

Taxonomic revision of the Recent and Holocene representatives of the Family Darwinulidae (Crustacea, Ostracoda), with a description of three new genera

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Abstract

The Darwinulidae, the only surviving family of the superfamily Darwinuloidea, are revised and 28 extant species are retained. Twenty-six species (2 of which as yet formally undescribed) are allocated to 5 genera, 3 of which are here described as new; 2 species have an uncertain position within the family because of their insufficient original description and are listed here as *species inquirendae*. The new genera are characterised on combinations of soft part and valve characters, but the chaetotaxy of the limbs seems most conservative and most suitable for the identification of genera. *Darwinula* s.s. and *Microdarwinula* are, with regard to Recent species, monospecific. *Alicenula* nov.gen. is erected to comprise the 3 species of the former *serricaudata*-group. *Vestalenula* nov.gen. comprises the 8 species of the *pagliolii-boteai* group, as well as *Darwinula danielopoli*, which, together with two undescribed species from Cuba and Tunisia, is placed in a special group within this new genus. *Penthesilenula* nov.gen. comprises two species-groups, with 10 species in total: 7 species in the *incae*-group, exclusively occurring in the southern Hemisphere, and 3 species in the *africana*-group. The latter group also contains *P. malayica* and *P. brasiliensis*, which occur on at least three continents; the latter species appears to have a higher incidence of morphological variability than the other extant darwinulids. The species-groups in the latter two genera are here used for convenience; no taxonomic value should at present be attached to them. Problems related to clonal taxonomy in general are briefly discussed. It is demonstrated that a systematic revision of an ancient asexual lineage can lead to a taxonomy which at the same time reflects natural phylogeny and is workable, i.e. is based on recognisable taxa.

Keywords: Recent Ostracoda, Darwinulidae, morphology, clonal taxonomy, biodiversity, ancient asexuals.

Additional keywords: *Darwinula*, *Microdarwinula*, *Alicenula* gen.nov., *Penthesilenula* gen.nov., *Vestalenula* gen.nov.

Résumé

Les Darwinulidae, unique famille de la superfamille Darwinuloidea ayant survécu, sont révisés et vingt-huit espèces ont été retenues ici. Vingt-six espèces (dont deux non encore décrites formellement) sont attribuées à cinq genres, dont trois ici décrits comme nouveaux; en raison de leur description originale incomplète, deux espèces occupent une position incertaine au sein de la famille et sont présentées ici comme *species*

inquirendae. Les nouveaux genres sont décrits sur la base des combinaisons des parties molles et des caractères des valves, mais la chétotaxie des membres paraît très stable et convient le mieux à l'identification des genres. Concernant les espèces Récentes, *Darwinula* s.s. et *Microdarwinula* sont monospécifiques. *Alicenula* nov.gen. a été érigé afin de contenir les trois espèces de l'ancien groupe *serricaudata*. *Vestalenula* nov.gen. comprend les huit espèces du groupe *pagliolii-boteai*, de même que *D. danielopoli* laquelle est placée, avec deux autres espèces non-décrites de Cuba et de Tunisie, dans un groupe spécial à l'intérieur de ce nouveau genre. *Penthesilenula* nov.gen. comprend deux groupes d'espèces, comptant un total de dix espèces: sept espèces du groupe *incae*, rencontrées exclusivement dans l'Hémisphère Sud, et trois espèces du groupe *africana*. Ce dernier groupe comprend également *P. malayica* et *P. brasiliensis*, que l'on trouve sur trois continents au moins; la fréquence de variabilité morphologique semble être plus élevée chez cette dernière espèce que chez les autres darwinulides existants. Les groupes d'espèces dans les deux derniers genres sont utilisés ici pour des raisons de convenance; aucune valeur taxonomique ne doit leur être attachée pour le moment.

Des problèmes concernant la taxonomie clonale en général sont brièvement discutés. Il est démontré qu'une révision systématique d'un ancien lignage asexué peut conduire à une taxonomie qui non seulement reflète la phylogénie naturelle, mais qui est en même temps réalisable, c.-à-d. basée sur des taxons reconnaissables.

Mots clés: Ostracodes Récents, Darwinulidae, morphologie, taxonomie clonale, biodiversité, anciens asexués.

Mots clés supplémentaires: *Darwinula*, *Microdarwinula*, *Alicenula* gen.nov., *Vestalenula* nov.gen., *Penthesilenula* nov.gen.

Introduction

JUDSON & NORMARK (1996) called the darwinulid ostracods 'ancient asexual scandals'. Several genetic theories dictate that asexual lineages should be short-lived and evolutionary dead ends, but the fossil record indicates that Darwinulidae as a group have persisted for at least 100 Ma, maybe as much as 200 Ma, without sexual reproduction. This makes this group unique, as the only other suspected ancient asexual group are the bdelloid rotifers, but absence of fossils in that lineage hampers estimates of the duration of their persistence as an asexual group (BUTLIN & GRIFFITHS, 1993). Darwinulid

ostracods thus have great potential for research on tempo and mode of biological evolution, without the possibility of generating high genetic variability by recombination. Some important findings have already contributed towards our understanding of this extended persistence of the group. The most common representative, *Darwinula stevensoni*, shows a strikingly low intraspecific morphological and genetic variability and this is assumed to be indicative of a slow molecular evolution in this organism (ROSSETTI & MARTENS, 1996; SCHÖN *et al.* 1998).

Darwinuloidea are exclusively non-marine, but make up less than 5% of the total specific diversity of extant non-marine ostracod faunas (MARTENS, 1998). This strikingly low specific diversity is also indicative of slow evolution, in this case low speciation rates. However, extant biodiversity is the net result of speciation and extinction (on local levels, including immigration) ratios. If this group speciates slowly, then its continued persistence indicates that also extinction rates are low. This will be further discussed below.

The present contribution revises the Recent Darwinulidae, based on both newly collected and known type materials. This work forms the necessary basis for future research projects on this group, and is timely, as identification of darwinulid species and genera was up to now very difficult (sometimes impossible), and this for several reasons. Firstly, original descriptions were often incomplete or even simply wrong. Whenever possible, types were therefore checked and are here re-described. In a number of cases, types had to be assumed lost or were damaged (e.g. when valves are kept in glycerine, details of the internal anatomy had disappeared) and certain characters in some species thus still remain unknown. Secondly, darwinulids in general are very small and important morphological characters are often detectable under powerful magnifications only; therefore, in some cases, details of limbs and valves were observed with SEM. Finally, because of the slow evolutionary rate in this group, morphological differences between species are often small, albeit constant. Taxonomic appraisal of an ancient asexual lineage requires the application of somewhat different species concepts (see below).

Most genera and species can now unequivocally be characterised and identified. The data matrix with morphological characteristics derived from the present revision has been used for a cladistic analysis, the result of which confirms our taxonomic decision to allocate most of *Darwinula* s.l. to new genera. These cladistic results will, together with the molecular-based phylogeny, be presented elsewhere.

Abbreviations used in text and figures

L: left; R: right; Le: length; W: width; H: height; V: valve; Cp: carapace; Cms: central muscle scar(s); dv: dorsal view; vv: ventral view; lv: lateral view; iv: internal view; ev: external view; A1: Antennula; A2: Antenna; Md: Mandibula; Mx: Maxillula; T1-3: thoracic limbs; P-abd: Postabdomen; Fu: Furca; h: hook-like process on

A2; exo: exopodite on A2; Ac: ventral aesthetasc clump on A2; pd: 'poil darwinuloïde'; ps: 'poil stevensoni'; a, b, c, α , s_{1-3} , t, w, x, y, z: specific setae on limbs; γ_{1-3} : aesthetascs on A2.

Nomenclature proposed by DANIELOPOL (1970), and adapted by ROSSETTI & MARTENS (1996) and ROSSETTI *et al.* (1996), is used in the description of chaetotaxy of soft parts. Recent evidence has shown that the Maxilla is missing in Ostracoda and that there are three thoracopods (SMITH & MARTENS, in press, MEISCH, in prep.). We follow this view.

Material used for the present revision is listed in appendices to this paper.

Taxonomic descriptions

Class	Ostracoda LATREILLE, 1806
Subclass	Podocopa G.W. MÜLLER, 1894
Order	Podocopida SARS, 1866
Suborder	Podocopina SARS, 1866
Infraorder	Darwinulocopina SOHN, 1988
Superfamily	Darwinuloidea BRADY & NORMAN, 1889
Family	Darwinulidae BRADY & NORMAN, 1889 syn.: Microdarwinulidae KASHEVAROVA & NEUSTRUEVA, 1982

Diagnosis

Small- to medium-sized ostracods (0.4-0.8 mm), elongate, sub-squarish or rounded in lv. Hinge adont or with medial groove, anterior and posterior cardinal teeth on RV, cardinal ridge and sockets on LV, valve margins without selvages or (continuous) inner or outer lists, fused zones very narrow with few straight and very short marginal pore canals. Some groups with a ventro-caudal keel on RV (remnant of outer list), or with internal ventral or caudal teeth on LV (remnants of inner list), other taxa devoid of any such features. All species (except in *Microdarwinula*) with brooding cavity. Cms arranged in a rosette or in two parallel vertical rows.

Eye present. A2 without natatory setae. Md and Mx with large respiratory plates. First thoracopod (called Maxillula in lit.) a maxilliped, with three-segmented palp. Second and third thoracopod walking limbs. Fu, if present, reduced to single seta. P-abd present or absent.

Remarks

1. The phylogenetic scheme presented below supports the view that the family Microdarwinulidae KASHEVAROVA & NEUSTRUEVA, 1982 is not a natural entity and constitutes a synonym of Darwinulidae.

2. Small details of the chaetotaxy (e.g., "sclerotization" of appendages, presence of setulae, barbulate setae, spines, hirsute parts, etc.) will not be discussed here as they are mostly at the limit of observation with light microscopy and are scarcely workable for diagnostic purposes.

Ecology and distribution

This group occurs worldwide and in all climatic zones. Although in general not very common, the species can be found in a wide range of habitats, including lakes, rivers, springs, groundwater, etc., but also in more marginal biotopes such as (semi-) terrestrial habitats. Drought-resistant stages (present in both other non-marine lineages, Cytheroidea and Cypridoidea) have not yet been described for Darwinulidae.

Genera and species

Five genera are here distinguished on both valve and soft part features: the type genus *Darwinula* BRADY & ROBERTSON, *Microdarwinula* DANIELOPOL, while three new genera, *Alicenula* nov.gen., *Vestalenula* nov.gen. and *Penthesilenula* nov.gen., are here described. The genus *Vestalenula* nov.gen. is divided into two species-groups: the *boteai* and *danielopoli* groups; *Penthesilenula* nov.gen. comprises the *incae* and the *africana* groups. These species-groups will be used in this revision for convenience; at present, no taxonomic rank should be allocated to them. Species-groups and lineages previously proposed by MARTENS & ROSSETTI (1997), MARTENS *et al.* (1997) and ROSSETTI *et al.* (1998) are now encompassed into the Linnean hierarchy presented below.

Two new synonymies are here proposed. Firstly, based on the study of the type material, it could unequivocally be demonstrated that *Darwinula sphenoides* ROME from Lake Kivu is a junior synonym of *Darwinula stevensoni* BRADY & ROBERTSON. Secondly, the discovery of a specimen of *Penthesilenula brasiliensis* (PINTO & KOTZIAN) from South Africa with double Fu, indicates that *Darwinula dicastrii* LÖFFLER, described from South America, is in all probability a junior synonym of *P. brasiliensis*. Both synonymies are more extensively discussed below.

Darwinula managuensis SWAIN & GILBY, 1965 and *D. yaquensis* SWAIN, 1967 are here listed as doubtful species, as the incomplete original description does not allow us to determine the exact generic position of these species within the family, nor even their validity as independent species (see below). Two as yet not formally described, but most likely valid, species are also listed (DANIELOPOL, 1980).

In all, 28 extant species of the family Darwinulidae are to date recognised.

Key to the genera – valves only

- 1 a. Cp rounded in lv, no externally visible brood pouch *Microdarwinula*
 b. Cp elongate or sub-squarish in lv, with externally visible brood pouch 2
- 2 a. RV without postero-ventral keel, LV with or without internal teeth 3
 b. RV with postero-ventral keel, LV with antero-ventral internal tooth *Vestalenula*

- 3 a. LV without internal teeth 4
 b. LV with internal teeth *Penthesilenula*
- 4 a. RV overlapping LV, $Le > 0.65$ mm *Darwinula*
 b. RV overlapping LV or LV overlapping RV, $Le \leq 0.65$ mm *Alicenula*

Key to the genera – valves and soft parts

- 1 a. Cp rounded in lv, no externally visible brood pouch *Microdarwinula*
 b. Cp elongate or sub-squarish in lv, with externally visible brood pouch 2
- 2 a. RV without postero-ventral keel, LV with or without internal teeth. A1 with two dorsal setae on first segment; second segment with one dorso-apical seta and three ventral setae. A2 expodite with two setae and a spine 3
 b. RV with postero-ventral keel, LV with antero-ventral internal tooth. A1 with one dorsal seta on first segment; second segment with two ventral setae, dorso-apical seta absent. A2 expodite with one seta and a spine *Vestalenula*
- 3 a. LV without internal teeth. Last segment of Md-palp with less than five claws (three or four), penultimate segment with seta *y* short or absent 4
 b. LV with internal teeth. Last segment of Md-palp with five claws, penultimate segment with seta *y* long *Penthesilenula*
- 4 a. RV overlapping LV, $Le > 0.65$ mm. Second segment of A1 endopodite with two large dorsal setae. Md-palp, penultimate segment with seta *z* long, seta *y* short; last segment with 'poil *stevensoni*'; setae *a* and *b* present *Darwinula*
 b. RV overlapping LV or LV overlapping RV, $Le \leq 0.65$ mm. Md-palp, penultimate segment with seta *z* short, seta *y* absent; last segment without 'poil *stevensoni*', seta *a* absent *Alicenula*

Genus *Darwinula* BRADY & ROBERTSON in JONES, 1885
syn. Polycheles BRADY & ROBERTSON, 1870
syn. Darwinella BRADY & ROBERTSON, 1872

Type species (by original designation):
Polycheles stevensoni BRADY & ROBERTSON, 1870

DIAGNOSIS

Elongate and rather large (c 0.7 mm) darwinulids, without internal teeth in the LV and without ventral keel on the

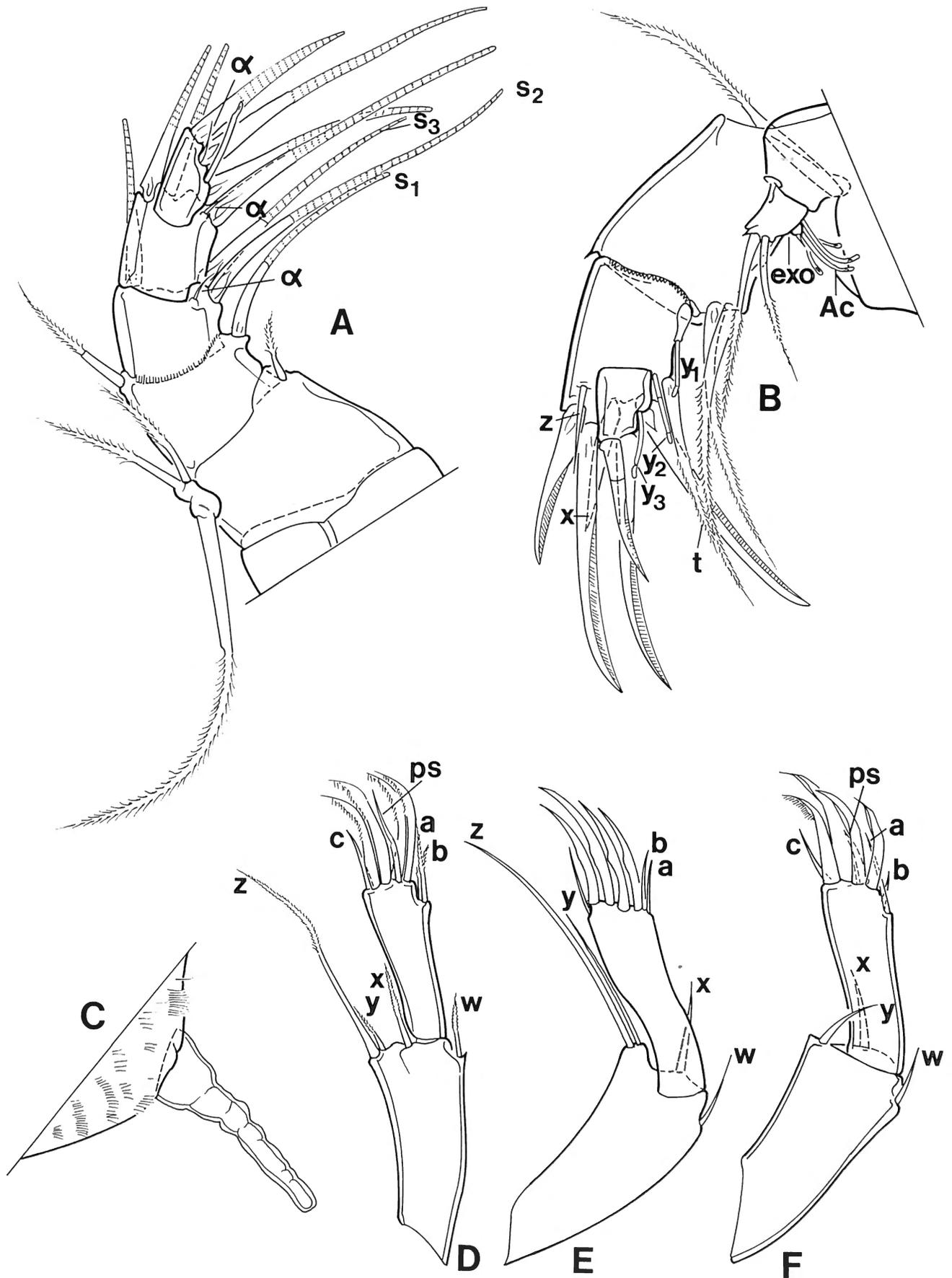


Fig. 1. - *Darwinula stevensoni* BRADY & ROBERTSON. A-D: Lake Pääjärvi, Finland; E, F: Lake Kivu, Zaire.
 A. A1 (OC1824). B. A2 (idem). C. P-abd (OC1822). D. Md-palp, endopodite (OC1825). E. Md-palp, endopodite (from ROME & DEDECKER, 1977, Pl. 5, Fig. H). F. Md-palp, endopodite, seta z missing (I.G.25.476 - OC766B).

RV. Hinge adont. Valves with R/L overlap. Dorsal margin evenly sloping, not rounded or straight over part of its length. Cms always situated towards the front in adult specimens. Large caudal brooding cavity externally visible. In frontal view, LV and RV almost symmetrical, not oblique. First segment of A1 with two dorsal setae, second segment with one dorsal and three ventral setae; fourth segment of endopodite with two dorsal setae. A2 with two long setae and a spine on exopodite; first endopodal segment with two ventro-apical setae. Seta *y* much shorter than seta *z* on penultimate Md-palp segment. Penultimate segment of T1 palp with two setae. P-abd present. Fu absent in adults, present in juveniles.

REMARKS

Due to the description of three new genera (see below), *Darwinula* s.s. is now, as far as extant fauna is concerned, monospecific. The present diagnosis is therefore much more restricted than before (SOHN, 1987; 1988). As all five genera presently recognised are characterised on both soft part and valve features, it should be possible to allocate at least the Mesozoic and the Cenozoic species of the former *Darwinula* s.l. to one of these genera, but this will be discussed elsewhere.

DISTRIBUTION

The single species in this genus, *Darwinula stevensoni*, has a cosmopolitan distribution.

1. *Darwinula stevensoni* BRADY & ROBERTSON, 1870
(Figs 1A-F, 24D, 27A-D)

- Argilloecia aurea* BRADY & ROBERTSON, 1870 (partim)
Polycheles stevensoni BRADY & ROBERTSON, 1870
Darwinella stevensoni (BRADY & ROBERTSON, 1870) BRADY & ROBERTSON, 1872
Darwinula stevensoni (BRADY & ROBERTSON, 1870) BRADY & ROBERTSON, 1885
Darwinula improvisa (TURNER, 1895) G.W. MÜLLER, 1912 (partim)
Darwinula aurea (BRADY & ROBERTSON, 1870) G.W. MÜLLER, 1912 (partim)
Darwinula protracta ROME, 1953 (syn. in ROSSETTI & MARTENS, 1996)
Darwinula variabilis TAGLIASACCHI, 1968 (syn. in ROSSETTI & MARTENS, 1996)
Darwinula sphenoides ROME, 1977 **nov.syn.**

TYPE LOCALITY

Somerton Broad, Norfolk, England (see SOHN, 1987); other original localities reported by BRADY & ROBERTSON (1870).

LECTOTYPE

Female Cp, Hancock Museum (Newcastle-upon-Tyne) no. 1.56.08 (designated by SOHN, 1987).

DIAGNOSIS

Valves pearly white, with smooth surface and widely spaced setae; RV overlapping LV on all sides except at the hinge. Seen ventrally, shell ovoid, posterior part rounded, forming a brood chamber, anterior part pointed; margin of the RV sinuous anteriorly and straight at the posterior 3/5; greatest width at about 2/3 of the length. In lateral view, shell elongate, greatest height in the posterior quarter; posterior margin more broadly rounded than the anterior one, the latter more pointed and slightly curved towards the ventral side; ventral margin almost straight, dorsal margin gently curved. Central ms consisting of 9-12 spots arranged in a circular rosette. First segment of A1 with two dorsal setae and one ventro-apical seta, second segment with one dorsal and three ventral setae; fourth segment with two large dorsal setae (*s*₂ and *s*₃). A2 exopodite with unequal bristles, one half as long as the other one. Second segment of Md-palp bearing four terminal setae, three short (*y*, *x* and *w*) and one larger (*z*), the latter reaching beyond the tip of the next segment; third segment with four apical claws, two subterminal setae (*a* and *b*) and two terminal setae, one shorter (*c*) and the other wider in the first half (*ps*). Penultimate segment of T1 palp with two setae of equal length. Fu absent in adult specimens. P-abd conical, vermiform.

MEASUREMENTS

ROSSETTI & MARTENS (1996), based on measurements of 30 specimens from Finland, Belgium and Italy: RV: Le=686-771 µm, H=288-322 µm. LV: Le=669-746 µm, H=263-305 µm.

LITERATURE

Redescriptions in PINTO & SANGUINETTI (1958), SOHN (1987), ROSSETTI & MARTENS (1996), ROSSETTI *et al.* (in press). Biology and ecology in SCHEERER-OSTERMAYER (1940), MCGREGOR & WETZEL (1968), MCGREGOR (1969), RANTA (1979), SOHN (1990), MBAHINZIREKI *et al.* (1991), GRIFFITHS & BUTLIN (1994).

REMARKS

Synonymies of *D. protracta* ROME, 1953 and *D. variabilis* TAGLIASACCHI, 1968 with *D. stevensoni* are discussed in ROSSETTI & MARTENS (1996). We propose here to consider *D. sphenoides* ROME, 1977 a synonym of *D. stevensoni*. To distinguish *D. sphenoides* from other congeners with RV overlapping LV (*D. stevensoni* and *D. protracta*), ROME

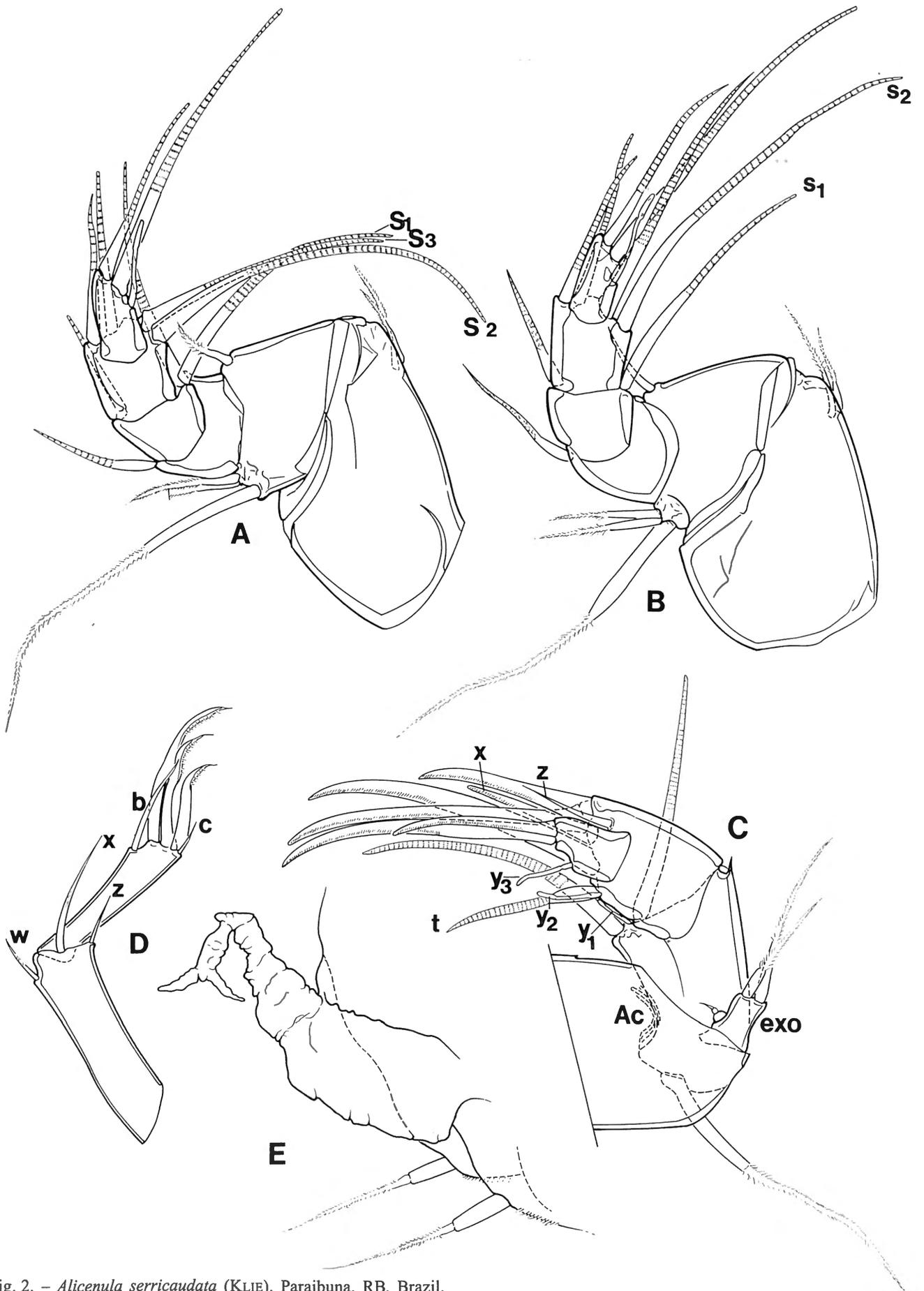


Fig. 2. – *Alicenula serricaudata* (KlIE). Paraibuna, RB, Brazil.

A. A1 (OC2157). B. A1, seta s_3 missing (OC2156). C. A2 (idem). D. Md-palp, endopodite (idem). E. Fu and P-abd (idem).

& DEDECKER (1977 : 256) took into account the following taxonomic characters: number of spots in the Cms; number of claws in the last two segments of A2 endopodite; chaetotaxy of Md-palp. The number of spots in the Cms (according to ROME & DEDECKER (*loc. cit.*), 9 in *D. stevensoni*, 10 in *D. sphenoides* and 11 in *D. protracta*) cannot be regarded as a valid specific character in Darwinulidae (ROSSETTI & MARTENS, 1996; WAKEFIELD, 1996). ROME's comparison of the A2 morphology of *D. sphenoides* with that of *D. stevensoni* was inadequate, since it was based on the inexact description of the chaetotaxy of the latter species by KLIE (1935 : 60). Finally, re-analysis of the type material of *D. sphenoides* from Lake Kivu (Zaire) allowed us to ascertain that in the ROME's description of the Md-palp of *D. sphenoides* (Pl. 5, Fig. H) setae *y* and *a* are incorrectly drawn and the seta *ps* was missed (Fig. 1F). In general, no apparent differences in chaetotaxy between *D. sphenoides* and *D. stevensoni* exist. We therefore consider these taxa as synonyms.

2. One specimen of *Darwinula stevensoni* from Lake Montorfano (Italy) presented anomalous T1 with asymmetrical limbs, while all other appendages, as well as valves, showed a normal morphology (ROSSETTI & MARTENS, 1996, Fig. 7). This specimen has been considered an isolated case of teratology.

Genus *Alicenula* nov.gen.

Type species (here designated):

Darwinula serricaudata KLIE, 1935

Other species allocated

D. furcabdominis, *D. inversa*

DERIVATION OF NAME

The little girl Alice, from *Alice in Wonderland* and *Through the looking glass*, managed to escape the Red Queen, much like the ancient asexual darwinulids seem to escape the effects of Muller's Ratchet, mutation load and, indeed, the Red Queen! This is of course also a tribute to Alice's creator, Lewis Carroll.

DIAGNOSIS

Elongate darwinulids, without internal teeth in the LV and without ventral keel on the RV. Hinge adont. Le mostly c 0.6 mm. Valves with R/L or with L/R overlap. Dorsal margin evenly sloping, not rounded or straight over part of its length. Cms always situated towards the front in adult specimens. Large caudal brooding cavity externally visible. First segment of A1 with two dorsal setae, second segment with one dorso-apical seta and three ventral setae. A2 with two long setae and a spine on exopodite; first endopodal segment with two ventro-apical setae. Seta *y* on penultimate segment of Md-palp absent. Adults with Fu. P-abd mostly large and "spinuous".

