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 inquirenda. 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 serricudata-group. Vestalenula nov.gen. comprises the 8 species of the pagliollii-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. Penthesilenum 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. brasilensis, 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., Penthesilenum nov.gen., 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 inquirenda. Les nouveaux genres sont décrits sur la base des combinaisons des parties molles et des caractères des valves, mais la chétotaxie des membres parait 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 serricudata. Vestalenula nov.gen. comprend les huit espèces du groupe pagliollii-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. Penthesilenum 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. brasilensis, 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, ancients asexués.

Mots clés supplémentaires: Darwinula, Microdarwinula, Alicenula gen.nov., Vestalenula nov.gen., Penthesilenum 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; lv: internal view; ev: external view; A1: Antenna; 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 darwinuloide'; ps: 'poil stevensoni'; a, b, c, a, s1-3, t, w, x, y, z: specific setae on limbs; y1-3: aesthetasc on A2.

Nomenclature proposed by Danielopoulos (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. Møller, 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-square 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.
Taxonomic revision of the Recent and Holocene representatives of the Family Darwinulidae

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 DANIELLOP, 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 daniellopoli 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 & ROSETTI (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 RÖM 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 (DANIELLOP, 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<0.65 mm Alicenula

Genus Darwinula BRADY & ROBERTSON in JONES, 1885
   syn. Polycheles BRADY & ROBERTSON, 1870
   syn. Darwinivella 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.
Darwinula sphenoides
Darwinula variabilis
Darwinula protracta
(1870).

other original localities reported by

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 (s2 and s3). A2 exopodite with unequal bristles, one half as long as the other one. Second segment of Md-palp bearing four terminal setae, three short (x, y 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, vermiciform.

MEASUREMENTS

LITERATURE

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.
& 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 Darwinulinae (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):
Darianula serricaudata Klie, 1935

Other species allocated
D. furcaboraminis, 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 c present 2
b last segment of Md-palp with four apical claws, seta c absent A. furcaboraminis

2 a LV overlapping RV b RV overlapping LV

A. serricaudata A. inversa

2. Alicenula serricaudata (Klie, 1935)
(Figs 2A-E, 24A-C, 27E)


TYPE LOCALITY

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

HOLOTYPE


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 furcaboromnis* (KEYSER). Everglades National Park, Florida. From KEYSER (1975, Pl. 6).
Fig. 4. – *Alicenula inversa* (MARTENS & ROSSETTI). Molopo, North West Province, RSA.
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. Penultimate segment of Md-palp bearing three distal claws, a small internal seta (c) and a sub-terminal external seta (b); seta a absent. Penultimate segment of Md-palp with two short 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 serricata data*, Klie (1935) did not describe the morphology of the A1. Pinto & Kotzian (1961) figured the A1 of *D. serricata data espinosa* from Rio Grande do Sul (Brazil) with one dorsal seta (s) on the second endopodal segment. In all the investigated specimens from Paraiba (R.B., Brazil), we found two dorsal setae (s2 and s3) on the second segment of A1 endopodite, except one specimen in which seta s3 was absent (Fig. 2B). We are therefore inclined to consider such differences as a variation occurring in *Alicenula serricata data*.

3. *Alicenula furcatabdominis* (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 Penthesiliena* 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).


**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


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 Danielopoli, 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 seta 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 Alice nula 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


KEY TO THE SPECIES

1 a. keel on RV short (boteai-group) 2
   b. keel on RV elongate (danielopoli-group) V. danielopoli

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 . V. lundi
   b. in LV, valves sloping with rounded dorsal margin V. marlieri

5 a. first segment of A1 endopodite with one ventro-apical seta, first segment of A2 endopodite with two ventro-apical setae V. pagliolii
   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 V. boteai
   b. P-abd conical, Fu consisting of a widened base (Le=1.5xW) carrying a seta V. molopoensis

7 a. size >0.60 mm V. daps
   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).
I. The boteai-group

CHARACTERISTICS

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


TYPE LOCALITY


HOLOTYPE

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

DIAGNOSIS

Elongate valves (Le>2xH), 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 μm, H=197 μm; RV: Le=425 μm, H=191 μm (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-square 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. — *Vestalemula cuneata* (KLIE). Kikuyu, Kenya. From KLIE (1939).
A. A1 (fig. 69). B. A2 (fig. 70). C. Md-palp, endopodite (fig. 71).
Fig. 7. – *Vestallenula daps* (HARDING). Lake Te-Nggano, Rennel Island, Solomon Islands. Type material.
(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. Collected 23.10.1951 by T. Wolff.

**HOLOTYPE**

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

**DIAGNOSIS**

Cylindrical; 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 ventral 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.

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**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**


**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; 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**

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).

(Figs 9A-D, 25N-P)

**TYPE LOCALITY**


**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. 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**


**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. 10. – *Vestalenula marieri* (Kiss). Luhanga stream, Zaire. Type material.
Fig. 11. – *Vestalenula molopoensis* (MARTENS & ROSSETTI). Molopo, North West Province, RSA.
Fig. 12. *Vestalenula paglioli* (Pinto & Kotzian). Rio Grande do Sul, Brazil. Topotype material.

