Redescription and morphological variability of *Darwinula stevensoni* (BRADY & ROBERTSON, 1870) (Crustacea, Ostracoda)

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Abstract

The species *Darwinula stevensoni* is extensively redescribed. Morphological variability of both valves and soft parts is assessed in several geographically and climatically distant populations and is found to be minimal or non-existant. Only size significantly varies between populations and this can be attributed to the differences in ambient temperatures during the larval development. Number and shape of muscle scars also vary, but this both within and between populations. Valve shape and chaetotaxy of limbs are remarkably constant. One female from an Italian population has aberrant Mx2-palps, but this specimen is considered a teratological case.
Earlier records of males of *D. stevensoni* and the taxonomic position of the infraorder Darwinulocopina within the suborder Podocopina are briefly rediscussed. A hypothesis on the biological strategy of darwinulids is tested using data on morphological variability and taxonomic diversity.
Key-words: reproduction, diversity, evolution, taxonomy.

Résumé

L'espèce *Darwinula stevensoni* est redécrite en détail. La variabilité morphologique, aussi bien des valves que des parties molles, est évaluée dans plusieurs populations géographiquement et climatiquement éloignées les unes des autres, et s'est avérée négligeable ou inexistante. Seule la taille varie de façon significative d'une population à l'autre, ce qui peut être attribué à la différence de température de l'environnement au cours du développement larvaire. Le nombre et la forme des attaches musculaires sont également variables, aussi bien, cependant, entre différentes populations qu'à l'intérieur d'une même population. La forme des valves et la chétotaxie des pattes sont remarquablement stables. Une femelle d'une population italienne présente d'aberrants palpes M×2, mais c'est un cas tératologique. Les mentions précédentes de mâles *D. stevensoni* et la position taxonomique des Darwinulocopina au sein des Podocopina sont reconsidérées. Une hypothèse sur la stratégie biologique des darwinulides est vérifiée à l'aide de données sur la variabilité morphologique et la diversité taxonomique.
Mots-clefs: reproduction, diversité, évolution, taxonomie.

Introduction

The Darwinuloidea are, together with the Bdelloidea, one of the two prominent examples of so-called ancient asexuals (BUTLIN & GRIFFITHS, 1993, JUDSON & NORMARK, 1996), organisms which have persisted over geologically long periods of time without sexual reproduction. According to ruling theory, such lineages are doomed to early extinction for several reasons: co-evolving parasites ('Red Queen' hypothesis of HAMILTON (1980), not VAN VALEN, 1973), Muller's ratchet and mutation-load-reduction-theory (MAYNARD SMITH, 1986, JUDSON & NORMARK, *loc. cit.*). Nevertheless, Darwinulidae indeed appear to have survived without sexual reproduction at least since the end of the Cretaceous (c. 70 Ma), or the Jurassic (c. 120 Ma) (SOHN, 1988), but as quotations of some Mesozoic males are doubtful, possibly since the Permian (250 Ma) (SCHOEN et al., 1996). It should be noted that 'asexuality' has always equalled to 'absence of males', both in extant populations and in fossil assemblages.

A European research network, consisting of six laboratories in five countries, has investigated the evolutionary ecology of reproductive modes of the three extant lineages of non-marine ostracods with a variety of techniques: morphological and morphometrical analyses, clonal autecology, starch-gel electrophoresis of allozymes and amplification and automated sequencing of both mitochondrial and nuclear DNA. Three species, one of each lineage, were investigated and *Darwinula stevensoni* (BRADY & ROBERTSON, 1870) was the obvious representative of the Darwinuloidea. The present paper forms part of this concerted research effort and reports on morphological variability of both valves and soft parts in several geographically isolated populations from Europe and Africa; the clonal and genetic variability of the same populations will be reported on elsewhere. *Darwinula stevensoni* is extensively redescribed. Earlier redescriptions of this species (PINTO & SANGUINETTI, 1958, SOHN, 1987) give an incomplete picture of the chaetotaxy and were thus unsatisfactory for our purposes, which included detailed morphological comparisons within and between populations. The position of the Darwinulocopina within the Podocopida is briefly discussed. A hypothesis on the biological strategy of *Darwinula* is outlined and is tested using the present morphological evidence.

Materials and methods

The morphology of both soft parts and valves of specimens of four populations (Finland, Belgium, Italy and South Africa) was investigated with both Scanning Electron Microscopy (SEM) and light microscopy. Illustrations of valves and limbs of representative specimens are here reproduced. Specimens from the following localities were investigated (Fig. 1):

Lake Pääjärvi, Lammi Biological Station, Finland.
Coordinates: N 61°03'02" E 25°02'32"
Date: 14.11.1995
Coll.: K. Martens & K. Salonen
Habitat: medium-sized lake, material collected in littoral at 1-2m deep, on soft mud. No ice at time of collecting. Station: near field station, stations 'c' and 'e' of RANTA (1979)
pH = 7.0
EC = 85.8 μS/cm
water temperature = 4.0 °C.

Hollandersgatkreek, NW Belgium
Coordinates: N 51°15'47" E 03°31'58"
Date: 18.5.1995
Coll.: K. Martens & M.E. Montenegro
Habitat: slightly saline lake, sandy bottom, animals collected at c 1-1.5m deep, along edge of littoral Typha-stand.
pH = 8.8
EC = 3.44 mS/cm (S= 2.0)
water temperature = 12.8 °C

Canale Corniano, Italy
Coordinates: N 45°10'06" E 10°44'44"
Date: 15.4.1996
Coll.: G. Gentile
Habitat: Material collected in littoral at 1m depth in the final stretch of a polluted canal (Canale Corniano), flowing into to Lake Superiore of Mantova, a large wetland situated along the low course of the Mincio River (a tributary of the Po River).
pH = 7.5
EC = 490 μS/cm
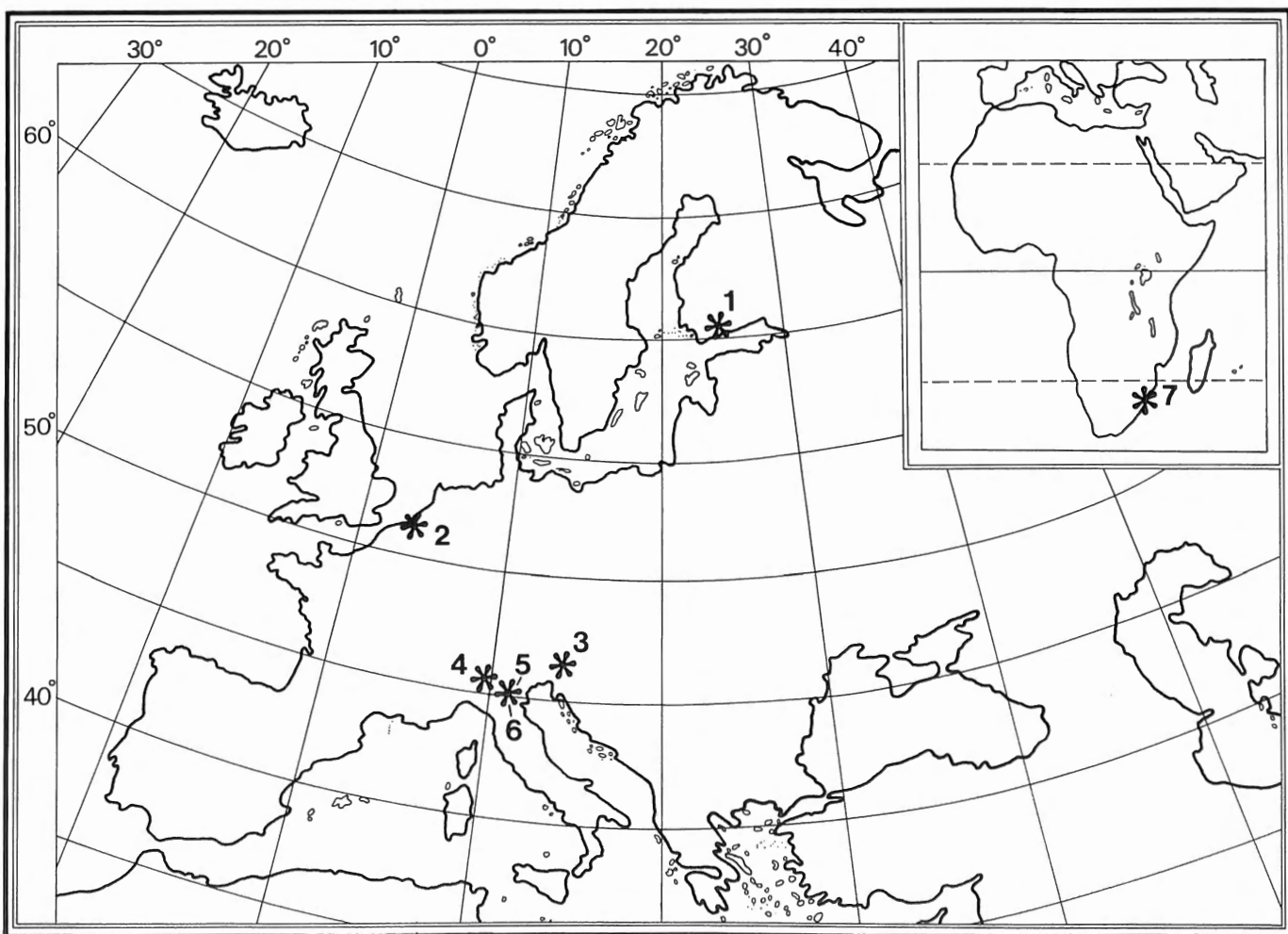water temperature = 14.3 °C

Fig. 1. – Location of sampling sites (1: Pä; 2: Ho; 3: Os; 4: Mo; 5: IM; 6: CC; 7: Si).

