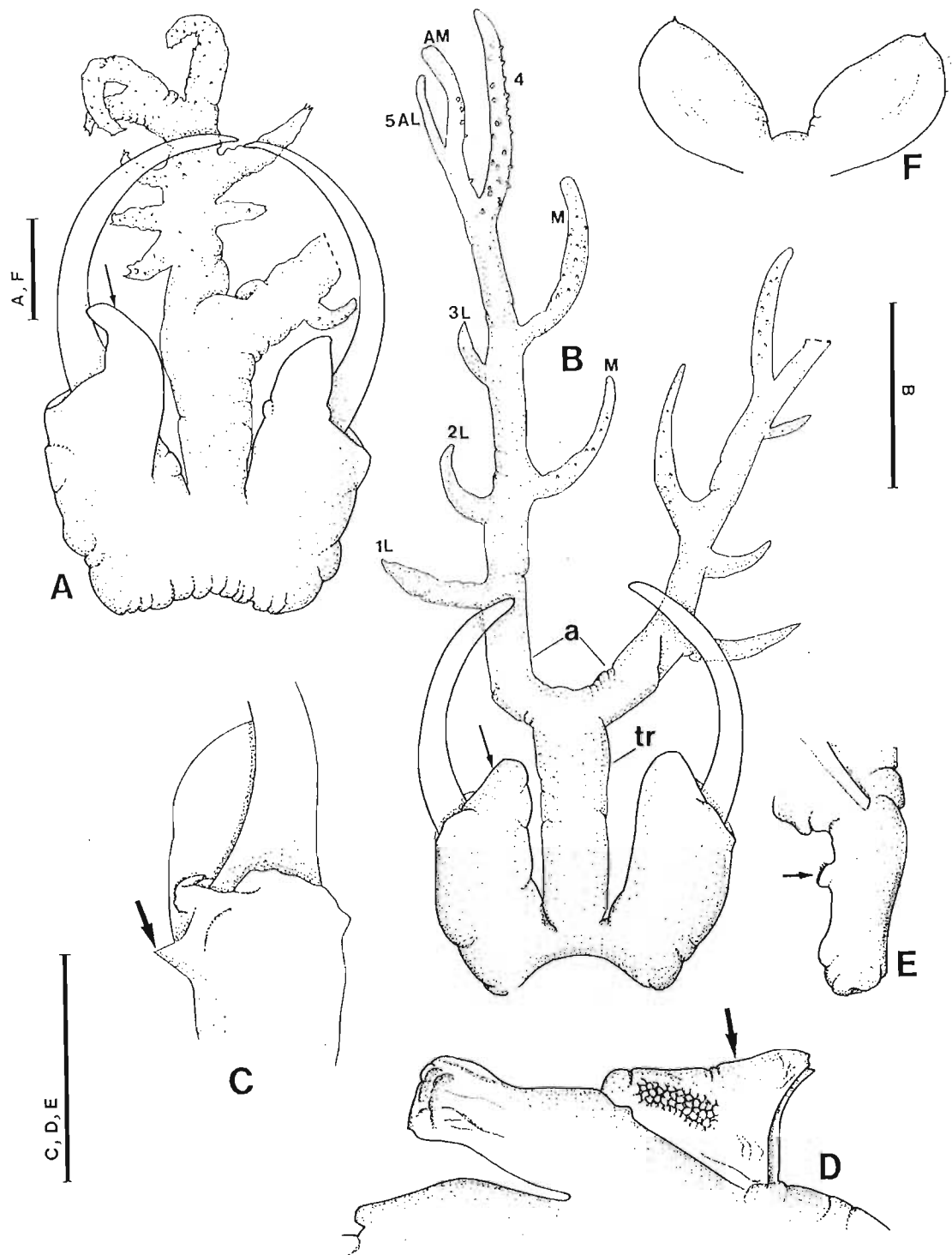


Figure 3. *Branchinella ornata*

A = MNSHI 102319. Dorsal view of male antennae and frontal appendage with right arm not shown. Arrow indicates leaf-like extension of basal joint. B = SMN 51237. Dorsal view of antennae and frontal appendage with apical region of right arm not shown, arrow indicates blunt, leaflike extension of basal joint. a = arms; tr = trunk. C = Ventral view of proximal region of basal joint showing triangular projection (indicated by arrow) (MNHSI 102319). D = Lateral view of penes showing large, triangular processes (indicated by arrow) (MNHSI 102319). E = Ventral view of penis, arrow indicates median projection (MNHSI 102319) F = Dorsal view of female antennae (MNHSI 102319). Scale = 1,0 mm.

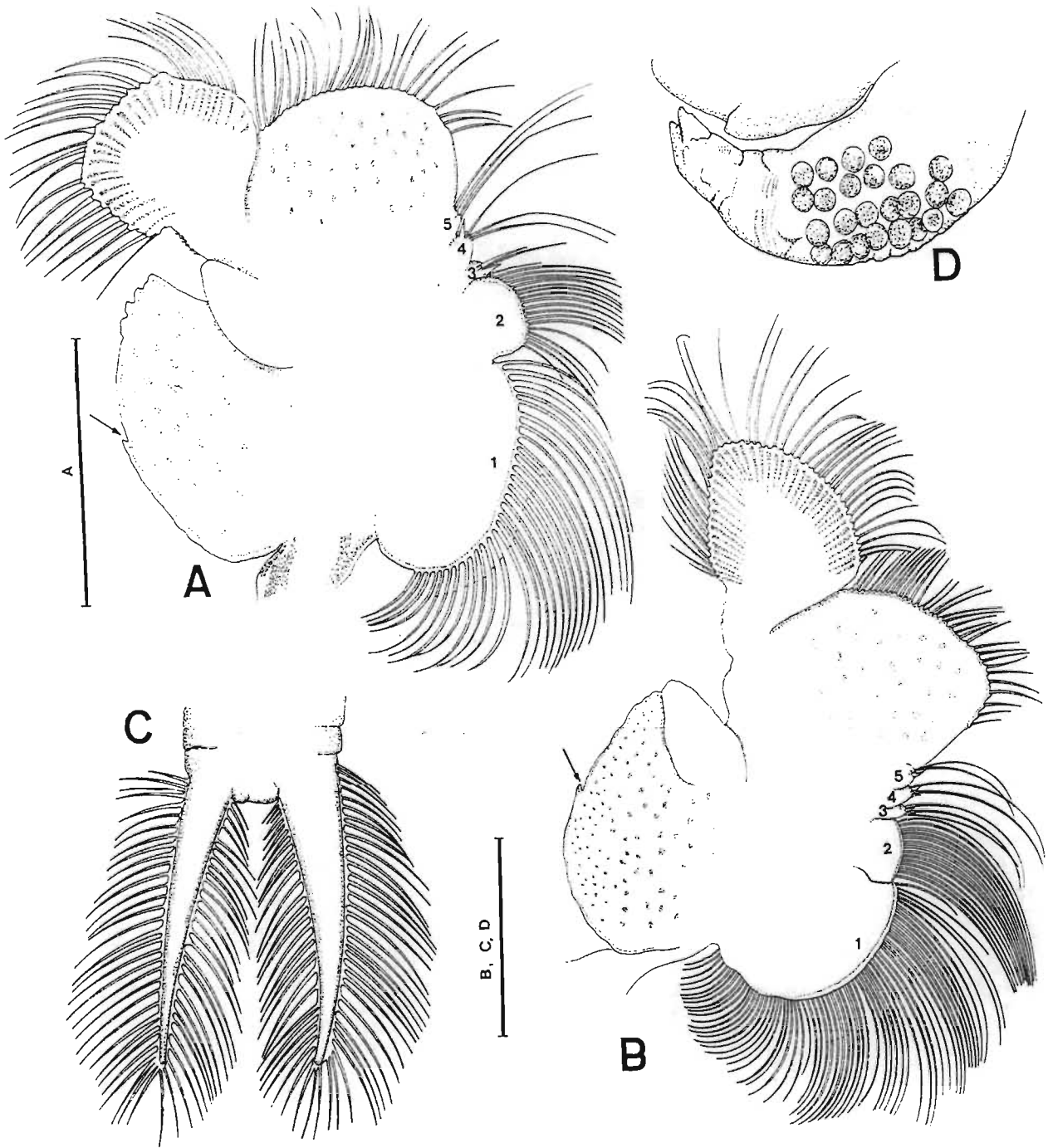


Figure 4. *Branchinella ornata* (MNSHI 102319)

A = Anterior surface of right thoracopod 1, arrow indicates notch in pre-epipodite. B = Anterior surface of right thoracopod 5, arrow indicates notch in pre-epipodite. C = Cercopods. D = Lateral view of brood pouch. Scale = 1,0 mm.