DIFFERENTIAL DIAGNOSIS

The new genus is distinguishable by the presence of a large and "spinuous" P-abd. From all other genera, except *Darwinula*, it can be distinguished by the absence of internal teeth on the LV and further from *Vestalenula*, by the absence of an external postero-ventral keel on the RV. The new genus can be distinguished from *Darwinula* primarily on soft part features, mainly in the Md-palp and by the presence of a Fu in the adults. Two out of three species have a R/L overlap unlike *D. stevensoni*, all species are significantly smaller than the latter taxon.

KEY TO THE SPECIES

- | | |
|--|-------------------------|
| 1 a last segment of Md-palp with three apical claws, seta <i>c</i> present | 2 |
| b last segment of Md-palp with four apical claws, seta <i>c</i> absent | <i>A. furcabdominis</i> |
| 2 a LV overlapping RV | <i>A. serricaudata</i> |
| b RV overlapping LV | <i>A. inversa</i> |

2. *Alicenula serricaudata* (KLIE, 1935)

(Figs 2A-E, 24A-C, 27E)

syn. *D. serricaudata espinosa* PINTO & KOTZIAN, 1961 (in MARTENS & ROSSETTI 1997).

TYPE LOCALITY

Different localities in Ivory Coast (Tourni, Danané, Man, at km 43 on road from Odienné to Touba, at km 100 on road from Odienné to Bougouni). Coll. on various dates between 04.02.1931 to 30.03.1931 by C. ALLAUD and P.A. CHAPPUIS.

HOLOTYPE

Not designated. Syntypes: Zoologisches Museum der Universität Kiel CR-292; 1434 (presently at the Zoologisches Museum Hamburg).

DIAGNOSIS

Medium-sized darwinulid. Cp elongate; in lv, dorsal margin markedly sloping towards the front. Hinge adont. LV overlapping RV on all sides. Postero-ventral keel on RV and internal teeth in LV absent. Cms consisting of 6 large spots. First segment of A1 with two dorsal setae; second segment with one dorso-apical seta and three ventral setae, two short, subequal, and one longer; third segment with one dorsal and one ventral seta; fourth segment with one ventral seta and one or two dorsal setae (see below).

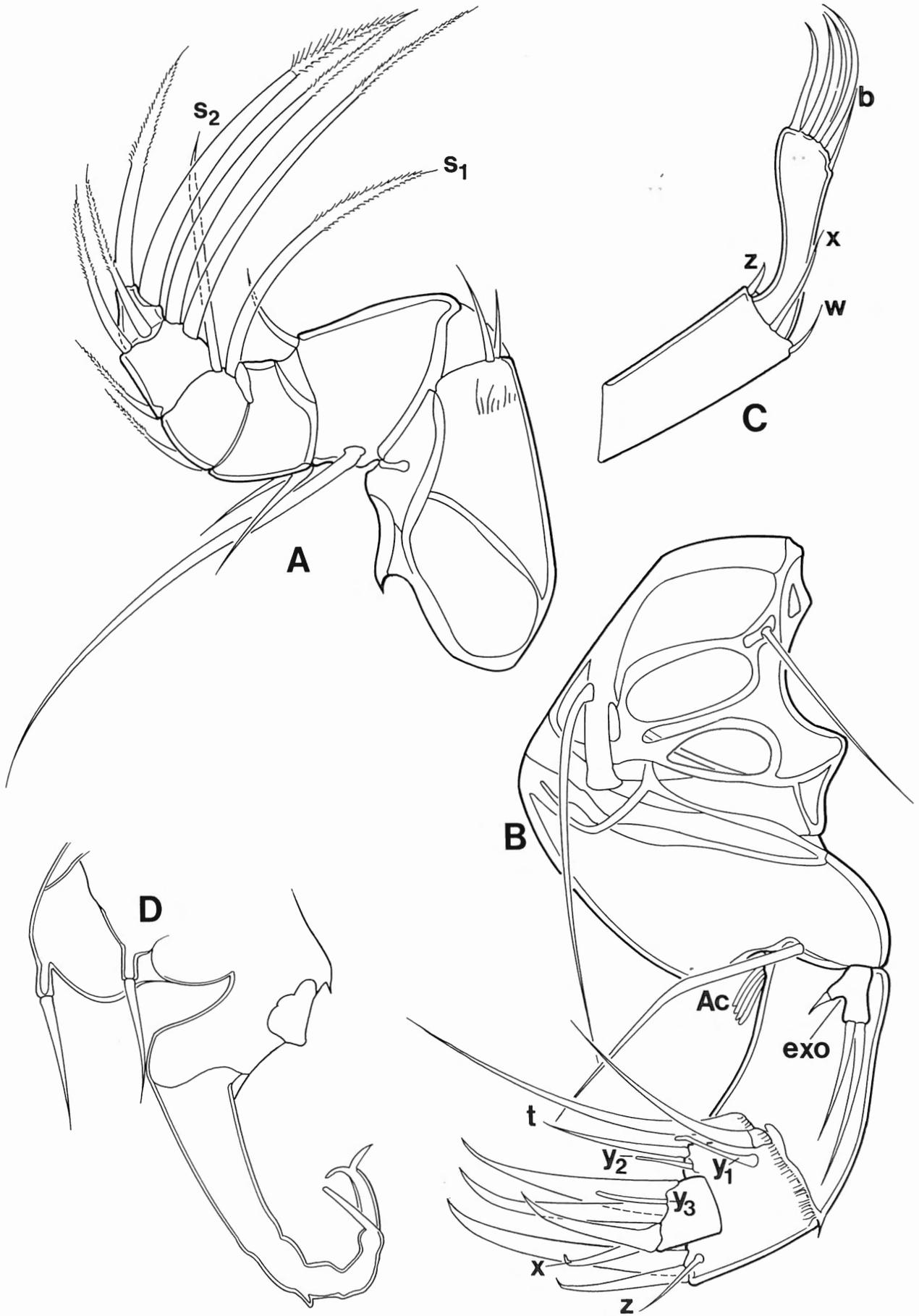


Fig. 3. - *Alicenula furcabdominis* (KEYSER). Everglades National Park, Florida. From KEYSER (1975, Pl. 6).
 A. A1. B. A2. C. Md-palp, endopodite. D. Fu and P-abd.

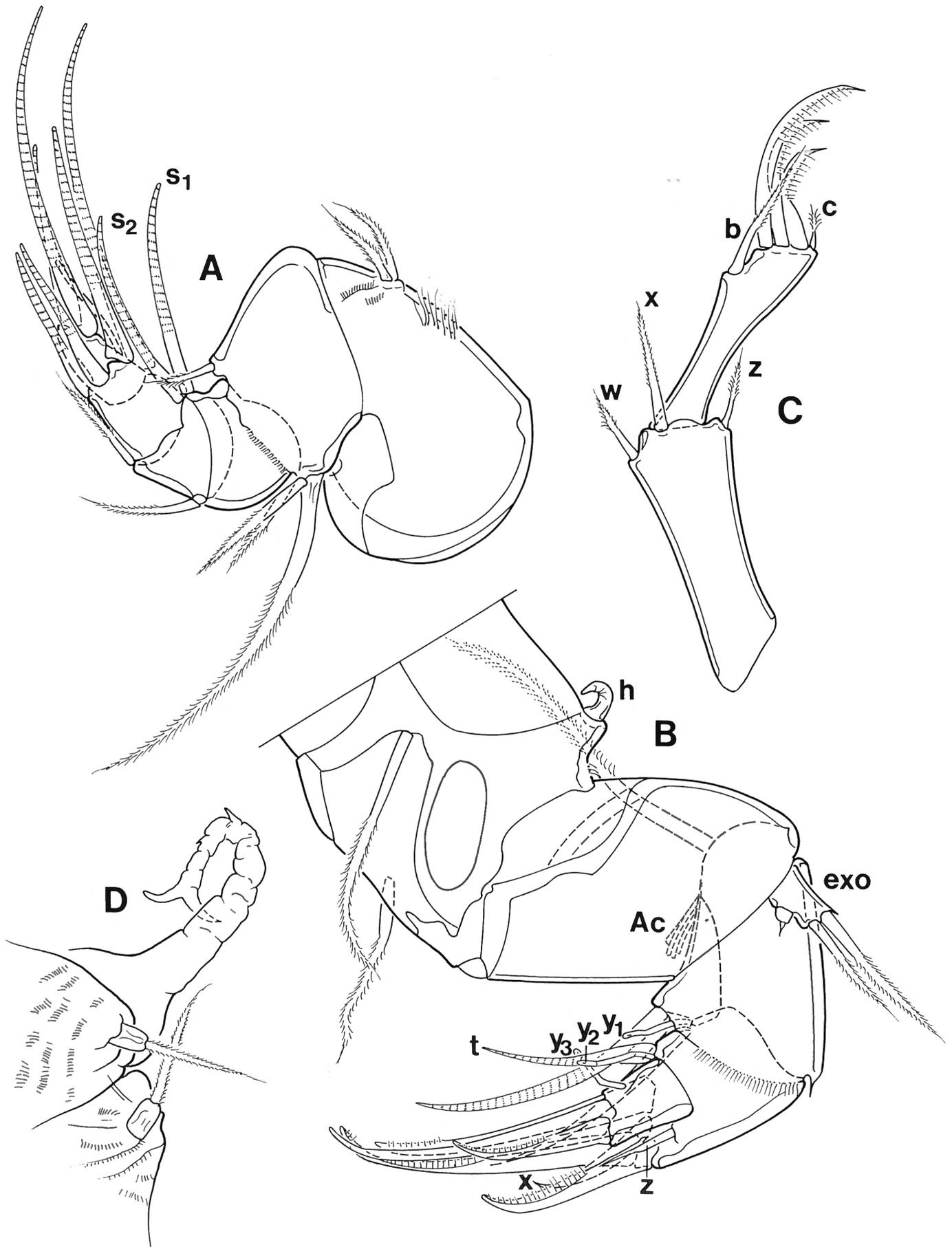


Fig. 4. - *Alicenula inversa* (MARTENS & ROSSETTI). Molopo, North West Province, RSA.
 A. A1 (OC2117). B. A2 (OC2116). C. Md-palp, endopodite (idem). D. Fu and P-abd (OC2112).

A2 exopodite with two setae and a short lateral spine; first segment of endopodite with two ventro-apical setae. Penultimate segment of Md-palp with two short lateral setae (*w* and *z*) and one medial seta (*x*), the latter twice as long as the former ones; seta *y* absent. Terminal segment of Md-palp bearing three distal claws, a small internal seta (*c*) and a sub-terminal external seta (*b*); seta *a* absent. P-abd elongate, curved and distally bifurcate, set with few small spine-like expansions. Fu consisting of a narrow base bearing a hirsute distal seta.

MEASUREMENTS

KLIE (1935): Le=0.62 mm, W=0.22 mm, H=0.23 mm.
PINTO & KOTZIAN (1961): Le=0.49-0.57 mm, W=0.22 mm, H=0.18-0.22 mm.

LITERATURE

KLIE (1935); PINTO & KOTZIAN (1961); MARTENS & ROSSETTI (1997).

REMARKS

In the original description of *Darwinula serricaudata*, KLIE (1935) did not describe the morphology of the A1. PINTO & KOTZIAN (1961) figured the A1 of *D. serricaudata espinosa* from Rio Grande do Sul (Brazil) with one dorsal seta (*s*₁) on the second endopodal segment. In all the investigated specimens from Paraibuna (R.B., Brazil), we found two dorsal setae (*s*₂ and *s*₃) on the second segment of A1 endopodite, except one specimen in which seta *s*₃ was absent (Fig. 2B). We are therefore inclined to consider such differences as a variation occurring in *Alicenula serricaudata*.

3. *Alicenula furcabdominis* (KEYSER, 1975) (Figs 3A-D, 24E, 27F,G)

TYPE LOCALITY

North River, Everglades National Park, Florida, USA.
Approximate coordinates: 80°54'20"W, 25°20'30"N.

HOLOTYPE

Universität Hamburg (Germany), Zoologisches Museum, no. K 30328. *Remark*: Dr D. KEYSER (Hamburg) kindly sent some paratypes of his species for examination. Some valves in this collection belong to the *incae*-group of *Penthesilenula* nov.gen., as they possess the typical internal teeth on the LV. As no soft parts of these specimens were available, their specific status cannot be determined; in any case it constitutes the northernmost locality of this lineage.

DIAGNOSIS

Medium-sized darwinulid. In lv, Cp elongate, dorsal margin evenly sloping towards the front; posterior and anterior ends broadly rounded. LV overlapping RV. LV without internal teeth, RV without keel. Hinge adont. Cms with c 7 spots. First segment of A1 with two dorsal setae, second segment with three ventral setae and one dorsal seta; third and fourth segments with one dorsal and one ventral seta each. A2 exopodite with a short spine and two setae of different length; first endopodal segment carrying two large dorsal setae. Penultimate segment of Md-palp with seta *z* very reduced, seta *x* c twice as long as seta *w*, seta *y* absent; last segment with four distal claws and seta *b* in sub-apical position, setae *a* and *c* absent. Penultimate segment of T1 palp with one seta. Fu a seta with a short cylindrical base. P-abd a long and curved process with a barbed end.

MEASUREMENTS

KEYSER (1975): RV: Le=0.50-0.52 mm, H=0.21 mm;
LV: Le=0.49-0.51 mm, H=0.20-0.21 mm.

LITERATURE

KEYSER (1975).

4. *Alicenula inversa* (MARTENS & ROSSETTI, 1997) (Figs 4A-D, 27H-K)

TYPE LOCALITY

Dolomitic spring at Marico Oog, Molopo Oog area, North West Province (former Transvaal), RSA. Approximate coordinates: 25°47'30"S, 26°22'10"E. Coll. 01.11.1993 by K. MARTENS.

HOLOTYPE

Albany Museum (Grahamstown, RSA), no. AM-TDW-7A.

DIAGNOSIS

Medium-sized darwinulid. Cp elongate, posterior part moderately enlarged. Valves unequal, RV overlapping LV on all sides. Postero-ventral keel on RV and internal teeth in LV absent. Central ms with 6-7 spots arranged in a circular rosette. First segment of A1 with two dorsal setae, second segment with one dorsal seta and three ventral setae, two short, subequal, and one longer; third and fourth segments with one dorsal and one ventral seta each. A2 exopodite with two long setae and a short lateral spine; first segment of endopodite with two ventro-apical setae. Penultimate segment of Md-palp with two short

lateral setae (*w* and *z*) and one medial seta (*x*), the latter twice as long as the former ones; seta *y* absent. Terminal segment of Md-palp bearing three distal claws, a small internal seta (*c*) and a sub-terminal external seta (*b*); setae *a* absent. P-abd elongate, curved and distally bifurcate, set with few small spine-like expansions. Fu consisting of a narrow base bearing a hirsute distal seta.

MEASUREMENTS

MARTENS & ROSSETTI (1997): Le=510-520 µm (n=3), W=200-210 µm (n=2), H=210 µm (n=1).

LITERATURE

MARTENS & ROSSETTI (1997).

REMARKS

One specimen of *A. inversa* from the type locality presented asymmetrical T3, one limb being normal and one aberrant, the latter with two subapical, ventral setae on the last endopodal segment. No differences from the normal form were observed in either remaining soft parts or valve shape (see MARTENS & ROSSETTI, 1997, Fig. 2J).

Genus *Vestalenula* nov.gen.

Type species (here designated):

Darwinula boteai DANIELOPOL, 1970.

DERIVATION OF NAME

Named after the Vestals, six virgins dedicated to a life of chastity, who tended the sacred fire kept perpetually burning in the temple of Vesta (Goddess of the hearth) in Rome.

DIAGNOSIS

Small darwinulids, with valves elongate or short and subquadrate. RV with a postero-ventral, external keel, the latter short (*boteai* group) or elongate (*danielopoli* group). LV with long or short internal antero-ventral tooth, no caudal or caudo-ventral internal teeth. Hinge adont. Le mostly c 0.6 mm or less. Valves with L/R overlap. Dorsal margin straight over part of its length. Cms always situated towards the front in adult specimens. Large caudal brooding cavity externally visible.

First segment of A1 with one dorsal seta, second segment with two ventral setae; fourth segment without ventro-apical seta. A2 with one long setae and a spine on exopodite. Seta *y* on penultimate Md-palp segment short; last segment with five apical claws. Adults mostly with Fu (exception: *V. inconspicua*?), P-abd smooth or absent.

DIFFERENTIAL DIAGNOSIS

The new genus is primarily characterised by the presence of a postero-ventral external keel and by a unique set of soft part characters, mainly in the A1 and A2. From *Darwinula* and *Alicenula* nov.gen. it can further be distinguished by the size and the presence of a large antero-ventral internal tooth in the LV; from *Penthesilenula* nov.gen. further by the absence of caudal or postero-ventral internal teeth in the LV and from *Microdarwinula* by the presence of an externally visible brood pouch and a straight (not rounded) dorsal margin.

REMARKS

For a number of species allocated to this genus, the diagnostic characteristics of the valves are not known, because the original description does not mention them or because the types are either lost or with decalcified valves. These species are placed in this genus based on soft part characters; future collections of new material will falsify these allocations.

OTHER SPECIES ALLOCATED

D. cuneata, *D. daps*, *D. inconspicua*, *D. marlieri*, *D. molopoensis*, *D. lundi*, *D. pagliolii*, *D. danielopoli*.

KEY TO THE SPECIES

- | | |
|--|-----------------------|
| 1 a. keel on RV short (<i>boteai</i> -group) | 2 |
| b. keel on RV elongate (<i>danielopoli</i> -group) | <i>V. danielopoli</i> |
| 2 a. P-abd present | 3 |
| b. P-abd absent | 7 |
| 3 a. Le/H ratio >2.2 | 4 |
| b. Le/H ratio <2.2 | 5 |
| 4 a. in lv, valves sub-squarish with dorsal margin straight | <i>V. lundi</i> |
| b. in lv, valves sloping with rounded dorsal margin | <i>V. marlieri</i> |
| 5 a. first segment of A1 endopodite with one ventro-apical seta, first segment of A2 endopodite with two ventro-apical setae | <i>V. pagliolii</i> |
| b. first segment of A1 endopodite without ventro-apical seta, first segment of A2 endopodite with one ventro-apical seta | 6 |
| 6 a. P-abd elongate, Fu consisting of a widened base (Le=3xW) carrying a seta | <i>V. boteai</i> |
| b. P-abd conical, Fu consisting of a widened base (Le=1.5xW) carrying a seta | <i>V. molopoensis</i> |
| 7 a. size >0.60 mm | <i>V. daps</i> |
| b. size <0.60 mm | 8 |

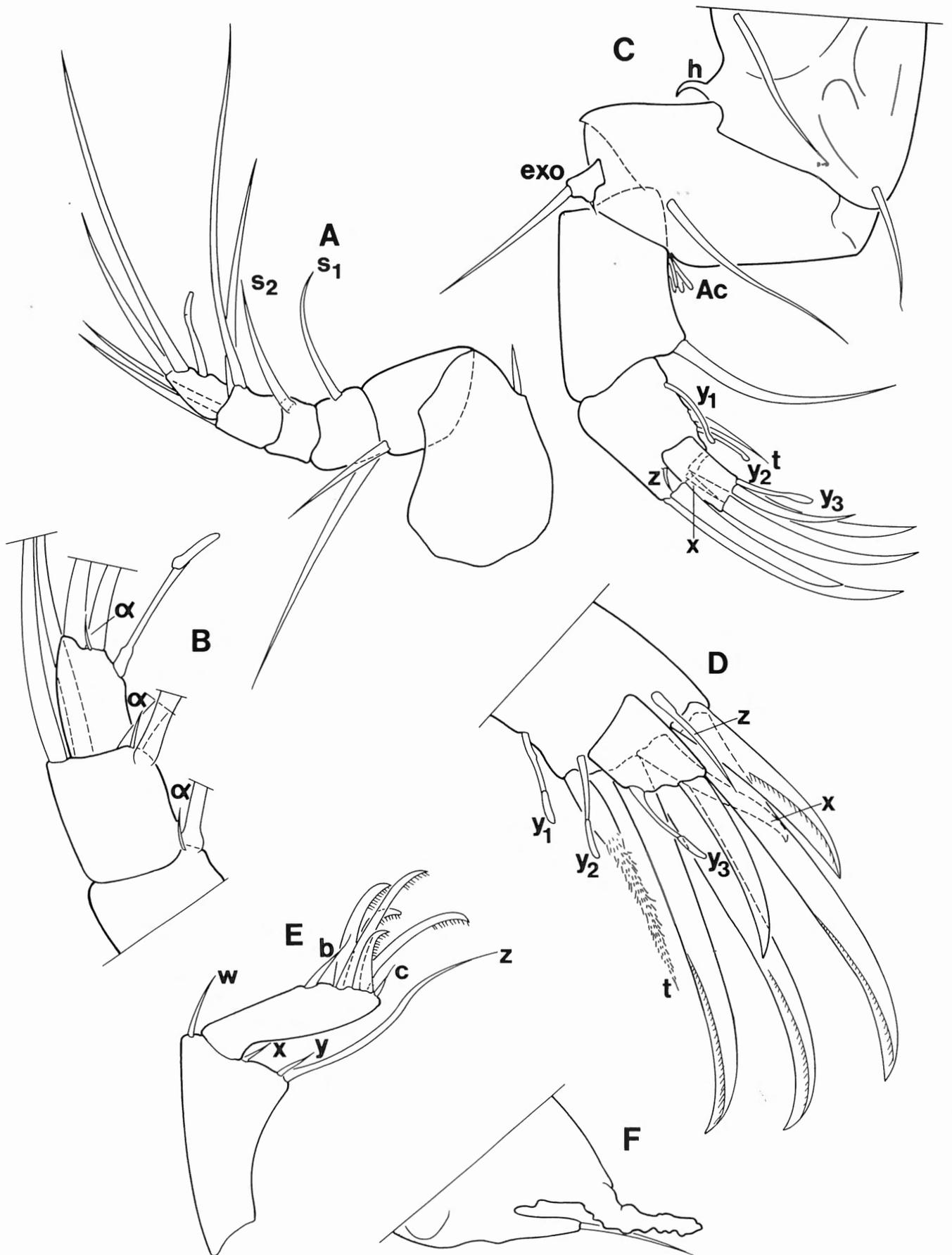


Fig. 5. – *Vestalenula boteai* (DANIELOPOL). River Mraconia, Rumania. From DANIELOPOL (1970).
 A. A1 (fig. 2A). B. A1, detail (fig. 2B). C. A2 (fig. 2D). D. A2, detail (fig. 2D). E. Md-palp, endopodite (detail of fig. 1D).
 F. Fu and P-abd (fig. 1F).

- 8 a. penultimate segment of Md-palp with seta
z short, last segment without seta c *V. inconspicua*
b. penultimate segment of Md-palp with seta
z long, last segment with seta c *V. cuneata*

I. The *boteai*-group

CHARACTERISTICS

Antero-ventral internal tooth on LV and external ventral keel on RV both rounded and short.

5. *Vestalenula boteai* (DANIELOPOL, 1970) (Figs 5A-F, 25A-C, 27L,M)

TYPE LOCALITY

Interstitial of river Mraconia, 2 km from confluence with river Danube, at c 25 km W of Orsova, Dept. Caras-Severin, Rumania. Approximate coordinates: 44°42'N, 22°20'E. Coll. F. BOTEAI (25.10.1968), D. TABACARU and D.L. DANIELOPOL (06.10.1969).

HOLOTYPE

Not designated. Material deposited in the following collections: Speleological Institute "E. Racovitza" (Bucharest, Rumania); Museum of Natural History "G. Antipa" (Bucharest, Rumania); British Museum (Natural History) (London, UK), R.B.I.N.Sc. (Brussels, Belgium).

DIAGNOSIS

Elongate valves ($Le > 2 \times H$), with dorsal margin straight over c half the length and running parallel to ventral margin; $LV > RV$ in dv. RV with a small and rounded (not elongate) postero-ventral keel, ventro-caudal valve margin in this valve inwardly displaced. LV with a small antero-ventral internal tooth; postero-ventral tooth missing. A1 with one dorsal seta on first segment; second segment with two ventral setae, dorso-apical seta absent. A2 exopodite with one long and one short spine-like seta; first endopodal segment of A2 with one large ventro-apical seta. Fu and P-abd present.

MEASUREMENTS

From figures in DANIELOPOL (1970): LV: $Le = 0.42$ mm, $H = 0.19$ mm; RV: $Le = 0.41$ mm, $H = 0.17$ mm; $W = 0.19$ mm. New measurements: LV: $Le = 455$ μ m, $H = 197$ μ m; RV: $Le = 425$ μ m, $H = 191$ μ m (LV and RV belong to different specimens).

LITERATURE

DANIELOPOL (1970); MARTENS *et al.* (1997).

6. *Vestalenula cuneata* (KLIE, 1939) (Figs 6A-C, 25D-F)

TYPE LOCALITY

Moss spring at the foot of Kikuyu, near Maji ya Moto, Kenya. Coll. 17.11.1932 by P.A. CHAPPUIS.

HOLOTYPE

Universität Hamburg (Germany), Zoologisches Museum, no. 294.

DIAGNOSIS

Cp sub-squarish in lv, maximum height at the posterior third; dorsal margin decidedly leaning forward in the anterior half. LV overlapping RV. Cms consisting of c 12 spots arranged in a rather oval rosette. A1 with one dorsal seta on the first segment and two ventral setae on the second one; third and fourth segments with one dorsal seta each. A2 exopodite with one large seta; first endopodal segment with one ventro-apical seta. Penultimate segment of the Md-palp with seta z long and seta y very short; second segment bearing five claws and a short seta (c) distally and one seta (b) in sub-apical position. Penultimate segment of T1 palp with one seta. Fu a seta slightly longer than its relatively broad base. Posterior part of the body short and broadly rounded; P-abd absent.

MEASUREMENTS

KLIE (1939): $Le = 0.46$ mm, $W = 0.23$ mm, $H = 0.23$ mm.

LITERATURE

KLIE (1939).

REMARKS

The type material does not provide additional information on valve morphology; as the carapaces are stored in glycerine, they are completely decalcified.

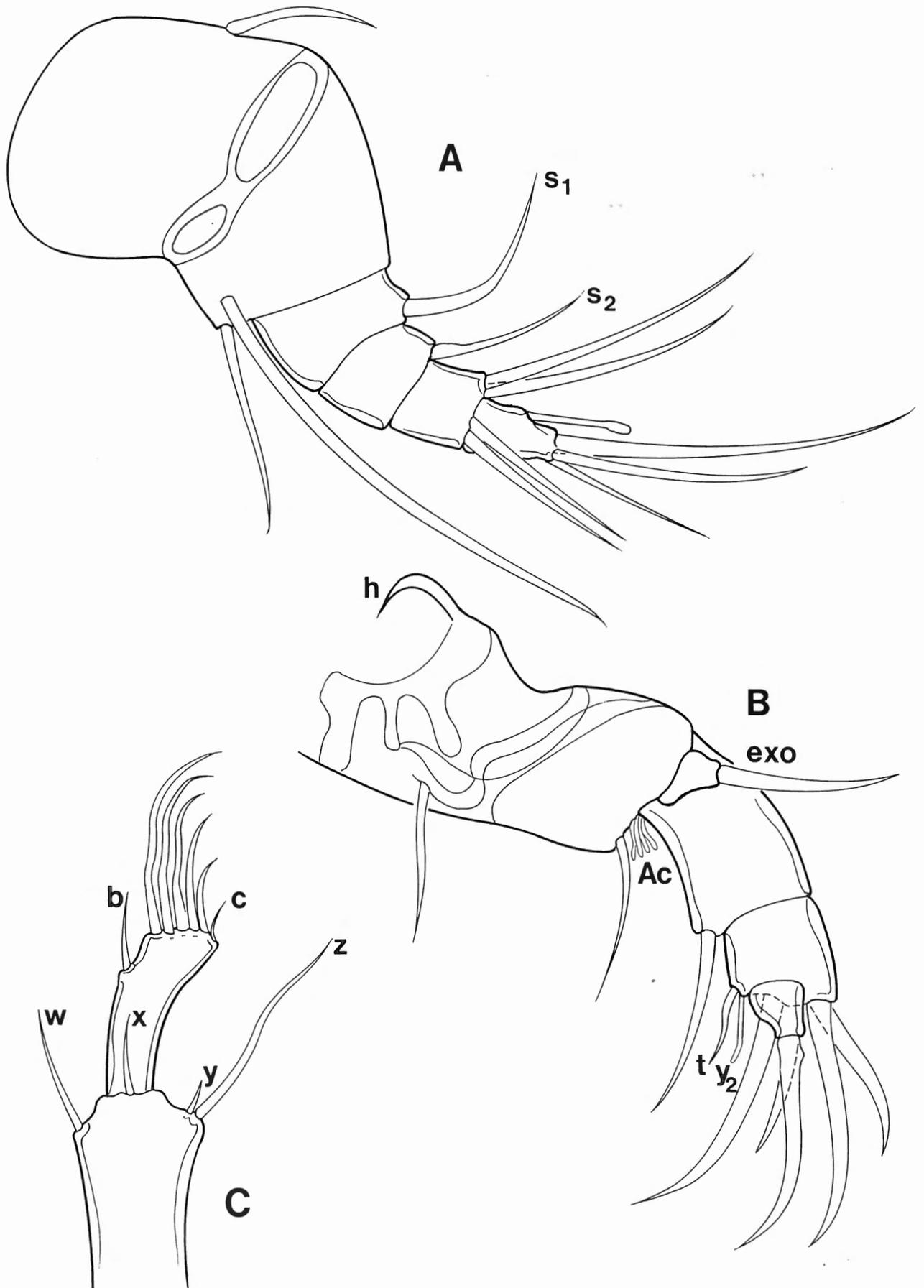


Fig. 6. - *Vestalenula cuneata* (KLIE). Kikuyu, Kenya. From KLIE (1939).
 A. A1 (fig. 69). B. A2 (fig. 70). C. Md-palp, endopodite (fig. 71).