Lake Sibaya, KwaZulu-Natal, R. South Africa
Coordinates: S 27°25'13" E 32°41'53"
Coll.: K. Martens, M. Hamer & M. Coke.
Date: 16.10.94
Habitat: oligotrophic lake, situated very near to the ocean, with sediments generally consisting of clean white sand. Age is presumed Holocene (max 0.01 Ma). Station: southernmost arm of lake, at pumping station, opposite water level gauge jetty. At edge of emergent macrophyte (*Typha*, *Phragmites*) stands, amongst submerged macrophytes on very muddy and organically rich sediment. Max depth of collecting: c. 1 m.
pH = 8.6
EC = 684 μS/cm
water temperature = 22.0 °C

Specimens of three other Austrian and Italian populations are also illustrated (Fig. 1):

– Ossiacher See, Austria (N 46°40' E 13°57') (Lab culture).
– Lake Montorfano, Italy (N 45°46'57" E 09°08'15"). Sampling date: 25.4.1996. Coll.: V. Rossi & G. Gentile.
– Lake Inferiore of Mantova, Italy (N 45°09'08" E 10°48'21"). Sampling date: 11.4.1996. Coll.: G. Rossetti & G. Gentile.

Line drawings of limbs are all made with camera lucida. Valves are prepared for SEM by washing in absolute EtOH and simply drying in air. Error on SEM magnifications is ±5%. In *Darwinula stevensoni* often all specimens from a preserved recent sample have tightly closed valves, which makes dissection without damage to at least one of the valves very difficult. We developed the following simple technique: glue a piece of double-sided sticky tape in a small Petri dish and attach the carapace to it. Use a very fine brush (no. 000) bearing a small piece of the same tape to push against the edge of the overlapping valve (the RV in *D. stevensoni*); after a while the valves will open slightly. Then open carapace completely with either brush or fine needle. Add 100% EtOH to the mounted carapace in the Petri dish. The valves will come loose from the tape. Soft parts are then dry and presumed lost, but can, when needed, be re-soaked again overnight in a phosphate rich detergent.

Limbs are prepared for SEM photography in much the same way, namely by submerging and dissecting the body in absolute EtOH and then drying the limbs in air. For limbs, no glue or sticky tape is used, they are directly stuck on a cover slip glued to the stub, and remain attached when dried. This has several advantages: small setae and claws cannot sink into the glue and the background of the micrograph is more uniformous.

Right and left valves of ten specimens from Lake Pää-järvi, Hollandersgatkreek and Canale Corniano populations were measured to the nearest 4 μm under a light microscope. Length and greatest height of each valve were recorded. Size differences among populations were analyzed by one-way ANOVA test (SOKAL & ROHLF, 1981).

Nomenclature proposed by DANIELOPOL (1968, 1970) is used in the description of the chaetotaxy of Antennula and Antenna and the morphology of the mandibular masticatory process (Fig. 2).

Abbreviations used in text and figures

Soft parts

A1	antennula
A2	antenna
in	incisor on Md coxa
LaMo	*lamina molaris*
Md	mandibula
Mx1	maxilla
Mx2	maxillula
Pg	guidance seta ('poil de guidance') on Md coxa
Pl	'poil laciniforme' on Md coxa
RMo	molar region on Md coxa
T(1–2)	thoracic limbs
Abd	abdomen

Valves

Cp	carapace
ms	muscle scars
RV	right valve
LV	left valve
dv	dorsal view
vv	ventral view
llv	left lateral view
iv	internal view

Sampling sites

Pä	Lake Pääjärvi (Finland)
Ho	Hollandersgatkreek (Belgium)
Os	Ossiacher See (Austria)
Mo	Lake Montorfano (Italy)
IM	Lake Inferiore Mantova (Italy)
CC	Canale Corniano (Italy)
Si	Lake Sibaya (South Africa)

Figured specimens (all adult females)

OC.1817-1824: Pä; OC.1825-1837: Ho; OC.1838: Os; OC.1839-1845: Mo; OC.1846-1849: IM; OC.1850-1857: CC; OC.1858-1863: Si. All specimens stored in the Ostracod Collection of the Royal Belgian Institute of Natural Sciences, Brussels.
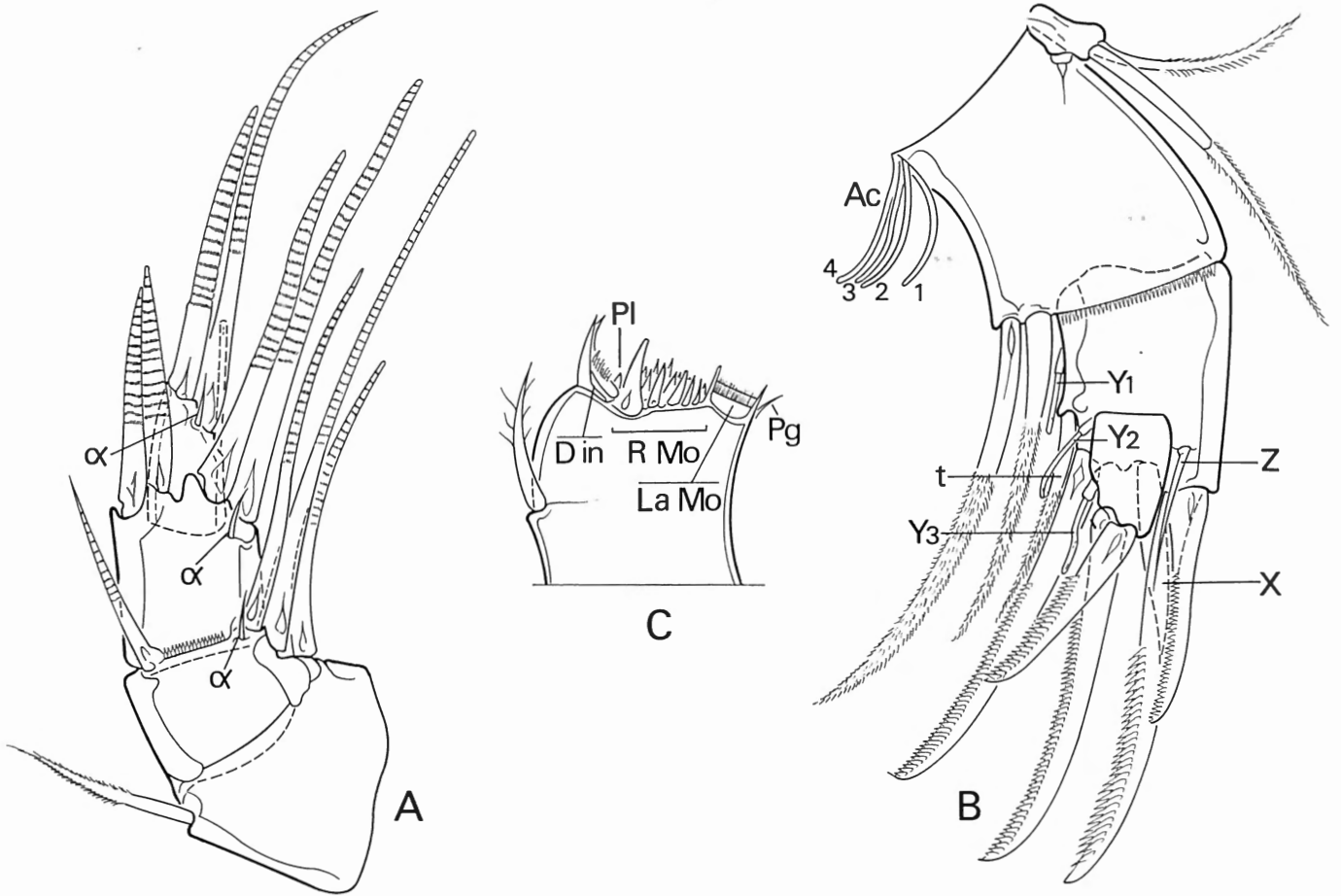
Fig. 2. – Terminology used in description of darwinulid appendages (from DANIELOPOL 1968, 1970).
A. A1, endopodite. B. A2 (Ac: aesthetasc clump). C. Md, masticatory process.