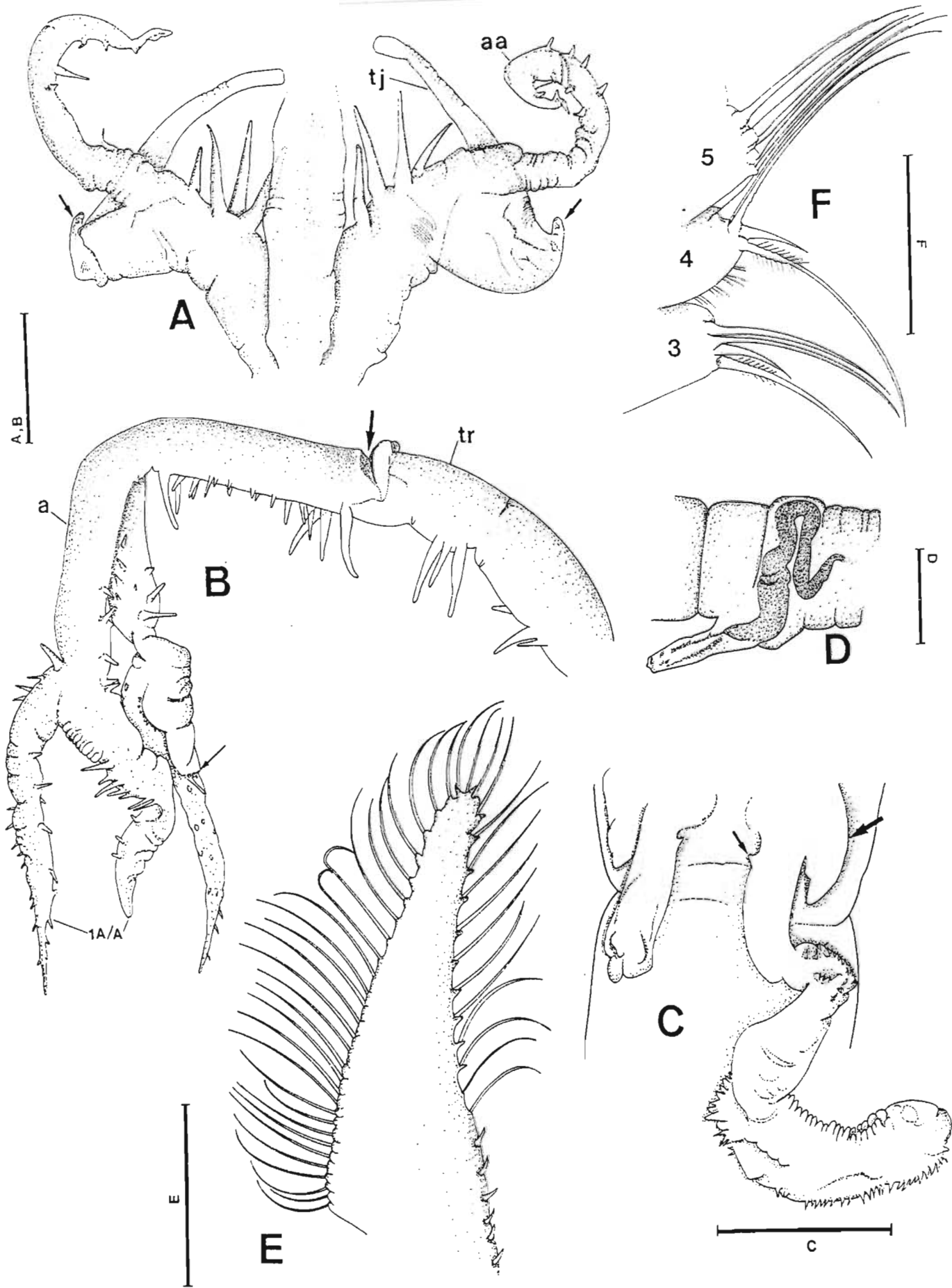


Figure 5. *Branchinella ondonguae* (AM LEN 187A)

A=Dorsal view of male antennae. aa=antennal appendage; tj=terminal joint, scale = 1,0 mm. B=Lateral view of frontal appendage with terminal branch of right arm damaged (shown by small arrow); a=arm; tr=trunk. Large arrow indicates deep dorsal fold, scale = 1,0 mm). C=Ventral view of penes, with left apical region everted. Large arrow indicates leaf-like extension of segment, small arrow indicates median projection, scale = 1,0 mm). D=Lateral view of genital segments of male showing vas deferens, scale = 1,0 mm. E=Exopodite of the second leg. F=Detail of a segmented appendage.

SOUTH AFRICA

Transvaal

Kruger National Park, SE of Pafuri, Nyandu Flats

22°30'S/31°25'E

Potchefstroom

26°42'S/27°06'E

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- * indicates publications not seen.

CHAPTER 7

ANOSTRACAN DIVERSITY, BIOGEOGRAPHY AND STATUS IN SOUTHERN AFRICA

ABSTRACT

Most of the southern African anostracan species have distinct distribution patterns which appear to be influenced by aspects of rainfall and temperature. Ten biogeographic categories were identified and these show certain broad similarities to those of other faunal groups. The most obvious difference between the anostracan distribution patterns and those of other aquatic animals, is however, the absence of anostracans from flowing waters and permanent impoundments. The Great Escarpment forms a distinct barrier between coastal margin and inland species which are, in some streptocephalids, closely related. In the case of the species occurring along the eastern part of southern Africa, dispersal and subsequent isolation from the original population rather than vicariance appears to have resulted in speciation. Life history characteristics also influence distribution and because of their relatively long life cycle, *Streptocephalus* species are excluded from shallow, highly ephemeral rockpools such as those in the Drakensberg which are inhabited by *Branchipodopsis*. Habitat type has an additional influence on anostracan distribution; those large pans which fill episodically are inhabited mainly by easily dispersed, widespread species, while pools which fill frequently are often occupied by endemic species. Forty-six species, distributed between four known and a possible three new genera, and four families are known from southern Africa. This high level of species richness probably results from the wide range of climatic regions present in the subregion. Other factors such as the lack of recent glaciations in southern Africa and the possible origin of two genera in Gondwanaland may also have contributed to the large number of species, 39 of which are endemic. The current status of the anostracan fauna, in terms of the number of specimens and localities from which a species has been collected, is presented in the form of a table. Many populations occur in protected game and nature reserves, but those outside such areas may be threatened mainly by reclamation of land for agriculture and urbanisation. However, the temporary pools of large parts of southern Africa have not been sampled, and a great deal more research is necessary before distribution, diversity and status of species can be assessed with complete confidence.

INTRODUCTION

Anostracans produce drought resistant cysts or eggs which are reported to be passively dispersed by wind, via the digestive system of birds, or by adhering to the body of birds or mammals (Procter, Malone & DeVlaming 1964; Thiéry 1987). As a result of such dispersal, and because temporary pools are not confined to specific regions or waterways, species of anostracans and other branchiopods could be expected to have wide distributions. This supposition has, however, been challenged by a number of authors (Belk & Cole 1975; Wiman 1979; Fryer 1988; Williams 1988), mainly on the basis of differentiation of populations, even within a relatively small area. Restricted gene flow between populations results in local adaptations and possible speciation. Branchiopod eggs, it is now believed, are adapted to resist, rather than promote dispersal to habitats which may be unsuitable for their survival.

Williams & Busby (1991) provided an alternative view on the biogeography of temporary pool inhabitants based on the distribution of the notostracan, *Triops australiensis* in Australia. They suggested that episodically-filled temporary pools would be inhabited only by easily-dispersed species, since the irregularity of filling would not allow the evolution of local adaptations and thus speciation.

Brendonck, Thiéry & Coomans (1990) investigated the branchiopod fauna of the Galapagos islands which exhibited definite affinities with South and North American species and thus indicated that dispersal had occurred. They suggested that the nature of the new habitat, in terms of its similarity to the original one and the biota of the habitat, particularly the presence of competitors and predators, plays a major role in determining the success of colonising branchiopods. Belk (1977) found that temperature determined the distribution of species in Arizona by controlling the hatching success of eggs and, to a lesser extent, by its effects on adult survival.

On a more global scale, Bănărescu (1990) described the distribution patterns of anostracan families and genera, and discussed these mainly in relation to their possible origin and continental drift. He did, however, emphasise temperature as an explanation for the presence or absence of taxa in certain areas.

Chemical heterogeneity of habitats, particularly in relation to salinity, and thermal variation resulting from pools filling during different seasons and from the distribution of pools along altitudinal and latitudinal gradients was found to be an important factor influencing anostracan diversity in Arizona (Belk 1977). Thirty-six species of Anostraca, distributed between four genera, each of which belongs to a separate family, have been described from the southern African subregion. Descriptions of an additional six species have not yet been published, three possible new genera have been identified, and *Artemia parthenogenetica* may be a valid record from Namibia. Therefore, the anostracan fauna could consist of a possible 46 species, which represents about a fifth of the total number of species described worldwide. This high species richness, and the factors influencing local species richness are addressed here.

Barnard (1929) mapped the distribution of certain anostracan species, but he believed that insufficient records were available to analyse distribution. Although large parts of southern Africa have still not been investigated, a significant increase in the number of localities from which anostracans have been collected will allow at least a tentative examination of patterns in distribution.

The significance of anostracans and temporary freshwater habitats has been overlooked in southern Africa and it is quite likely that both described and undiscovered species have become extinct through man's activities during the latter part of the last century. Recently, an awareness of the importance of biodiversity and invertebrate conservation has started to develop in South Africa and a number of projects on the distribution and status of certain invertebrate groups have been initiated. Temporary pools and their inhabitants are yet to receive the attention they deserve and as an initial step towards this aspect of the Anostraca of southern Africa, a list of species, a summary of their distribution, and a comment on their status in terms of the number of specimens and localities from which they have been collected has been compiled.

THE SOUTHERN AFRICAN SUBREGION

The northern limits of southern Africa have been differently defined, depending on the faunal group with which a particular study has dealt. The definition of the subregion as including those countries lying south of the Zambezi and Kunene rivers (Namibia, Botswana, Zimbabwe, southern Mozambique, South Africa and those independent countries within her borders, namely Swaziland and Lesotho) is one frequently used and which forms a major line of separation for some organisms. This definition was accepted for the present study largely because little or no material for the countries lying immediately to the north of this boundary (Angola, Zambia, Malawi and Tanzania) has been collected.

Africa is about 100 million years old and after the division of Pangea, about 180 million years ago, formed the central part of Gondwanaland. Tectonic plate movements resulted in the Australian and Antarctic, Indian and South American landmasses moving away from Africa at the beginning of the Cretaceous. Apart from a slight northwards movement, Africa remained almost in its original position. Subsequent to its separation from Gondwanaland, the African landscape has been sculptured mainly by the effects of erosion, and since no Pleistocene ice age was experienced in Africa, no recent glaciation effects are evident. Southern Africa has a rather uniform topography, and consists of a high interior plateau, which is thought to represent the central elevated region of Gondwanaland, with a broad basin in the Kalahari (Fig. 1). This plateau is separated from a marginal zone along the coast which varies in width from 60km in the west to 240km in the east and which tilts towards the sea. The Great Escarpment, which is formed by a number of mountain ranges, separates the marginal and plateau regions (Fig. 1). Thick lava flows, produced in the Jurassic, covered the underlying rock and protected these mountains from weathering.