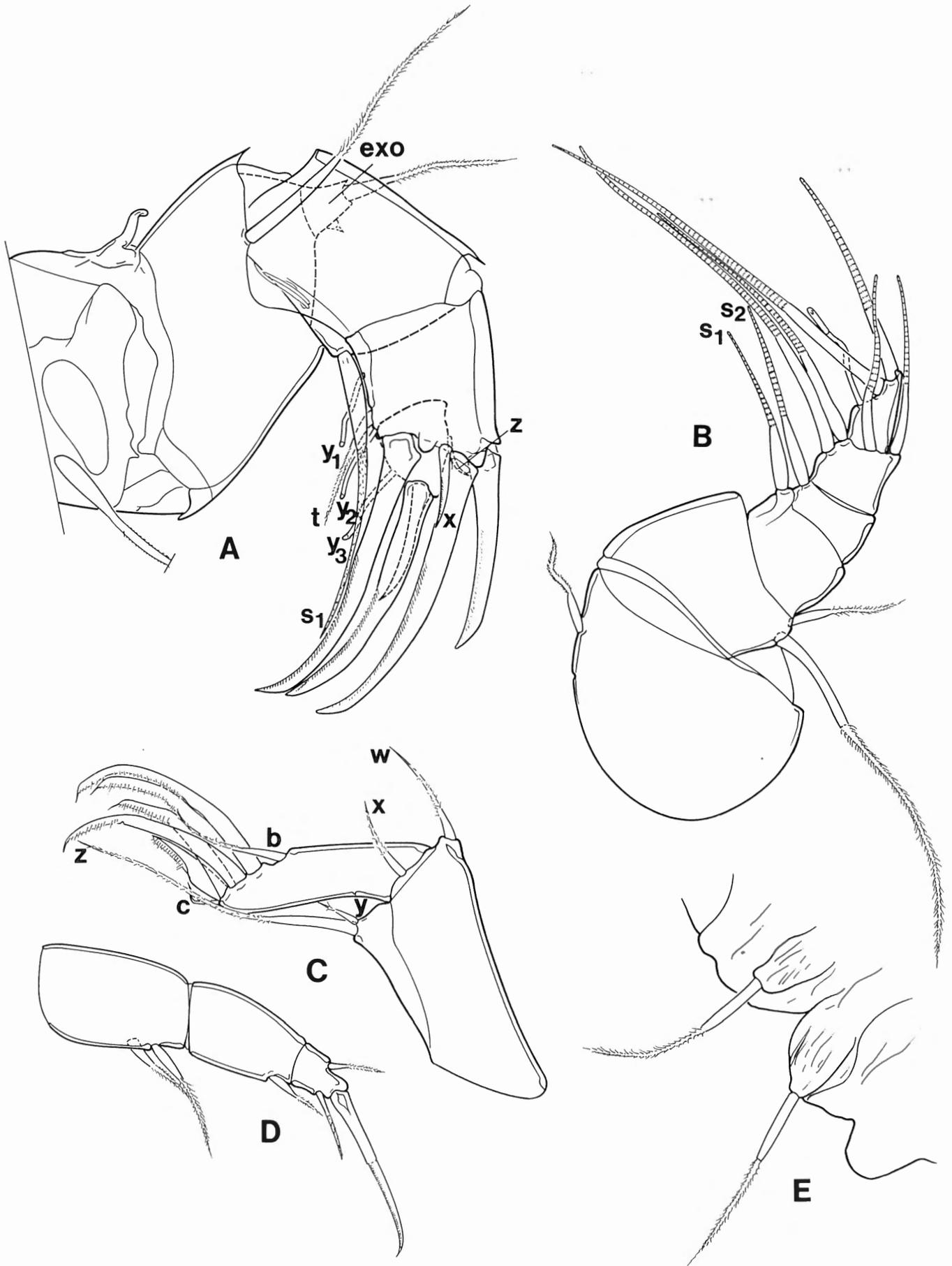


Fig. 7. – *Vestalenula daps* (HARDING). Lake Te-Nggano, Rennel Island, Solomon Islands. Type material.
 A. A1. B. A2. C. Md-palp, endopodite. D. T1, endopodite. E. Fu and Abdomen.

7. *Vestalenula daps* (HARDING, 1962)
(Figs 7A-E, 25G,H)

TYPE LOCALITY

Found in the stomachs of the fish *Eleotris fusca*, caught in Lake Te-Nggano (the largest saline lake in the Pacific - salinity 4.56‰), Rennel Island, Solomon Islands. Coll. 23.10.1951 by T. WOLFF.

HOLOTYPE

Zoological Museum (Copenhagen, Denmark), no. CRU-2651.

DIAGNOSIS

Cp ovoid; in lv; valves relatively high and decidedly sloping, maximum height behind the middle, posterior margin more broadly rounded than the anterior one, the latter with a more pronounced bend; LV overlapping RV at both ends. First segment of A1 with one dorsal seta, second segment with two ventral setae, the shorter one less than 1/3

the length of the other one; third and fourth segments with one dorsal seta each. A2 exopodite with one seta and a short spine; first endopodal segment carrying one large ventro-apical seta. Penultimate segment of Md-palp with seta *y* short and seta *z* long; last segment with five terminal claws, a short internal seta (*c*) and an external seta (*b*). Penultimate segment of T1 palp with a sub-apical seta. Fu consisting of an enlarged base bearing a seta. P-abd absent.

MEASUREMENTS

HARDING (1962): Le=0.63 mm, W=0.33 mm, H=0.30 mm.

LITERATURE

HARDING (1962).

REMARKS

The type material consists of two dissected specimens with soft parts in sealed slides and seven specimens stored in alcohol, the latter with decalcified valves.

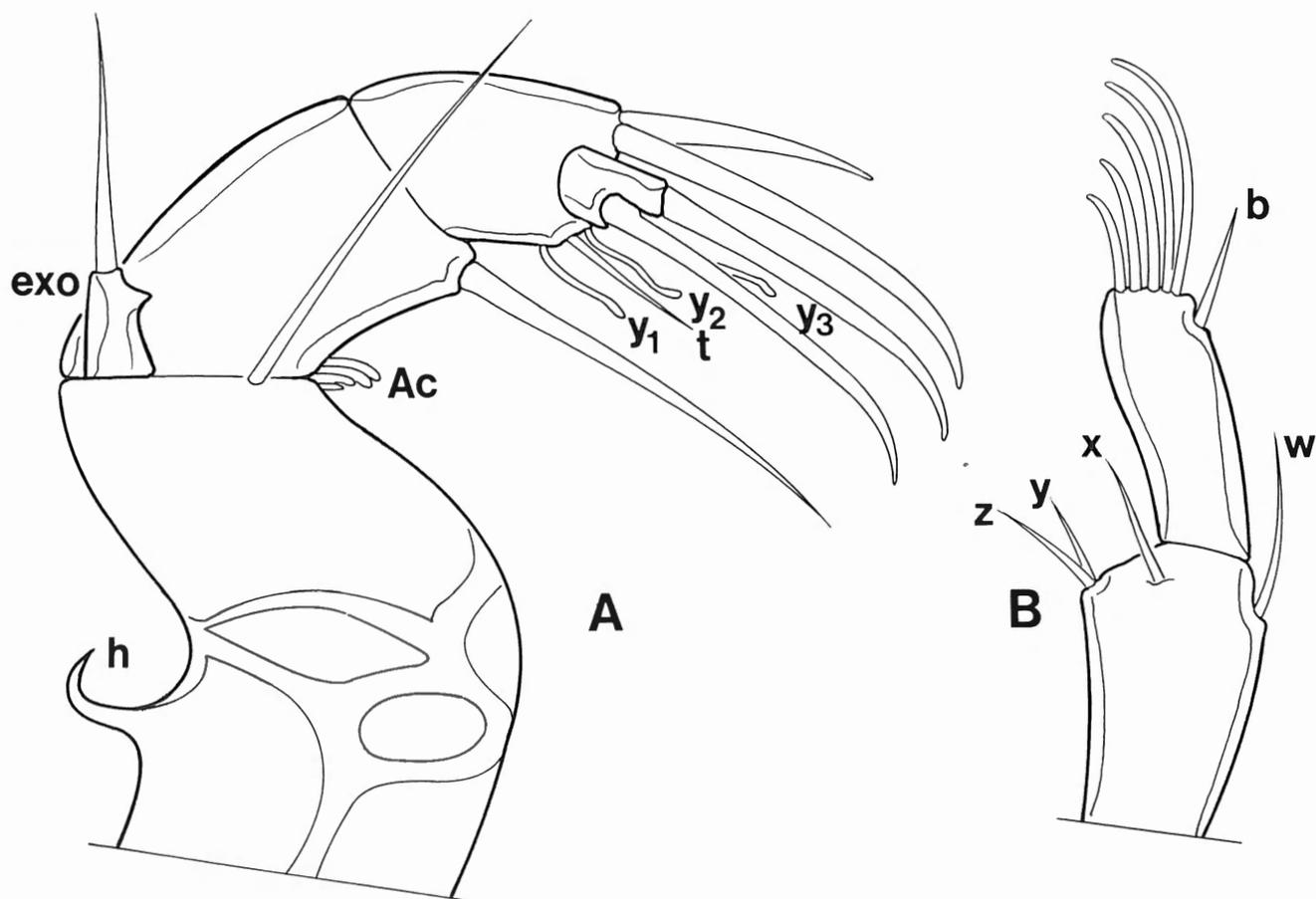


Fig. 8. - *Vestalenula inconspicua* (KLIE). Bandama river, Ivory Coast. From KLIE (1935).
A. A2 (fig. 51). B. Md-palp, endopodite (fig. 52).

8. *Vestalenula inconspicua* (KLIE, 1935)
(Figs 8A,B, 25I,J)

TYPE LOCALITY

Rocky banks of the Bandama river, Ivory Coast. Coll. 14.02.1931 by C. ALLAUD and P.A. CHAPPUIS.

HOLOTYPE

Zoologisches Museum der Universität Kiel CR-293 (presently at the Zoologisches Museum Hamburg).

DIAGNOSIS

Small-sized valves, sub-squarish in lv, maximum height at the posterior third, dorsal margin evenly sloping towards the front; LV overlapping RV; Cms with c 6 spots. A2 exopodite with one seta and a lateral spinula; first segment of endopodite carrying one ventro-apical seta. Setae *y* and *z* on the first segment of Md-palp both short; second segment with five terminal claws, setae *a* and *c* absent. Fu and P-Abd absent.

MEASUREMENTS

KLIE (1935): Le=0.46 mm, H=0.23 mm.

LITERATURE

KLIE (1935).

REMARKS

The type material of *Darwinula inconspicua* has not been investigated. The above description is based on the descriptions and illustrations by KLIE (1935).

9. *Vestalenula lundi* (NEALE & VICTOR, 1978)
(Figs 9A-D, 25N-P)

TYPE LOCALITY

Sandy riverbank with coarse gravel in Sabaragamuwa Province, Sri Lanka. Approximate coordinates: 6°49'N, 80°22'E. Coll. 09.02.1962 by P. BRINK, H. ANDERSON and L. CEDERHOLM.

HOLOTYPE

British Museum (Natural History) (London, UK), no. 1977.76.

DIAGNOSIS

Small-sized darwinulid. Cp elongate; in lv, sub-squarish with posterior end broadly rounded and dorsal margin decidedly sloping towards the front. LV overlapping RV; hinge adont. Number of spots in the ms unknown. RV without keel; internal teeth in LV absent. First segment of A1 with one dorsal seta, second segment with two ventral setae; third and fourth segments carrying one dorso-apical seta each. A2 exopodite with one large seta; first segment of endopodite with one ventro-apical seta. Penultimate segment of Md-palp with seta *y* short and seta *z* long; last segment with five terminal claws and a subterminal external seta (*b*). Fu consisting of a conical base bearing a seta. P-abd as a widened, smooth process.

MEASUREMENTS

NEALE & VICTOR (1978): Le=0.40 mm, W=0.21 mm, H=0.17 mm.

LITERATURE

NEALE & VICTOR (1978).

REMARKS

1. The original description of chaetotaxy of *V. lundi* by NEALE & VICTOR (1978 : 1084, Figs 7-12), is incorrect for several characters; which is why the type material is re-illustrated here (Fig. 9).

2. Due to the decalcification of valves, the type material does not allow a definitive assessment on presence or absence of a ventral keel on RV and internal teeth on LV.

10. *Vestalenula marlieri* (KISS, 1959)
(Figs 10A-E, 25K-M)

TYPE LOCALITY

Luhanga stream, northern extremity of the Lake Tanganyika, Zaire. Coll. 22.06.1958 by G. MARLIER.

HOLOTYPE

Royal Museum for Central Africa (Tervuren, Belgium), no. R.G. 50330.

DIAGNOSIS

Small-sized darwinulid; in lv, valves sloping, greatest height at the posterior third; in dv, Cp pear-shaped; LV

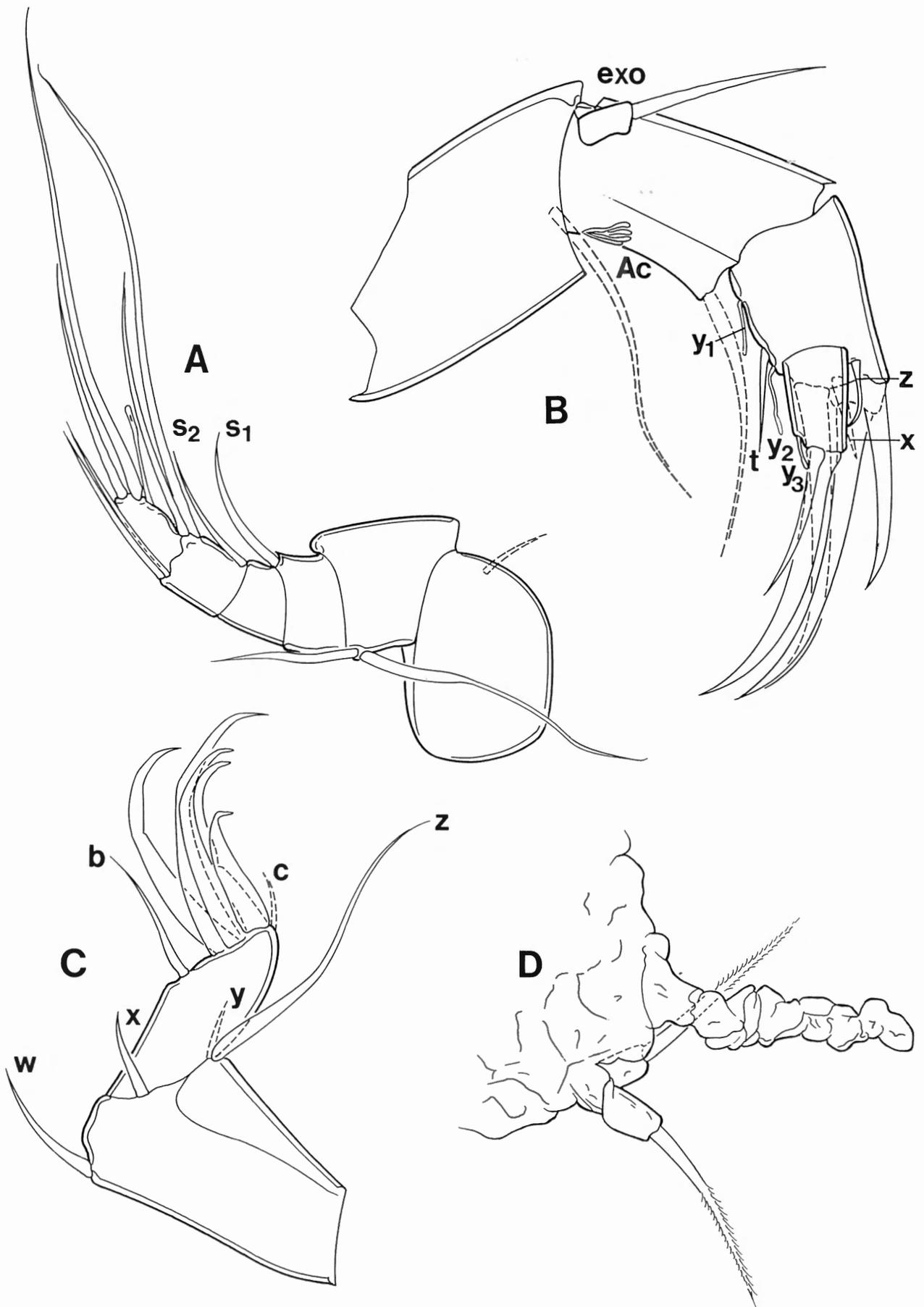


Fig. 9. – *Vestalenula lundi* (NEALE & VICTOR). Sabaragamuwa Province, Sri Lanka. Type material. A. A1. B. A2. C. Md-palp, endopodite. D. Fu and P-abd.

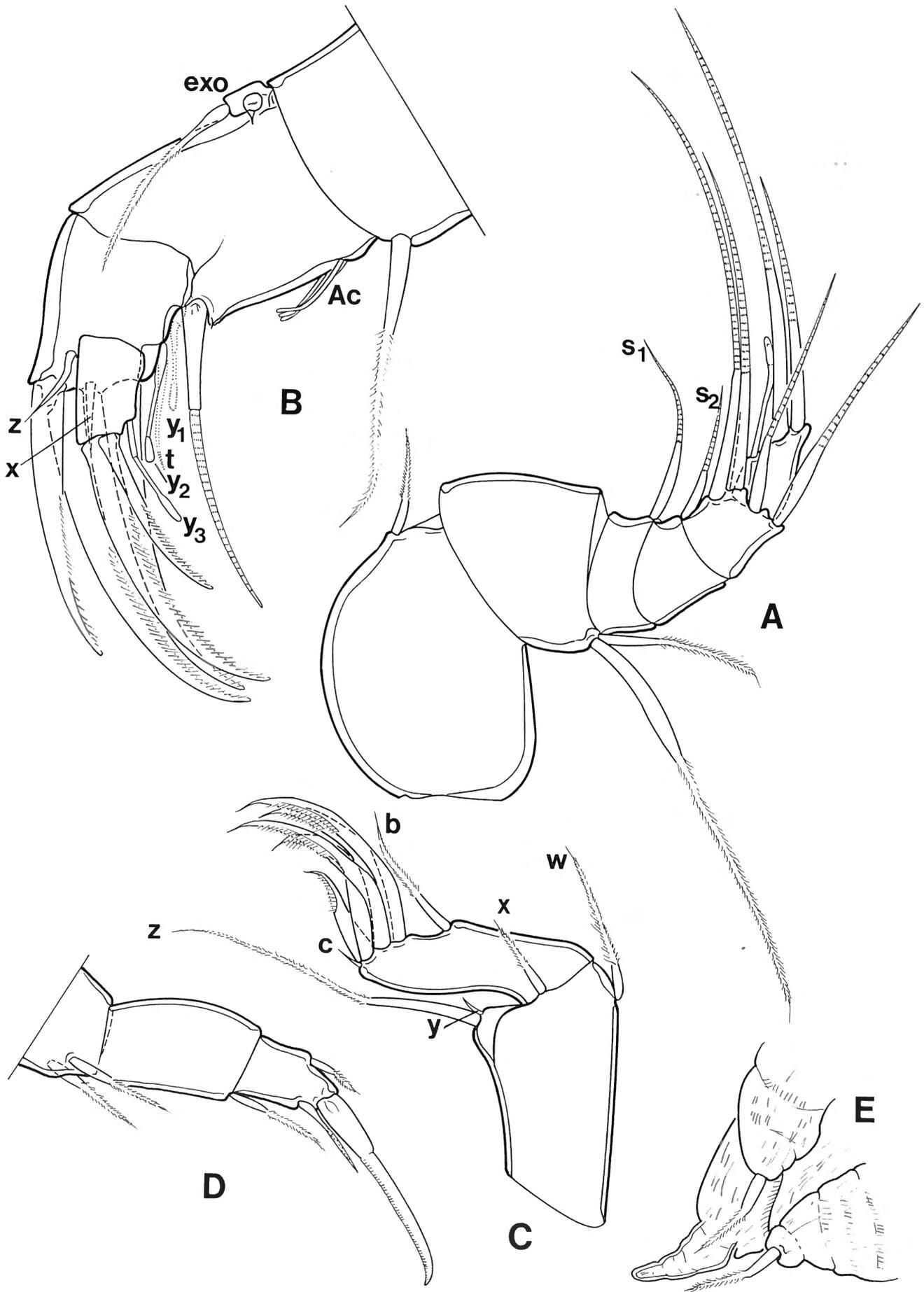


Fig. 10. – *Vestalenula marlieri* (KISS). Luhanga stream, Zaire. Type material.
 A. A1. B. A2. C. Md-palp, endopodite. D. T1, endopodite. E. Fu and P-abd.

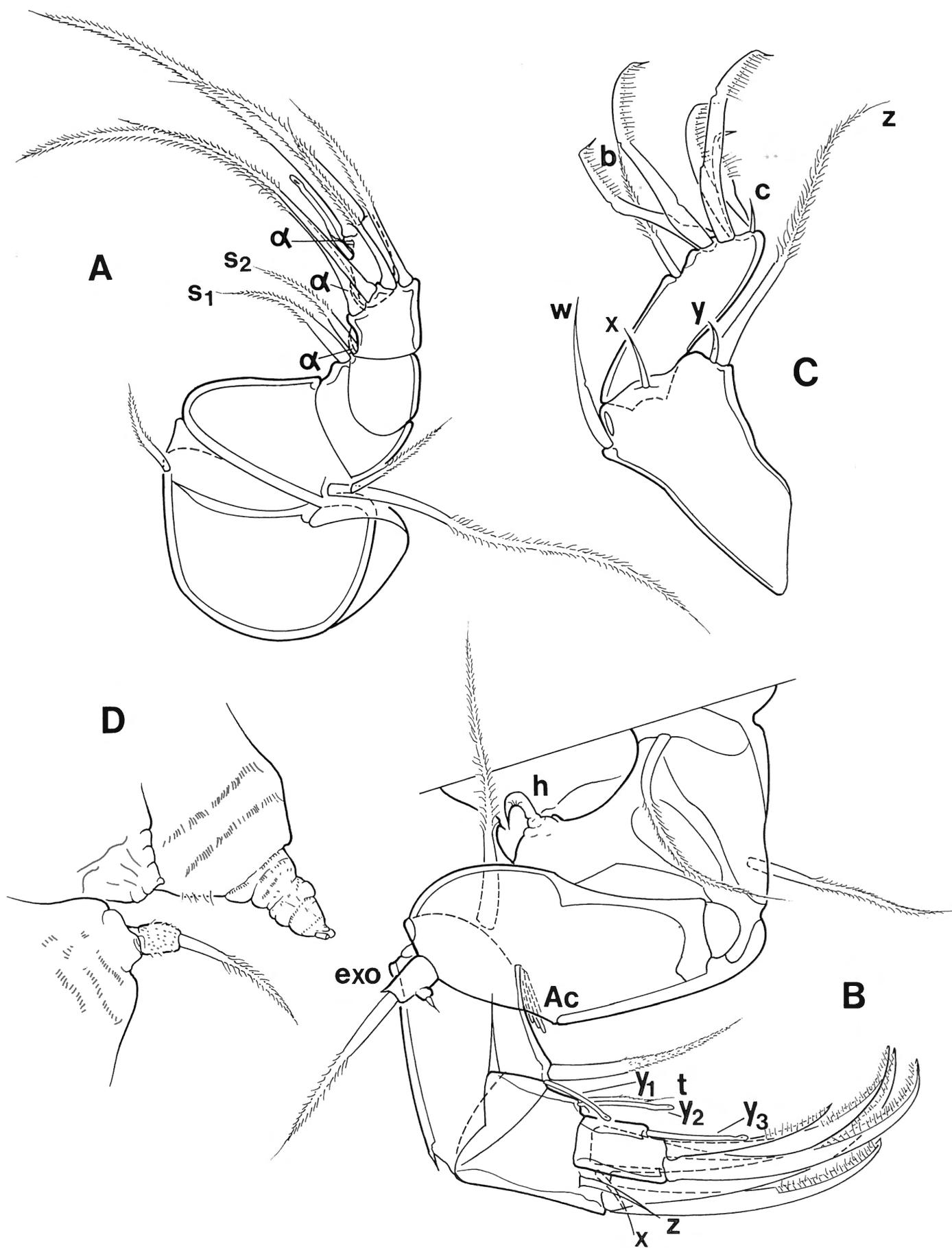


Fig. 11. – *Vestalenula molopoensis* (MARTENS & ROSSETTI). Molopo, North West Province, RSA.
 A. A1 (OC2100). B. A2 (OC2098). C. Md-palp, endopodite (idem). D. Fu and P-abd (OC2100).

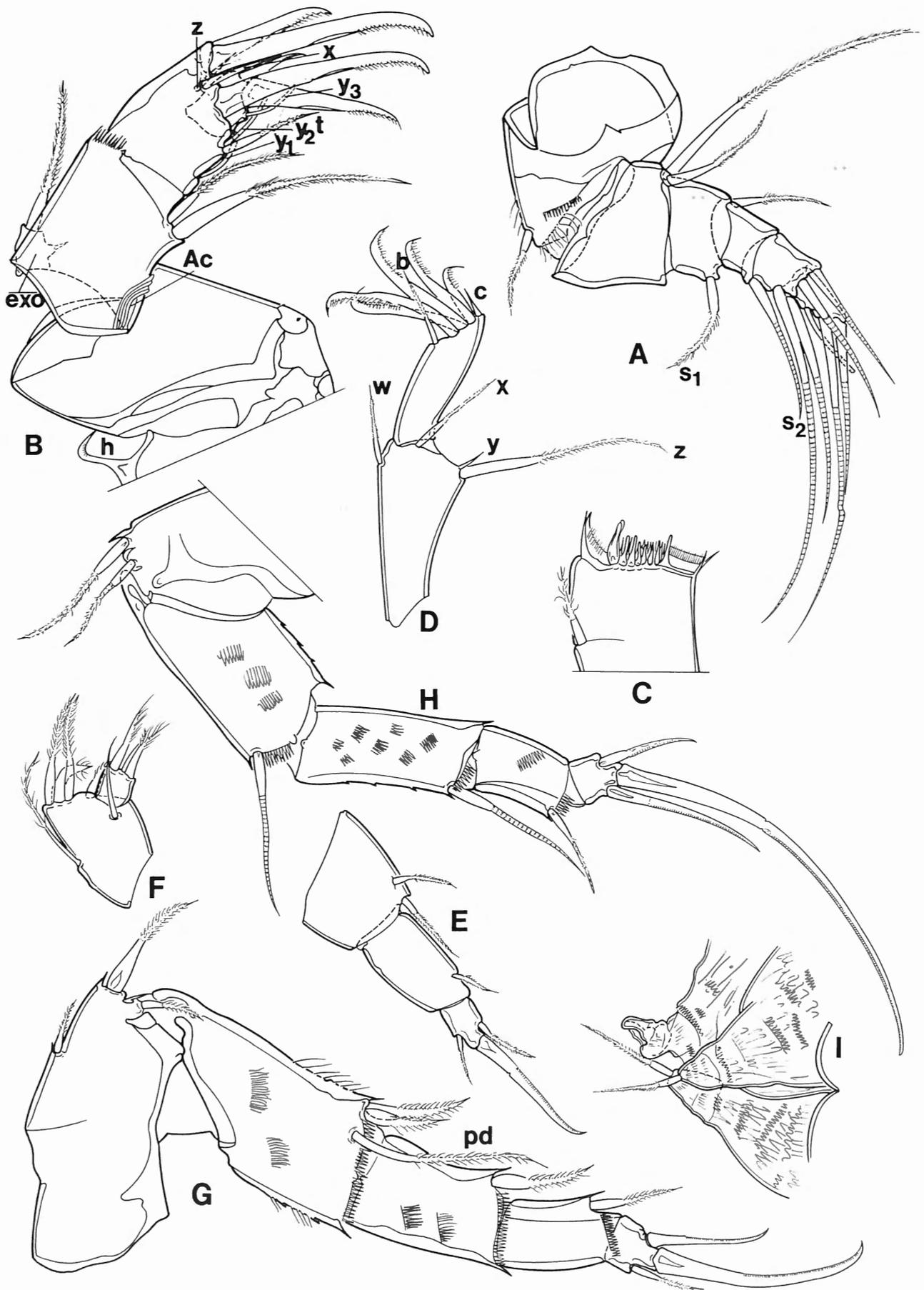


Fig. 12. – *Vestalenula pagliolii* (PINTO & KOTZIAN). Rio Grande do Sul, Brazil. Topotype material.

A. A1 (OC2161). B. A2 (OC2160). C. Md, masticatory process (idem). D. Md-palp, endopodite (OC2161). E. T1, endopodite (idem). F. Mx-palp (idem). G. T2 (OC2160). H. T3 (idem). I. Fu and P-abd (idem).

overlapping RV. First segment of A1 with one dorsal seta, second segment with two ventral setae, one *c* 2.5 times as long as the other one; third and fourth segments with one dorsal seta each. A2 exopodite with one seta and a small spine; first segment of endopodite with one ventro-apical seta. First segment of Md-palp with seta *y* minute and seta *z* very long; terminal segment with five apical claws, seta *c* very short, seta *a* absent. Penultimate segment of T1 palp with one apical seta. Fu an enlarged mound bearing a seta. P-abd a conical protuberance.

MEASUREMENTS

KISS (1959): Le=0.42 mm, W=0.22 mm, H=0.20 mm.

LITERATURE

KISS (1959).

REMARKS

The type material consists of dissected soft parts (re-illustrated in Fig. 10) only. No additional information on valve morphology, and more in particular the presence or absence of a keel on the RV and internal teeth on the LV, is therefore available.