Taxonomic description

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
Genus	*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) BRADY & ROBERTSON, 1872
Darwinula stevensoni (BRADY & ROBERTSON, 1870) BRADY & ROBERTSON, 1885
Darwinula improvisa TURNER, 1895
Darwinula aurea (BRADY & ROBERTSON, 1870) G.W. MÜLLER, 1912 (partim)
Darwinula variabilis TAGLIASACCHI, 1968 **nov. syn.**
Darwinula protracta ROME, 1953 **nov. syn.**

REDESCRIPTION

Carapace (Figs. 9A-R, 10A-M, 11A-H) cigar-shaped. Valves thin with smooth surface and widely spaced setae, pearly white, with dark spots above the adductor attachment transparent through the valves, more evident in fresh specimens than in preserved ones. Valves unequal, RV overlapping LV on all sides except at the hinge. Seen ventrally, shell ovoid, posterior part rounded, forming a brood chamber, anterior extremity rather pointed; margin of the RV sinuous anteriorly and quite straight at the posterior three fifths; 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. Internal surface of valves from smooth to weakly sculptured; central ms consisting of 9-12 spots arranged in a circular rosette. Calcified inner lamellae absent. Hingement adont, with one groove on both valves. Pigmented eye fused, usually well marked, in frontal position.

A1 (Figs. 3A, 4A, 5A, 6A, 8A,B). Uniramous, short and stout. Protopodite consisting of two segments, the first one rather enlarged with two short setae in dorsal position, the second one bearing a short dorsal seta. Exopodite rudimentary, with two short setae and one long seta pointing backwards. Endopodite four-segmented; first podomere with one ventral and one dorso-apical seta, the latter longer; second podomere with two dorso-apical bristles, the one nearly twice as long as the other, and one shorter ventro-apical bristle; third podomere with four apical bristles, two ventral and two dorsal, the latter longer; fourth podomere with two apical bristles and an aesthetasc at the ventral side; last three segments of endopodite with ventro-distal "alpha" setae.

A2 (Figs. 3B, 4B, 5B, 6B, 8C-H). Protopodite two-segmented, proximal segment with two dorsal setae and a sturdy ventral hook, distal segment with one long seta. One-segmented exopodite with three setae, two long apical ones and one lateral conical one, the latter reduced. Endopodite three-jointed; first segment with a group of 4-5 aesthetascs in ventral, proximal position, this segment with an expanded distal corner corresponding to the insertion of two long setae; dorso-apical margin ending as a spine; second segment with four distal claws of different lengths, one of which rather small (X), one seta (t) and two aesthetascs (Y1 and Y2) on the ventral margin and one short subapical seta (Z); third endopodite segment inserted on the second segment in subapical position, with two distal claws and one ventral aesthetasc (Y3).

Md (Figs. 3C,D, 4C,D, 5C,D, 6C,D, 8I,J). Consisting of sclerotized coxa and three-segmented palp, the latter corresponding to basis and two-segmented endopodite. Masticatory process divided into three part: an external "incisor", a "molar region" and an internal *"lamina molaris"*. Incisor consisting of an acuminate tooth, partially fused with a very thin external spine, the former hirsute and with an additional small spine ("poil laciniforme") at the internal edge; molar region formed by "lamellar teeth" of different sizes, the outermost larger, with bifide apex rather flattened in lateral view; *lamina molaris* provided with a basal plate carrying a series of subequal, closely spaced slender setae and, at the inner edge, with a thin, curved "guidance seta" (poil de guidance); one subapical seta inserted along the external margin; proximal part of coxa curved and pointed (not figured). Basal joint of palp bearing 8 long feathery fan-arranged apical setae and a group of 5-6 subapical setae of different size, some with a widened base (not figured). Exopodial branchial plate small and delicate, consisting of 8 hirsute rays (not figured). First podomere of endopodite apically widened, with four terminal setae, three short and one longer, the latter reaching beyond the next segment; second podomere narrow, with two subterminal and two terminal setae, the longer one wider in the first half, and four apically hirsute, subequal claws.

Mx1 (Figs. 3E,F, 4E,F, 5E,F, 5E,F, 8K). Masticatory part consisting of three endites with indeterminate number of apical setae (not figured). Palp two-segmented; first segment rather broad, with two sub-terminal setae, one on the external edge and one close to the second endite, and four distal setae, two curved and plumose, two straight and hirsute, three of which grouped at the external corner; second segment small, with one thin median seta and two larger unequal setae, provided with a double row of setulae. Branchial plate large, with four long reflexed setae at the proximal, external margin, followed by a small conical seta and then by 23-26 hirsute rays; inner, proximal margin of the respiratory plate hirsute, except along the insertion of the masticatory process.

Mx2 (Figs. 3G, 4G, 5G, 6G). Protopodite with many distal setae (not figured); two isolated long, unequal setae close to the articulation with the endopodite. Epipodal branchial plate bearing 11 respiratory rays, and set with thin setulae at the free margin. Three-jointed endopodite; first and second segment both with two lateral setae along the anterior edge; third segment shorter with two unequal subapical setae and a strong terminal claw, the latter about three times the length of the last segment.

T1 (Figs. 3H, 4H, 5H, 6H, 8L). Protopodite one-segmented, with three ventral setae, one short proximal and two long distal ones. Endopodite four-jointed; first segment long, with two unequal ventro-apical setae and one long seta ("poil darwinuloïde" - DANIELOPOL 1968) more inward, slightly longer than the next segment; second and third podomere with one apical seta each; last segment short, with one stout apical claw, flanked by two subapical claws, the ventral one longer than the dorsal one and slightly less than half the length of the distal claw.
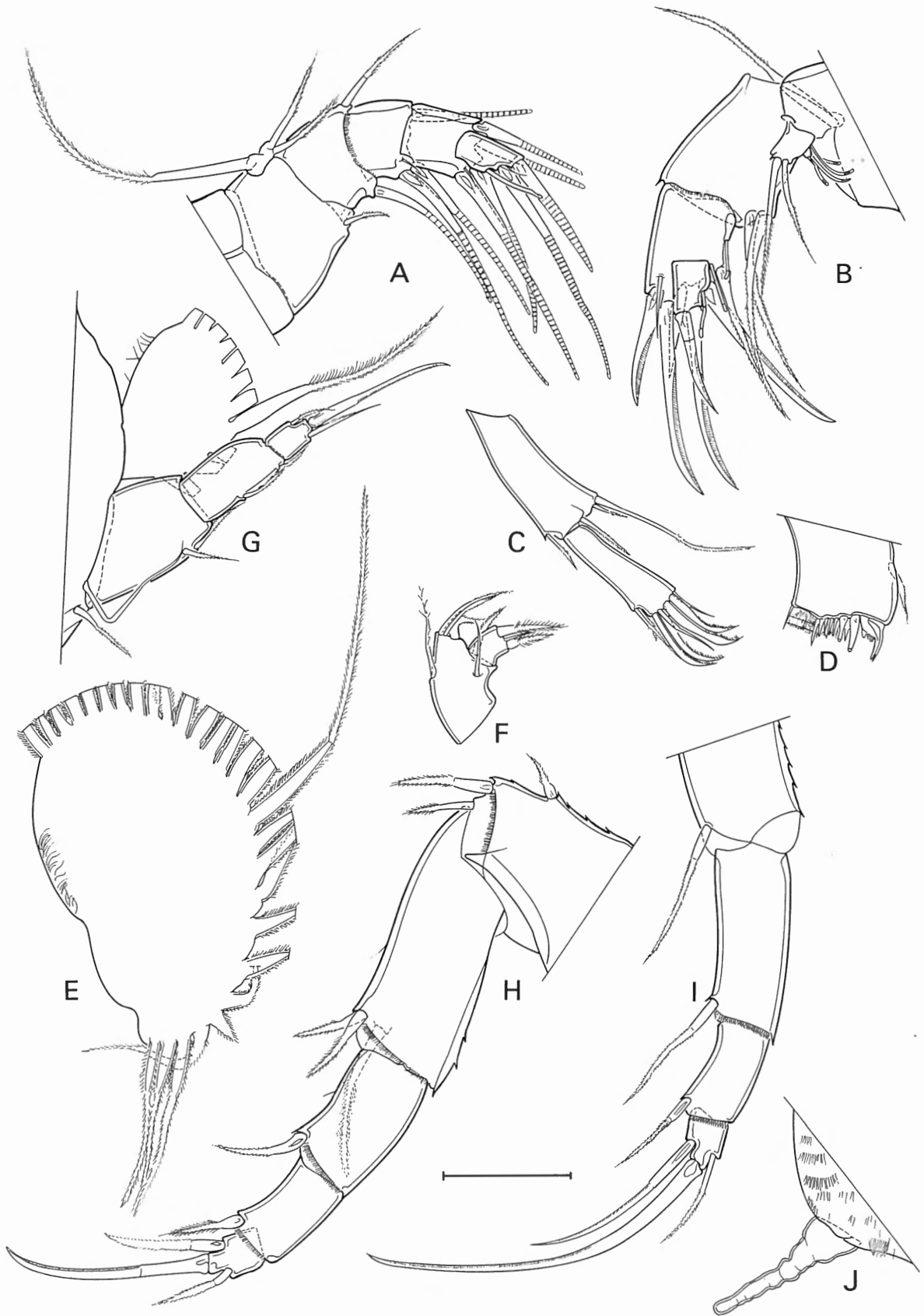
Fig. 3. – *Darwinula stevensoni* BRADY & ROBERTSON. Lake Pääjärvi, Finland.
A. A1 (OC.1824). B. A2 (OC.1824). C. Md, endopodite (OC.1825). D. Md, masticatory process (OC.1824). E. M×1, branchial plate (OC.1824). F. M×1, palp (OC.1817). G. M×2 (OC.1824). H. T1 (OC.1824). I. T2 (OC.1824). J. Abd (OC.1822). Note that the aberrant position of the A2 exopodite in Fig. 3B is due to a twist during slide preparation. Scale = 49 μm for A-J.