The southern African climate is affected largely by the presence of the cold Benguela and warm Agulhas currents moving northwards and southwards on the west and east coasts respectively. Proximity to the equator and topographic variation are additional influences on climate. Southern Africa has always been a semi-arid region, and on the subcontinent precipitation decreases uniformly westwards from the Escarpment across the plateau. Along the southern and eastern coastal margins, topographic irregularities complicate the general trend. Distribution of the mean January precipitation is similar to that for the year, with only

the south-western Cape region experiencing a winter rainfall maximum. The Port Elizabeth coastal strip is the only all-year rainfall region, with a double annual rainfall maximum, while the dry west coast area is a zone with no clearly defined maximum, but with a predominantly winter rainfall.

MATERIALS AND METHODS

Distribution records were obtained from various museum collections, and a number of surveys of previously unsampled areas were carried out. Localities presented in publications which included records of southern African anostracan species were also used. Only those species which have been collected from more than one locality have been grouped into the various biogeographic categories and their distribution mapped, but all species have been included in the species richness analysis. The index of species richness, which simply indicates the number of species in a given area, has been used in this study rather than diversity indices which include information on how relative abundances are distributed and, according to Samways (1994), have little conceptual value. Any reference to diversity in this work, therefore, implies species richness. For this exercise, the map of southern Africa was divided into two by two degree grids and species present in each grid were plotted. In the case of two localities within the grid for a single species, only one of these has been indicated.

Depending on their apparent effect on species distribution, either the relevant isohyet or the Effective Temperature (ET) isolines have been plotted on the biogeographic category maps. ET values were obtained from Stuckenberg (1969). This index of temperature stresses the biological importance of summer, and expresses the relative warmth and duration of the warm period of the year. ET measures warmth on a temperature scale, specifying temperatures at the beginning and end of the warm period, and implicates the duration of that period. An increase in ET can be associated with an increase in the proportion of the year with temperatures warmer than the ET.

RESULTS

Species distribution

The anostracan fauna of southern Africa exhibits distinct distribution patterns and has been divided into ten biogeographic categories, the names of which have been modified from a combination of biomes presented for other faunal groups (Smithers 1983; Skelton 1993). The twelve species which have been collected from only a single locality have been excluded from these categories since they cannot be said to exhibit any distribution pattern. *Artemia* has also been excluded since the genus is dependant largely on a specific habitat type, and will therefore have a distribution controlled by that of saline pools rather than the factors which influence the other anostracans of southern Africa. The following ten biogeographic categories for the southern African anostracans are presented in figures 2-5, with categories 3 and 5 illustrated in figure 3; 4,7 and 9 in figure 4 and 6, 8 and 10 in figure 5.

1. *Widespread species*. Only two species (*S. cafer* and *B. wolfi*) occur over the width of southern Africa, from east to west, and along much of the length of the region, and for *B. wolfi*, are present in montane, arid and tropical zones. It is, however, possible that a number of species have been incorporated together as *B. wolfi* since a large amount of variation in antennal morphology is evident in specimens from different areas.

2. *Arid South-West species*. These species occur in the arid and semi-arid regions of Namibia and the Karoo where average annual rainfall is largely less than 300 mm. The range of the different species varies somewhat, with, for example, *S. papillatus* and *B. browni* occurring only south of the Namibian border. The locality for *S. proboscideus* on the Transvaal/ Botswana border is the most eastern record for this category, and falls into an area where annual rainfall averages 500 mm. The northern Namibian localities for this species are also in a higher rainfall area than the rest of the arid south-west zone (Fig. 2).

3. *Southern Savanna species*. The average rainfall in most of the area inhabited by this large category of species is 500 mm, although the localities in the southern Transvaal do have a higher value than this, and the localities for *S. macrourus*, *S. cladophorus* and *S. namibiensis* fall into the Karoo desert biome. The distributions of the species included in this group, however, indicates that they are largely excluded from those arid regions of Namibia

and the northern Cape where more than 35% of the annual rainfall is unpredictable and the annual rainfall is below 300 mm (Fig. 3). The single locality in the latter region for *S. indistinctus* was from Brehm (1958) and the identity of this species has not been verified.

4. *Highveld species*. Only one species, *S. cirratus*, is included in this category, which overlaps, to some extent with the previous one. This species is, however, restricted to altitudes between 1000 and 1500 m, and is bounded by a 15°C ET isoline (Fig. 4).

5. *Cape West Coast species*. Again, a single species, *S. purcelli*, is included in this category. This species is unusual since its range includes the relatively wet locality of Cape Town and extends northwards along the coastal margin where, in some localities, rainfall is less than 100 mm per annum. The single locality at 30°S/20°E is the furthest inland and falls outside the winter rainfall limits (Fig. 3). A single specimen was, however, collected from this locality, which had an unusually high number of streptocephalid species, perhaps as a result of recent episodic flooding of the region.

6. *Cape East Coast species*. Three species are restricted to the east coast region of the Cape, with ranges extending from Cape Town, north-eastwards to just north of Port Elizabeth (Fig. 5). The annual rainfall of this region is predominantly over 400 mm and precipitation occurs either in winter or throughout the year.

7. *East Cape Inland species*. These species are distributed between the coastal and escarpment regions of the eastern part of southern Africa. The two closely related species included in this category are restricted to different areas, with *S. dregei* occurring in the more arid, low altitude parts of the eastern Cape, while *S. spinicaudatus* occurs in the higher parts as well as in the Transkei (Fig. 4) where annual rainfall is higher and ET lower as a result of the altitude.

8. *Eastern Escarpment species*. Six species, all of the genus *Branchipodopsis* have been collected from the Drakensberg mountains which form the divide between the marginal region and the interior plateau in the eastern part of southern Africa (Fig. 5). Only two of these species, however, have been collected from more than one locality. The record of *B. drakensbergensis* from Benoni in the southern Transvaal appears somewhat curious since this

area has a lower altitude than the Drakensberg and is not quite part of the mountain range, but there is an altitudinal link between this locality and the Great Escarpment (Fig. 1). The species of this category are distributed within the 14 and 15°C ET isolines (Fig. 5).

9. *Tropical/Subtropical species*. These species extend from north-eastern Natal into Swaziland and northwards into the eastern Transvaal and southern Zimbabwe (Fig. 5). Rainfall averages over this region vary from 250-500 mm in southern Zimbabwe, to over 750 mm in parts of north-eastern Natal. This entire region forms part of the marginal area of southern Africa and is less than 1000 m in altitude. The species included in this category are distributed in one of the warmest ET regions (18°C) and the 17°C ET isoline appears to form a distinct barrier to the movement of these species inland (Fig. 5).

10. *Zimbabwean species*. This category has been established solely for *S. trifidus* which is restricted to Zimbabwe, with a single locality just over the Zambian border, but two other species (*S. vitreus* and *S. wirminghausi* sp. nov.), which have only been collected from a single locality in western Zimbabwe, could also be included. Although this category overlaps with the Southern savanna group to some extent, it has been separated since those species belonging to it are distributed in a southern and south-western direction, while *S. trifidus* appears to have a range extending northwards, excluding regions where ET falls below 17°C (Fig. 5).

Species richness

Table 1 includes all 46 anostracan species reported from southern Africa in this study, the distribution, status and biogeographic group (GR) to which each has been allocated and whether they are endemic to the region. The term "common" indicates that large numbers of specimens have been collected from a number of habitats. "Uncommon" refers to species which may have been collected from a number of localities, but in low numbers (usually less than 10 specimens). Cases where species have been collected from a single habitat, on one occasion only, are described as 1 locality, common, if many specimens were collected, or "rare" if less than 10 specimens were collected. Endemic species (E) are indicated by "Y", while those which occur outside the subregion are indicated as "N", followed by CA for central and/or east Africa, NA for North Africa, E for Europe and COS for cosmopolitan. Those species for which descriptions are not yet published, are marked by a "*", those of uncertain

identity by a "#", and unconfirmed records are indicated by a "?". These designations and groupings are based on data presently available, and additional collecting will result in changes to many of them.

In summary, of the 46 species recorded from southern Africa, 38 are endemic to the region. Only two species, *Branchinella spinosa* and the unconfirmed *Artemia parthenogenetica*, have distributions which include other continents. None of the families are endemic to Africa, and three of the four genera represented have a wide global distribution. Only *Branchipodopsis* is concentrated in southern Africa, with 16 of the 21 species described restricted to the subcontinent. The three unidentified genera collected from southern Africa are endemic.

<i>B. hodgsoni</i>	common, E Cape coast	6	Y
<i>B. kalaharensis</i>	common, Kalahari	3	Y
<i>B. karroensis</i>	common, 1 locality, Karoo	2	Y
<i>B. scambus</i>	uncommon, Grahamstown area	7	Y
<i>B. wolfi</i>	common, most of subregion	1	N, CA
<i>B. tridens</i>	common, Namibia, N Cape	2	Y
<i>B. kaokoensis</i>	rare, 1 locality, N Namibia	2	Y
<i>B. natalensis</i>	rare, 1 locality, Natal/OFS border	8	Y
<i>B. simplex</i>	rare, 1 locality, N Namibia	2	Y
<i>B. drepane</i>	rare, 1 locality, central Namibia	2	Y
<i>B. drakensbergensis</i> *	common, Drakensberg, S Transvaal	8	Y
<i>B. underbergensis</i> *	common, 2 localities, Drakensberg	8	Y
<i>B. dayae</i> *	rare, 2 localities, NW Cape, W Cape coast	2/ 4	Y
<i>B. hutchinsoni</i> *	common, 1 locality, Karoo	2	Y
<i>B. barnardi</i> *	common, 1 locality, Drakensberg	8	Y
Gen.nov. A#	rare, 2 localities, NE Natal	9	Y
Gen.nov.B#	common, 1 locality, Grahamstown	7	Y
Gen.nov.C#	common, 1 locality, Namib desert	2	Y
<i>A. salinial tunisiana?</i>	common, E, W Cape coast	4/ 5	N,E NA,
<i>A. parthenogenetica?</i>	rare, 1 locality, Namibia	2	N, COS
<i>B. ornata</i>	rare, N Namibia, Botswana, S Transvaal	3	Y
<i>B. ondonguae</i>	rare, N Namibia, E Transvaal	3	N, NA
<i>B. spinosa</i>	rare, 1 locality, N Botswana	3	N,E NA,

Factors influencing species richness

In order to determine which regions were occupied by the greatest number of species, and whether certain climatic conditions were particularly conducive to a rich fauna, the distribution of all anostracan species collected from southern Africa was plotted (Fig. 6). Table 2 presents the six grids in which the most species have been collected and data on various aspects of the climate prevalent in the grid area. A more detailed analysis in which the significance of climatic factors influencing species diversity could be ranked would almost certainly prove erroneous at this stage since, as can be seen from figure 6, large areas have not been sampled and for most parts of the map in which species are not indicated, this may not be an accurate reflection of the species diversity, but may rather indicate a lack of sampling in the area.