11. *Vestalenula molopoensis* (MARTENS & ROSSETTI, 1997) (Figs 11A-D, 27N-Q)

TYPE LOCALITY

Riverine pools, Marico river, Molopo Oog area, North West Province (former Transvaal), RSA. Approximate coordinates: 25°46'40"S, 26°26'00"E. Coll. 02.11.93 by K. MARTENS.

HOLOTYPE

Albany Museum (Grahamstown, RSA), no. AM-TDW-26A.

DIAGNOSIS

Medium-sized darwinulid. Cp enlarged in the posterior part. Valves short and quite high, LV overlapping RV on all sides; LV with a round anterior internal tooth, RV with a short postero-ventral keel. Central ms with 7-8 relatively large spots. First segment of A1 with one dorsal seta; second segment with two unequal setae ventrally (one *c* 3 times as long as the other one); third and fourth segments with only one dorso-apical seta each. A2

exopodite with one long seta and a short lateral spine; first segment of A2 endopodite carrying only one ventro-distal seta. First segment of Md-palp endopodite with seta *z* much longer than seta *y*; second segment with five apical claws, one short internal seta (*c*) and one subapical internal seta (*b*). Fu consisting of a broad, hirsute base bearing a seta. P-abd having a conical, digitiform shape.

MEASUREMENTS

MARTENS & ROSSETTI (1997): Le=478-519 µm (n=3); W=240 µm (n=2); H=240 µm (n=1).

LITERATURE

MARTENS & ROSSETTI (1997).

12. *Vestalenula pagliolii* (PINTO & KOTZIAN, 1961) (Figs 12A-I, 25Q-S, 28A,B)

TYPE LOCALITY

Riverine pools at km 119.5 on road from Pôrto Alegre to Tramandai, Rio Grande do Sul, southern Brazil. Coll. I.D. PINTO and Y.T. SANGUINETTI.

HOLOTYPE

Museu de Paleontologia do Universidade do Rio Grande do Sul (Brazil), no. MP-0-8.

DIAGNOSIS

RV with a small, rounded keel and LV with small antero-ventral internal tooth. Shape subequal to that of *V. boteai*, but significantly higher and less elongate (RV: Le(2xH). Most soft part features as in *V. boteai*, but third segment of A1 with one ventro-apical seta and A2 with two large ventro-apical setae on the first endopodal segment (checked in topotype material).

MEASUREMENTS

PINTO & KOTZIAN (1961): Le=0.45-0.52 mm; H=0.21-0.25 mm; W=0.21 mm. New measurements: LV: Le=456 µm, H=213 µm; RV: Le=485 µm, H=221 µm, (LV and RV belong to different specimens).

LITERATURE

PINTO & KOTZIAN (1961); MARTENS *et al.* (1997).

REMARKS

The European populations of this species available for study were all fossil. No soft parts of European specimens could thus be studied. Original description of the chaetotaxy of this species (PINTO & KOTZIAN 1961) was extensive for that time, but does not allow full comparison with the present-day descriptions, therefore topotype material from Brazil is re-illustrated here (Fig. 12).

II. The *danielopoli*-group

CHARACTERISTICS

Antero-ventral internal tooth on LV and external ventral keel on RV elongate, not short and round.

REMARKS

DANIELOPOL (1980) mentioned and partly illustrated two other species in this lineage, which he named *Darwinula* sp. A and *D.* sp. B. These are briefly discussed below.

13. *Vestalenula danielopoli* (MARTENS *et al.* 1997) (Fig. 28C-F)

TYPE LOCALITY

In calcareous silt sediment (Holocene, Subatlanticum) at Mùcheln, Sachsen-Anhalt, Geiseltal, 45 km W of Leipzig, Germany. Approximate coordinates: 51°18'11"N, 11°50'25"E. Coll. 17.11.1966 by D. MANIA.

HOLOTYPE

Royal Belgian Institute of Natural Sciences (Brussels, Belgium), Ostracod Collection, no. OC2085.

DIAGNOSIS

Carapace sub-squarish, dorsal margin straight over more than half the length; RV with an elongate (not short and rounded) ventral keel and LV with antero-ventral internal tooth large and elongate, posterior internal tooth absent. Soft part features unknown.

MEASUREMENTS

MARTENS *et al.* (1997): Le=455-499 μm (n=3), H=215 μm (n=1), W=228-246 μm (n=2).

LITERATURE

MARTENS *et al.* (1997).

Genus *Penthesilenula* gen.nov.

Type species (here designated):

Darwinula inca DELACHAUX, 1928

DERIVATION OF NAME

Named after Penthesilea, queen of the Amazons, daughter of Ares and Aphrodite; killed by Achilles. Achilles mourned her death when he tore off her helmet and saw her beauty.

*Ducit Amazonidum lunatis agmina peltis
Penthesilea furens, mediisque in milibus ardet,
aurea subnectens exsertae cingula mammae,
bellatrix, audetque viris concurrere virgo.*

Vergil's Aeneid, book 1.

*Penthesilea in her fury leads
the rank of crescent-shielded Amazons.
She flashes through her thousands; underneath
her naked breast, a golden girdle; soldier-
virgin and queen, daring to war with men.*

DIAGNOSIS

Small (Le=c 0.4 mm) to relatively large darwinulids (Le=c 0.8 mm), sub-squarish in lateral view, with dorsal margin straight over at least part of its length, anterior margin narrowly rounded, caudal margin nearly straight. Hinge adont. Cms always situated towards the front in adult specimens. Large caudal brooding cavity externally visible. In frontal view, LV and RV almost symmetrical, not oblique. LV generally overlapping RV on all sides except dorsal side. LV either with two rounded internal teeth (antero-ventral and postero-ventral in *africana*-group) or with one pointed caudal internal tooth (*incae*-group). RV without postero-ventral keel. First segment of A1 with two dorsal setae, second segment with three ventral setae and one dorsal seta. A2 exopodite with two long setae and a spine, first endopodal segment with two ventro-apical setae. Setae γ and z on penultimate segment of Md-palp both long, subequal.

DIFFERENTIAL DIAGNOSIS

The new genus differs from *Darwinula* s.s. and from most species of *Alicenula* nov.gen. in the sub-squarish shape of the valves in lateral view, in the presence of internal teeth in the LV and in the length ratio of Md-palp setae γ and z . It differs from *Microdarwinula* by the presence

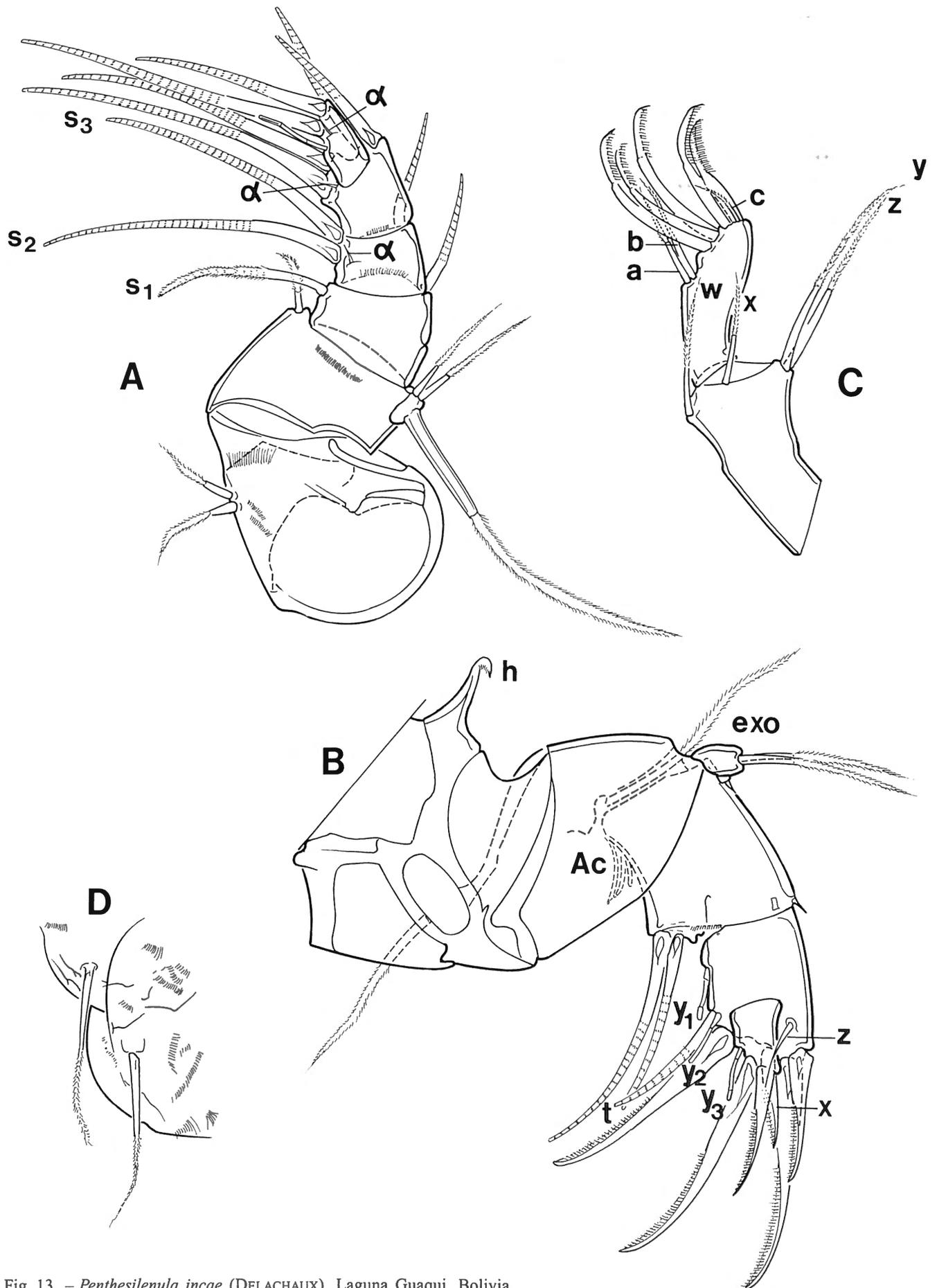


Fig. 13. – *Penthesilenula incae* (DELACHAUX). Laguna Guaqui, Bolivia.

A. A1 (OC1794). B. A2 (idem). C. Md-palp, endopodite (idem). D. Fu and Abdomen (OC1795).

of a brooding cavity (external carapace shape), the less pronounced cardinal teeth on the hinge of the RV, and by the presence of two dorsal setae on the first segment of the A1. The new genus can at first glance be confused with species from *Vestalenula* nov.gen., but differs from them in the absence of a ventral keel on the RV, the presence of either a postero-ventral or caudal internal tooth in the LV (absent in *Vestalenula* nov.gen.), the presence of two (not one) dorsal setae on the first segment of A1 and three (not two) ventral setae on the second segment, the presence of two (not one) ventro-apical setae on the first endopodal segment of the A2 and the presence of two (not one) long setae on the A2 exopodite and, finally, by the fact that setae y and z on the Md-palp are both long ($y < z$ in *Vestalenula* nov.gen.).

REMARKS

As reported above for the genus *Vestalenula* nov.gen., for a number of species allocated to the genus *Penthesilenula* nov.gen. the diagnostic characteristics of the valves are not known, either because of the inadequate original descriptions or because the types are lost or badly preserved. These species are therefore placed in the genus *Penthesilenula* nov.gen. on the basis of the soft part morphology; future collections of new material will have to validate these generic allocations.

DISTRIBUTION

Two valves belonging to this genus were found amongst the original type material of *A. furcabdominis*. Without soft parts it is impossible to obtain a specific status, but as this record occurs in the northernmost locality of the *incae*-group it is here included in the distribution map (Fig. 31).

OTHER SPECIES ALLOCATED

D. aotearoa, *D. araucana*, *D. kohanga*, *D. reboa*, *D. setosa*, *D. sphagna*, *D. africana*, *D. brasiliensis*, *D. malayica* (see below).

KEY TO THE SPECIES

- | | |
|---|--------------------|
| 1 a. LV with internal tooth along caudal margin,
no postero-ventral tooth (<i>incae</i> -group) | 2 |
| b. LV with postero-ventral internal tooth,
no caudal tooth (<i>africana</i> -group) | 6 |
| 2 a. LV overlapping RV | <i>P. araucana</i> |
| b. RV overlapping LV | 3 |
| 3 a. size >0.70 mm | 4 |
| b. size <0.70 mm | 5 |

- | | |
|--|------------------------|
| 4 a. Le/H ratio <2.2, P-abd absent | <i>P. incae</i> |
| b. Le/H ratio >2.2, P-abd present | <i>P. kohanga</i> |
| 5 a. in lv, dorsal margin distinctly slanting
forward, anterior end slender | <i>P. aotearoa</i> |
| b. in lv, dorsal margin slightly curved,
anterior end rounded | <i>P. sphagna</i> |
| 6 a. second segment of A1 endopodite with
one large dorsal seta | <i>P. malayica</i> |
| b. second segment of A1 endopodite with
two large dorsal setae | 7 |
| 7 a. second segment of A1 endopodite with
ventro-apical seta | <i>P. brasiliensis</i> |
| b. second segment of A1 endopodite without
ventro-apical seta | <i>P. africana</i> |

I. The *incae*-group

CHARACTERISTICS

LV without postero-ventral internal teeth, but with pointed caudal internal tooth.

14. *Penthesilenula incae* (DELACHAUX, 1928)
(Figs 13A-D, 28G-J)

TYPE LOCALITY

Lake Huaron, Region of Huancavelica, Department of Junin, Peru. Approximate coordinates: 13°23'S, 72°15'W. Coll. by E. GODET in 1915.

HOLOTYPE

Repository unknown.

DIAGNOSIS

Large-sized darwinulid. Cp elongate, posterior part broadly enlarged. Valves unequal, LV overlapping RV on all sides. LV with posterior internal teeth. Cms with 13-14 small spots arranged in a nearly circular rosette. First segment of A1 with two dorsal setae, second segment with one short dorso-apical seta and three ventral setae, two short, subequal, and one longer; third segment with one ventral and one dorsal seta (s_1), fourth segment with one ventral seta and two dorsal setae (s_2 and s_3). A2 exopodite with two long setae and a short lateral spine; first segment of endopodite with two ventro-apical setae. Penultimate segment of Md-palp with two long, subequal setae (y and z) internally, one medial seta (x), and one external seta (w),

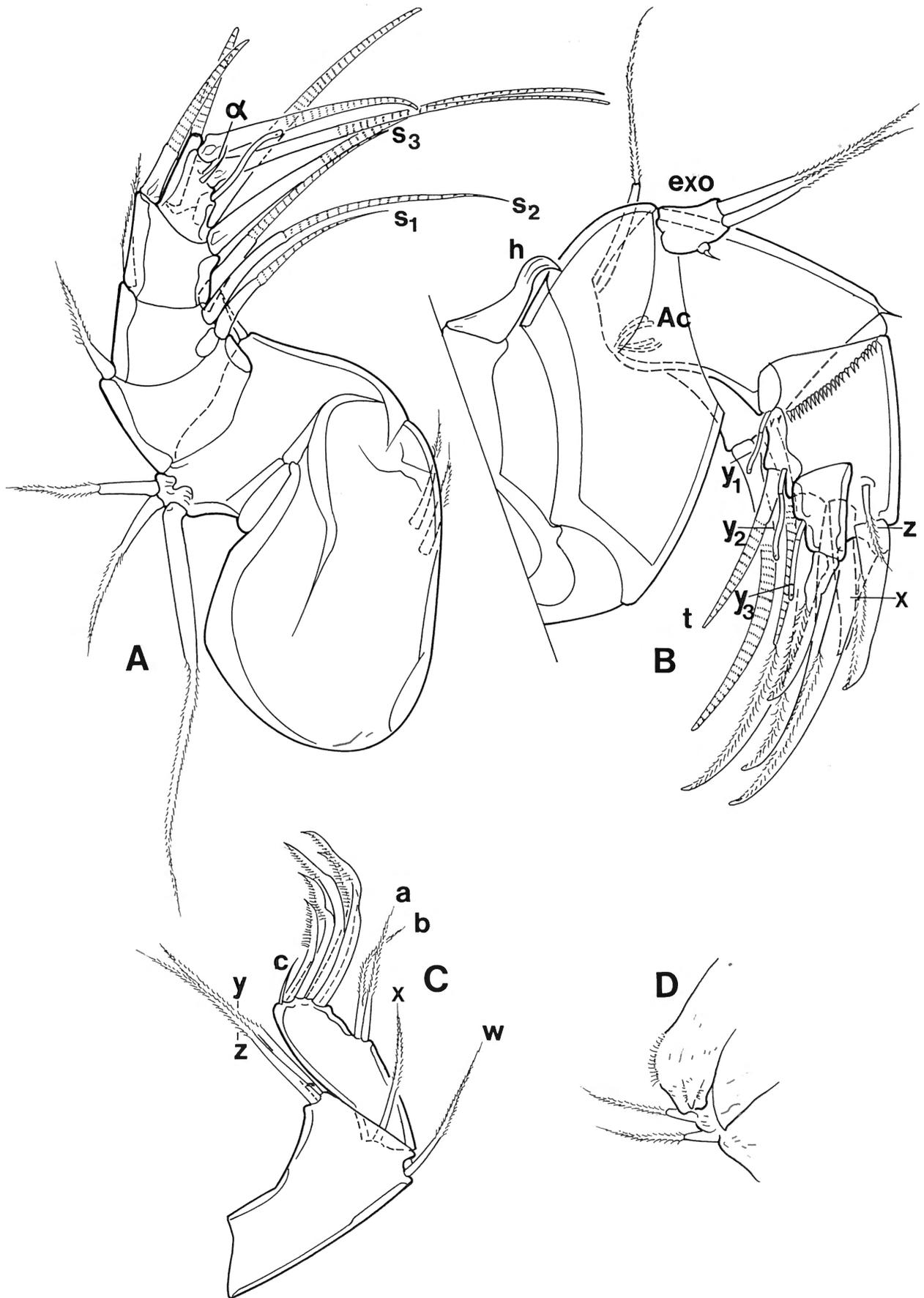


Fig. 14. – *Penthesilenula aotearoa* (ROSSETTI *et al.*). Karori Stream, New Zealand.

A. A1 (OC2145). B. A2 (OC2146). C. Md-palp, endopodite (OC2144). D. Fu and Abdomen (OC2146).

the latter two shorter than the former ones; terminal segment with five claws of different length, two subapical, external setae (*a* and *b*) and one smaller internal seta (*c*), the latter half as long as the former two. P-abd absent. Fu present as a long seta.

MEASUREMENTS

DELACHAUX (1928): Le=0.87 mm, W=0.45 mm, H=0.40 mm.
ROSSETTI *et al.* (1996): Le=772-804 µm (n=4).

LITERATURE

DELACHAUX (1928); ROSSETTI *et al.* (1996).

15. *Penthesilenula aotearoa* (ROSSETTI *et al.*, 1998) (Figs 14A-D, 28K-N)

TYPE LOCALITY

Small (dammed) swamp, overflowing into the Karori Stream, Kinnoull Station, Makara, Wellington, New Zealand. Approximate coordinates: 41°19'S, 174°41'E. Grid ref. R27 512 865. Coll. 30.10.96 by S.H. EAGAR.

HOLOTYPE

Royal Belgian Institute of Natural Sciences (Brussels, Belgium), Ostracod Collection, no. OC2143.

DIAGNOSIS

Medium-sized darwinulid. Cp ovoid. Valves sub-squarish, LV overlapping RV on all sides. LV with posterior and antero-ventral teeth; RV without postero-ventral keel. Hinge adont. In lv, maximum height at the posterior third; posterior margin more broadly rounded than anterior one; dorsal margin distinctly slanting forward. Cms consisting of clearly separated spots arranged in a nearly circular rosette. First segment of A1 with two dorsal setae, second segment with one small dorso-apical seta and three ventral setae, two subequal and one longer directed backwards; third segment with two apical setae, one dorsal (*s*₁) and one ventral, fourth segment with two long dorso-apical setae (*s*₂ and *s*₃) and a shorter ventro-apical seta. A2 exopodite with two long setae and a short lateral spine; first segment of A2 endopodite with two ventro-apical setae. Penultimate segment of Md-palp with seta *z* as long as seta *y*, last segment bearing two setae (*a* and *b*) inserted in sub-apical position along the external edge and, distally, five claws of different length and one small, internal seta (*c*). Fu a seta slightly widened proximally. P-abd absent.

DIFFERENTIAL DIAGNOSIS

Penthesilenula aotearoa spec. nov. has *P. sphagna* as its closest congener, a semi-terrestrial species found in a *Sphagnum* swamp in New Zealand (see below). *Penthesilenula aotearoa* can be distinguished from *P. sphagna* by the size of the Cp (larger in *P. aotearoa*), by the different shape of valves in lv (anterior end decidedly more slender in *P. aotearoa*), by the position of setae *a* and *b* on the distal segment of the Md-palp (more apically in *P. sphagna*), and by the presence in *P. aotearoa* of two sub-apical setae on the first podomere of the T1 endopodite (for *P. sphagna* only one seta is figured).

MEASUREMENTS

ROSSETTI *et al.* (1998): Le=585-610 µm (n=5), W=289-293 µm (n=2), H=293-311 µm (n=3).

LITERATURE

ROSSETTI *et al.* (1998).

16. *Penthesilenula araucana* (LÖFFLER, 1961) (Figs 15A-C, 26A)

TYPE LOCALITY

Region of Villarrica and Puyehue, Central Chile. Coll. in 1953-54 by L. BRUNDIN, K. THOMASSON and H. LÖFFLER.

HOLOTYPE

Unknown.

DIAGNOSIS

Medium-sized darwinulid. In lv, Cp sub-squarish; maximum height at about the middle; both ends broadly rounded, dorsal margin gently sloping towards the front. RV overlapping LV. A2 exopodite with two long setae; first segment of endopodite with two ventro-apical setae. Penultimate segment of Md-palp with setae *y* and *z* both long; last segment bearing five distal claws and two subapical setae (*a* and *b*), seta *c* absent. Fu consisting of a simple seta. P-abd absent.

MEASUREMENTS

LÖFFLER (1961): Le=560 µm, W=233 µm, H=265 µm.

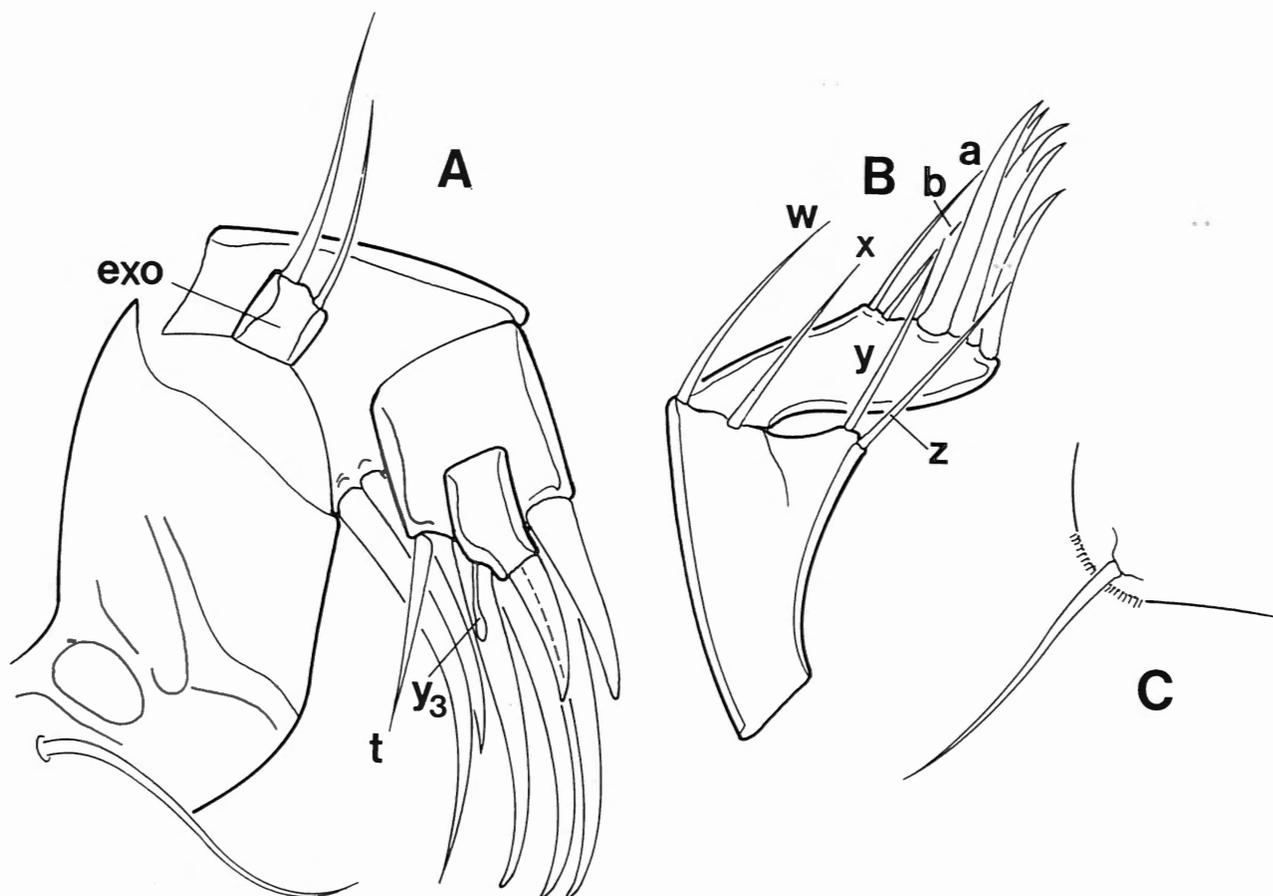


Fig. 15. – *Penthesilenula araucana* (LÖFFLER). Region of Villarrica and Puyehue, Central Chile. From LÖFFLER (1961).
A. A2 (fig. 242). B. Md-palp, endopodite (detail of fig. 241). C. Fu (fig. 243).

LITERATURE

LÖFFLER (1961).

**17. *Penthesilenula kohanga* (ROSSETTI *et al.*, 1998)
(Figs 16A-D, 28O-Q, 29A)**

TYPE LOCALITY

Small (dammed) swamp, overflowing into the Karori Stream, Kinnoull Station, Makara, Wellington, New Zealand. Approximate coordinates: 41°19'S, 174°41'E. Grid ref. R27 512 865. Coll. 30.10.96 by S.H. EAGAR.

HOLOTYPE

Royal Belgian Institute of Natural Sciences (Brussels, Belgium), Ostracod Collection, no. OC2151.

DIAGNOSIS

Large darwinulid. Valves elongate, LV overlapping RV; LV with a posterior (but no anterior) internal tooth, RV

without postero-ventral keel. Hinge adont. Cms consisting of clearly separated spots arranged in a circular rosette. First segment of A1 with two dorsal setae, second segment with one short dorso-apical seta and three ventral setae, two shorter, subequal and one c. 2.5 times the length of the other two; third segment with one ventral and one dorsal seta (s_1); fourth segment bearing two dorso-apical setae (s_2 and s_3) and one ventro-apical seta. A2 exopodite with two long setae and a short lateral spine; first segment of A2 endopodite with two ventro-apical setae. Penultimate segment of Md-palp with seta z as long as seta y ; setae x and w of about the same length; last segment with two external, sub-apical setae (a and b) and distally five unequal claws and one short, internal seta (c). Fu consisting of a simple seta. P-abd an elongate, digitiform protuberance.

MEASUREMENTS

ROSSETTI *et al.* (1998): Le=720-840 μm (n=7), W=340-380 μm (n=4), H=330-370 μm (n=4).

LITERATURE

ROSSETTI *et al.* (1998).

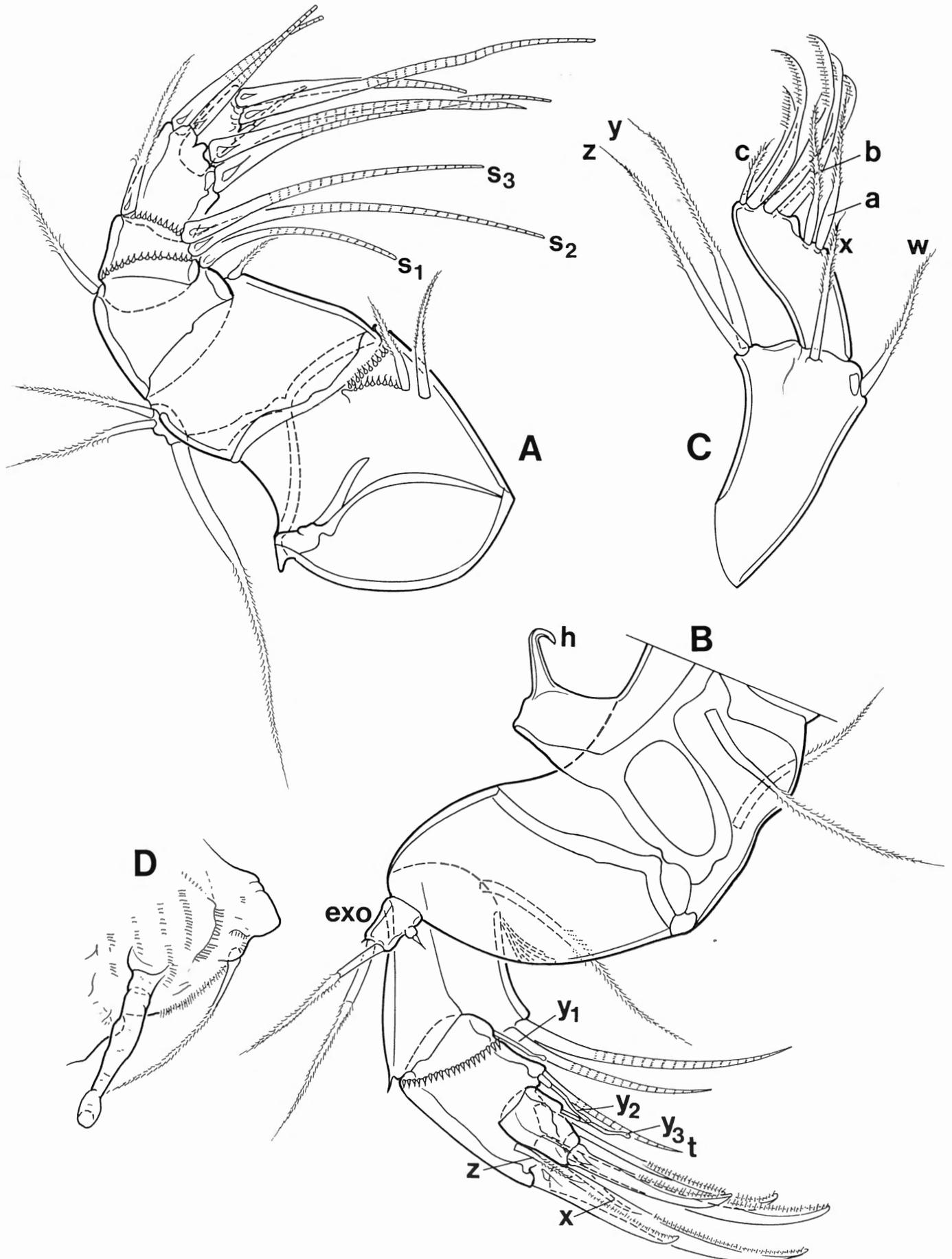


Fig. 16. – *Penthesilenula kohanga* (ROSSETTI *et al.*). Karori Stream, New Zealand.