Fig. 4. – *Darwinula stevensoni* BRADY & ROBERTSON. Hollandersgatkreek, Belgium.
   A. A1 (OC.1830). B. A2 (OC.1834). C. Md, endopodite (OC.1829). D. Md, masticatory process (OC.1834). E. M×1, branchial plate (OC.1832). F. M×1, palp (OC.1831). G. M×2 (OC.1830). H. T1 (OC.1830). I. T2 (OC.1830). J. Abd (OC.1829).
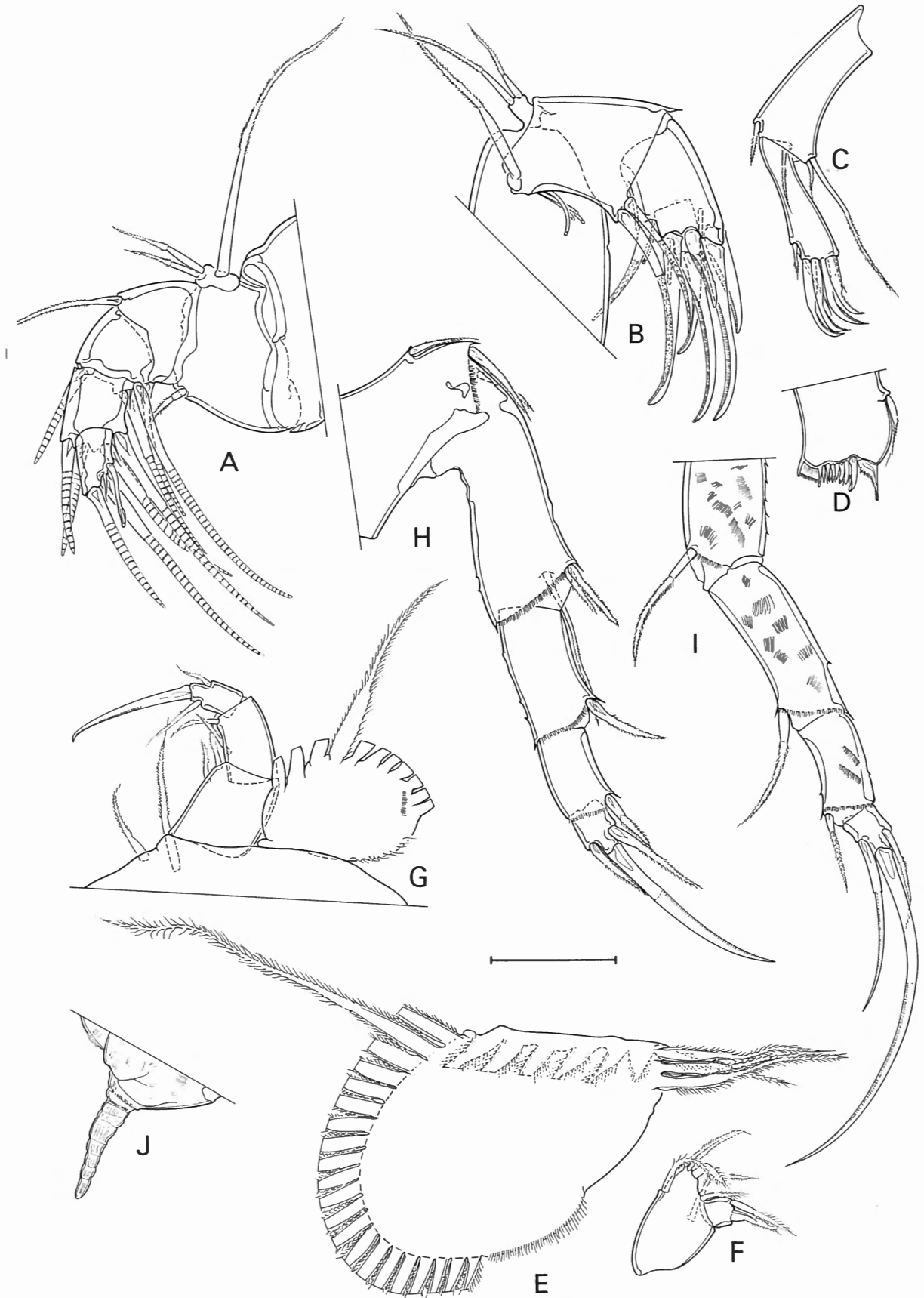   Scale = 49 μm for A-J.

Fig. 5. – *Darwinula stevensoni* BRADY & ROBERTSON. Canale Corniano, Italy.
A. A1 (OC.1855). B. A2 (OC.1855). C. Md, endopodite (OC.1856). D. Md, masticatory process (OC.1856). E. M×1, branchial plate (OC.1857). F. M×1, palp (OC.1857). G. M×2 (OC.1856). H. T1 (OC.1853). I. T2 (OC.1854). J. Abd (OC.1856).
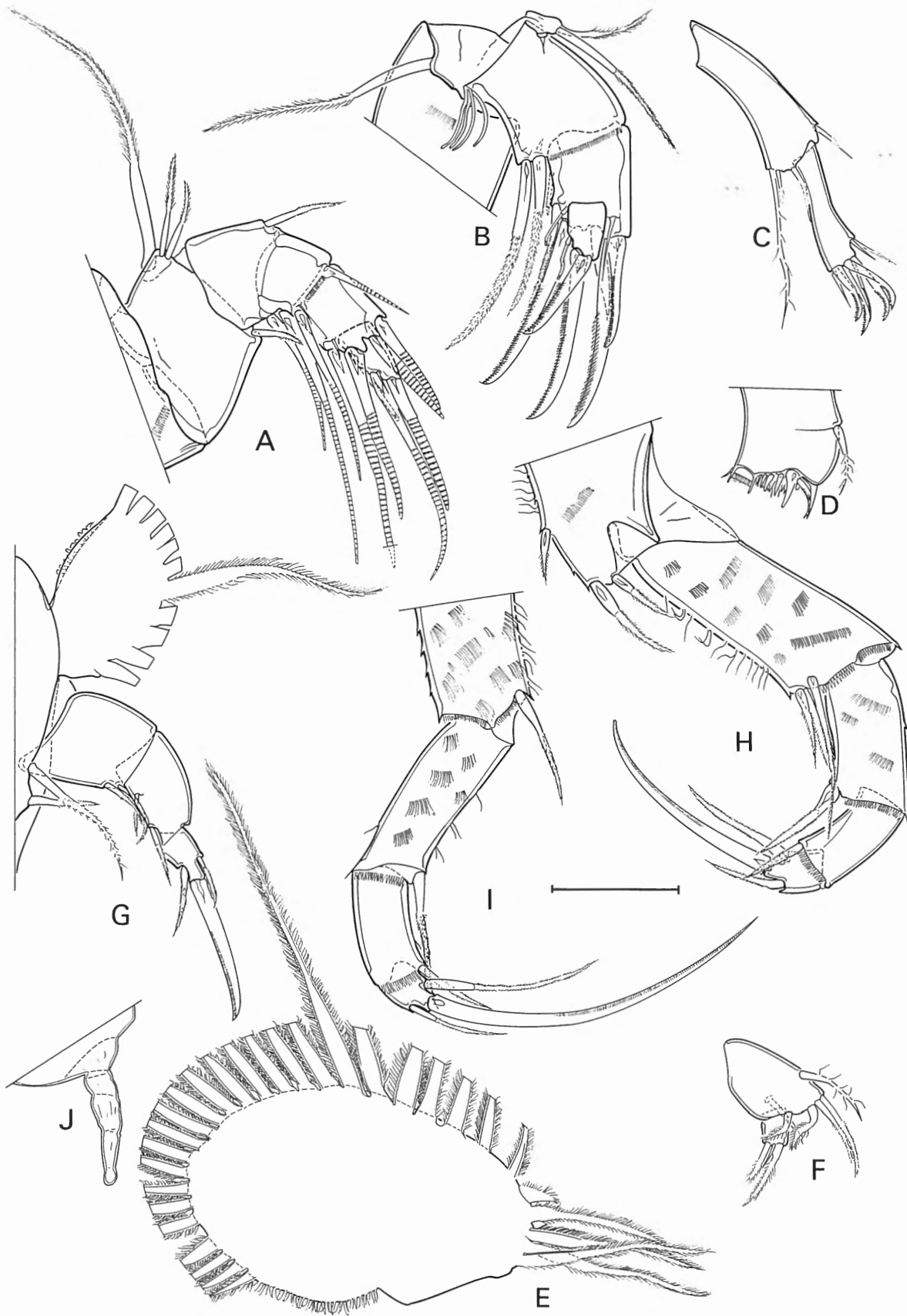Scale = 49 μm for A-J.