The number of species present within two degree latitude lines has also been calculated and is indicated on figure 6. Again, however, the results of this count may simply be a manifestation of the amount of sampling in different areas, and, in addition, there is the effect of the width of the continent at different latitudes. It is, nevertheless, interesting to note that the latitude which includes the greatest number of species (28-30°), includes species from four of the biogeographic categories identified, and crosses four of the ecoregions identified by Skelton (1993) (Fig. 7).

Table 2. Two degree grids of southern Africa with the highest species diversity and associated climatic conditions.

Grid no Grid co-ordinates	1 (18/14)	2 (30/20)	3 (26/28)	4 (32/18)	5 (32/24)	6 (28/28)
Anost. biogeog. cat: Ecoregions (Skelton):	2 6	2/4 6	3 3	5/6 5	7 3	8 4
No. genera No. spp.	2 8	2 7	3 7	3 6	3 6	1 6
Altitude (masl)	500- 1000	500- 1000	1000- 1500	0-1500	0-1500	1500- 3000
Annual rainfall (mm)	300- 500	100- 200	600- 1000	100- 800	400- 800	700- 1500
*Variability of rainfall	40-60%	35%	20%	20%	20%	20%
Annual T°C	22,5	17,5	16,5	17,5	17,5	12,0
ET °C	16	15-16	15	15-16	15-16	14-15
January mean T°C	32,5	32,0	29,0	25,0	26,0	24,0
#Annual evaporation (mm)	300	350	250	250	200	200

*Variability of rainfall is a measure, expressed as a percentage, of the relative unpredictability of the mean annual rainfall. This is an important consideration in southern Africa since two regions may have similar mean annual rainfall figures, but the one area may remain dry for most of the year and receive all its rain over a matter of days in the form of thundershowers (Lovegrove 1993).

#Another important consideration in terms of rainfall is the rate at which moisture may be lost through evaporation and this is measured by the amount of water lost (in mm) from experimental pans.

The grid which has the highest level of species richness falls into the Kaokoveld region of northern Namibia, a region defined as an arid savanna desert biome by Lovegrove (1993). This biome stretches diagonally across northern Namibia, across the southern and central Kalahari Desert in Botswana to about 26°E and into the northern Cape as far south as 29°.

Most of the biome comprises level plains which form part of the Kalahari Basin. The northwestern part of the biome, Kaokoveld, has a number of endemic birds and reptiles, and overall, the arid savanna supports a rich fauna. The second grid in the table, which supports seven species also falls into a desert biome, the Nama Karoo which has its centre in the plateau of the Cape.

The remainder of the species-rich grids fall into a wide range of climatic regions, including the winter-rainfall south-west Cape, the year-round rainfall Port Elizabeth area, the montane Drakenberg, and the central plateau, Highveld region of the southern Transvaal. All three of the southern African regions, the marginal, Escarpment and plateau have areas which support a diverse anostracan fauna.

In terms of genera, the two Cape coastal areas have *Artemia* as the third genus, while the southern Transvaal grid has a representative of *Branchinella* in addition to *Branchipodopsis* and *Streptocephalus*. The Drakensberg grid is unique in that it supports only a single genus, *Branchipodopsis*.

DISCUSSION

Southern Africa supports one of the most diverse anostracan faunas in the world, and in addition, most of the forty-six species identified to date, are endemic to the region. The species richness would appear to be an effect of the heterogenous, in terms of climate, nature of southern Africa. Belk (1977) suggested that temperature, particularly in relation to the time of year at which pools were filled, influenced the anostracan species diversity of Arizona. In most parts of southern Africa, there is only one rainfall season, which eliminates the possibility of a cold-adapted species hatching during the winter-filling in addition to a warm-adapted one in the summer. This type of system may, however, account for the large number of species which are present in the Port Elizabeth grid (Fig. 6), where there is both a summer and winter rainfall peak. As illustrated by figure 6 and table 2, there is no single climatic region which favours anostracan diversity, and it is most likely the large number of climatic types, related to altitude, latitude and western or eastern position, as suggested by Belk (1977) for Arizona, which has resulted in the richness of the fauna. The fact that the greatest number of anostracan species occur across the latitudes which include the most climatic regions, provides evidence for this. In addition, the wide range of temporary pool habitats,

from the large pans of the Kalahari and the pan belt, to animal wallows and rockpools, could also contribute to the evolution of a rich fauna, as could the fact that no Pleistocene glaciation was experienced in southern Africa which allowed radiation of the anostracan fauna.

There are, however, other considerations relating to species diversity. Bănărescu (1990), based on evidence from present distribution, suggested that the Branchiopodidae had a Gondwanian origin, with the ancestral Branchiopodinae in the eastern part of Gondwanaland. Sixteen of the approximately 21 species of *Branchipodopsis*, a member of that family, occur in southern Africa. According to Briggs (1987), such concentrations of a particular taxon usually indicates a centre of origin for that taxon. The presence of three unidentified genera belonging to the Branchiopodinae also indicates an origin of the subfamily consistent with that proposed by Bănărescu (1990).

A controversy currently exists regarding the origin of the Streptocephalidae, which has over half its described species distributed in Africa, and many of these are confined to southern Africa. This concentration of species appears to indicate a southern Gondwanaland origin for the monogeneric family. However, no *Streptocephalus* species occur in South America or Australia and this fact has led to the belief that the streptocephalids had a Laurasian origin, and moved into Africa after the break up of Gondwanaland (Belk 1984). A major adaptive radiation in Africa is given as the reason for the present species diversity on the continent. As an alternative, Bănărescu (1990) suggested that the streptocephalids could have originated in Africa, and later dispersed to Madagascar, Europe, South and East Asia and from the latter area to North America and the Antilles, but neither to Australia nor South America. The distance between these continents is probably too great to allow the dispersal of eggs by wind or birds. This suggestion would indicate that the dispersal was rather recent since the North American species have not yet had time to reach South America. The latter alternative seems the more feasible of the two options since *Streptocephalus* is the most thermophilous of all fairy shrimp genera (Bănărescu 1990) and it would appear unlikely to have originated in the cold Laurasian area or to have survived recent glaciations which occurred in the northern hemisphere. Additional evidence for an African origin is provided by the extremely diverse morphology of the African streptocephalids as opposed to the American and Asian members of the genus and the success, in terms of both abundance in temporary pools and distribution in southern Africa, of the genus. Unfortunately, there is no fossil

evidence to substantiate either possible origin.

Branchinella is also reported to have a Gondwanaland origin by Bănărescu (1990), but the centre of origin was given as South and East Asia rather than Africa. The presence of only three species of the genus, none of which are particularly abundant or widely distributed in the southern part of the continent is obviously a result of dispersal southwards.

Those factors which influence anostracan species richness also affect their distribution. The climate, in particular mean annual rainfall and the predictability of this, and, in relation to altitude, the temperature, appears to limit the distribution of anostracan species to certain regions. Only two species, *S. cafer* and *B. wolffi* do not exhibit any pattern in terms of distribution but it is probable that the latter includes a number of species which are difficult to separate based purely on antennal morphology. The remainder of the southern African species are apparently confined to specific areas predominantly by their ability to survive only under certain climatic conditions. Although the limits and exact nature of these abilities and conditions have yet to be investigated, cases of species having distributions which follow certain climatic conditions are evident from figures 2-5. An example of this is the distribution shown by species included in the "Southern Savanna" biogeographic category. These species are excluded from the central and southern regions of Namibia and the Great Karoo probably as a result of the aridity and unpredictability of the rain in these areas. The unique nature of the rainfall patterns in the southern Cape probably restricts the distribution of those species which occur along the east and west coastal regions. While rainfall is probably the dominant factor influencing distributions in the western half of southern Africa, those anostracan species which occur in the eastern half of the subcontinent exhibit distribution patterns which correlate more strongly with temperature.

The importance of temperature on the egg hatching success and thus the distribution of anostracan species was shown by Belk (1977). Temperature would probably have a similar type of effect on distribution in southern Africa, but which indices of temperature (annual mean, maximum, minimum, monthly averages) have the most significant influence is difficult to determine. The use of ET, which stresses the biological importance of the summer months, was used in this study since summer is the predominant rainfall season over most of southern Africa, and the duration of the summer and the temperature extremes experienced

during this period would most likely influence anostracan distribution. Stuckenberg (1969) illustrated the distribution of a number of snake and frog species together with ET isolines and showed that this climatic factor was significant for these animals. Some species of southern African anostracans occur over a relatively wide range of ET but others, particularly the Highveld species *S. cirratus*, and the Tropical/Subtropical species are distinctly bounded by the 15°C and 17°C ET isolines respectively. In both these cases ET is closely correlated to topography. Steep ET gradients, such as those observed where abrupt changes in topography occur, such as at the East Cape and Natal Drakensberg along the eastern part of South Africa, were found to cause faunal discontinuities by Stuckenberg (1969). A similar phenomenon is evident in the anostracans, but rather than resulting in a faunal discontinuity, steep ET gradients appear to present a distinct barrier, and species are limited to one side of the Escarpment. A clear example of this is provided by the Subtropical/Tropical species, particularly *S. bidentatus* (Fig. 4) which is restricted to the area east of the Drakensberg mountain range (Fig. 1). A break in the Escarpment at the Limpopo river has allowed this *S. bidentatus*, and a number of other species, to inhabit the southern region of Zimbabwe but the Matopos to the west and the Inyanga mountains to the east probably present a barrier, in the form of a steep ET gradient, to their dispersal further into Zimbabwe. The East Cape Inland species, *S. dregei*, too, is restricted to the coastal margin, possibly by the ET associated with the high altitudes of the Escarpment. Of course, it could be argued that the Escarpment may act purely as a physical barrier to dispersal inland by wind, and other dispersal mechanisms.