A. A1 (OC2151). B. A2 (*idem*). C. Md-palp, endopodite (*idem*). D. Fu and P-abd (*idem*).

18. *?Penthesilenula reposita* (CHAPMAN, 1963)
(Fig. 26B-D)

syn. *Darwinula* sp. HORNIBROOK, 1955

TYPE LOCALITY

Ross Creek, Dunedin, New Zealand. Found in swamps, particularly in peaty areas. Coll. 13.03.1960 by M.A. CHAPMAN.

HOLOTYPE

Otago Museum, Dunedin, New Zealand. Accession number not reported.

DIAGNOSIS

Medium-sized darwinulid; in lv, Cp kidney-shaped, maximum height at the posterior third, anterior end rather pointed. LV larger than RV.

MEASUREMENTS

CHAPMAN (1963): Le=0.64 mm, W=0.34 mm, H=0.28 mm.

LITERATURE

HORNIBROOK (1955); CHAPMAN (1963).

REMARKS

According to CHAPMAN (1963), the specimens illustrated by HORNIBROOK (1955) belong to this species. We here follow this opinion.

Only A2, Md and T2 have been figured by CHAPMAN (1963, Pl. XIII, Figs 1-4), and those without a satisfactory detail. A more complete and accurate description of chaetotaxy may in time change the taxonomic position of this species. The more so, because this species has a rather atypical kidney-shaped valves, which resemble the Cretaceous species *Darwinula oblonga* ROEMER. MARTENS *et al.* (1997) already mentioned that *D. oblonga* might well represent a separate lineage within the Darwinulidae, of which *D. schneiderae* OLTEANU, 1995 and *?Penthesilenula reposita* might be Pliocene, resp. Recent, representatives.

19. *Penthesilenula setosa* (DADAY, 1902)
(Figs 17A,B, 26E-H)

TYPE LOCALITY

Amenkelt, Santa Cruz, Patagonia, Argentina. Coll. by F. SILVESTRI (1899 or 1900).

HOLOTYPE

Budapest Museum (Hungary), no. IV/P-183.

DIAGNOSIS

Medium-sized darwinulid. LV overlapping RV. Cms consisting of 9 spots arranged very close to each other. A2 exopodite carrying two large setae; first segment of endopodite with two ventro-apical setae. Penultimate segment of Md-palp with setae *y* and *z* both long, extending beyond the distal margin of the next segment; last segment of Md-palp with five claws and one internal seta (*c*) apically and two long setae (*a* and *b*) inserted on the distal fourth of the external margin, the latter two *c* 3 times as long as the former one. P-abd absent. Fu not described.

MEASUREMENTS

DADAY (1902): Le=0.60 mm, W=0.24 mm, H=0.28-0.33 mm.

LITERATURE

DADAY (1902).

REMARKS

Possibly *Penthesilenula setosa* will in time have to be considered a senior synonym of *P. incaea*. The inadequate original description of the former species (based on one "ziemlich stark macerirt" female) and the type material consisting of a crushed specimen only (the same used for the description) do not allow a decision to date. *Penthesilenula incaea* (c 0.8 mm) is larger than *P. setosa* (0.6 mm), but the difference in size may be due to an incorrect measurement.

20. *Penthesilenula sphagna* (BARCLAY, 1968)
(Figs 18A-C, 26I-L)

TYPE LOCALITY

Sphagnum swamp, Ardmore, Auckland district, New Zealand. Coll. 14.05.1967 by M.H. BARCLAY.

HOLOTYPE

Dominion Museum, Wellington, New Zealand. Accession number not reported.

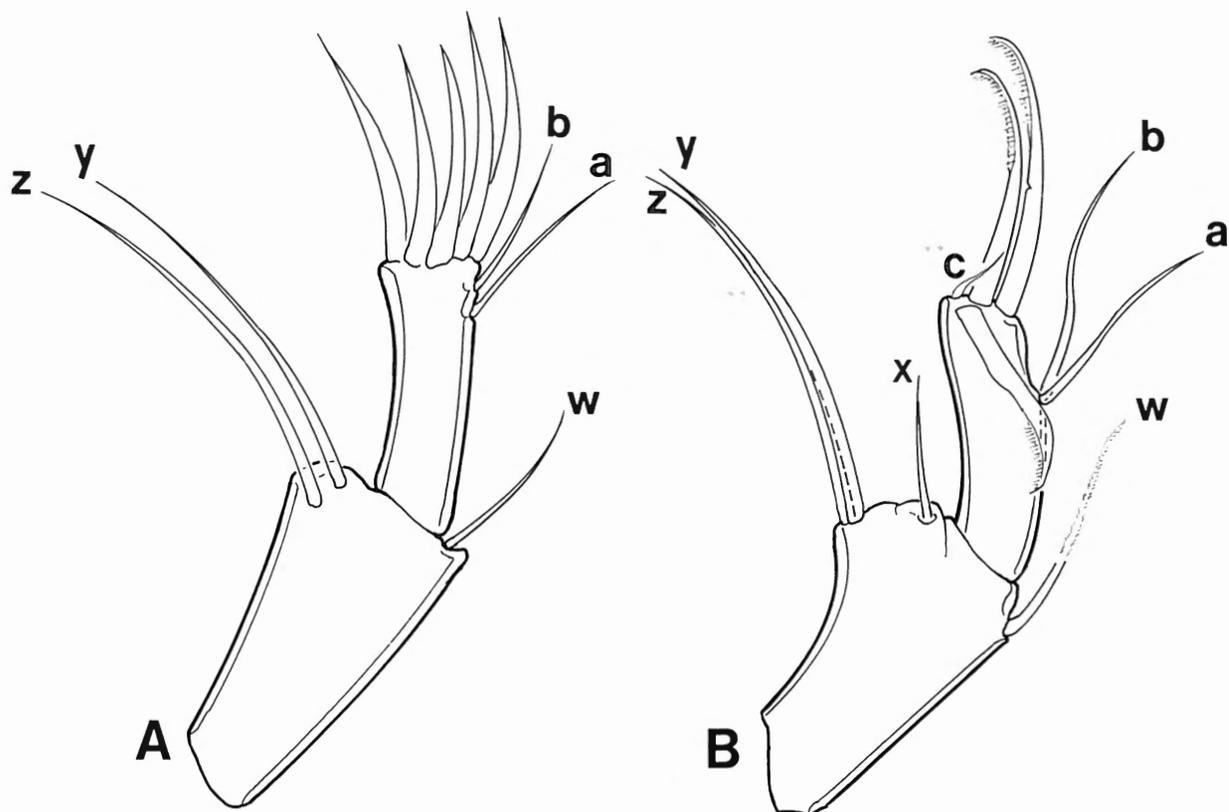


Fig. 17. – *Penthesilenula setosa* (DADAY). Amenkelt, Santa Cruz, Patagonia, Argentina. A: from DADAY (1902); B: type material. A. Md-palp, endopodite (detail of fig. 17). B. Md-palp, endopodite.

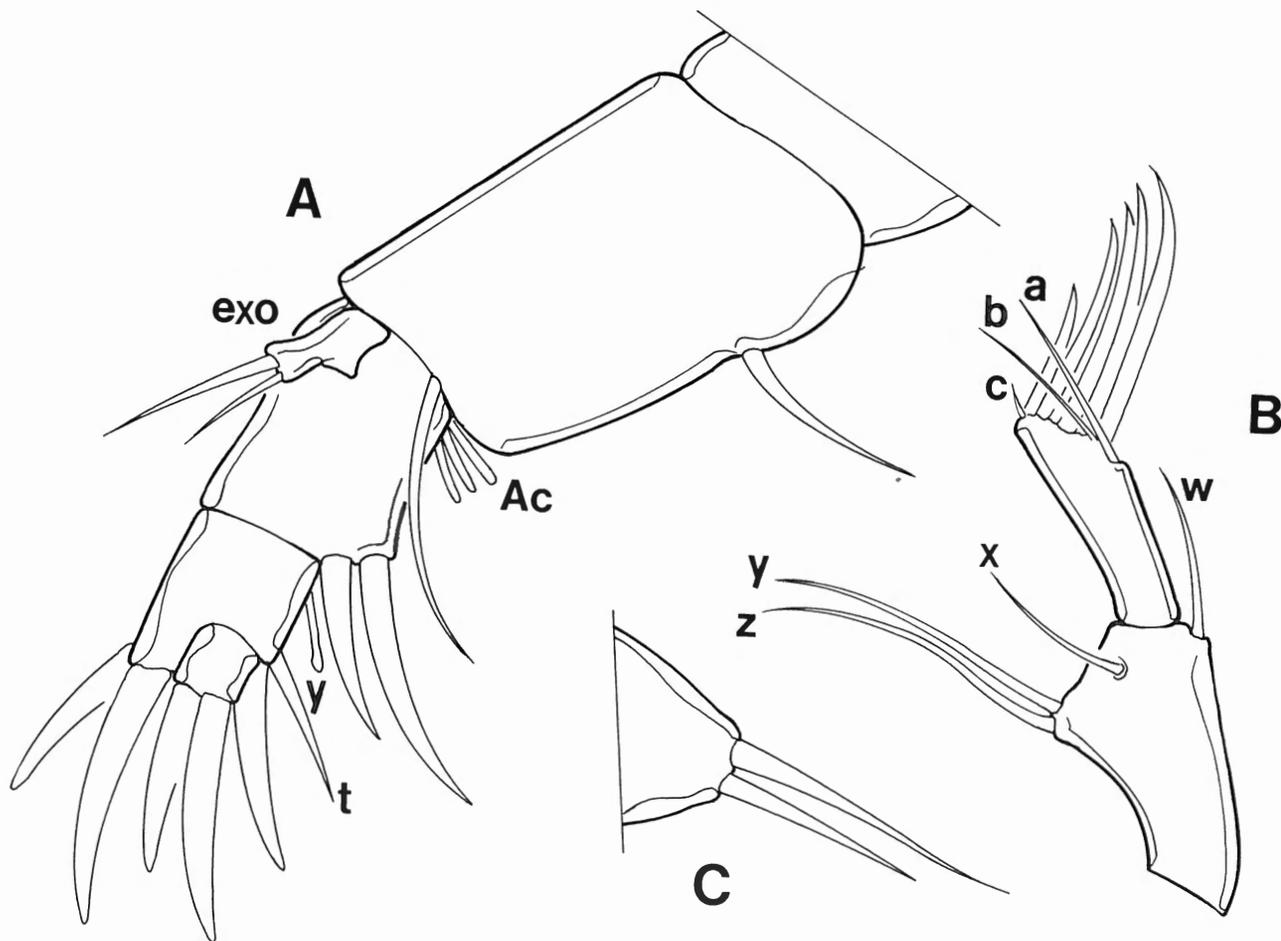


Fig. 18. – *Penthesilenula sphagna* (BARKLAY). Ardmore, Auckland district, New Zealand. From BARCLAY (1968). A. A2 (fig. 2e). B. Md-palp, endopodite (fig. 2f). C. Fu (fig. 2g).

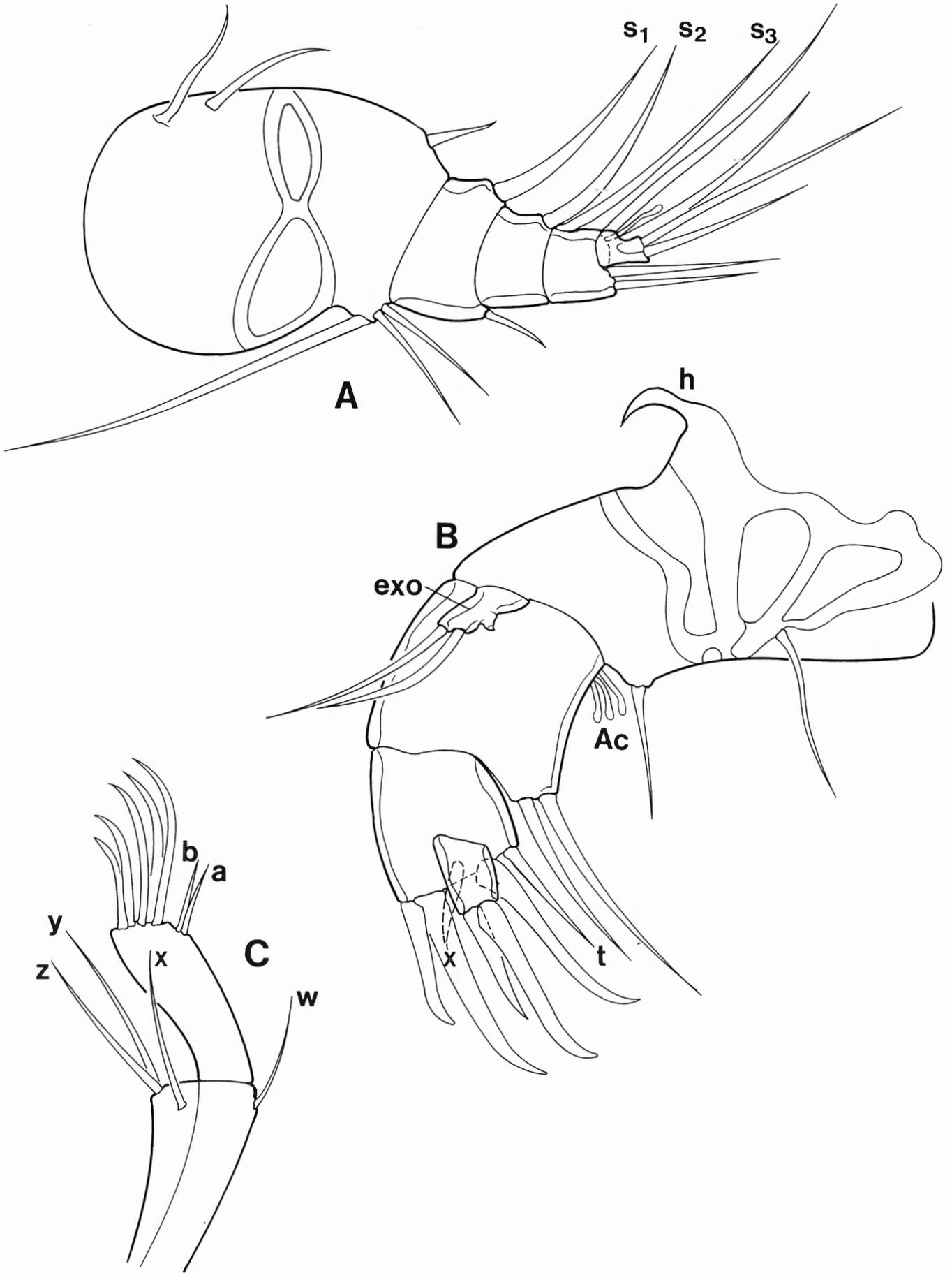


Fig. 19. - *Penthesilenula africana* (KLIE). West Africa. A, B: from KLIE (1939); C: from KLIE (1935).
A. A1 (fig. 63). B. A2 (fig. 64). C. Md-palp, endopodite (fig. 48).

DIAGNOSIS

Small darwinulid. LV slightly overlapping RV both anteriorly and posteriorly. In lv, sub-squarish in shape; both ends rounded, anterior narrower than posterior. Cms a rosette with c 9 spots. A2 exopodite with two setae and a lateral spine; first segment of A2 endopodite with two ventro-apical setae. Setae *y* and *z* on the penultimate segment of Md-palp both long; last segment with five claws and a small, internal seta (*c*) terminally and two internal, subapical setae (*a* and *b*). Fu a seta. P-abd absent.

MEASUREMENTS

BARCLAY (1968): Le=0.43 mm (LV), Le=0.42 mm (RV), W=0.12 mm, H=0.25 mm.

LITERATURE

BARCLAY (1968); EAGAR (1994).

II. The *africana*-group

CHARACTERISTICS

LV with antero-ventral and postero-ventral rounded teeth; carapace generally small (Le<0.6 mm), more consistently sub-quadrate than in the previous species-group.

21. *Penthesilenula africana* (KLIE, 1935) (Figs 19A-C, 26M-O)

TYPE LOCALITY

In a moss spring at km 21 on road from Man to Touba (Ivory Coast). Coll. 07.03.1931 by C. ALLAUD and P.A. CHAPPUIS.

HOLOTYPE

Universität Hamburg (Germany), Zoologisches Museum, no. 291.

DIAGNOSIS

Small-sized darwinulid. In lv, Cp decidedly sub-squarish, with dorsal margin gently sloping towards the front. LV overlapping RV. Cms with c 10 spots. First segment of A1 with two dorsal setae, second segment with three ventral setae and one dorsal seta; third segment with one

dorsal and one ventral seta; fourth segment carrying two dorsal setae. A2 exopodite with two subequal setae and one lateral spine; first segment of A2 endopodite with two ventro-apical setae. Setae *y* and *z* of the Md-palp subequal, reaching the distal margin of the next segment. Last segment of Md-palp with five distal claws of different length and two sub-apical setae *a* and *b*, seta *c* absent. Fu as a conical protuberance carrying a simple seta. P-abd absent.

MEASUREMENTS

KLIE (1935): Le=0.48 mm, W=0.22 mm, H=0.24 mm.

LITERATURE

KLIE (1935; 1939).

REMARKS

The type material consists of decalcified carapaces without soft parts. No information on the presence of keel on RV, internal teeth on LV and type of hingement is thus available.

22. *Penthesilenula brasiliensis* (PINTO & KOTZIAN, 1961) (Figs 20A-D, 26P,Q, 29B-H)

syn. *Darwinula dicastrii* LÖFFLER, 1966 **nov.syn.**

TYPE LOCALITY

Of *brasiliensis*: Riverine pools at km 119.5 on road from Pôrto Alegre to Tramandai, Rio Grande do Sul, southern Brazil. Coll. I.D. PINTO and Y.T. SANGUINETTI.

Of *dicastrii*: Caleu, Cerro el Roble, Province of Santiago, Chile. Coll. 30.12.1963 by F. DI CASTRI.

HOLOTYPE

Of *brasiliensis*: Museu de Paleontologia do Universidade do Rio Grande do Sul (Brazil), no. MP-0-11.

Of *dicastrii*: Unknown.

DIAGNOSIS

Valves relatively short and high, LV>RV on all sides, RV without postero-ventral keel, LV with small antero-ventral and large postero-ventral internal teeth. Hinge adont. Cms a rosette of c 9 relatively large scars. First segment of A1 with two dorsal setae; second segment with dorso-

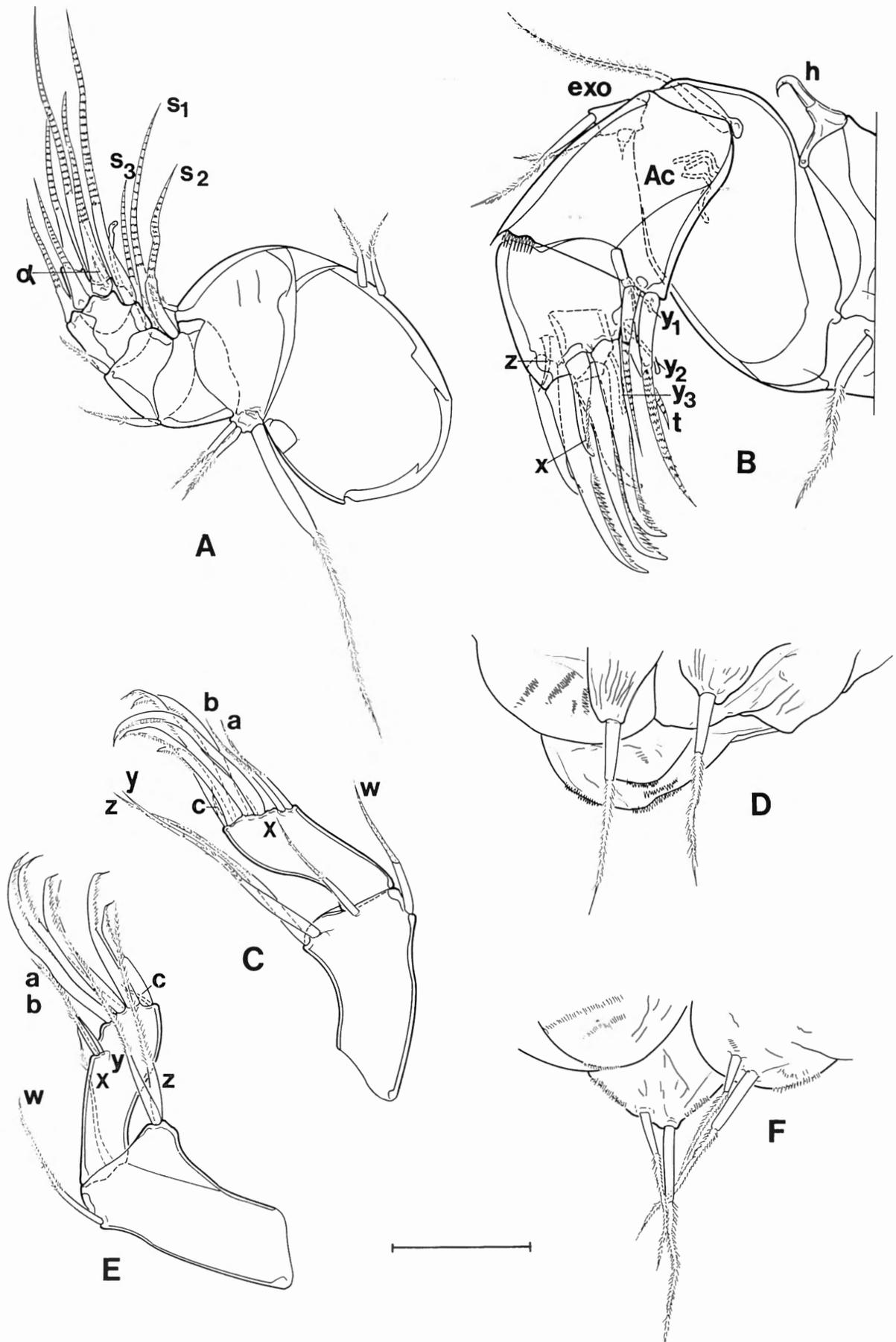


Fig. 20. – *Penthesilenula brasiliensis* (PINTO & KOTZIAN). Drakensberg, RSA.
 A. A1 (OC2165). B. A2 (idem). C. Md-palp, endopodite (OC2166). D. Fu and Abdomen (OC2165). E. Md-palp, endopodite (OC2167). F. Fu and Abdomen (idem).

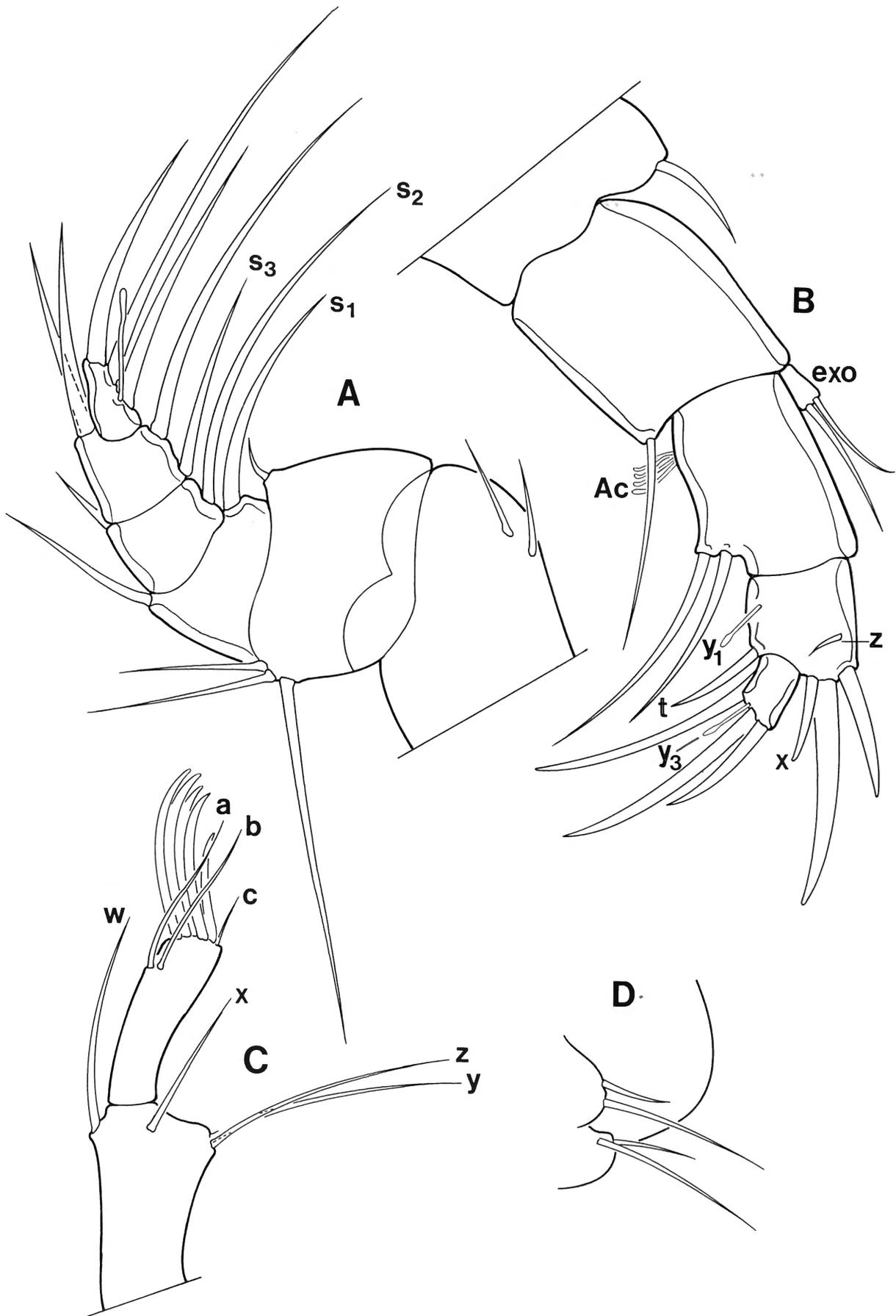


Fig. 21. - *Darwinula dicastrii* (LÖFFLER). Caleu, Chili. From LÖFFLER (1966, Pl. 1).