Fig. 6. – *Darwinula stevensoni* BRADY & ROBERTSON. Lake Sibaya, South Africa.
A. A1 (OC.1858). B. A2 (OC.1858). C. Md, endopodite (OC.1859). D. Md, masticatory process (OC.1859). E. M×1, branchial plate (OC.1859). F. M×1, palp (OC.1859). G. M×2 (OC.1858). H. T1 (OC.1858). I. T2 (OC.1858). J. Abd (OC.1859).
Scale = 49 μm for A-J.

T2 (Figs. 3I, 4I, 5I, 6I). Protopodite one-segmented, with two ventro-apical setae (not figured). Endopodite four-segmented; first three segments bearing one distal seta each; last segment with a long, curved apical claw, a subapical ventral claw about half the length of the central claw and a shorter dorso-apical seta.

Furca absent in adult specimens.

Abdomen (Figs. 3J, 4J, 5J, 6J, 8M) ending as a conical, vermiform process (postabdomen).

Male unknown.

MEASUREMENTS

See Tables 1 and 2.

Table 1
Results of one-way ANOVA's on length (L, in μm) and height (H, in μm) of RV and LV in *Darwinula stevensoni*. N = 30 for each test (10 per population); Pä = mean value for specimens from Pä; Ho = mean value for specimens from Ho, CC= mean value for specimens from CC

Valve	L/H	Pä	Ho	CC	F(2,27)	P	Sign.
RV	L	734	752	706	24.987	0.000	***
RV	H	303	312	298	9.137	0.001	***
LV	L	718	730	691	15.950	0.000	***
LV	L	290	288	278	7.867	0.002	***

Table 2
Measurements of valves (length = L, in μm and height = H, in μm) of *D. stevensoni*, pooled values of three populations (Pä, Ho, CC); N = 30

Valve	L/H	minimum	maximum	mean ± S.D.
RV	L	686	771	730 ± 24
RV	H	288	322	304 ± 10
LV	L	669	746	713 ± 23
LV	H	263	305	286 ± 9

REMARKS

The above redescription amends and corrects the one by SOHN (1987) in the following details:
• "alpha" setae on third and fourth podomeres of the A1 endopodite and aesthetasc on the fourth segment of A1 endopodite were not mentioned.
• there is a third setae on the A2 exopodite;

• the clump of aesthetascs on the second podomere of the A2 are figured in Plate 2, Figs. 7, 11, but were not mentioned in the description;
• the chaetotaxy of the second podomere of the A2 was missing;
• the third podomere of endopodite of the A2 has 2 distal claws and one aesthetasc, not "three long and one short claws";
• the basal podomere of the endopodite of the Md does not have "one long and one shorter seta", but four apical setae;
• the Mx1 palp was described as follows: "the first joint of the palp has three long bristles and the end joint of the palp has two". Actually, the first segment bears 6 setae and the second segment 3 setae.
• we prefer to follow the nomenclature of DANIELOPOL (1968) and consider a four-jointed endopodite, not exopodite, for T1 and T2.
• certain other details are different (for example number of branchial rays), but these are difficult to interpret. They might follow either from difficulties during observation or might constitute "normal" variability (see below).

MORPHOLOGICAL VARIABILITY OF *D. stevensoni*

The most marked differences between the populations presently investigated are in carapace size (Tabs. 1,2; Figs. 9, 10); one-way ANOVA's performed on length and height measurements of 3 populations (Pä, Ho, CC) are all highly significant. Differences in food and salinity, but especially in temperature, during the larval development can cause significant differences in adult size (MARTENS et al., 1985) and we thus attribute size differences to these epigenetically active environmental factors. There are also occasional small differences in carapace shape (for example slightly different L/H ratio, curvature of postero-ventral corner etc), but, although difficult to quantify, these appear to be similar within and between populations and in any case are neglectable.

Although conserving a general pattern in the shape of the muscle scars (ms) in *Darwinula stevensoni*, the number of spots varies amongst individuals of the same population, is not related to development stage and may even be different in the two valves of the same specimen. Therefore, ms seem to have low diagnostic importance at the taxonomic levels lower than superfamily (PINTO & KOTZIAN, 1961; SOHN, 1976, 1987), although WAKEFIELD (1994, in press) used ms patterns for the identification of species and growth stages in fossil *Darwinula*. In the populations of *D. stevensoni* analyzed in the present study, number of ms varies between 9 and 12, and this is in accordance with the range commonly reported for this species (Table 3); in most specimens the number of ms in the RV is larger than in the LV (Fig. 11). Differences amongst populations were further observed in size of appendages, although morphometric analyses were not carried out. In any case, no evident variations
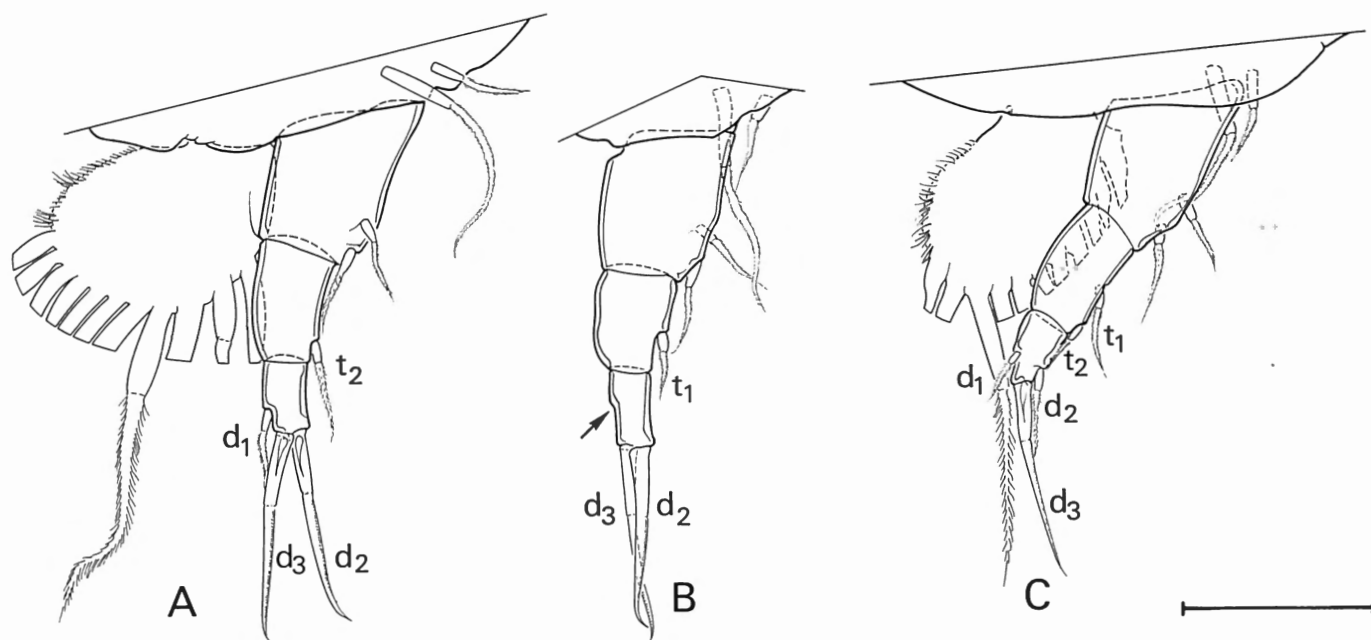
Fig. 7. – *Darwinula stevensoni* BRADY & ROBERTSON. Lake Montorfano, Italy.
　　　　A,B. M×2 (OC.1841): aberrant form. C. M×2 (OC.1842): normal form.
　　　　Scale = 49 μm for A-C.

were noticed in size ratios between podomeres or in length ratios in the chaetotaxy.