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 endopodite with 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 consisting of a broad, hirsute base 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


TYPE LOCALITY
Riverine pools at km 119.5 on road from Porto 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 Mücheln, 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 incae 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 furans, medisique in milibus ardet,
aurea subnectens exsertae cingula mammæ,
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 ventropapal setae. Setae y 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 y and z. It differs from Microdarwinula by the presence
Fig. 13. *Penthesilenula incae* (DELACHAUX). Laguna Guaqui, Bolivia.
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*
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. furcatabdominis*. 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. repoa*, *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 (incae-group) 2
   b. LV with postero-ventral internal tooth,
   no caudal tooth (africana-group) 6
2 a. LV overlapping RV  
   b. RV overlapping LV  *P. araucana* 3
3 a. size >0.70 mm  4
   b. size <0.70 mm  5
4 a. Le/H ratio <2.2, P-abd absent  *P. incae*
   b. Le/H ratio >2.2, P-abd present  *P. kohanga*
5 a. in LV, dorsal margin distinctly slanting
   forward, anterior end slender  *P. aotearoa*
   b. in LV, dorsal margin slightly curved,
   anterior end rounded  *P. sphagna*
6 a. second segment of A1 endopodite with
   one large dorsal seta  *P. malayica*
   b. second segment of A1 endopodite with
   two large dorsal setae  7
7 a. second segment of A1 endopodite with
   ventro-apical seta  
   b. second segment of A1 endopodite without
   ventro-apical seta  *P. brasiliensis*

**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 (s1), fourth segment with one ventral
seta and two dorsal setae (s2 and s3). 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.
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**


**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 (s1) and one ventral, fourth segment with two long dorso-apical setae (s2 and s3) 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 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.

**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).


**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. Peulultimate 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**

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

**TYPE LOCALITY**

**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 (s1); fourth segment bearing two dorso-apical setae (s2 and s3) 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): L=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.
18. *Penthesilenula repoa* (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. XII, 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 repoa* might be Pliocene, resp. Recent, representatives.  

19. *Penthesilenula setosa* (Day, 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**  
Day (1902): Le=0.60 mm, W=0.24 mm, H=0.28-0.33 mm.  

**Literature**  
Day (1902).  

**Remarks**  
Possibly *Penthesilenula setosa* will in time have to be considered a senior synonym of *P. incae*. 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 incae* (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**  

**Holotype**  
Dominion Museum, Wellington, New Zealand. Accession number not reported.
Fig. 17. — Penthesilena 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. — Penthesilena 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. — Pentheslenula 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-aquarish, 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 LOFFLER, 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: Ca-leu, 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. - *Penthesilena brasiensis* (Pinto & Kotzian). Drakensberg, RSA.
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 (s₁) and one ventral seta; fourth segment with two dorsal setae (s₂ and s₃) 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 μm (n=3), W=233-239 μm (n=2), H=245 μm (n=1).


LITERATURE

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

DIAGNOSIS

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 Agraffard, Ireland (D.I. 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 maiyica (MENZEL, 1923) (Figs 22A-C, 26U)

DIAGNOSIS

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.

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 zimmeri* (MENZEL). Lake Caldarusani (Judet Ilfov), Rumania. From DANIELOPOL (1968).
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.,

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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

(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 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, Nícaragua.

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. ?Darvinula 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 Aqua, 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.*

**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

A. LV, ev (fig. 1C). B. RV, iv (fig. 1B). C. Cp, dv (fig. 1A). D. Cp, Liv (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, Liv (fig. 49). K. LV, iv (fig. 1). L. RV, iv (fig. 2). M. Cp, dv (fig. 3). N. Cp, Rlv (fig. 5). O. Cp, Liv (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).

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. Polypheletic 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 \( P. \) \( brasilienensis \) with double \( F_u \) 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 polypheletic 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 if the double \( F_u \) originated once and subsequently expanded its distribution over several continents. The case is similar to that of interspecific hybrids, for example \( A e r i m e n a \) \( p a r t h e n o g e n e t i c a \), 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 polypheletic 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 (\( M A Y R \) 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 \( H e r p e t o c y p r i s \) (\( G O N Z A L E Z \) \( M O Z O \) 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 \( H O L M A N \) (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

\( M A R S H A L L \) 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 \( F R Y E R \) (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 (\( S C H O N \) et al., 1998; \( S C H O N \) & \( M A R T E N S \), 1998). If such silent genes are switched on after a certain time, they can introduce strong biases into any phylogeny scheme, but especially in that of ancient asexual groups. Certain darwinulids indeed show aberrant features which might be ascribed to such
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 enveloped 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:

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

2. **Valve overlap**:
   - mostly specific, sometimes generic
   - Shape of keel: species-group

3. **Internal teeth on LV**:
   - mostly specific

4. **Chaetotaxy A1 and A2**:
   - mostly generic

5. **Mx, T1, T2, T3**:
   - mostly generic

6. **Fu and P-abd**:
   - constant within the family

**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 Darwinuloida, 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 events.
Fig. 29 – A.: *P. kohanga*; B-H.: *P. brasiliensis*; I-L.: *Microdarwinula zimmeri*. 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).