A. A1 (fig. f). B. A2 (fig. g). C. Md-palp, endopodite (fig. e). D. Fu and Abdomen (fig. j).

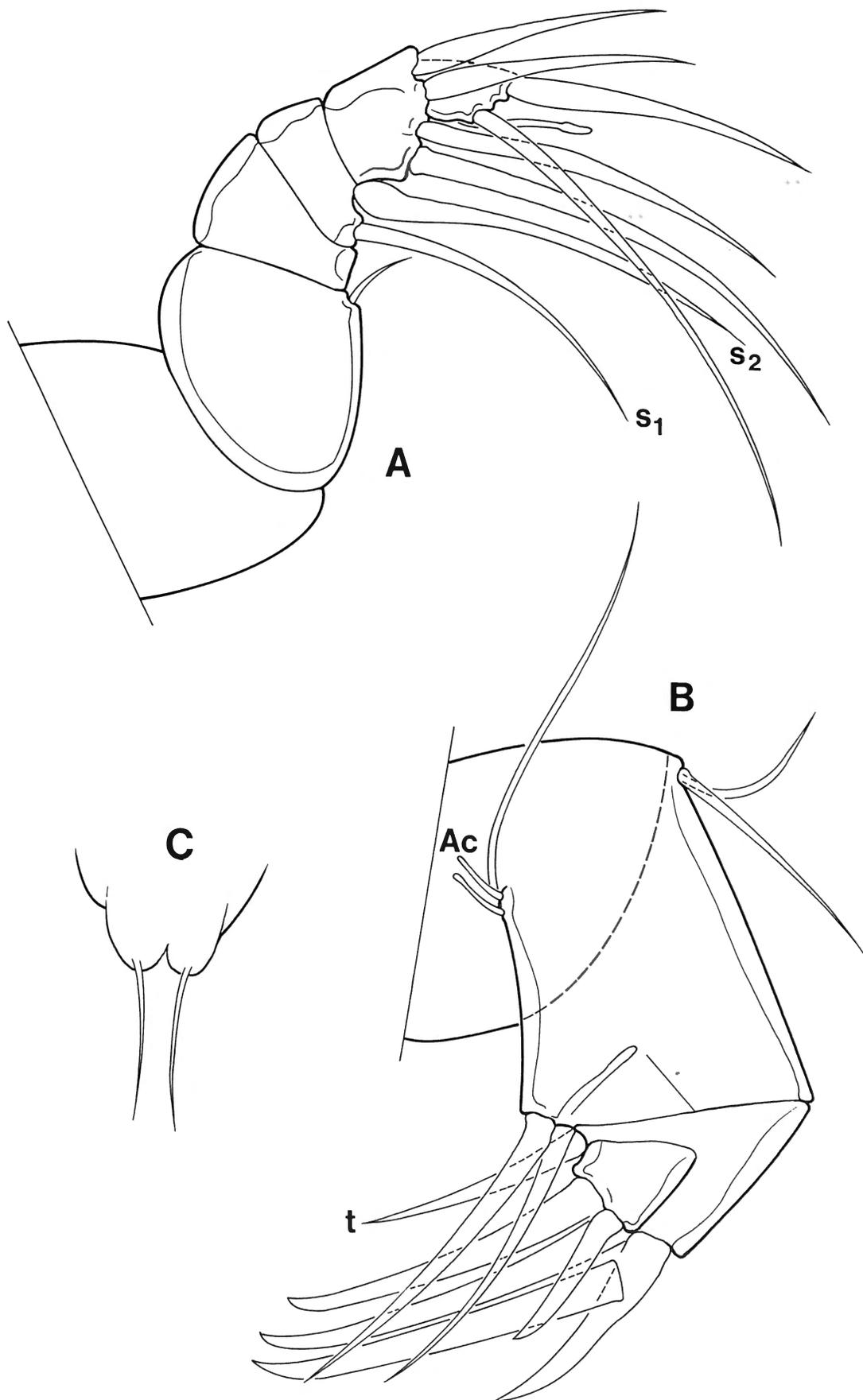


Fig. 22. – *Penthesilenula malayica* (MENZEL). West Java, Indonesia. From MENZEL (1923).
 A. A1 (fig. 2.1). B. A2 (fig. 2.2). C. Fu and Abdomen (fig. 5).

apical seta and three ventral setae, two shorter, subequal and one long (the latter c 3 times as long as the former ones); third segment with one dorsal (s_1) and one ventral seta; fourth segment with two dorsal setae (s_2 and s_3) and one ventral seta. A2 exopodite with two long setae and one lateral spine; first segment of endopodite with two ventro-apical setae. Penultimate segment of Md-palp with setae y and z both long, reaching halfway the apical claws on the next segment; last segment carrying five apical claws, one short internal seta (c) and two subapical external setae (a and b). Fu consisting of a long seta. P-abd absent.

MEASUREMENTS

Of *brasiliensis*: PINTO & KOTZIAN (1961): Le=0.47-0.55 mm, H=0.21-0.28 mm, W=0.22 mm. MARTENS *et al.* (1997): Le=490-508 μ m (n=3), W=233-239 μ m (n=2), H=245 μ m (n=1).

Of *dicastrii*: LÖFFLER (1961): LV: Le=485 μ m, H=225 μ m; RV: Le=473 μ m, H=212 μ m.

LITERATURE

PINTO & KOTZIAN (1961); LÖFFLER (1966); MARTENS *et al.* (1997).

DISTRIBUTION

Apart from the type locality in Brazil, the species has also been reported from southern France (Clue de la Fou, MARTENS *et al.*, 1997). Three further European populations of *Penthesilenula brasiliensis* were discovered in part of the type material of *Darwinula stevensoni* in the Brady collection (Hancock Museum, Newcastle-upon-Tyne), nl. White Loch, Kirkcudbright, Scotland (see also MARTENS *et al.*, 1997), Lough Inagh and Lough Agraiffard, Ireland (D.J. HORNE, pers. comm.). Finally, the species is here also reported from rivers and streamlets in the Drakensberg area of South Africa, further confirming the intercontinental distribution of this species.

REMARKS

1. The chaetotaxy of first and second segment of A1 endopodite is erroneously described in the text of MARTENS *et al.* (1997 : 101), while in Fig. 1A (1997: 102) it is correctly represented. MARTENS *et al.* (*loc. cit.*) further illustrated a specimen collected at Clue de la Fou (Southern France) with normal soft part morphology but aberrant valves (Figs 1M,N): with hinge and valve overlap reversed, i.e. RV overlapping LV; LV without internal teeth; RV with at least a postero-ventral internal tooth. The potential importance of this specimen is discussed below.

2. The collections of *P. brasiliensis* from South Africa contained one specimen with double Fu, much like was described for *Darwinula dicastrii* which in any case belongs in *Penthesilenula* (Fig. 20F). In all other aspects, the specimen agreed in its morphology with *P. brasiliensis*. This specimen conforms in all aspects with the original description of *P. dicastrii*, except for small differences in the length of setae x and w of the penultimate segment of Md-palp. The double Fu could be both genetically or epigenetically induced; we assume that it is the latter. In this case, the soft part morphology of *P. dicastrii* is identical to that of *P. brasiliensis* and we consider both species synonymous, with *P. brasiliensis* having priority.

23. *Penthesilenula malayica* (MENZEL, 1923) (Figs 22A-C, 26U)

TYPE LOCALITY

In moss springs (water temperature 45-50 °C) along the road from Cibodas (previously spelled Tjibodas) to Gedeh at 2100 m a.s.l., West Java, Indonesia.

HOLOTYPE

Repository unknown.

DIAGNOSIS

Medium-sized darwinulid. Cp sub-squarish in lv; LV overlapping RV. Number of spots in the ms c 8. Second segment of A1 with dorso-apical seta. First and second segment of A2 with one dorsal seta each. A2 exopodite with two large setae. First segment of A2 endopodite carrying two ventro-apical setae. Penultimate segment of Md-palp with setae y and z both long; last segment with five terminal claws and a subapical seta b . Fu as a seta inserted on a conical base. P-abd in form of a smooth, cylindrical process.

MEASUREMENTS

MENZEL (1923): Le=0.46 mm, W=0.24 mm, H=0.20 mm.

LITERATURE

MENZEL (1923); KLIE (1932; 1935).

REMARKS

1. Only A1 (in all probability some setae on first two segments were missing from the illustrated specimen),

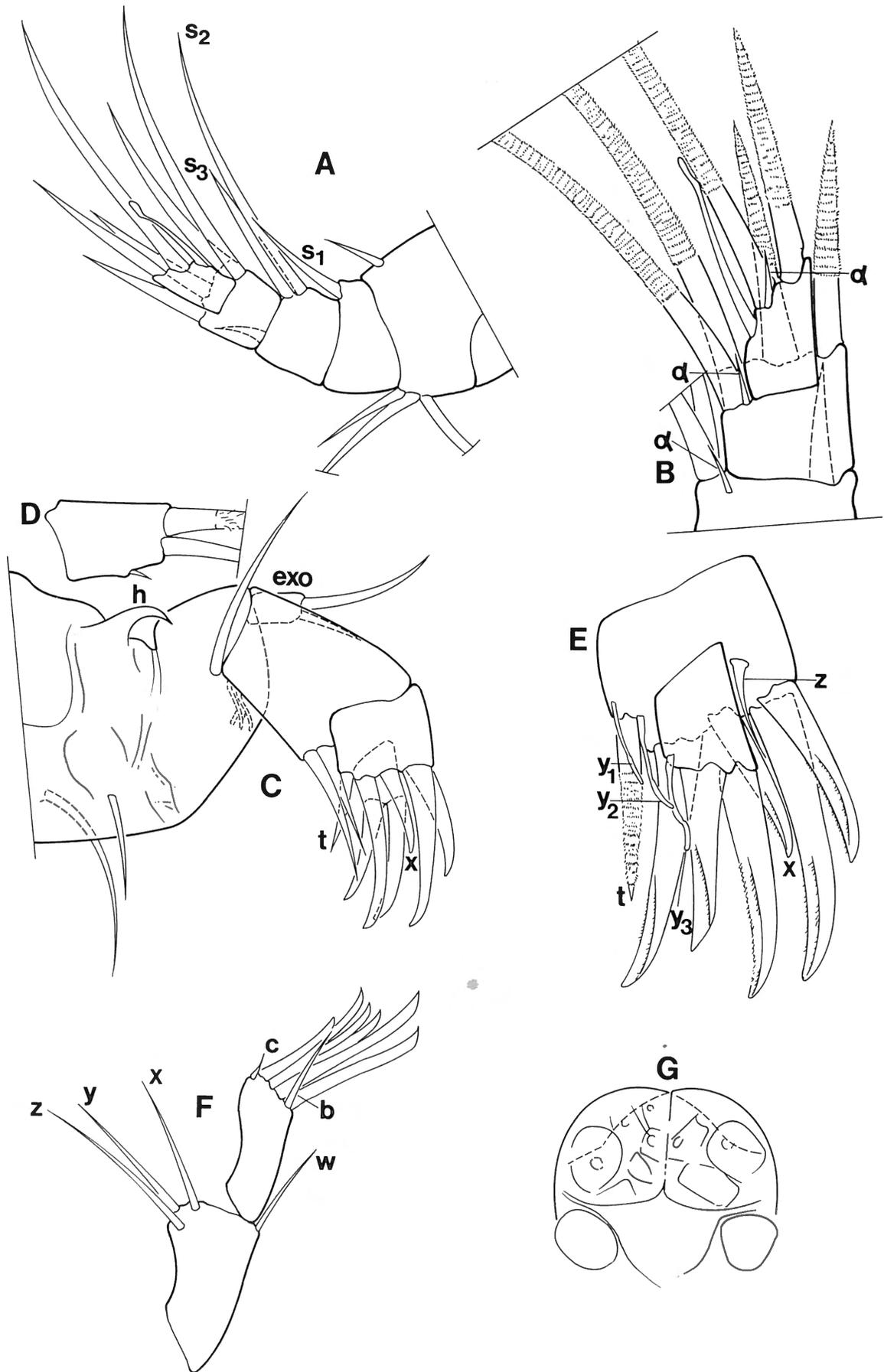


Fig. 23. - *Microdarwinula zimneri* (MENZEL). Lake Caldarusani (Judet Ilfov), Rumania. From DANIELOPOL (1968).
 A. A1 (fig. 12). B. A1, detail (fig. 13). C. A2 (fig. 14). D. A2, detail exopodite (fig. 15). E. A2, detail (fig. 16). F. Md-palp, endopodite (detail of fig. 17). G. Abdomen (fig. 28).

A2, T2, T3 and LV have been illustrated by MENZEL (1923, Figs 2-5).

2. The records of *P. malayica* in Sunda Islands (KLIE 1932) and West Africa (KLIE 1935) have to be considered with caution, as the absence of complete descriptions does not allow a full comparison with the original population described by MENZEL (1923).

Genus *Microdarwinula* DANIELOPOL, 1968

DIAGNOSIS

Small (<0.40 mm) animals, with rounded Cp, without externally visible brood pouch. Cms large (not reduced in size with the rest of the carapace) and central (not anteriorly displaced). Cp with L/R overlap. Hinge with prominent but smooth ridge in LV, RV with groove and prominent anterior and posterior cardinal teeth. RV without keel; LV with large antero- and postero-ventral internal

teeth. A1 with two dorsal setae on first segment, one dorsal seta and three ventral setae on second segment. A2 with two long setae and a spine on the exopodite; first endopodal segment with two long ventro-apical setae. Setae *y* and *z* on penultimate Md-palp segment long and subequal; terminal segment with six claws. Fu and P-abd absent, also in juveniles.

DIFFERENTIAL DIAGNOSIS

The genus is primarily characterised by its valve features, rounded shape in lateral view and absence of an externally visible brood pouch, through which it is distinguishable from all other Darwinulidae. Its chaetotaxy is largely congruent with *Penthesilenula* nov.gen., (except for the presence of one (not two) dorsal seta on the first segment of the A1) and with *Darwinula s.s.* and *Alicenula* nov.gen. (except in the length ratio of the setae *y* and *z* and number of terminal claws on Md-palp). *Microdarwinula* differs in several soft part features from *Vestalenula* nov.gen.,

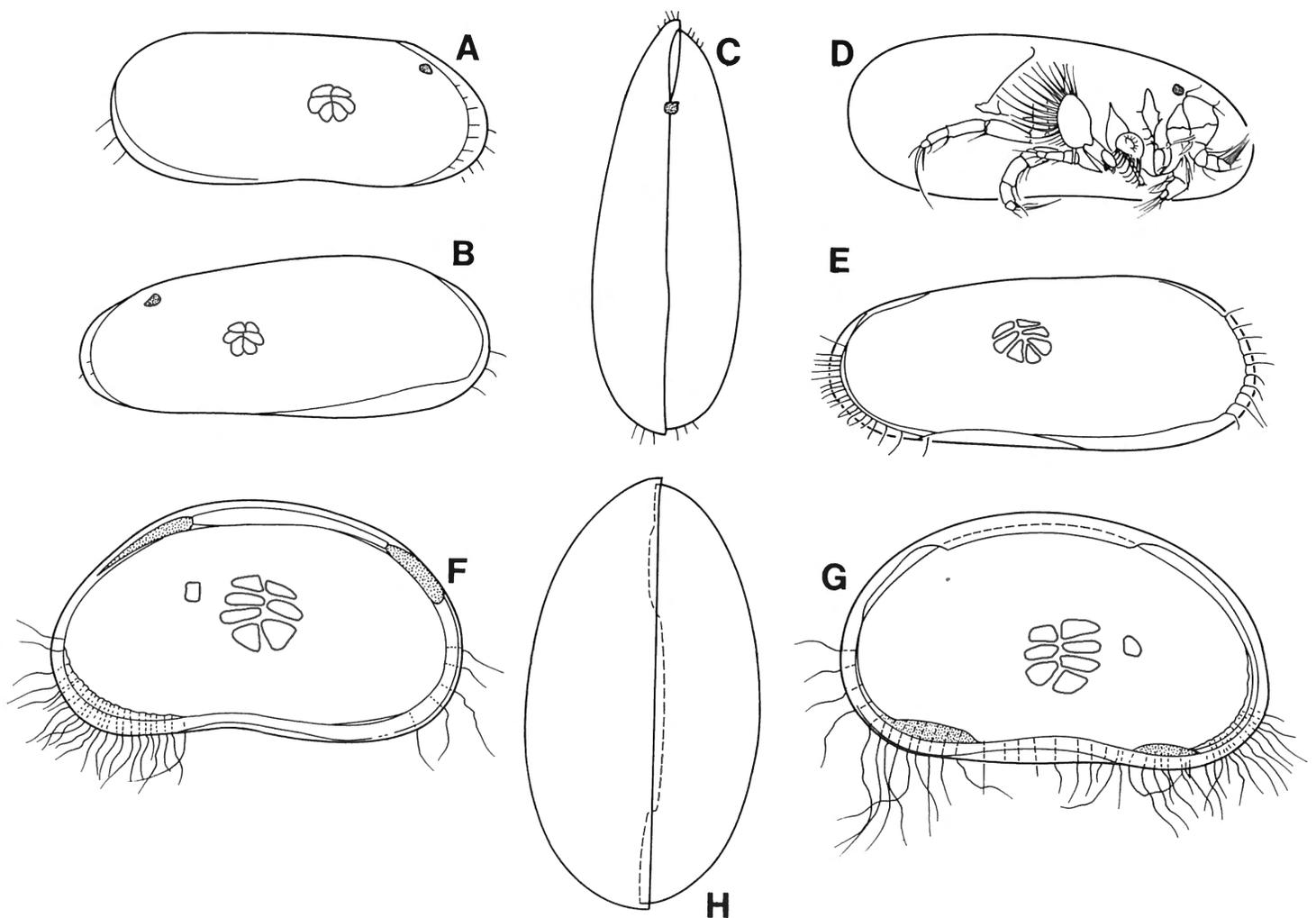


Fig. 24 – A-C: *Alicenula serricaudata* (KLIE) (from KLIE, 1935). D: *Darwinula stevensoni* BRADY & ROBERTSON (from SYWULA, 1974). E: *Alicenula furcabdominis* (KEYSER) (from KEYSER, 1975). F-H: *Microdarwinula zimneri* (MENZEL) (from DANIELOPOL, 1968). A. Cp, Rlv (fig. 41). B. Cp, Llv (fig. 37). C. Cp, dv (fig. 42). D. LV, iv (fig. 11A). E. RV, iv (fig. 6). F. RV, iv (fig. 7). G. LV, iv (fig. 6). H. Cp, dv (fig. 8).

especially in those of the A1 and A2 (see differential diagnosis of *Vestalenula* nov.gen.).

REMARKS

LI (1959, cited in ZHANG SHEN & WU QING-YAO, 1986) described *Sinodarwinula guanzhuangensis* from the Late Cretaceous - Early Tertiary of China. The genus strongly resembles *Microdarwinula* in outline (no posterior brooding cavity and rounded dorsal margin in lateral view) and is equally small (Le=0.33 mm). However, the species *Sinodarwinula guanzhuangensis* is certainly not conspecific with *Microdarwinula brevis*, as the former is more elongate. It is not impossible that *Microdarwinula* DANIELOPOL, 1968 will in time turn out to be a junior synonym of *Sinodarwinula* LI, 1959; but the incomplete description at present does not allow to check for important valve features, such as internal teeth of the LV, cardinal teeth of the hinge on the RV, etc. We therefore provisionally maintain *Sinodarwinula* and *Microdarwinula* as valid genera until re-examination of type material (or of new specimens) is possible. In any case, the discovery of *Sinodarwinula* pushes the origin of darwinulid lineages without brood pouch back from 20 Ma (the oldest record of *Microdarwinula zimmeri* - as *Darwinula brevis* STRAUB, 1952) to 60-70 Ma.

Type species (by original designation):

Darwinula zimmeri MENZEL, 1916

24. *Microdarwinula zimmeri* (MENZEL, 1916) (Figs 23A-G, 24F-H, 29I-L)

syn. *Darwinula brevis* STRAUB, 1952

TYPE LOCALITY

East Usambara, Amani, Tanzania. Coll. 23-27.08.1910 by C. ZIMMER.

HOLOTYPE

Repository unknown.

DIAGNOSIS

Small (<0.40 mm) animals, with rounded Cp, no brood pouch and Cms large and in the middle of the valve, consisting of c 6-7 scars. LV overlapping RV on all sides. Hinge with prominent but smooth ridge in LV, RV with groove and prominent anterior and posterior cardinal teeth. RV without keel; LV with large antero- and postero-ventral internal teeth. A1 with two dorsal setae on first segment, one dorsal and three ventral setae on second segment;

third segment with one dorsal seta; fourth segment with one ventral and two dorsal setae. Exopodite of A2 with two longer, apical setae and one short, conical lateral seta; first endopodal segment with two large apical setae. Md-palp with penultimate segment with four apical setae: *y* and *z* both long, *x* and *w* not reaching tip of terminal segment; the latter with six unequal apical claws and two unequal lateral setae (*b* and *c*'), one on each side. Fu absent, also in juveniles. P-abd absent.

MEASUREMENTS

MENZEL (1916): Le=0.30 mm, H=0.15 mm, W=0.14 mm.

DANIELOPOL (1968): LV: Le=0.34-0.37 mm, H=0.18-0.21 mm; RV: Le=0.35-0.36 mm, H=0.19-0.20 mm, W=0.18-0.20 mm.

LITERATURE

MENZEL (1916); DEVOTO (1965); DANIELOPOL (1968): full re-description; MARTENS *et al.* (1997).

Species inquirendae (Recent species only)

REMARKS

HOLMES (1997) reported the occurrence of *Darwinula* sp. gr. *stevensoni* and *D.* sp. gr. *africana* from waterbodies in the western part of Jamaica, without providing any morphological description. These records will not further be considered in the present revision.

25. ?*Darwinula managuensis* SWAIN & GILBY, 1965 (Not figured)

Type locality

Lake Managua, Nicaragua.

HOLOTYPE

United States National Museum, Washington D.C., USA. Accession number not reported.

MEASUREMENTS

SWAIN & GILBY (1965): Le=0.43 mm, H=0.20 mm.

LITERATURE

SWAIN & GILBY (1965).

26. ?*Darwinula yaquensis* SWAIN, 1967
(Not figured)

TYPE LOCALITY

Eastern nearshore part of Middle Gulf of California, Mexico.

HOLOTYPE

University of Minnesota Paleontological Collections. Accession number not reported.

MEASUREMENTS

SWAIN (1967): RV: Le=0.45 mm, H=0.18 mm.

LITERATURE

SWAIN (1967).

REMARKS

Most likely this species belongs in the genus *Darwinula* s.s., but it is insufficiently described to allow characterization.

27. ?*Vestalenula* sp. A
(Fig. 25T,U)

syn. *Darwinula* sp. A DANIELOPOL, 1980

LOCALITY

Cueva del Agua, Cuba.

MATERIAL

Material deposited at the Limnological Institute, Vienna (Austria).

LITERATURE

DANIELOPOL (1980).

REMARKS

This species belongs in the *danielopoli* group of the genus *Vestalenula* s.s.

28. ?*Vestalenula* sp. B
(Fig. 25V,W)

syn. *Darwinula* sp. B DANIELOPOL, 1980

LOCALITY

Oued Lebga, Tunisia.

MATERIAL

Material deposited at the Limnological Institute, Vienna (Austria).

LITERATURE

DANIELOPOL (1980).

REMARKS

This species belongs in the *danielopoli* group of the genus *Vestalenula* s.s.

Discussion

Taxonomy and nomenclature of ancient asexuals

When assessing the taxonomy of a certain clonal group, it is vital to determine what type of asexual taxon one is dealing with, as indeed several different types of asexuals exist. For example, *Artemia parthenogenetica* is an interspecific hybrid, as are most of the known examples of asexual lineages in vertebrates (fish and lizards); *Daphnia magna* has a cyclic parthenogenesis (the same populations reproduce sexually and asexually in different seasons and environmental conditions); many cypridinid ostracods have a geographical parthenogenesis, where sexual reproduction is geographically restricted to part of the areal, while parthenogenesis occurs in most if not all of the area where the species occurs. In all of the above examples, sexual reproduction is still possible and occurs at some stage in the life history of the organisms. Taxonomic concepts dealing with such organisms must take this into account and generally apply species concepts as clusters of clonal lineages around sexual roots (MALLET 1995).

In the case of ancient asexual groups, however, where no sexuality at all occurs, neither geographically, nor temporarily, nor taxonomically segregated, a different type of taxonomic concepts needs to be applied. The following facts need to be taken into account, when such a group is taxonomically revised.

1. *Small morphological differences*

It has been determined that both molecular and morphological evolution is slow in such groups. One must thus

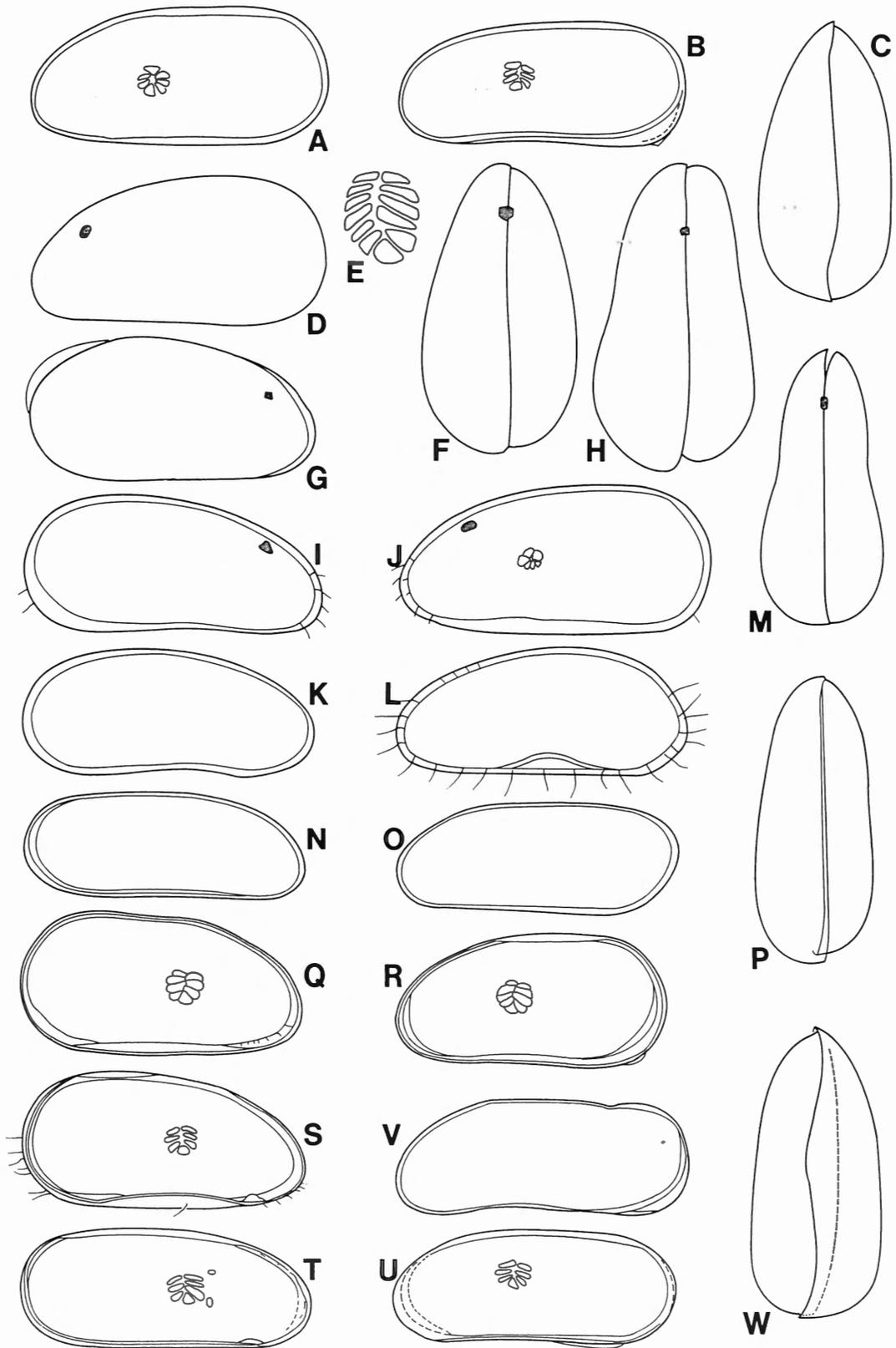


Fig. 25 - A-C: *Vestalenula boteai* (DANIELOPOL) (from DANIELOPOL, 1970). D-F: *Vestalenula cuneata* (KLIE) (from KLIE, 1939). G,H: *Vestalenula daps* (HARDING) (from HARDING, 1962). I,J: *Vestalenula inconspicua* (KLIE) (from KLIE, 1935). K-M: *Vestalenula marlieri* (KISS) (from KISS, 1959). N-P: *Vestalenula lundi* (NEALE & VICTOR) (from NEALE & VICTOR, 1978). Q-S: *Vestalenula pagliolii* (PINTO & KOTZIAN) (Q,R: from PINTO & KOTZIAN, 1961; S: OC2161). T,U: *Vestalenula* sp. A (from DANIELOPOL, 1980). V,W: *Vestalenula* sp. B (from DANIELOPOL, 1980).
 A. LV, ev (fig. 1C). B. RV, iv (fig. 1B). C. Cp, dv (fig. 1A). D. Cp, Llv (fig. 66). E. Cms (fig. 68). F. Cp, dv (fig. 67). G. Cp, Rlv (fig. 46). H. Cp, dv (fig. 52). I. Cp, Rlv (fig. 50). J. Cp, Llv (fig. 49). K. LV, iv (fig. 1). L. RV, iv (fig. 2). M. Cp, dv (fig. 3). N. Cp, Rlv (fig. 5). O. Cp, Llv (fig. 3). P. Cp, dv (fig. 4). Q. LV, iv (fig. 1). R. RV, iv (fig. 2). S. LV, iv. T. LV, iv (fig. 8A). U. RV, iv (fig. 8B). V. RV, iv (fig. 8D). W. Cp, vv (fig. 8C).