Number of aesthetascs in the clump on the second podomere of the A2 varied slightly: the most common pattern is a group of 4 aesthetascs, but 5 were occasionally observed (Figs. 8F, G).

Number of setae along the distal margin of the M×2 branchial plate varies between 24 and 27 and a similar variation (20-26) was also reported by SOHN (1987). As these structures are small and weakly sclerified, it is difficult to ascertain if this represents a bias in observed variation or if it reflects genuine variability. No differences were found in the number of respiratory rays of Md and Mx2 branchial plates, which showed a constant number of 8 and 11, respectively.

Small details (such as "sclerotization", presence of setulae, barbulate setae, spines, hirsute parts, etc.) are mostly at the limit of observation with light microscopy, and are thus not discussed here.

Fifteen gravid females of *D. stevensoni* from Lake Montorfano were dissected. One of these presented anomalous M×2, with asymmetrical limbs (Figs. 7A,B), both with only one lateral seta on the second endopodial segment (t1 and t2, respectively) and with d2 on the third endopodial segment claw-like and of the same length of d3; d1 was furthermore absent in one of the limbs (Fig. 7B, arrow). As all other appendages, as well as carapace morphology (Fig. 10M), were typical of *D. stevensoni*, this specimen is here considered an isolated teratology rather than a stable (clonal) morphology. A further argument for this is the observed asymmetry in its M×2, a feature not common in females, which indicates that this female had a deficient development.

Table 3

Carapace length (L, in mm) and number of muscle scars (N) in *Darwinula stevensoni* (n.r.: not reported)

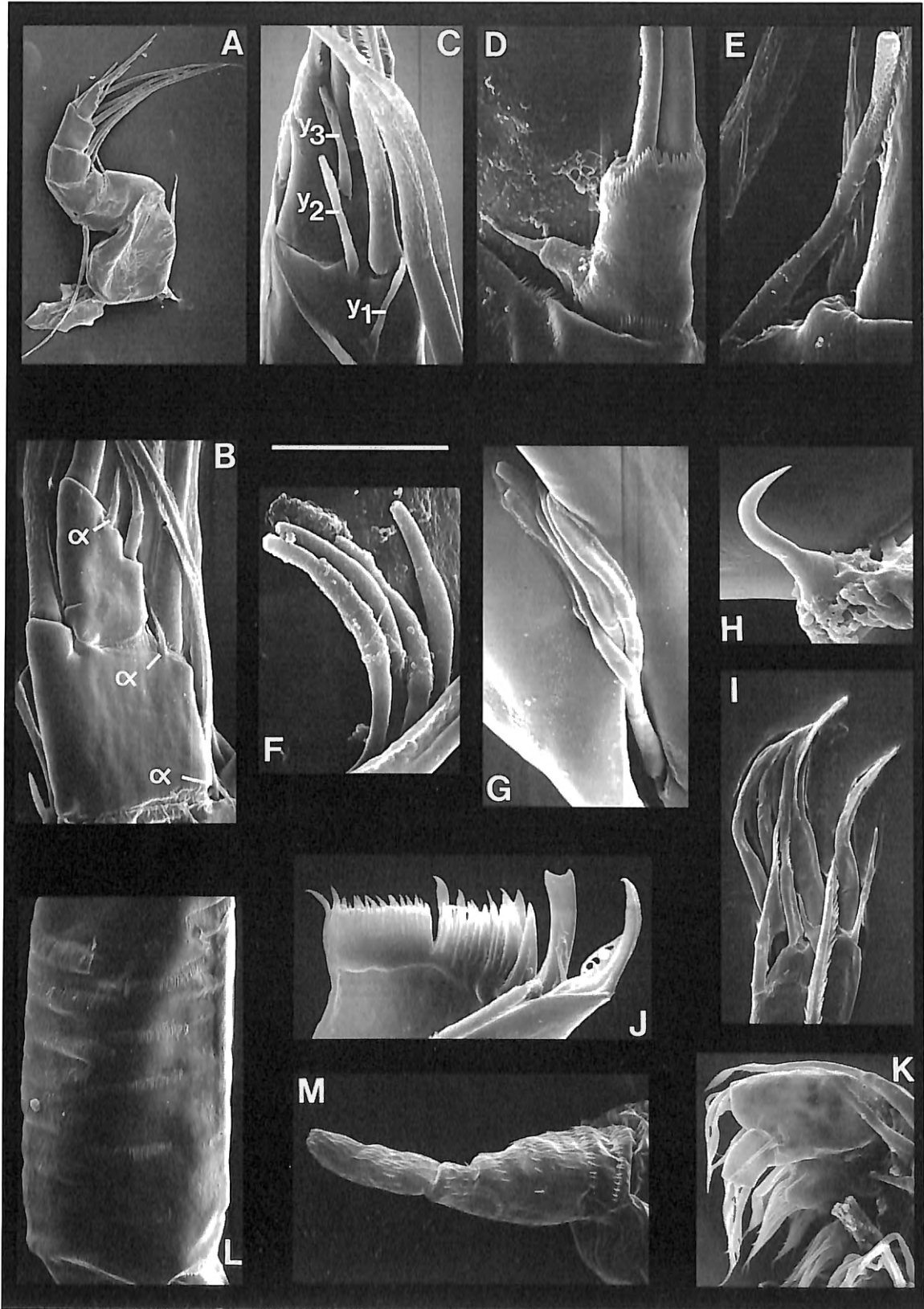|	L	N
BRADY & NORMAN (1889)	0.80	10-12
TURNER (1895) (*D. improvisa*)	0.68-0.70	n.r.
SARS (1928)	0.72	9
BRONSHTEIN (1947)	0.75	9
ROME (1953) (*D. protracta*)	0.78	11
PINTO & SANGUINETTI (1958)	0.75	9-10
TAGLIASACCHI-MASALA (1968) (*D. variabilis*)	0.65	7-11
SOHN (1976)	0.58-0.70	9-12
RANTA (1979)	0.65-0.68	n.r.