The patterns of anostracan distribution, because they appear to be governed largely by climate, are similar to those of a number of other faunal groups. The ecoregions illustrated by Skelton (1993) in his recent publication on the southern African freshwater fish (Fig. 7) are essentially applicable to the anostracans as well. Differences are, however, evident mainly in the Southern Savanna category of anostracans which extend into Skelton's (1993) Highveld region, and the absence of a distinct Tropical interior group of species, although this could be attributed to the lack of material from the areas included in this biome. The distribution of the diaptomid calanoids of southern Africa was investigated by Rayner (1990) and since many species of this group inhabit temporary waterbodies, some similarities with the anostracans could be expected. However, only those species confined to the Cape coast, such as *Lovenula simplex*, have a distribution which is distinctly common to both calanoids and anostracans.

The distribution of one species, *Lovenula falcifera*, overlaps to some extent with the Southern Savanna anostracans, but its range extends further into the eastern Cape. Some of the other species have a wider distribution, for example the Cape coastal species extend both east and westwards from Cape Town, and others have extremely limited distributions. Some of the more widespread species of diaptomids no doubt have such distributions as a result of their ability to be dispersed via rivers and streams and their survival in permanent waterbodies such as manmade impoundments. The fact that anostracans are excluded from such habitats has resulted in a distribution which differs in detail from other freshwater invertebrates, such as those discussed by Harrison (1978) and fish which have distributions corresponding largely to the position of major river systems. Since temporary waterbodies are almost ubiquitous in southern Africa, this type of restriction or influence is not seen in the anostracans, and even the presence of a distinct pan belt is not a key factor in the biogeography of these crustaceans.

The type of temporary pool does, however, influence the distribution of certain anostracans. Six species of *Branchipodopsis* occur in rockpools at high altitudes in the Drakensberg mountains, but no streptocephalids have been collected from these habitats or any other similar ones in other areas such as those at Augrabies Falls. Belk (1991) found that *S. texanus* did not occur in rockpools on top of Enchanted Rock, a large granite dome in Texas, but this species was present in pools at the base of the dome. *Branchinecta packardi*, however, was able to survive in the shallow, highly ephemeral summit rockpools and Belk (1991) suggested that this was a result of this species having a faster maturation rate and earlier reproduction when compared with *S. texanus*. In addition, *S. texanus* requires higher temperatures than those typically experienced during the more prolonged wet phases of the pools for successful egg hatching. *Branchinecta packardi* is not restricted to any particular season. A similar phenomenon appears to be operating in southern Africa, where the streptocephalids are excluded from rock pools in the Drakensberg and other areas. The type of habitat prevalent in an area is thus also an important consideration in anostracan distribution.

The type of habitat also affects distribution in the manner suggested by William & Busby (1991) in that easily dispersed species generally occupy episodically-filled pools in southern Africa. The large pans found in the pan belt in the northern Cape and those in

Namibia were inhabited by *B. tridens*, *S. ovamboensis* and *S. proboscideus*, all of which have relatively wide distributions and could thus be considered as easily dispersed. The latter two species exhibit no intraspecific variation and this indicates that populations are probably not genetically isolated from each other since they have not had sufficient generations to allow adaptations to local conditions. The small pools which may experience a number of refillings in a single rainy season, such as the Drakensberg rockpools, are inhabited by endemic species which have restricted distributions, indicative of local adaptations and consequential speciation, resulting from a large number of generations in a single wet season. The large amount of intraspecific variation evident in a number of species of *Branchipodopsis*, which typically inhabit smaller temporary pools of short, but more frequent wet phases, provides further support for local adaptations and thus populations restricted to a small area by their inability to be dispersed to habitats where different conditions prevail. There are, however, complicating factors involved in Williams & Busby's (1991) hypothesis. Small depressions, occasionally caused by game using salt deposits, are often situated within large, episodically-filled pans. These "microhabitats" will fill more frequently than the remainder of the pan, and they may thus allow a population with a specific set of adaptations or even an endemic species to evolve.

The barrier effect of the Escarpment, in terms of ET gradients and possibly also as a physical barrier to dispersal has been discussed above. Evidence for the effectiveness of this barrier is provided by the fact that only the two widespread species, *S. cafer* and *B. wolffi*, occur on both the central plateau and the coastal margin. All other species are distributed in one or the other of these regions. The formation of the Escarpment could provide an example of vicariance; biogeographic patterns produced by a particular kind of allopatric speciation in which a geographic barrier develops so that it splits a formerly continuous population. The formation of the Escarpment accompanied the rifting responsible for the splitting of Gondwanaland about 180 to 130 million years ago. The evolution of the passive margin of a plate involves subsidence in the rift zone as well as adjacent uplift due to thermal expansion of the crust during rifting. In southern Africa this uplift generated a hinge or flexural bulge which ultimately developed into the Great Escarpment. Later crustal adjustments, about 55 million years ago, enhanced this feature of the landscape (Thomas & Shaw 1991). Vicariance speciation was used to explain the endemism of the south-western Cape diaptomid calanoids by Rayner (1990) and could account for the large number of endemic members of a variety

of faunal and floral groups. The two streptocephalid species endemic to this region, *S. purcelli* and *S. dendyi*, were allocated to the same species group (Hamer et al. in press) and obviously share a common ancestor. These two species are quite morphologically distinct from the other southern African streptocephalids, which suggests an ancient isolation event, quite possibly the formation of the Escarpment.

The presence of one member of a species group on the coastal margin and another inland is relatively common within the southern African streptocephalids. Vicariance would appear to be an explanation for the evolution of the coastal species *S. gracilis* and its relative *S. papillatus* which inhabits the plateau. However, vicariance speciation through the formation of the Escarpment is not a simple explanation for the biogeographic patterns in all cases. One reason for this is geological; it is believed that the Escarpment was much wider than at present, its eastern margin was formed at the edge of the continent and has since retreated westwards, through erosion or changes in sea level. King (1967) suggests that the Drakensberg is presently situated 150km further inland than when it was formed. Most of the coastal plain around much of Africa is thought to have formed during the Pliocene, about 7 million years ago. The Escarpment could not really be said to have split a population in a true vicariance manner, since the land inhabited by the coastal species has only developed recently in relation to the formation of the barrier. Dispersal to the coastal margin once it had formed and later isolation possibly resulted in the current streptocephalid distribution patterns. However, it could be argued that after the upliftment of the margin, those populations inhabiting the regions near to the coast became isolated from those inland as erosion lowered the marginal area. An example of this type of speciation could be provided by *S. dregei*, *S. spinicaudatus* and *S. cirratus* which belong to the same species group. Each of these species is restricted to the marginal region, the eastern side of the Escarpment and the central plateau respectively and could have become isolated in response to the change in conditions associated with the altitudinal position of the population after upliftment and later erosion. The greater morphological difference between *S. dregei* and *S. cirratus* is indicative of a longer period of isolation between these two species than between *S. dregei* and *S. spinicaudatus*. The latter two species would have only separated once the eastern side of the Escarpment had retreated considerably, and the large amount of overlap in morphological characters exhibited by these two species suggests relatively recent speciation.

The north-eastern Natal region is inhabited by four streptocephalid species with members of their species group situated in the interior. Geological evidence has shown that in this area, the sea level was just below the Escarpment (the Lebombo mountains) and only during the Pleistocene did a series of lowerings of the sea level cause the coastline to shift progressively eastwards. Those species present on the Zululand coastal margin must have dispersed into this region only relatively recently. *Streptocephalus zuluensis*, *S. bidentatus*, *S. dendrophorus* and *S. bourquinii* all have closely related species (*S. kaokoensis*, *S. macrourus*, *S. cladophorus*, and *S. wirminghausi*) either situated in the Southern Savanna category range or with this type of distribution. The former assembly of species most likely originated from the more widely distributed latter, perhaps as populations became isolated through adaptations to the eroded, low lying areas of southern Zimbabwe and eastern Transvaal. From here, it would have been possible for these species to invade north-eastern Natal. Perhaps the factor responsible for the isolation of the low altitude species was the 18°C ET isoline associated with this region. This type of speciation is, therefore, of a typical allopatric type rather than vicariance speciation by the formation of the Escarpment. Unfortunately, the absence of an anostracan fossil record, as well as an incomplete distribution record for southern Africa, means that it is almost impossible to substantiate the above suggestions.

Similarly, discussion about the dispersal of anostracan eggs by various mechanisms and the frequency with which successful colonisation of new habitats and genetic exchange between populations occurs, is based largely on speculation or indirect evidence. For example, a number of studies have shown that anostracan eggs can survive the passage through the digestive system of various bird species, that the retention time for *Artemia* eggs is 12-24 hours, and that the eggs do adhere, in mud, to the legs and hooves of livestock (Thiéry 1987). In addition, anostracans have been found to inhabit many man-made dams in North America, which suggests that dispersal does occur. This type of evidence has also been witnessed in southern Africa, where *S. cafer* specimens were collected from a rice paddy established in the last few years on the Makatini Flats in north-eastern Natal. A number of temporary pools are situated in the vicinity of these paddies, and one particular pool is approximately 1 km away. However, it is interesting to note that ten branchiopod species have been recorded from this pool, and yet only one of these, which has a wide distribution and is able to survive in many different climatic regions and in various types of temporary pools, has been able to colonise

the new habitat successfully. Dispersal via flooding and in ephemeral rivers has not been documented, but it may occur. The presence of five streptocephalid species in a small pool in a dry river bed in the northern Cape could have resulted from recent heavy flooding over large areas in South Africa. The presence of more than one species of an anostracan genus is unusual (Dodson & Frey 1991), and the only other locality where this has been witnessed was in a large pan on the Makatini Flats where distinctly different habitat types within the pool could be identified (Hamer & Appleton 1991). In addition to the five streptocephalids, *Triops granarius*, two conchostracan genera, three species of *Daphnia* and three diaptomid species were also present in the pool, and most of the latter two group's representatives were outside their normal distribution range (N.A. Rayner University of Natal pers. comm.). The crustacean fauna, including the anostracans could, therefore have been concentrated in the river bed when the floods subsided, after having been carried for quite some distance. Dispersal is, therefore, most probably an infrequent phenomenon, the exact details about which we actually know very little.