Scale= 500 μm for A; 300 μm for B-H; 238 μm 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 Decker 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 (e.g. Darwinula sp. from Tasmania – DeDecker 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 brasilensis* (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 Decker, 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 endemics, or simply that their extant distribution is at present insufficiently known.

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**References**


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. furc abdominis* (Keys er); 3, *A. inversa* (Martens & Rossetti).
Taxonomic revision of the Recent and Holocene representatives of the Family Darwinulidae

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. martieri* (Kiss); 6, *V. molopoensis* (Martens & Rossetti); 7, *V. lunü* (Neale & Vicior); 8, *V. paglioli* (Pinto & Kottian); 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. sphagia* (Barclay); 8, ?Penthesilenula sp.
Fig. 31. – B. Map of distribution of the 'africana'-group of the genus Penthesilenula nov.gen.: 1, *P. africana* (KLIE); 2, *P. brasilienesis* (PINTO & KOTZIAN); 3, *P. malayica* (MENZEL).

Fig. 31. – C. Map of distribution of *Microdarwinula zimmeri* (MENZEL).

- Recent; ×: Fossil.
Taxonomic revision of the Recent and Holocene representatives of the Family Darwinulidae


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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 aotea roa** ROSETTI 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 Is., Solomon Is. from stomach of *Electris 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** ROSETTI 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  
Sabaramama 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 Tssebah, Moni 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.766BI  
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
- Hollandersgatkreek, Belgium, 20.05.1995, coll. K. Martens & M.E. Montenegro

**Alicenula furcatabdominis** (Keyser, 1975)

**Alicenula serricaudata** (Klie, 1935)

**Vestalenula boteai** (Danielopol, 1970)

**Darwinula** Brady & Robertson in Jones, 1885
- Polychaetes Brady & Robertson, 1870
- Darwinella Brady & Robertson, 1872

**Darwinula stevensoni** Brady & Robertson, 1870
- Argillioecia aurea Brady & Robertson, 1870 (partim)
- Polychaetes Brady & Robertson, 1870
- Darwinellia stevensoni (Brady & Robertson, 1870) Br. & Rob., 1872
- Darwinula stevensoni (Brady & Robertson, 1870) Br. & Rob., 1885
- Darwinula improviss (Turner, 1895) (syn. part. in G.W. MÖLLER, 1912)
- Darwinula aurea (Brady & Robertson, 1870) G.W. MÖLLER, 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 furcatabdominis** (Keyser, 1975)

**Vestalenula** nov.gen.
- Vestalenula boteai (Danielopol, 1970)
- Vestalenula cuanea (Klie, 1939)
- Vestalenula daps (Harding, 1962)
- Vestalenula inconspicua (Klie, 1935)
- Vestalenula lundi (Neale & Victor, 1978)

**Vestalenula pagliolii** (Pinto & Kotzian, 1961)
- White Loch, Kirkcudbright, Scotland, 06.09.1987, 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 inca** (Delachaux, 1928)

**Microdarwinula zimmeri** Menzel, 1916
- Ostroa, Germany (fossil), 30.02.1992, coll. R. Fuhrmann

Appendix 3: List of genera, species and synonyms

**Darwinula** Brady & Robertson in Jones, 1885
- Polychaetes Brady & Robertson, 1870
- Darwinella Brady & Robertson, 1872

**Darwinula stevensoni** Brady & Robertson, 1870
- Argillioecia aurea Brady & Robertson, 1870 (partim)
- Polychaetes Brady & Robertson, 1870
- Darwinellia stevensoni (Brady & Robertson, 1870) Br. & Rob., 1872
- Darwinula stevensoni (Brady & Robertson, 1870) Br. & Rob., 1885
- Darwinula improviss (Turner, 1895) (syn. part. in G.W. MÖLLER, 1912)
- Darwinula aurea (Brady & Robertson, 1870) G.W. MÖLLER, 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 furcatabdominis** (Keyser, 1975)

**Vestalenula** nov.gen.
- Vestalenula boteai (Danielopol, 1970)
- Vestalenula cuanea (Klie, 1939)
- Vestalenula daps (Harding, 1962)
- Vestalenula inconspicua (Klie, 1935)
- Vestalenula lundi (Neale & Victor, 1978)

**Vestalenula marieri** (Kiss, 1959)
- Vestalenula molopoensis (Martens & Rossetti, 1997)
- Vestalenula pagliolii (Pinto & Kotzian, 1961)
- Vestalenula danielopolii (Martens et al. 1998)
- Vestalenula sp. A. Danielopol, 1980
- Vestalenula sp. B Danielopol, 1980

**Penthesilenula nov.gen.**
- Penthesilenula inca (Delachaux, 1928)
- Penthesilenula aotearoa (Rossetti et al. 1998)
- Penthesilenula araucana (Löffler, 1961)
- Penthesilenula kokanga (Rossetti et al. 1998)
- Penthesilenula reposa (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)

**Species inquirendae**
- ?Darwinula managuensis Swain & Gilby, 1965
- ?Darwinula yaquensis Swain, 1967