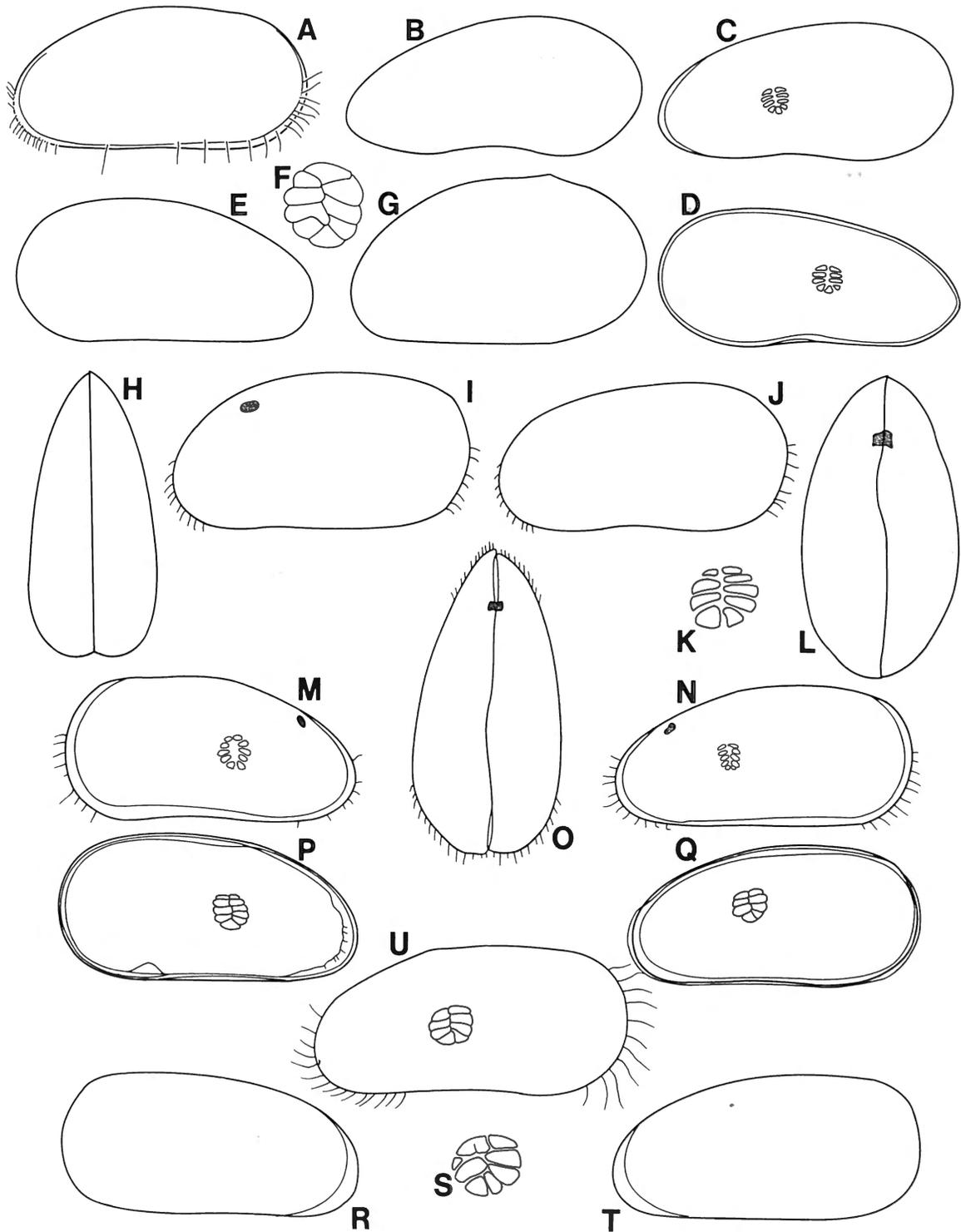
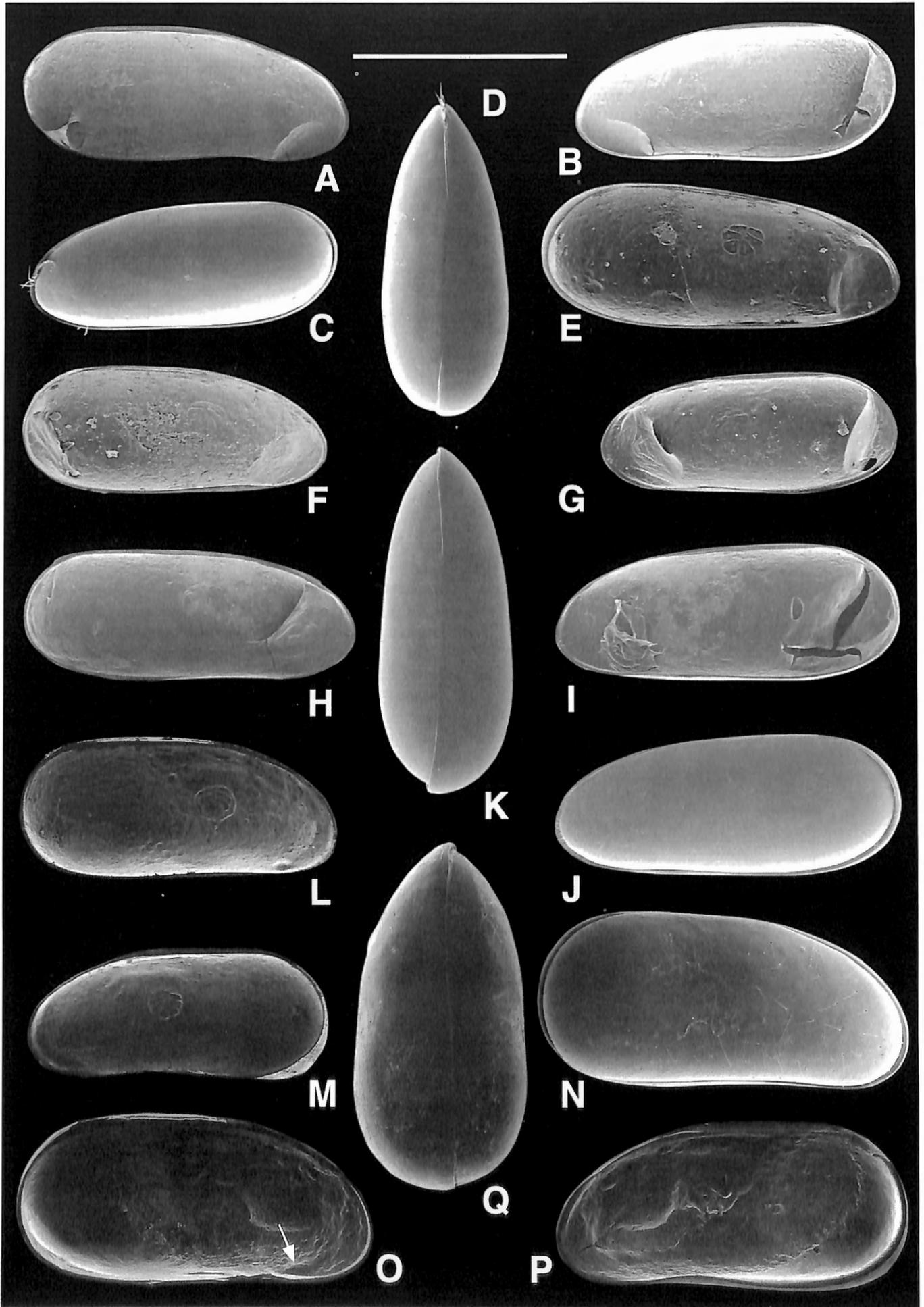


Fig. 26 - A: *Penthesilenula araucana* (LÖFFLER) (from LÖFFLER, 1961). B: ?*Penthesilenula reposita* (CHAPMAN) (from CHAPMAN, 1963). C,D: *Darwinula* sp. HORNIBROOK (= *P. reposita*) (from HORNIBROOK, 1955). E-H: *Penthesilenula setosa* (DADAY) (from DADAY, 1902). I-L: *Penthesilenula sphagna* (BARCLAY) (from BARCLAY, 1968). M-O: *Penthesilenula africana* (KLIE) (from KLIE, 1935). P,Q: *Penthesilenula brasiliensis* (PINTO & KOTZIAN) (from PINTO & KOTZIAN, 1961). R-T: *Darwinula dicastrii* LÖFFLER (from LÖFFLER, 1966). U: *Penthesilenula malayica* (MENZEL) (from MENZEL, 1923). A. LV, ev (fig. 239). B. LV, ev (Pl. XIII, fig. 1). C. LV, ev (fig. 15). D. LV, iv (fig. 16). E. RV, ev (fig. 14). F. Cms (fig. 21). G. LV, ev (fig. 15). H. Cp, dv (fig. 16). I. Cp, Llv (fig. 2a). J. RV, iv (fig. 2b). K. Cms (fig. 2c). L. Cp, dv (fig. 2d). M. Cp, Rlv (fig. 46). N. Cp, Llv (fig. 45). O. Cp, dv (fig. 47). P. LV, iv (fig. 7). Q. RV, iv (fig. 8). R. RV, ev (Pl. 1, fig. a). S. Cms (Pl. 1, fig. b). T. LV, ev (Pl. 1, fig. b). U. RV, iv (fig. 4).



give greater weight to small morphological differences than in the case of lineages with sexual or mixed reproduction, in which case a higher intraspecific variability must be allowed. A condition here is that such features must be stable, and thus occur consistently throughout one (or several) population(s).

2. Single specimens with aberrant characters

In principle, every clonal specimen has the potential to create a new lineage. If a certain specimen has acquired a morphologically visible character which distinguishes it from other specimens (either through a macro-mutation or through accumulation of several smaller mutations, together expressing the new morphological feature), then such a specimen could be considered to belong to a new species. Two factors are important here. Firstly, one must be certain that the new character is genetically induced, and not the result of developmental problems (i.e. during moulting). Secondly, the taxonomic principle that new species should never be described on one individual is even more important in such ancient asexual groups (see also point 1).

3. Polyphyletic origin

One can assume that speciation in such lineages occurs either through saltatory macromutation or through gradual accumulation of mutations. In both cases, similar morphologies can originate independently from each other at different times and in different places. An example of the latter would be that specimens of *P. brasiliensis* with double Fu originated in both South America and in Southern Africa. If this morphological aberration is indeed genetically induced, and if animals with this morphology are considered to belong to a different species, then this species could have had a polyphyletic origin. The example falls short of being perfect as to date we are not certain that the feature is stable within a population. Moreover, even if this is the case, then we still cannot determine whether indeed this feature originated at least twice on different continents or the double Fu originated once and subsequently expanded its distribution over several continents. The case is similar to that of interspecific hybrids, for example *Artemia parthenogenetica*, which can originate as a hybrid of two sexual parental species several times and in several places. As the ancestral stock of such species is always the same, there is a growing tendency

to consider such hybrids as valid species. The same must then be true for polyphyletic asexual speciation.

4. Morphological gaps

As biological species concepts are inapplicable to ancient asexuals, the one species concept that can be applied to such lineages is the morphological species concept, which requires morphological gaps between species (MAYR 1969). Asexual groups derived from extant sexual roots mostly form a cluster of closely related morphologies and to distinguish between intraspecific clonal lineages and asexual spin-offs forming different species is very difficult indeed, as was exemplified by the revision of the ostracod genus *Herpetocypris* (GONZALEZ MOZO *et al.*, 1996). Surprisingly, however, the different species of the Darwinulidae are easily recognisable as very few intermediate forms exist. This was already shown for another ancient asexual group by HOLMAN (1987), who found that in the bdelloid rotifers, fewer synonyms occur than in the cyclically sexual Monogononta. Bdelloid species are thus causing less taxonomic confusion, i.e. they are more easily distinguishable because of clear morphological gaps between species. The same is true for darwinulids. A reason for this is not immediately apparent; but two possible causes can be singled out. Firstly, slower molecular evolution means that fewer intermediate forms originate. Secondly, it also means that natural selection has longer time spans to weed out the less fit, intermediate forms.

5. Silent genes

MARSHALL *et al.* (1994) postulated that silent genes (i.e. the genes present in the genome but not being expressed during the lifetime of the organism) cannot survive longer than 10 Ma in any type of genome, but this hypothesis is contested by FRYER (pers. comm.), who offers evidence that such genes most likely can survive for much longer periods of time using examples of recurring atavistic morphologies. The latter hypothesis is further strengthened by the assumed higher efficiency of DNA repair mechanisms in at least a number of darwinulids (SCHÖN *et al.*, 1998; SCHÖN & MARTENS, 1998). If such silent genes are switched on after a certain time, they can introduce strong bias into any phylogeny scheme, but especially in that of ancient asexual groups. Certain darwinulids indeed show aberrant features which might be ascribed to such

Fig. 27. – A-D: *Darwinula stevensoni* BRADY & ROBERTSON; E: *Alicenula serricaudata* (KLIE); F,G: *Alicenula furcabdominis* (KEYSER); H-K: *Alicenula inversa* (MARTENS & ROSSETTI); L,M: *Vestalenula boteai* (DANIELOPOL); N-Q: *Vestalenula molopoensis* (MARTENS & ROSSETTI). Origin of illustrated specimens: A-D = Lake Pääjärvi, Finland; E = Paraibuna, RB, Brazil; F,G = Paurotis Pond, Everglades N.P., Florida, USA; H-K, N-Q = Molopo, North West Province, RSA; L,M = Nitratál, Slovakia (fossil).

D. stevensoni: A. LV, iv (OC1818). B. RV, iv (idem). C. Cp, left lv (OC1821). D. Cp, dv (OC1820).

A. serricaudata: E. LV, iv (OC2156).

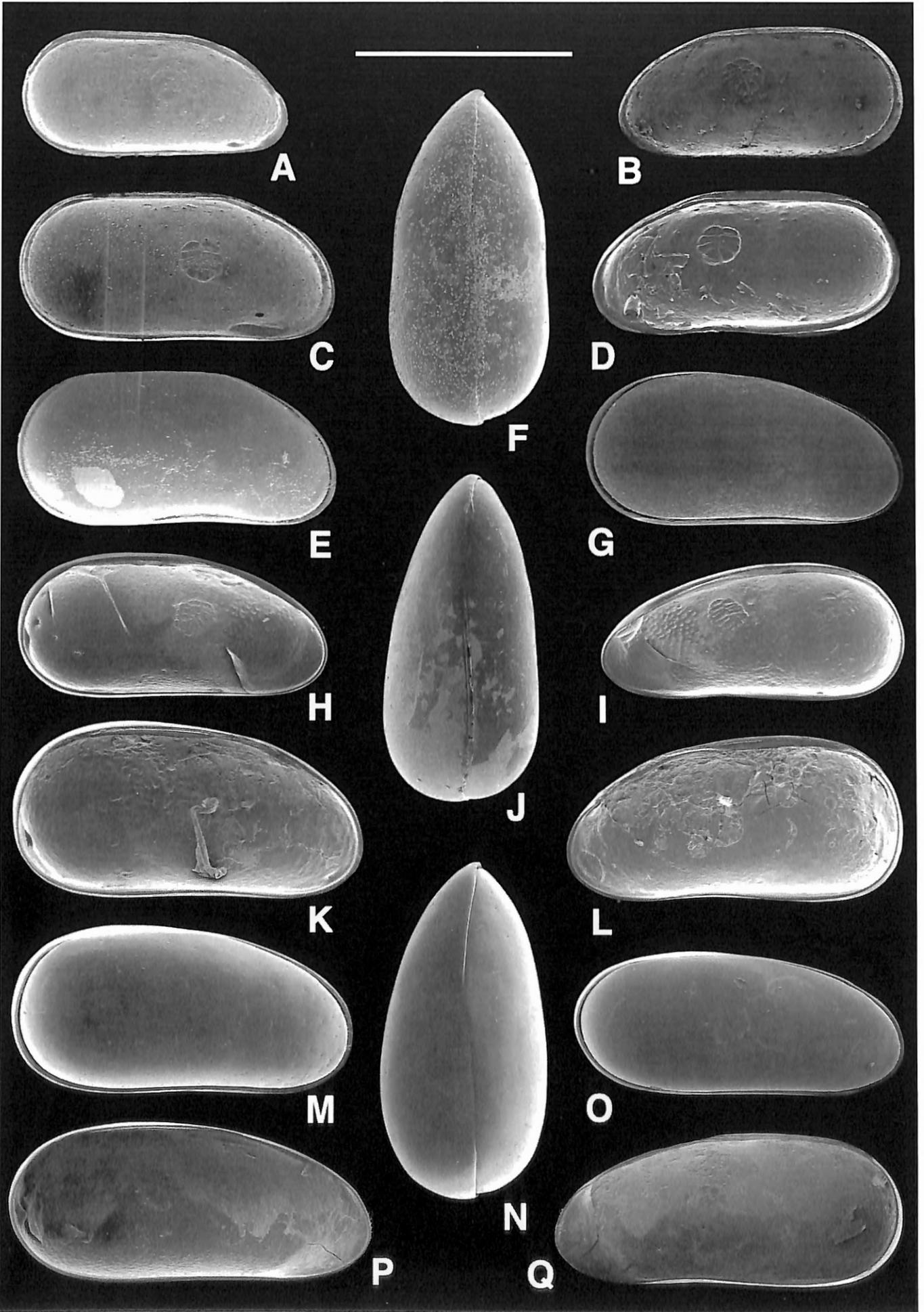
A. furcabdominis: F. LV, iv (OC2174). G. RV, iv (idem).

A. inversa: H. LV, iv (OC2116). I. RV, iv (idem). J. Cp, left lv (OC2115). K. Cp, dv (OC2113).

A. boteai: L. LV, iv (OC2168). M. RV, iv (OC2169).

A. molopoensis: N. LV, iv (OC2100). O. RV, iv (idem). P. Cp, right lv (OC2108). Q. Cp, dv (OC2105).

Scale = 417 µm for A-D; 343 µm for F-G; 325 µm for E,H-K; 308 µm for L-M; 299 µm for N-Q.



phenomena. For example, presence or absence of P-abd in different species in *Vestalenula* nov.gen. and *Penthesilenula* nov.gen., valve overlap reversals in different species, etc. Such phenomena could lead to mosaic evolution, in which possession of similar features no longer reflects common descent, thus rendering the reconstruction of phylogenetically valid taxonomies impossible. However, the present revision shows that such characters seem to occur at the specific level only, and that they are relatively easily recognisable amongst the various other features which do comply with the general diagnosis of species clusters (either genera or species-groups within genera).

In spite of these potential hazards, we conclude that it is possible to construct a trustworthy taxonomy of ancient asexuals, both reflecting the natural phylogeny and being practically useful (with taxa being recognisable), as long as the above points are carefully considered.

Taxonomic value of characters

Species and genera in the Darwinulidae are mostly characterised by both valve and soft part features. As is usual for ostracods, it appears that the structure and shape of valves are more plastic, while soft part features tend to be more conservative. Therefore, chaetotaxy of limbs is generally used to characterise genera, while valve shapes are better suited as specific characteristics. This explains why species with very different valve shapes (short and subquadrate, long and elongate) can occur in the same genus. The reasons behind this are clear and not related to the special reproductive mode in darwinulids, they are valid for the majority of bivalved arthropods and certainly for most ostracods. Firstly, because the entire body has to be envelopped by the valves, the number of body appendages, of segments per appendage and the chaetotaxy in general are strongly reduced in ostracods as compared to other benthic crustaceans, for example harpacticoids. Secondly, the same bodyplan also makes that natural selection has a strong effect on valves, but a strongly reduced effect on the protected limbs. The latter are thus logically more conservative in evolution.

Structural valve features are very rare in Darwinulidae, as this group has no calcified inner lamella or any other complete marginal valve structure: presence or absence of ventral keel on RV (a remnant of an external list), cardinal teeth on RV and internal ventral and caudal teeth in LV (remnants on an internal list) are the only useful structural characteristics. However, these features mostly follow patterns congruent to those of the soft part features

and thus strengthen the validity of the genera. In a few cases, exceptions occur. For example, *Penthesilenula* nov.gen. comprises two species-groups with different patterns of internal teeth in the LV, although soft part features strongly indicate that all ten species indeed belong in one phylogenetic lineage.

Aberrant characters within a lineage (possibly as a consequence of a switched-on silent gene – see above) can help to characterise a species within a certain lineage, on the condition that the character is stable.

The following general rules became apparent during the present revision:

Shape and size of valves:	specific (exception: <i>Microdarwinula</i>)
Valve overlap :	mostly specific, sometimes generic
Keel on RV:	generic. Shape of keel: species-group
Internal teeth on LV:	generic or species-group
Chaetotaxy A1 and A2:	mostly generic, sometimes specific
Md-palp:	mostly generic, sometimes specific
T1:	specific in the case of <i>D. stvensoni</i>
Mx, T2, T3:	constant within the family
Fu and P-abd:	specific

Taxonomy of the Darwinulidae

The present revision deals with recent representatives only. This has the advantage that validity of taxa (both species and genera) is strengthened by both valve and soft part features. In a following step, the applicability of this new taxonomy of the Darwinulidae to fossil faunas will have to be tested. When dealing with well-preserved specimens, even of Mesozoic age, it will be possible to recognise most genera based on valve features mentioned above. However, species based on less well-preserved specimens will still have to be allocated to *Darwinula* s.l. This is not necessarily a problem. Although palaeontological and neontological taxonomies must be maximally integrated, they can still occasionally proceed independently from each other, as they rely on different methods, use different characters and reflect resolution at different levels.

Nevertheless, the strength of ostracods as a model group for the investigation of evolutionary processes lies in the fact that both neontological and palaeontological details are available. Fossil evidence is now required to complete the phylogeny of Darwinuloidea, showing whether the origin of the different lineages is situated in the Palaeozoic, the Mesozoic or the Cenozoic, which lineages are ancestral to others, providing absolute dating of phylogenetic

Fig. 28 – A,B: *V. pagliolii*; C-F: *V. danielopoli*; G-J: *Penthesilenula incae*; K-N: *P. aotearoa*; O-Q: *P. kohanga*. Origin of illustrated specimens: A,B = Cottbus, Germany (fossil); C,D = Mùcheln, Germany (fossil); E,F = Ostrau, Germany (fossil); G-J = Laguna Guaqui, Bolivia; K-Q = Karori stream, New Zealand.

V. pagliolii: A. LV, iv (OC2159). B. RV, iv (OC2158)

V. danielopoli: C. LV, iv (OC2086). D. RV, iv (idem). E. Cp, right lv (OC2090). F. Cp, dv (OC2088)

P. incae: G. Cp, right lv (OC1792). H. LV, iv (OC1794). I. RV, iv (idem). J. Cp, dv (OC1791).

P. aotearoa: K. LV, iv (OC2143). L. RV, iv (idem). M. Cp, right lv (OC2148). N. Cp, dv (OC2149).

P. kohanga: O. Cp, right lv (OC2170). P. 15. LV, iv (OC2151). Q. RV, iv (idem)

Scale= 530 µm for G-J; 500 µm for O-Q; 370 µm for A,B, K-N; 308 µm for L-F.

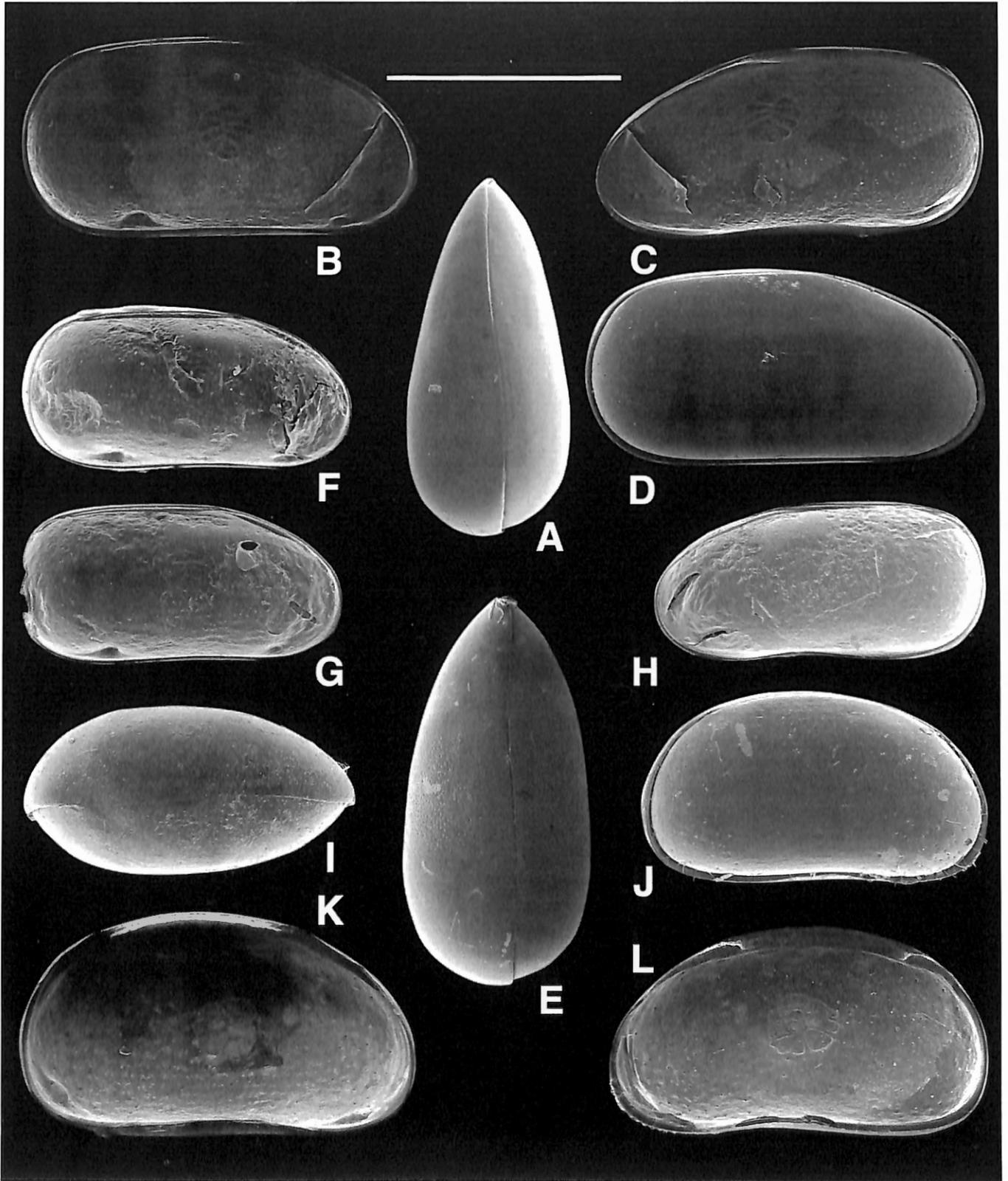


Fig. 29 – A.: *P. kohanga*; B-H.: *P. brasiliensis*; I-L: *Microdarwinula zimмери*. Origin of illustrated specimens: A= Karori stream, New Zealand; B-E; I-L= Clue de la Fou, France; F-H, Drakensberg area, South Africa.
P. kohanga: A. Cp, dv (OC2171).
P. brasiliensis: B. LV, iv (OC2164). C. RV, iv (idem). D. Cp, right lv (OC2162). E. CP, dv (OC2163). F. LV, iv (OC2166). G. LV, iv (OC2167 – specimen with double furca as in *P. dicastrii*). H. RV, iv (idem).
Microdarwinula zimмери: I. Cp, dv (OC2172). J. CP, right lv (no?). K. LV, iv (OC2173). L. RV, iv (idem).
 Scale= 500 μ m for A; 300 μ m for B-H; 238 μ m for I-L.

branching between the different genera and species-groups, etc. It is hoped that the present taxonomy of surviving taxa will facilitate the interpretation of the fossil faunas in a complete evolutionary framework. At that stage, these phylogenies can be applied to interpret other aspects of the history and biology of this group, such as, for instance, (palaeo-) zoogeography.

Distribution of Darwinulidae

Only the following preliminary remarks of the distribution of the species in this group can be offered, as most species are known from their type localities only and as no darwinulids at all have thus far been reported from vast areas, like China, most of Siberia etc. :

1. *Darwinula stevensoni* is the only darwinulid with cosmopolitan distribution. It occurs on all continents (including Australia, DE DECKKER pers.comm.), except Antarctica and can be found in a wide range of habitats. Both the wide distribution and its ecological tolerance offer support for the hypothesis that this species has a 'general purpose genotype' (LYNCH 1984) which is maintained by a very efficient DNA repair system (SCHÖN *et al.* 1998; SCHÖN & MARTENS 1998). Other darwinulids, not identified to species level, have been reported from Australia (eg. *Darwinula* sp. from Tasmania – DEDECKKER 1982). The total specific diversity of Australian darwinulids is expected to be quite high, when compared to other southern Hemisphere continents.

2. The *incae*-group of *Penthesilenula* nov.gen. occurs only in the southern Hemisphere and certainly for this group a Gondwana-origin seems plausible.

3. *Penthesilenula brasiliensis* (together with its congener *P. malayica*) occurs on at least three continents. This intercontinental distribution could be due to a superior dispersal system (compared to most other darwinulids) or to a great antiquity. The former species also seems to be the most plastic of the entire family, as several populations show specimens with clear morphological aberrations (double furca, valve reversal). The fossil *Darwinula* spec. from Tasmania (DE DECKKER, 1982) can at present not be identified to species level, but certainly belongs in the *africana*-group of *Penthesilenula*.

4. Most other species are known from their type localities only. At present we don't know if this really means that these are point endemisms, or simply that their extant distribution is at present insufficiently known.

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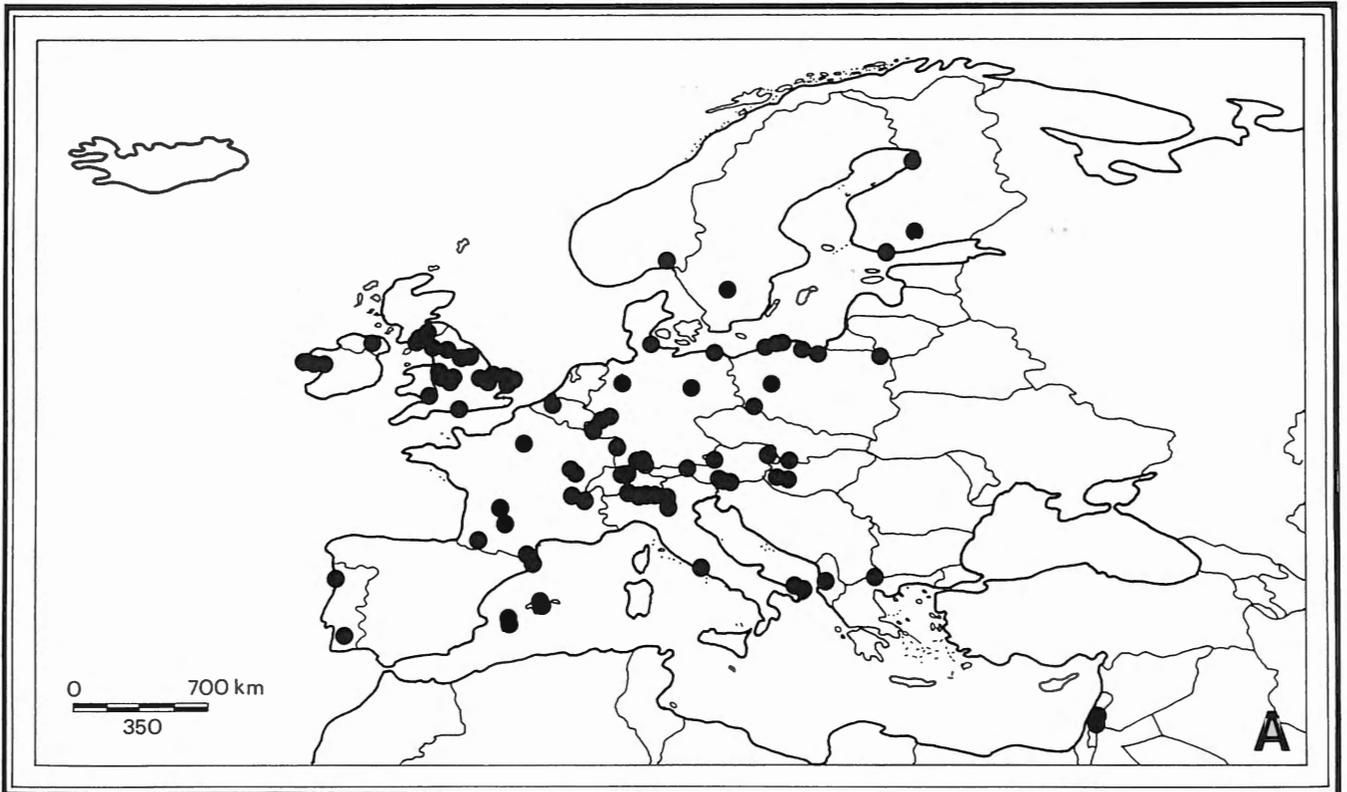


Fig. 30. – A. Records of *Darwinula stevensoni* BRADY & ROBERTSON in Europe (from NODE).