The latter statement applies to many aspects of anostracan research in southern Africa and for much of the above discussion it is important to consider the incompleteness of much of the data. Indeed, one of the most significant deductions which can be made from figure 6, is that there are still vast areas of the subcontinent which need to be investigated in terms of the anostracan fauna. In addition, table 1 clearly shows that the status of many identified species is in need of investigation. Many temporary pools occur in game reserves and are thus protected. However, in large areas of southern Africa, agriculture and urbanisation have destroyed a many of these habitats. In Natal, for example, only 10% of the original wetlands remain, and no anostracans were collected from much of this province. Hopefully, the data from this study will provide a basis and some direction for much needed future studies on the southern African Anostraca.

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The co-operation of the curators of those museums which provided specimens on loan for this study, the Natal Parks Board and the National Parks Board, and those individuals who collected specimens during the course of this study is much appreciated.

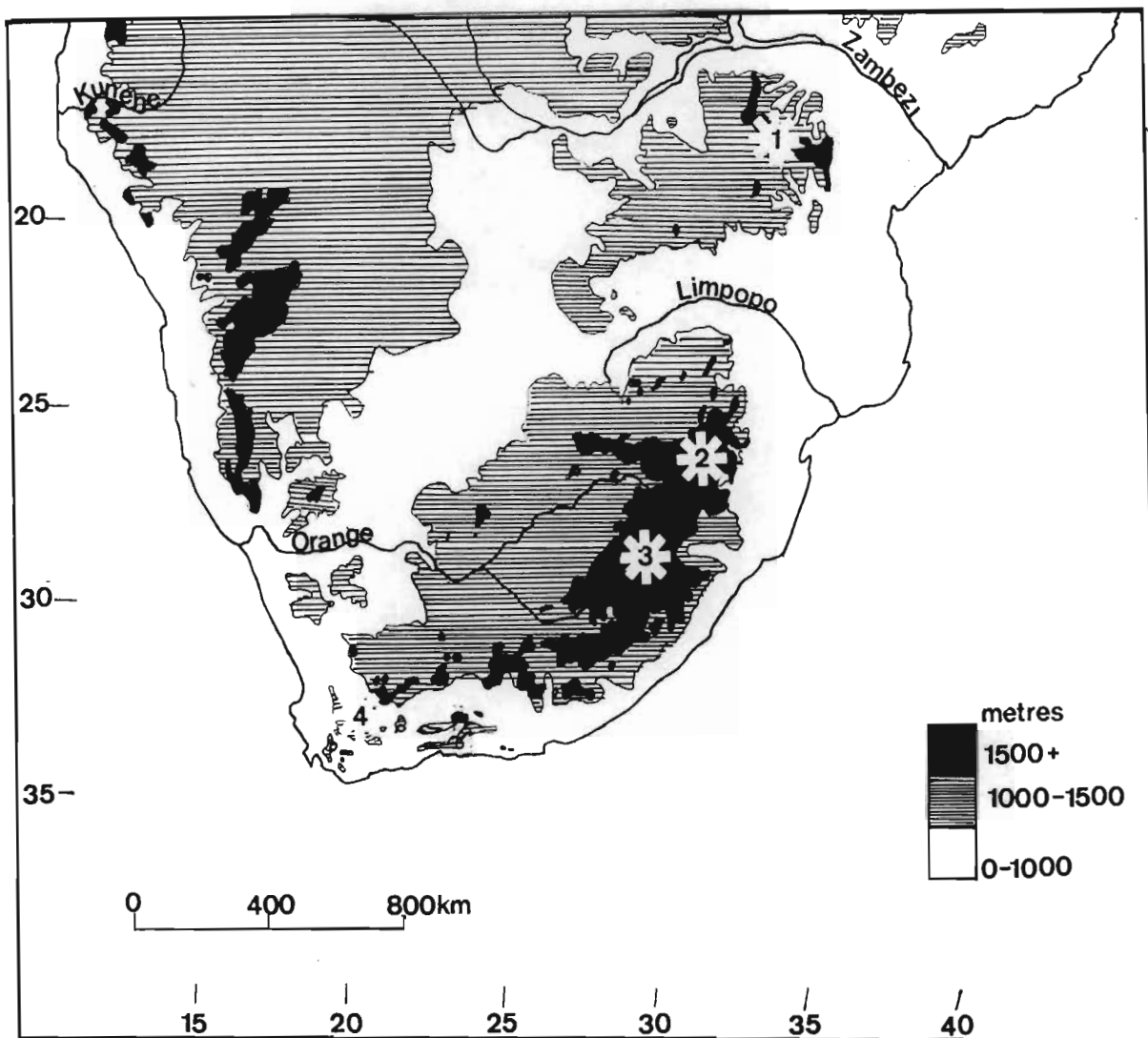


Figure 1. Map of southern Africa showing major altitudinal regions (from M.J.A. Werger 1978).
 1 = Inyanga mountains, Zimbabwe. 2 = Drakensberg. 3 = Cape Fold mountains.

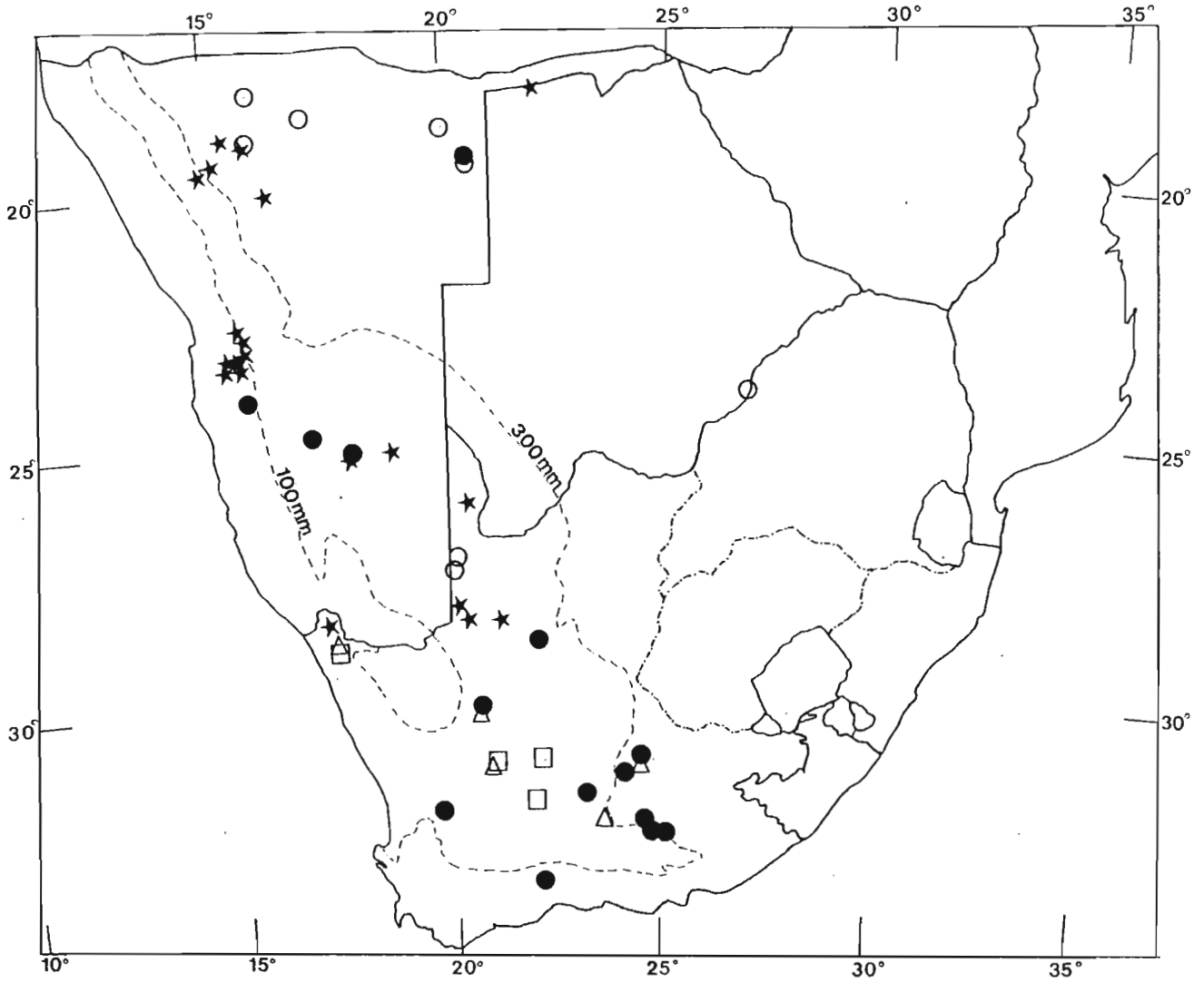


Figure 2. Map of southern Africa showing pattern of distribution of biogeographic category 2, "Arid South-West" species. ● *S. ovamboensis*, ○ *S. proboscideus*, △ *S. papillatus*, □ *B. browni*, and ★ *B. tridens*. 100 and 300mm isohyets are illustrated by the dotted line.