Fig. 8. – *Darwinula stevensoni* BRADY & ROBERTSON. A,D,E,F,H,J-M: Ho; B,G: Si; C,I: Pä.
A. A1 (OC.1836). B. A1, detail poils «alpha» (preparation not kept). C. A2, detail aesthetascs Y1-3 (preparation not kept). D. A2, detail exopodite (preparation not kept). E. A2, detail aesthetasc (OC.1835). F. A2, aeshetasc clump (preparation not kept). G. A2, aesthetasc clump (preparation not kept). H. A2, detail hook (OC.1836). I. Md, distal segment of palp (preparation not kept). J. Md, masticatory process (preparation not kept). K. Mx1, palp (OC.1837). L. T1, detail (OC.1837). M. Abd (OC.1837).
Scale = 114 μm for A; 26 μm for B and L; 23 μm for C; 12 μm for D; 9 μm for E,F; 11 μm for G; 21 μm for H and M; 24 μm for I; 16 μm for J; 42 μm for K.
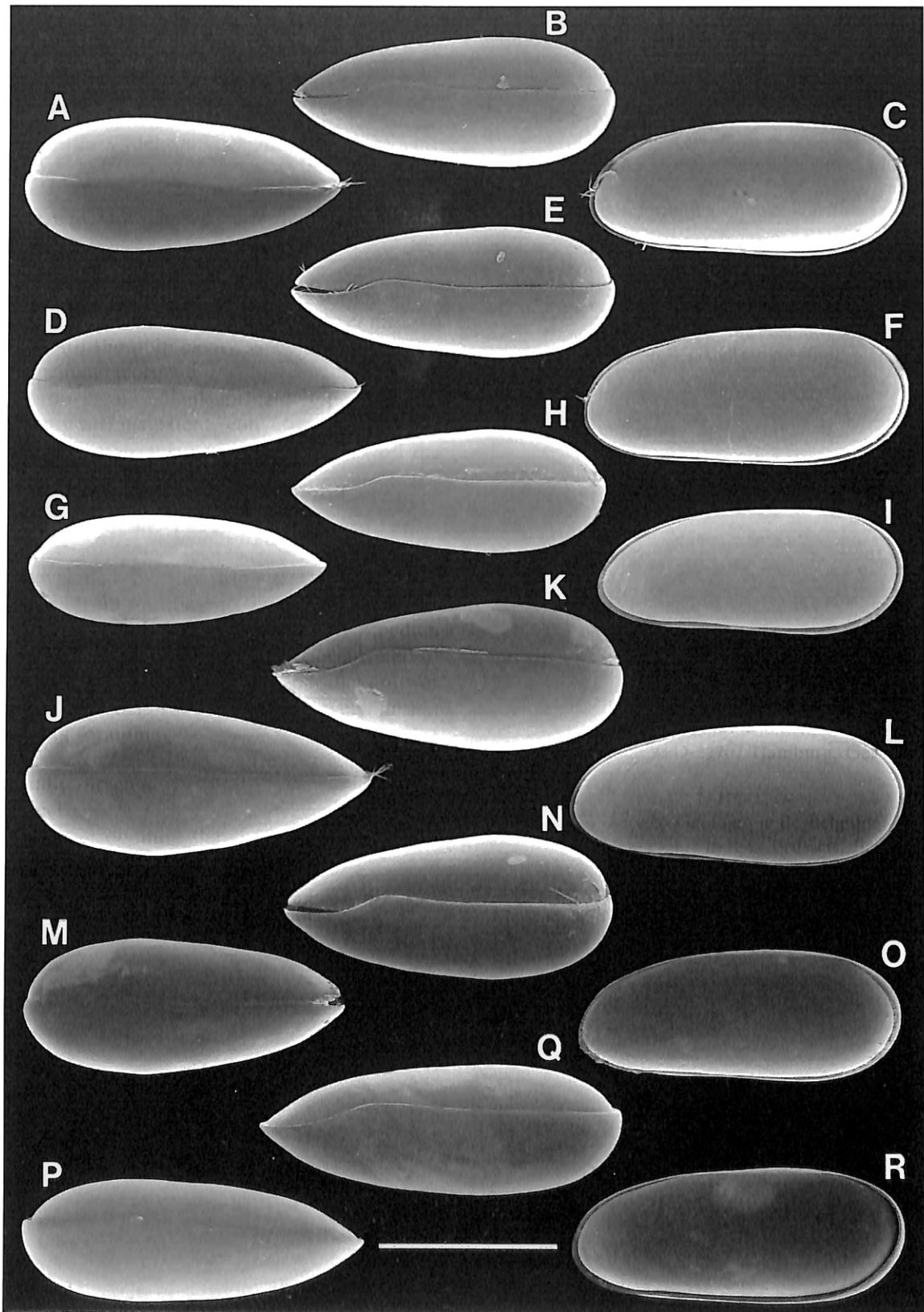
Fig. 9. – *Darwinula stevensoni* BRADY & ROBERTSON. A-C: Pä; D-F: Ho; G-I: Mo; J-L:IM; M-O: CC; Q-R: Si.
A. Cp, dv (OC.1820). B. Cp, vv (OC.1819). C. Cp, llv (OC.1821). D. Cp, dv (OC.1825). E. Cp, vv (OC.1826). F. Cp, llv (OC.1827). G. Cp, dv (OC.1845). H. Cp, vv (OC.1844). I. Cp, llv (OC.1843). J. Cp, dv (OC.1846). K. Cp, vv (OC.1847). L. Cp, llv (OC.1848). M. Cp, dv (OC.1851). N. Cp, vv (OC.1850). O. Cp, llv (OC.1852). P. Cp, dv (OC.1863). Q. Cp, vv (OC.1861). R. Cp, llv (OC.1862).
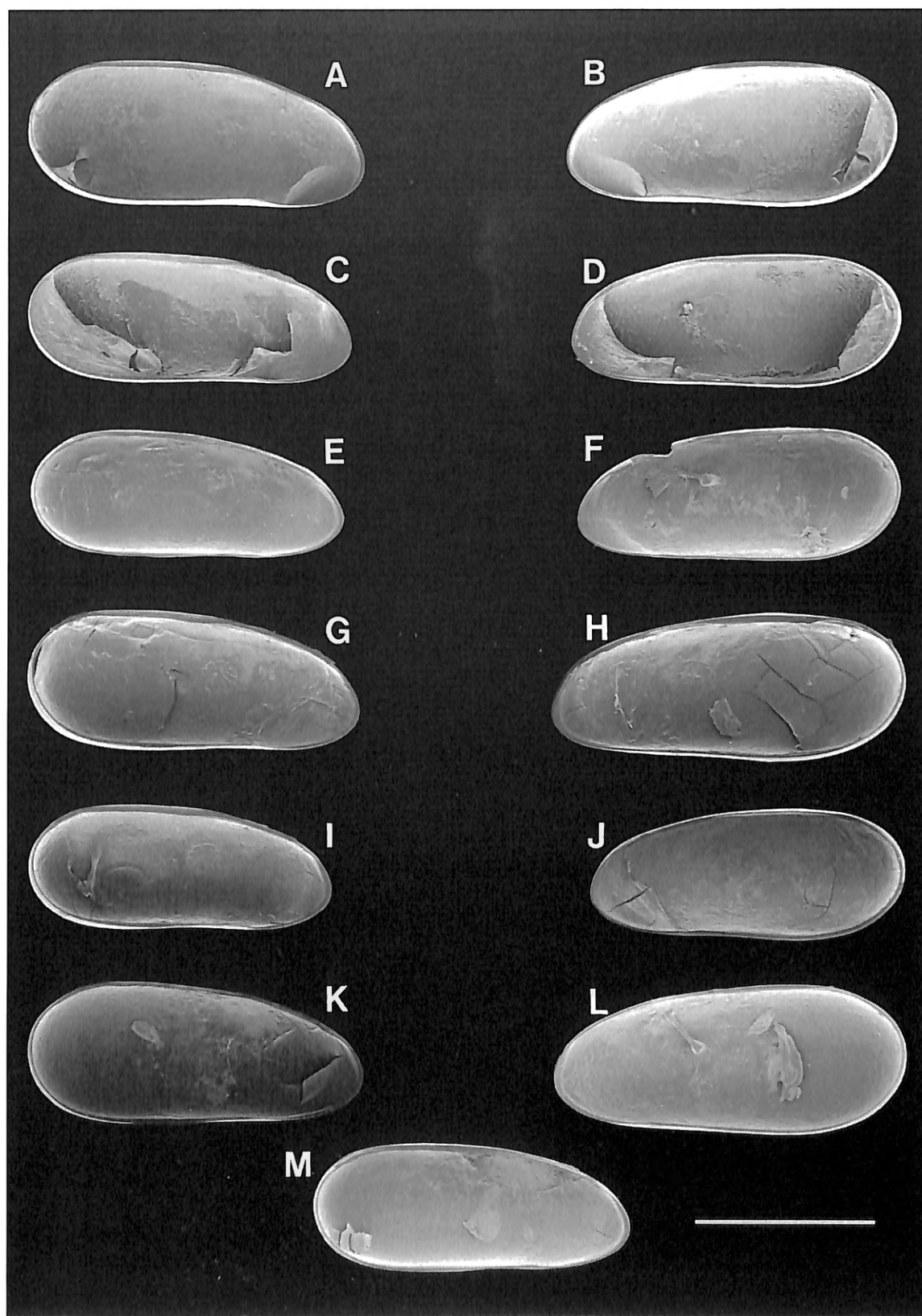Scale = 417 μm for A-R.