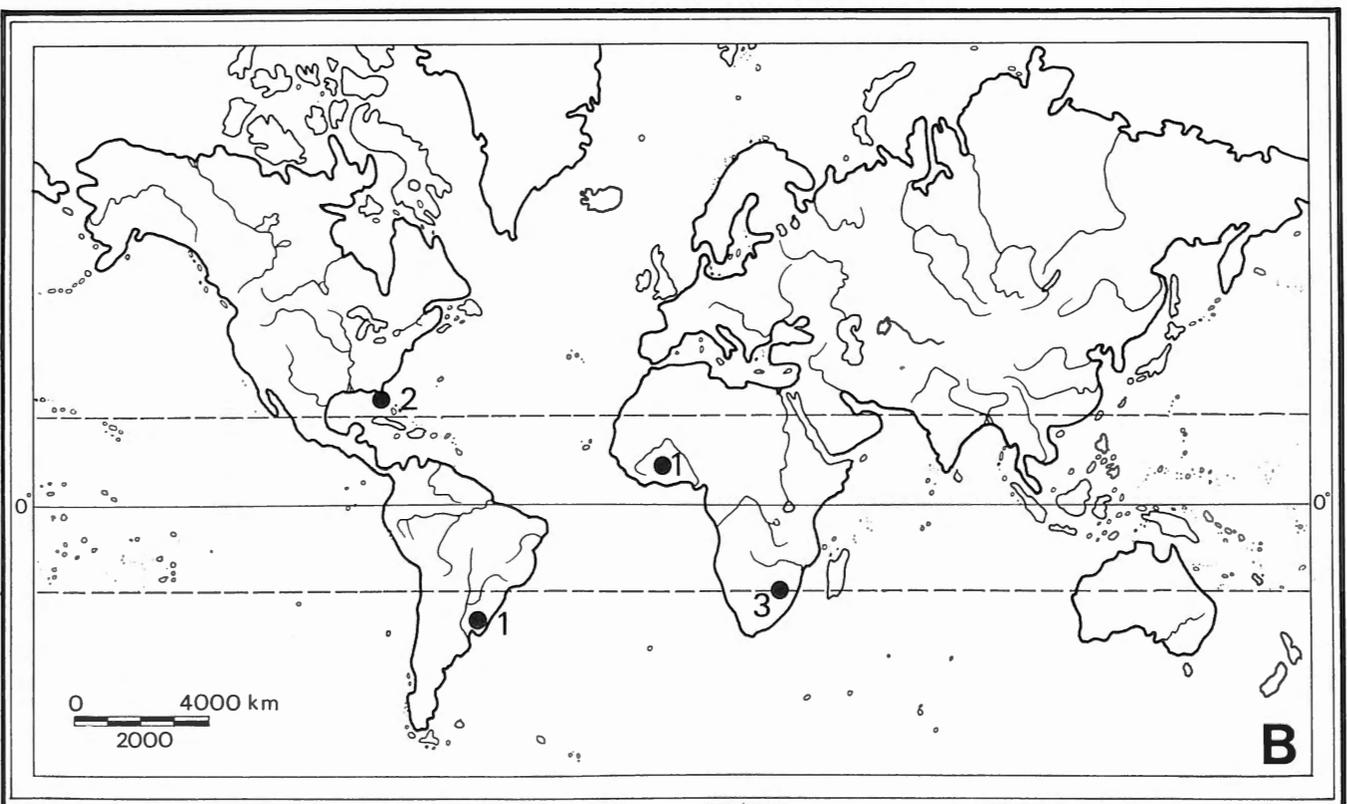


Fig. 30. – B. Map of distribution of the genus *Alicenula* nov.gen.: 1, *A. serricaudata* (KLIE); 2, *A. furcabdominis* (KEYSER); 3, *A. inversa* (MARTENS & ROSSETTI).

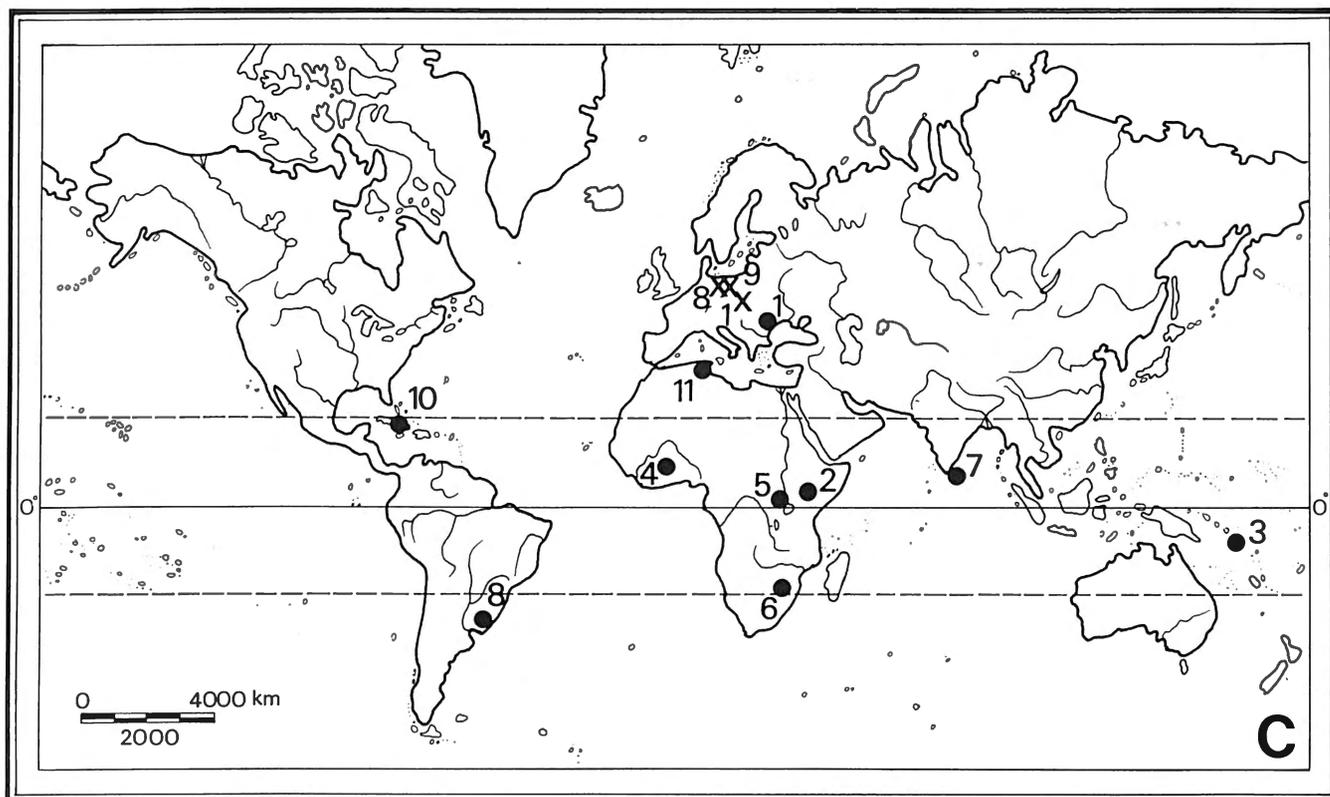


Fig. 30. – C. Map of distribution of the genus *Vestalenula* nov. gen.: 1, *V. boteai* (DANIELOPOL); 2, *V. cuneata* (KLIE); 3, *V. daps* (HARDING); 4, *V. inconspicua* (KLIE); 5, *V. marlieri* (KISS); 6, *V. molopoensis* (MARTENS & ROSSETTI); 7, *V. lundii* (NEALE & VICTOR); 8, *V. pagliolii* (PINTO & KOTZIAN); 9, *V. danielopoli* (MARTENS *et al.*); 10, ?*Vestalenula* sp. A DANIELOPOL; 11, ?*Vestalenula* sp. B DANIELOPOL.
●: Recent; ×: Fossil.

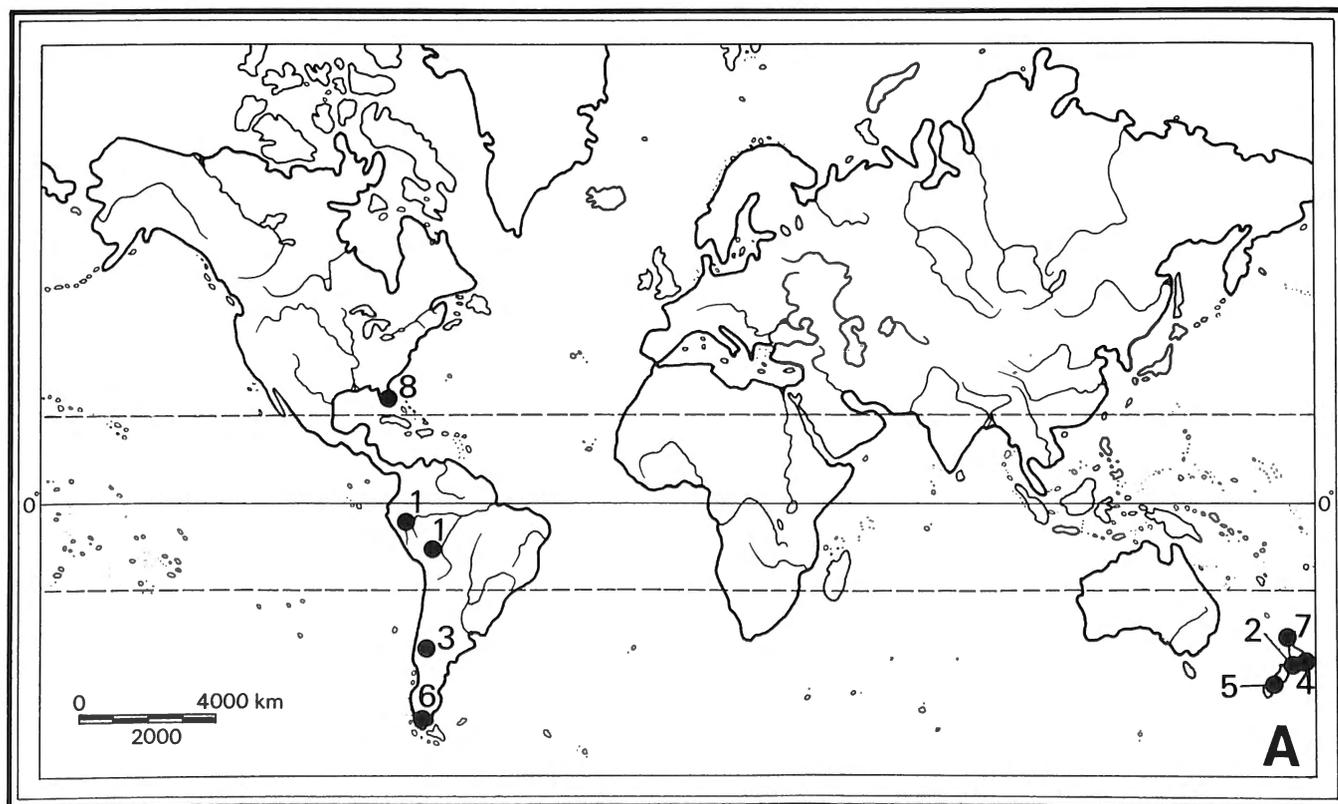


Fig. 31. – A. Map of distribution of the 'incae'-group of the genus *Penthesilenula* nov.gen.: 1, *P. incae* (DELACHAUX); 2, *P. aotearoa* (ROSSETTI *et al.*); 3, *P. araucana* (LÖFFLER); 4, *P. kohanga* (ROSSETTI *et al.*); 5, ?*Penthesilenula repoa* (CHAPMAN); 6, *P. setosa* (DADAY); 7, *P. sphagna* (BARCLAY); 8, ?*Penthesilenula* sp.

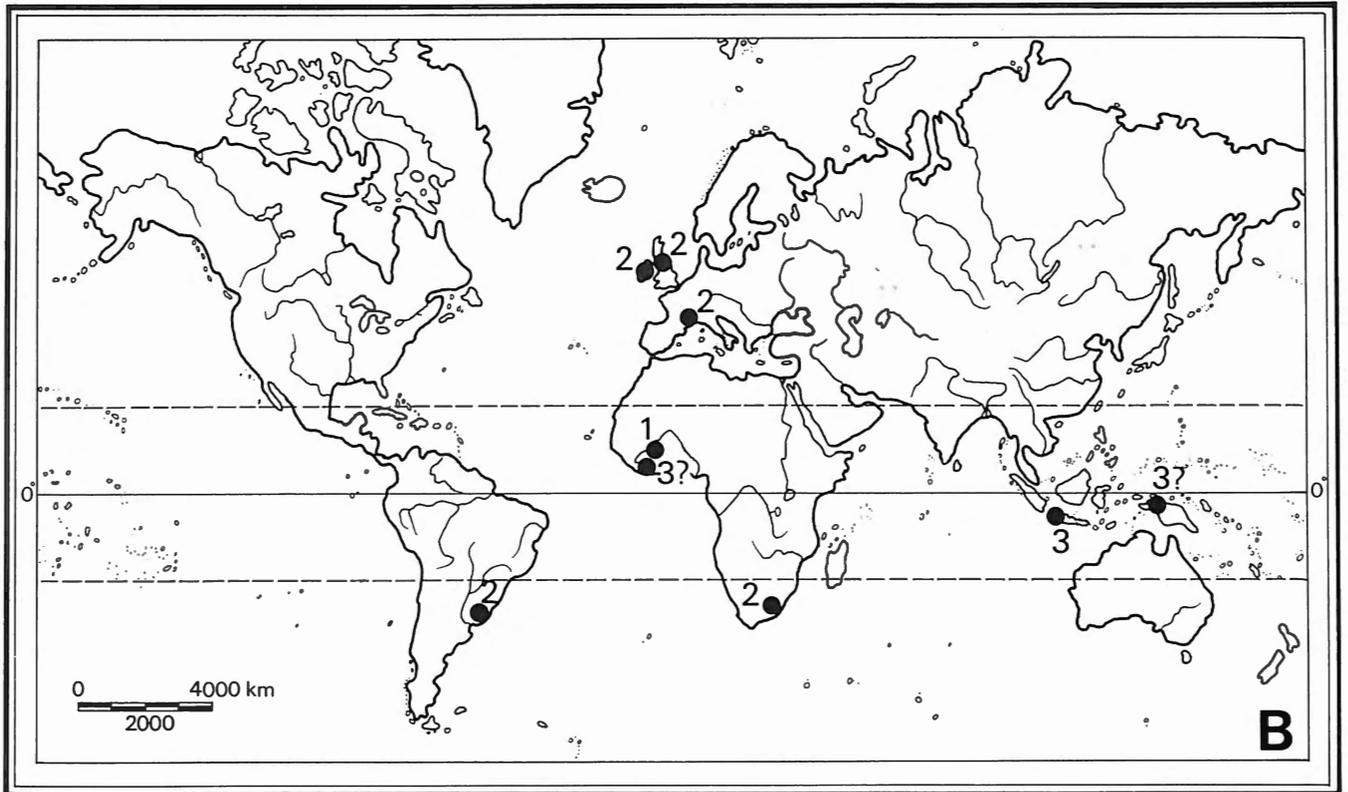


Fig. 31. – B. Map of distribution of the 'africana'-group of the genus *Penthesislenula* nov.gen.: 1, *P. africana* (KLIE); 2, *P. brasiliensis* (PINTO & KOTZIAN); 3, *P. malayica* (MENZEL).

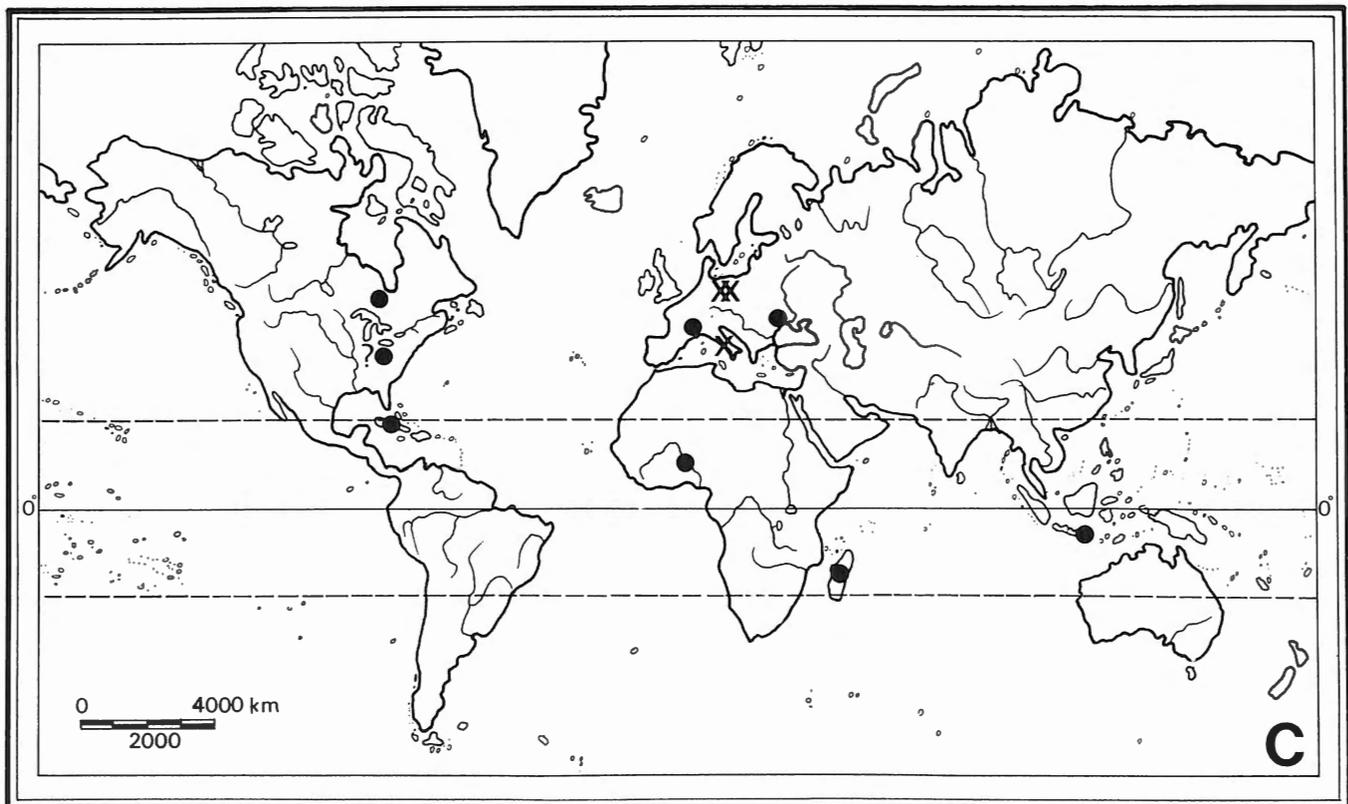


Fig. 31. – C. Map of distribution of *Microdarwinula zimmeri* (MENZEL).
●: Recent; ×: Fossil.

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Appendix 1: List of type materials investigated

- Darwinula africana* KLIE, 1935
Road from Man to Touba, km 21, Ivory Coast
07.03.1931
Coll.: C. ALLAUD and P.A. CHAPPUIS
Universität Hamburg, Zoologisches Museum
No. 291
Decalcified carapaces without soft parts
- Darwinula aotearoa* ROSSETTI *et al.*, 1998
Karori Stream, Kinnoull Station, Makara, Wellington, New Zealand
30.10.1996
Coll.: S.H. EAGAR
Ostracod Collection RBINSc Brussels
O.C.2143
An adult female, with soft parts dissected in glycerine in a sealed slide and valves stored dry
- Darwinula cuneata* KLIE, 1939
Omo Expedition, Kikuyu (Maji ya Moto= hot water spring), Kenya.
17.11.1932
Coll.: P.A. CHAPPUIS
Universität Hamburg, Zoologisches Museum
No. 294
Adult females with decalcified valves kept in glycerine
- Darwinula danielopoli* MARTENS *et al.*, 1997
Mücheln, Sachsen-Anhalt, Germany
17.11.1966
Coll.: D. MANIA
Ostracod Collection RBINSc Brussels
O.C.2085
A dried RV stored in a micropal slide
- Darwinula daps* HARDING, 1962
Lake Tegano, Rennel Isl., Solomon Is.
from stomach of *Eleotris fusca*
23.10.1951
Coll.: T. WOLFF
Copenhagen Museum
CRU-2651
Mounted slide
- Darwinula inversa* MARTENS & ROSSETTI, 1997
Marico Oog, Molopo Oog area, North West Province (former Transvaal), RSA
01.11.1993
Coll.: K. MARTENS
Albany Museum, Grahamstown, RSA
AM-TDW-7A
An adult female, with soft parts dissected in glycerine in a sealed slide and valves stored dry
- Darwinula kohanga* ROSSETTI *et al.*, 1998
Karori Stream, Kinnoull Station, Makara, Wellington, New Zealand
05.05.1996
Coll.: S.H. EAGAR
Ostracod Collection RBINSc Brussels
O.C.2151
An adult female, with soft parts dissected in glycerine in a sealed slide and valves stored dry
- Darwinula lundi* NEALE & VICTOR, 1968
Sabaragamuwa Province, Sri Lanka
19.02.1962
Coll.: P. BRINK, H. ANDERSON and L. CEDERHOLM
British Museum (Natural History)
Paratypes: Nos 1977.77-78: mounted slides
Nos 1977.79-85: specimens stored in alcohol with decalcified valves
- Darwinula marlieri* KISS, 1959
Luhanga River, Northern basin of Lake Tanganyika
22.6.1958
Coll.: G. MARLIER
Royal Museum for Central Africa, Tervuren
R.G. 50330 D/T./29.-31.
Mounted slides
- Darwinula molopoensis* MARTENS & ROSSETTI, 1997
Riverine pools, Marico River, Molopo Oog area, North West Province (former Transvaal), RSA
02.11.1993
Coll.: K. MARTENS
Albany Museum, Grahamstown, RSA
AM-TDW-26A
An adult female, with soft parts dissected in glycerine in a sealed slide and valves stored dry
- Darwinula protracta* ROME, 1953
Grotte Tsebahu, Mont Hoyo, Irumu, D.R.Congo.
10.3.1952
Coll.: N. LELEUP
Royal Museum for Central Africa, Tervuren
R.G. 40732-40733
Mounted slides
- Darwinula setosa* DADAY, 1902
Amenkelt, St. Cruz 27., Patagonia
Budapest Museum
IV/P-193
Mounted slide
- Darwinula sphenoides*, ROME, 1977
Lake Kivu, D.R. Congo
St. 1074 I.G. 25.476
Coll.: J. VERBEKE
Ostracod Collection RBINSc Brussels
O.C.766B1
Mounted slide

Appendix 2: List of other material used for the present paper

Only selected localities are given for *Darwinula stevensoni* and *Microdarwinula zimmeri* (see ROSSETTI & MARTENS, 1996; MARTENS *et al.*, 1997); for the other species, all localities are given.

Darwinula stevensoni BRADY & ROBERTSON, 1870

- Lake Pääjärvi, Finland, 14.11.1995, coll: K. MARTENS & K. SALONEN
- Hollandersgatkreek, Belgium, 18.05.1995, coll. K. MARTENS & M.E. MONTENEGRO
- Canale Corniano, Italy, 15.04.1996, coll. G. GENTILE
- Clue de la Fou, France, 30.06.1996, coll. K. MARTENS & D.L. DANIELOPOL
- Lake Sibaya, RSA, 16.10.1994, coll. K. MARTENS, M. HAMER & M. COKE

Alicenula furcabdominis (KEYSER, 1975)

- Paurotis Pond, Everglades N.P., Florida, USA, 13.02.1970, coll. D. KEYSER

Alicenula serricaudata (KLIE, 1935)

- Paraibuna, RB, Brazil, 28.11.1995, coll. M. KUHLMANN.

Vestalenula boteai (DANIELOPOL, 1970)

- Bojnice-Opatovce, Slovakia (fossil), 21.09.1966, coll. D. MANIA

Vestalenula pagliolii (PINTO & KOTZIAN, 1961)

- Cottbus, Germany (fossil), 12.08.1983, coll. R. FUHRMANN
- Tramandai, Brazil, 27.02.1964, coll. I.D. PINTO & Y.T. SANGUINETTI (leg. D. DANIELOPOL)

Penthesilenula brasiliensis (PINTO & KOTZIAN, 1961)

- Clue de la Fou, France, 30.06.1996, coll. K. MARTENS & D.L. DANIELOPOL
- White Loch, Kirkcudbrigh, Scotland, 06.09.1887, ex BRADY collection, Hancock Museum, Newcastle-upon-Tyne (no 1.47.20) (via D.J. HORNE)
- Drakensberg, RSA, 1995-96, Coll. K. MARTENS & M. HAMER

Penthesilenula incaea (DELACHAUX, 1928)

- Laguna Guaqui, Bolivia, 07.07.1995, coll. K. MARTENS & M.E. MONTENEGRO

?*Penthesilenula* sp.

- Paurotis Pond, Everglades N.P., Florida, USA, 13.02.1970, coll. D. KEYSER (K 38934) (=OC2175)

Microdarwinula zimmeri MENZEL, 1916

- Clue de la Fou, France, 30.06.1996, coll. K. MARTENS & D.L. DANIELOPOL
- Ostrau, Germany (fossil), 05.10.1992, coll. R. FUHRMANN

Appendix 3: List of genera, species and synonyms

Darwinula BRADY & ROBERTSON in JONES, 1885

Polycheles BRADY & ROBERTSON, 1870

Darwinella BRADY & ROBERTSON, 1872

Darwinula stevensoni BRADY & ROBERTSON, 1870

Argilloecia aurea BRADY & ROBERTSON, 1870 (partim)

Polycheles stevensoni BRADY & ROBERTSON, 1870

Darwinella stevensoni (BRADY & ROBERTSON, 1870) BR. & ROB., 1872

Darwinula stevensoni (BRADY & ROBERTSON, 1870) BR. & ROB., 1885

Darwinula improvisa (TURNER, 1895) (syn. part. in G.W. MÜLLER, 1912)

Darwinula aurea (BRADY & ROBERTSON, 1870) G.W. MÜLLER, 1912 (partim)

Darwinula protracta ROME, 1953 (syn. in ROSSETTI & MARTENS, 1996)

Darwinula variabilis TAGLIASACCHI, 1968 (syn. in ROSSETTI & MARTENS, 1996)

Darwinula sphenoides ROME, 1977 **nov.syn.**

Alicenula nov.gen.

Alicenula serricaudata (KLIE, 1935)

Darwinula serricaudata espinosa PINTO & KOTZIAN, 1961

Alicenula furcabdominis (KEYSER, 1975)

Alicenula inversa (MARTENS & ROSSETTI, 1997)

Vestalenula nov.gen.

Vestalenula boteai (DANIELOPOL, 1970)

Vestalenula cuneata (KLIE, 1939)

Vestalenula daps (HARDING, 1962)

Vestalenula inconspicua (KLIE, 1935)

Vestalenula lundii (NEALE & VICTOR, 1978)

Vestalenula marlieri (KISS, 1959)

Vestalenula molopoensis (MARTENS & ROSSETTI, 1997)

Vestalenula pagliolii (PINTO & KOTZIAN, 1961)

Vestalenula danielopoli (MARTENS *et al.* 1998)

Vestalenula sp. A. DANIELOPOL, 1980

Vestalenula sp. B DANIELOPOL, 1980

Penthesilinula nov.gen.

Penthesilenula incaea (DELACHAUX, 1928)

Penthesilenula aotearoa (ROSSETTI *et al.* 1998)

Penthesilenula araucana (LÖFFLER, 1961)

Penthesilenula kohanga (ROSSETTI *et al.* 1998)

?*Penthesilenula reposita* (CHAPMAN, 1963)

Darwinula sp. HORNIBROOK, 1955

?*Penthesilenula setosa* (DADAY, 1902)

Penthesilenula sphagna (BARCLAY, 1968)

Penthesilenula africana (KLIE, 1935)

Penthesilenula malayica (MENZEL, 1923)

Penthesilenula brasiliensis (PINTO & KOTZIAN, 1961)

Darwinula africana brasiliensis PINTO & KOTZIAN, 1961

Darwinula dicastrii LÖFFLER, 1961 **nov.syn.**

Microdarwinula DANIELOPOL, 1968

Microdarwinula zimmeri (MENZEL, 1916)

Darwinula brevis STRAUB, 1952

Species inquirendae

?*Darwinula managuensis* SWAIN & GILBY, 1965

?*Darwinula yaquensis* SWAIN, 1967