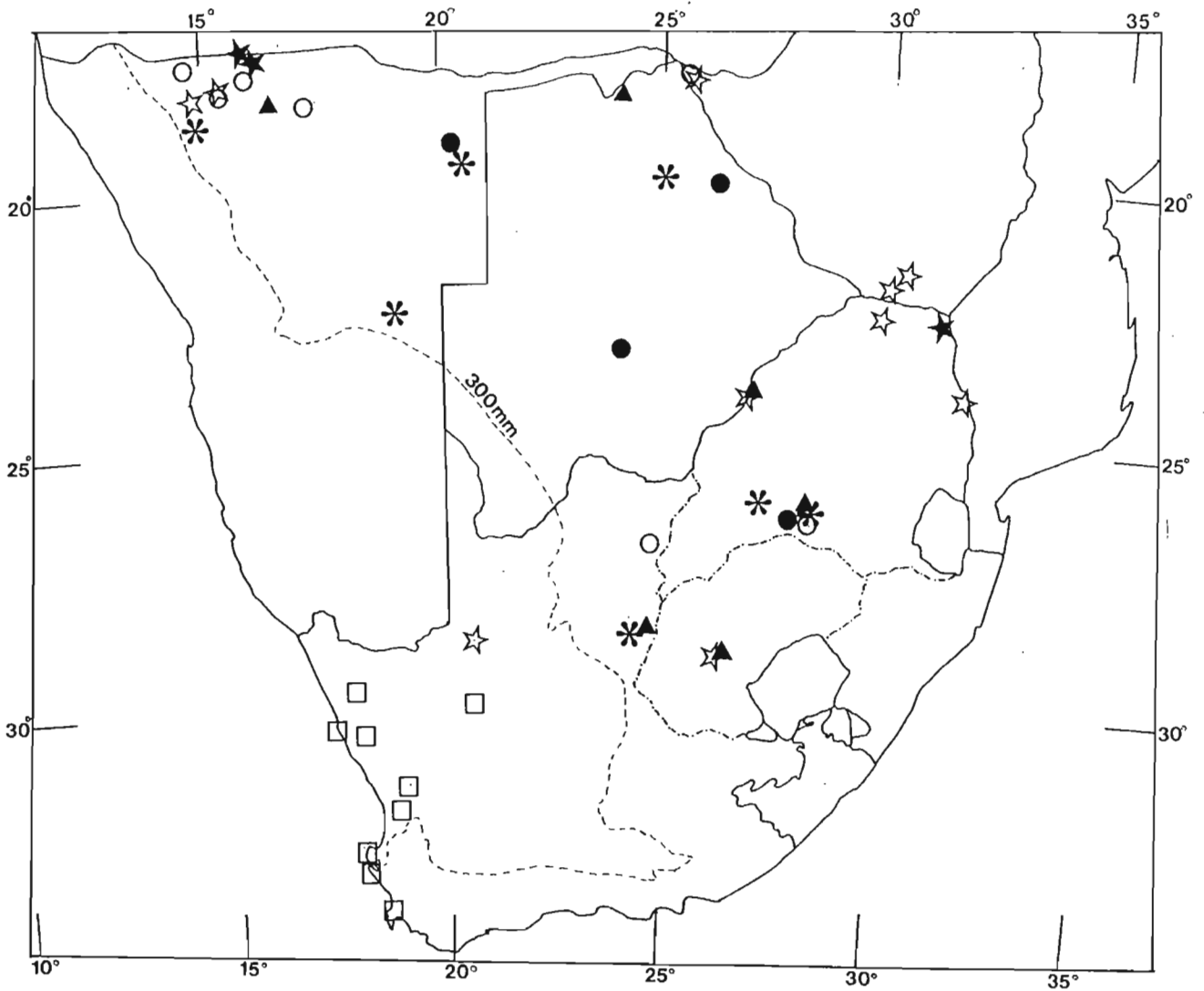


Figure 3. Map of southern Africa showing distribution patterns of biogeographic category 3, "Southern Savanna" species, ☆ *S. indistinctus*, ○ *S. cladophorus*, ▲ *S. macrourus*, * *S. namibiensis*, ★ *B. ondonguae* and ● *B. ornata*; category 5, "Cape West Coast" species □ *S. purcelli*. 300mm isohyet is illustrated by the dotted line.

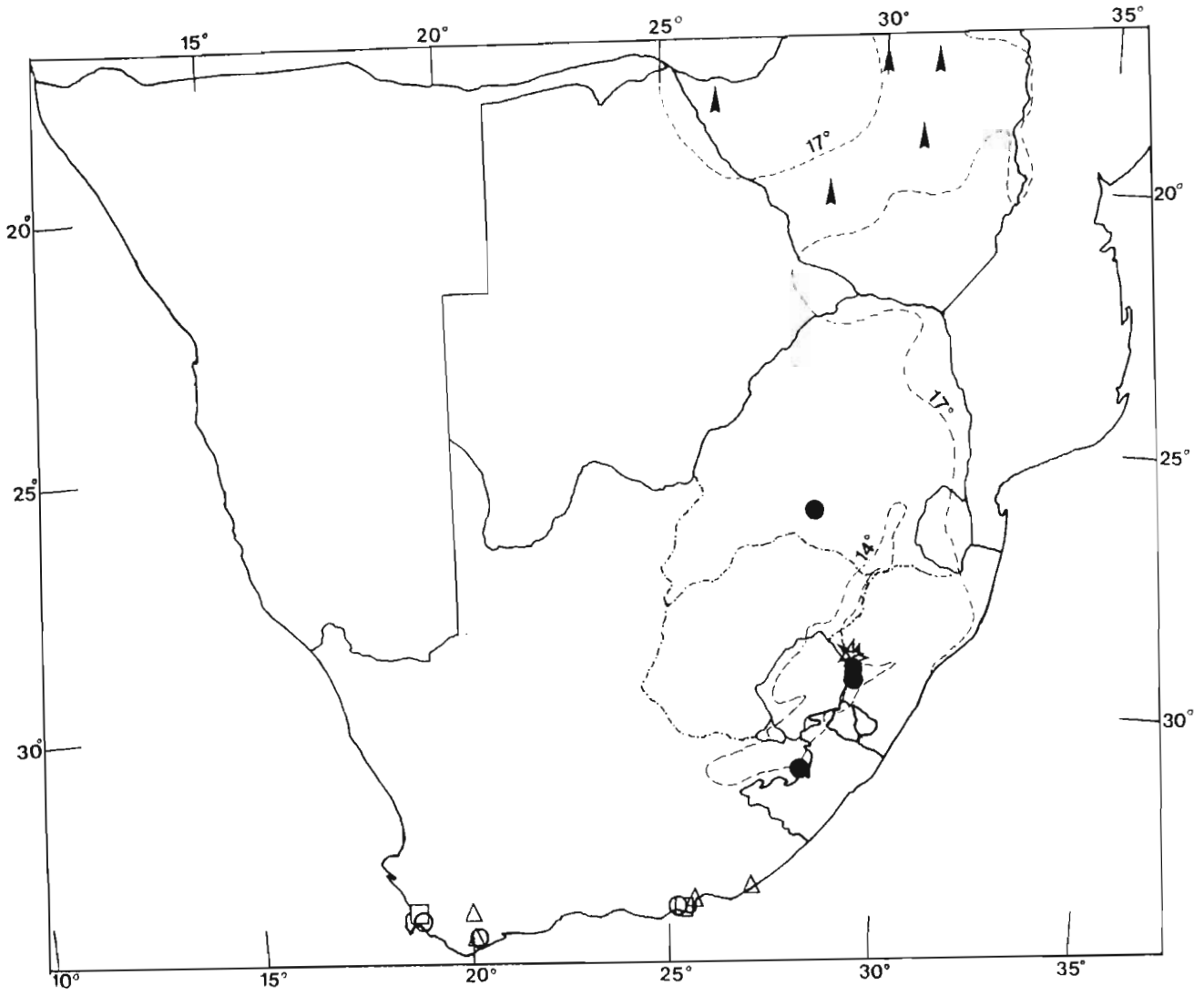


Figure 4. Map of southern Africa showing distribution pattern of biogeographic category 6 "Cape East Coast" species, ○ *S. dendyi*, □ *S. gracilis*, △ *B. hodgsoni*; category 8 "Eastern Escarpment" species, ● *B. drakensbergensis*, ☆ *B. underbergensis*, and category 10 "Zimbabwe" species, ▲ *S. trifidus*.

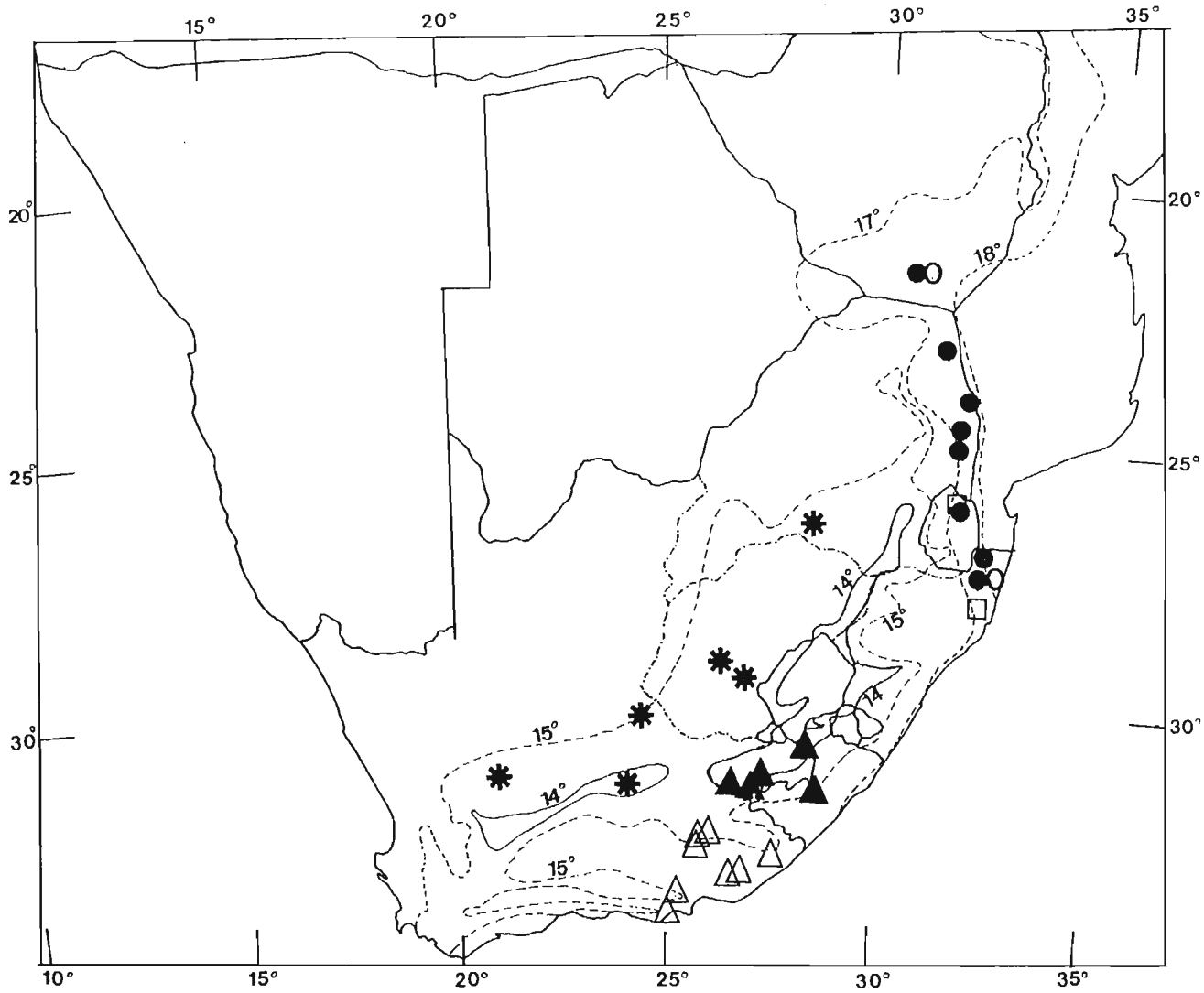
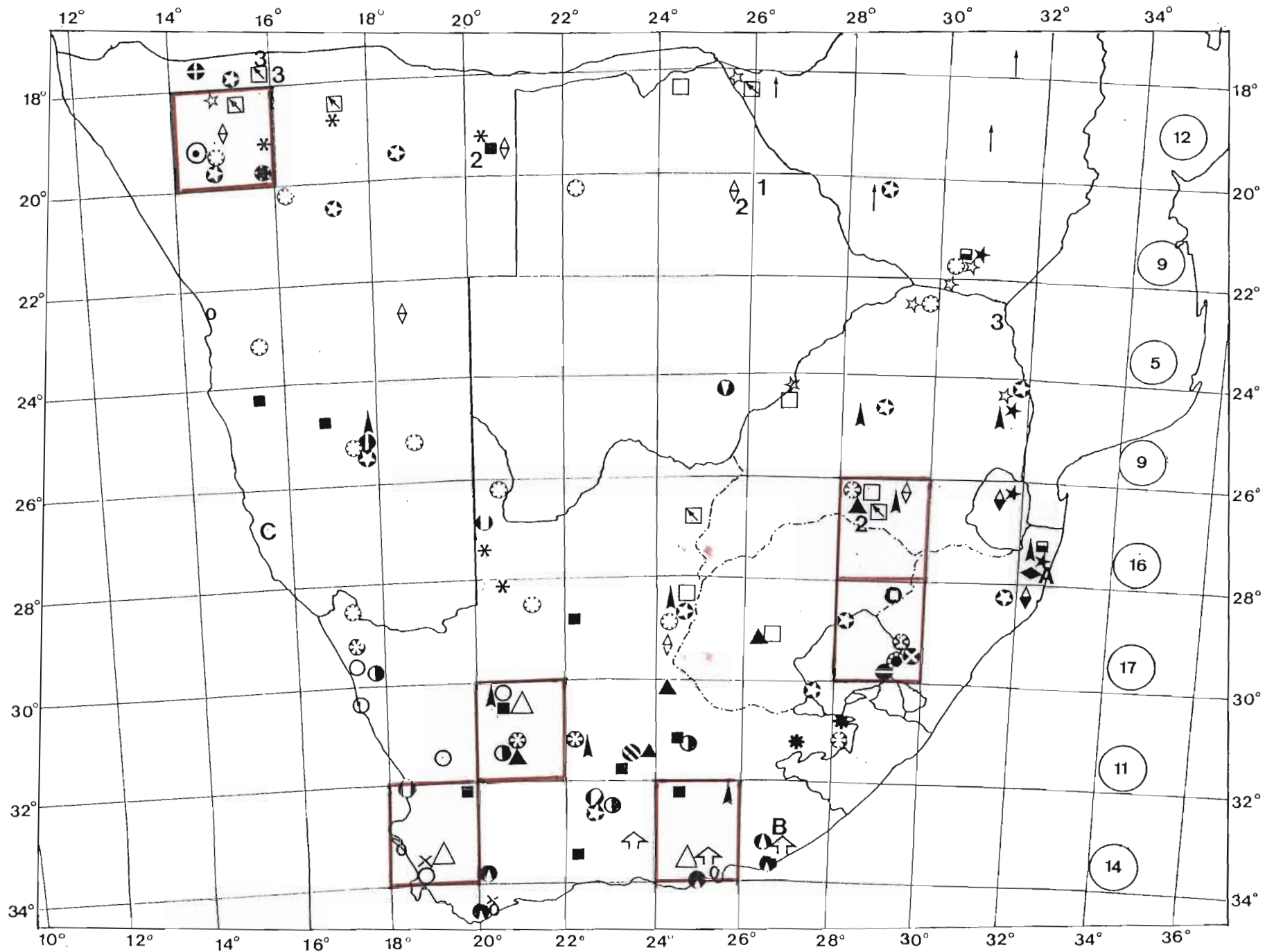


Figure 5. Map of southern Africa showing distribution pattern of biogeographic category 4 "Highveld" species, * *S. cirratus*; category 7 "Eastern Cape Inland" species, △ *S. dregei*, ▲ *S. spinicaudatus*, and category 9, "Tropical/ Subtropical" species, ● *S. bidentatus*, □ *S. bourquinii* and ○ *S. zuluensis*.



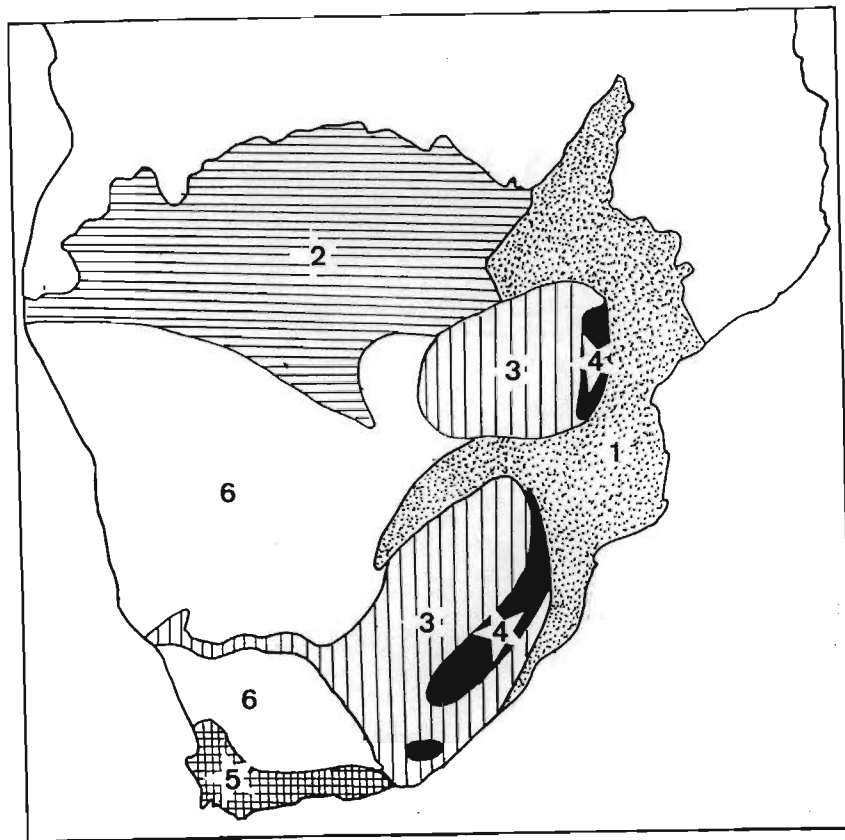


Figure 7. Aquatic ecoregions as presented by Skelton (1993). 1 = Tropical east coast region, including extensions along the Zambezi and Limpopo valleys. 2 = Tropical interior region. 3 = Highveld (temperate) region, which includes two subregions, the interior plateau of Zimbabwe, and the Transvaal-Orange Free State region extending to the coast in southern Natal and Transkei. 4 = Montane-escarpment region, fragmented into "islands". 5 = Cape Fold mountain region. 6 = Kalahari-Karoo-Namib region, generally arid.

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Annexes :
Bijlagen :

No
Nr

Vos réf.
Uw ref.

Date
Datum

9 October, 1992

To whom it may concern:

The African members of the genus Streptocephalus were revised in a series of four manuscripts by Luc Brendonck, University of Ghent (Belgium) and Michelle Hamer of the University of Natal, Pietermaritzburg, South Africa. The revision took the form of two papers on the egg morphology of which Brendonck was senior author, and two papers on adult morphology of which Hamer was senior author. It was agreed that the results of this research would be available for use in the doctoral theses of both students. It has, however, been noticed that the two manuscripts on adult morphology were included as sections XI.4 and XI.5 in the thesis "Study of the biology of large freshwater branchiopods, with special reference to the fairy shrimp Streptocephalus proboscideus (Frauenf.) (Crustacea: Branchiopoda: Anostraca)" submitted by Luc Brendonck in 1992. Michelle Hamer was only very briefly mentioned in the acknowledgements. The omission of a detailed acknowledgement from the thesis was a result of objections made by the co-supervisor to the inclusion of names other than that of his student in the thesis.

In this regard, Luc Brendonck hereby acknowledges that Michelle Hamer was responsible for the following contributions to chapters XI.4 and XI.5 of section XI (part I) of his thesis: Revision of African Streptocephalidae:

1. Examination and measurements of all material
2. All rough sketches
3. Ink figures 7a,d,e,f,g; 8a,b,d,e,f; 10a,b,d,e; 11a,b,d,e,f; 12a,b,d,e; 13a,d,e; 14a,c,d; 15a,c,f; 19a,b,f; 21a,c,e of XI.4 and 2a,c; 3a,c; 4a,c; 5a; 6a; 7a,b,d,e,g,h; 8a,f; 9a,b; 10a,b,c; 11a,b,e; 12a,b,c of XI.5
4. Morphological descriptions for all species revised in XI.4 and XI.5
5. Localities and maps presented in Figs 2-6 of chapter XI.4 and Fig. 1 of XI.5
6. Introductions and discussions of both sections (edited jointly by Hamer and Brendonck)
7. Keys XI.4.6 and XI.5.6
8. Establishment of species groups based on antennal morphology and the allocation of species to these


Dr Luc Brendonck