Fig. 10. – *Darwinula stevensoni* BRADY & ROBERTSON. A,B: Pä; C,D: Ho; E,F,M: Mo; G,H: IM; I,J: CC; K,L: Si.
A. LV, iv (OC.1818). B. RV, iv (OC.1818). C. LV, iv (OC.1828). D. RV, iv (OC.1828). E. LV, iv (OC.1840). F. RV,
iv (OC.1840). G. LV, iv (OC.1849). H. RV, iv (OC.1849). I. LV, iv (OC.1853). J. RV, iv (OC.1853). K. LV, iv (OC.1860).
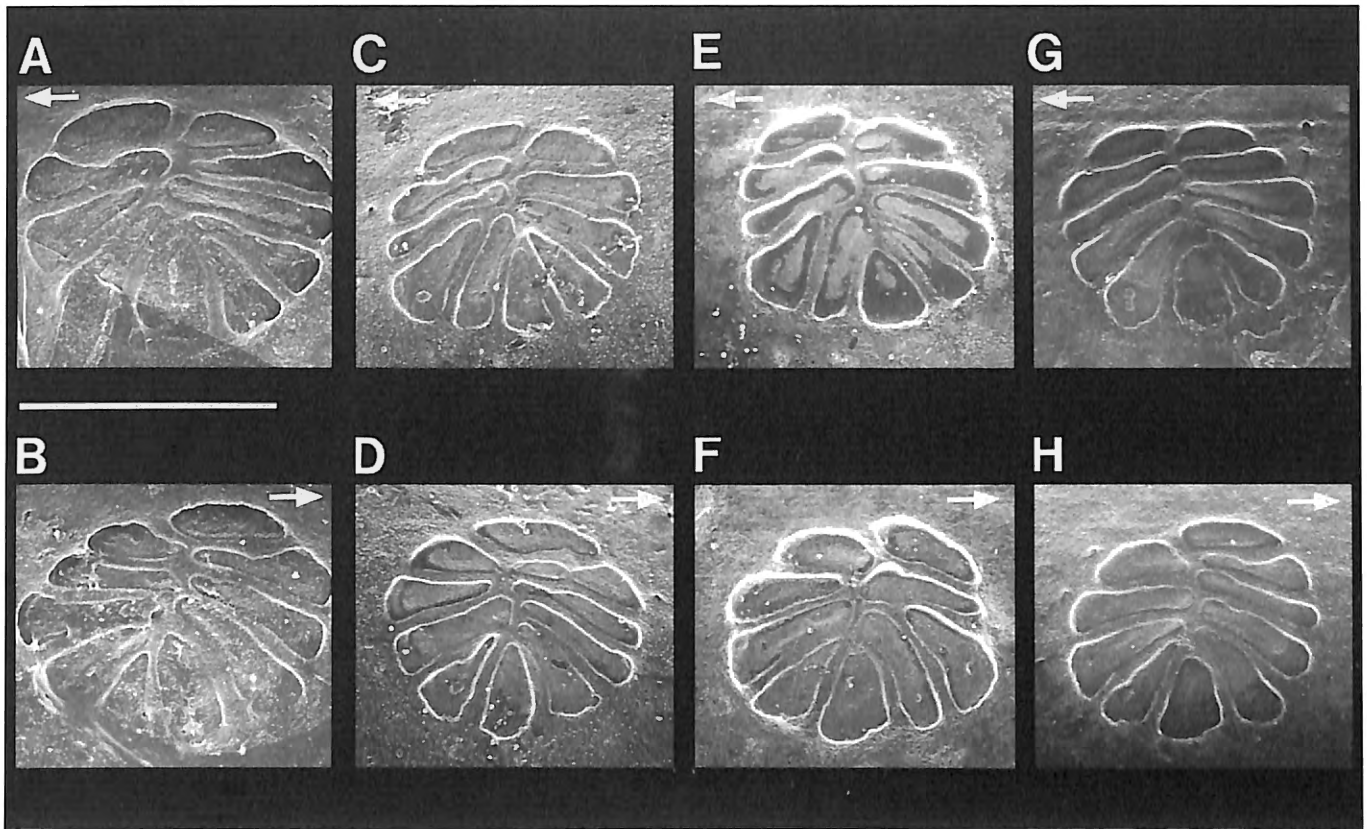L. RV, iv (OC.1860). M. LV, iv (OC.1841).
Scale = 417 μm for A-M.

Fig. 11. – *Darwinula stevensoni* BRADY & ROBERTSON. All specimens adult females. A,B: Ho; C,D: Os; E,F: Mo; G,H: CC.
A. RV, ms (OC.1833). B. LV, ms (OC.1833). C. RV, ms (OC.1838). D. LV, ms (OC.1838). E. RV, ms (OC.1839).
F. LV, ms (OC.1839). G. RV, ms (OC.1853). H. LV, ms (OC.1853).
Scale = 73 μm for A-H.

Discussion

NEW SYNONYMIES

Darwinula variabilis is very similar to *D. stevensoni* in its all round morphology. TAGLIASACCHI (1968, p. 627) listed the following features of *Darwinula variabilis*, a species collected from hyperthermal waters of Sardinia, as being different from *D. stevensoni*: number and position of muscle scars; setae on the basal segment of the mandibular palp as well as setae of the branchial plates of Md, M×1 and M×2 not plumose; absence of ventral seta on the first endopodial segment of T2; shape of abdominal process.

We propose to sink *D. variabilis* into the synonymy of *D. stevensoni*, because of the following reasons: (1) as is reported below, the number of muscle scars in *Darwinula* is not a valid taxonomic criterium, and moreover, the muscle scars figured for *D. variabilis* (TAGLIASACCHI, *loc. cit.*, Plate IV, p. 628) fall into the range of variability observed for *D. stevensoni*. (2) In many cases, detection of feathery setae in *Darwinula* can be difficult with a light microscope and again, this can therefore not be regarded as a valid specific character. (3) In the discussion, TAGLIASACCHI (1968: 627) cited the absence of one ventro-distal seta in the first endopodial segment of T2 as typical of *D. variabilis*; however both in the description and in the figures (Plate III, fig. L, p. 626) the presence of this seta is ascertained. (4) The shape of the abdominal process (postabdomen) in *D. variabilis* (Plate III, Fig. M, p. 626) does not differ from that of *D. stevensoni*.

Unfortunately, the type material of *D. variabilis*, stored at the University of Cagliari, was completely lost in a fire (TAGLIASACCHI, pers. com. 1996), so that the types cannot be reinvestigated. Moreover, recent sampling in the type locality did not confirm the occurrence of *Darwinula* sp. (DE MIRANDA RESTIVO et al., 1995), which makes the investigation of topotype material inpossible.

ROME (1953) described *Darwinula protracta* from a cave on Mont Hoyo, Irumu, Zaire, and indicated greater size (length = 0.78 mm, greatest height = 0.31 mm), greater number of muscle scars (11), different chaetotaxy of A2 (summarily reported but not figured) and of the mandibular palp as major differences with *D. stevensoni*. However, size and the number of muscle scars fit within the normal ranges of variability reported for *D. stevensoni* (see below). The incomplete description of the A2 in *D. protracta* makes a careful comparison of the chaetotaxy of this limb in both species impossible. Con-

tatrary to ROME's claim, the two distal segments of the mandibular palp of *D. protracta* (Plate II, Fig. 20, p. 40) are almost identical to those of *D. stevensoni*. ROME (*loc. cit.*) also doubted the presence of an eye in *D. protracta*, but he dissected only one specimen and even the interstitial *D. boteai* DANIELOPOL, 1970 has a pigmented eye. Because of the apparent absence of structural differences between both nominal species, we propose to consider *D. protracta* a synonym of *D. stevensoni*.

POSITION OF THE INFRAORDER DARWINULOCOPINA WITHIN THE SUBORDER PODOCOPINA

The Darwinulocopina were described as a suborder by SOHN (1988), but lowered to the rank of infraorder by MARTENS (1992), one of five within the suborder Podocopina. As is usually the case at such a high taxonomical level, it is very difficult to assess affinities between these lineages and few characters are available. For example, a spermpump outside of the hemipenis (Zenker organ) is present in Cypridocopina and in the Sigillioidea (this group still requires the formal erection of an infraorder - MARTENS, 1992), while the spermpump is incorporated within the hemipenis in Cytherocopina and in Bairdiocopina. Because no males of Darwinulocopina have ever been conveniently described, the position of this lineage remains unclear.

The presence of a clump of aesthetascs on the first endopodial segment of the A2 in *Darwinula stevensoni* (Figs. 2, 3B, 4B, 5B, 6B, 8F,G) might be useful in this regard. These structures are considered homologous with the group of six to eight aesthetascs in *Saipanetta* (Sigillioidea) and with the group of six in *Macrocypris* (Macrocypridoidea, Cypridocopina), but also with the single aesthetasc Y in Pontocyprididae and Cypridoidea (both Cypridocopina) (MADDOCKS, 1976, 1990). There are up to three setae-like structures (DANIELOPOL, 1972), possibly aesthetascs, in that position in a number of Bairdiocopina; there are no such aesthetascs in the Cytherocopina.

These observations provoke two remarks. First, if all of these structures are indeed homologous, then a convergent reduction in number of aesthetascs has occurred in at least 3 of the 5 lineages, namely in Bairdiocopina and Cypridocopina (partly) and in Cytherocopina (whole lineage?). As taxa with several aesthetascs in that position are present at least in Bairdiocopina and Cypridocopina, these observations can thus not be used to lodge Sigillioidea and Darwinulocopina in a separate group and the 5-partite division of the Podocopina remains unchallenged by these observations.

However, it can also be questioned if the clump of aesthetascs are indeed fully homologous with the single large aesthetasc Y in, for example, Cypridoidea (DANIELOPOL, 1972). Comparisons between the morphology of the clump-aesthetascs (Ac1-4) and of the other aesthetascs on the A2 in *D. stevensoni* (see above) revealed potentially important differences: the distal part of

aesthetascs Ac1-4 is smooth, in aesthetascs Y1-3 this surface is pitted, as is also the case in the single aesthetascs Y of most Cypridoidea (DANIELOPOL, 1973, 1978). Comparative investigations of these morphologies in the five lineages of the Podocopina are required to assess the homology of these structures, and hence of its validity as a taxonomic feature. Meanwhile, the presence of this clump of 4-5 aesthetascs in *Darwinula stevensoni* confirms the affinity of the Darwinulocopina to the Sigillioidea (McKENZIE, 1982), but does not allow both taxa to be grouped into a separate lineage.

PAST AND PRESENT DIVERSITY

The history of scientific discoveries in the Darwinulocopina, and more specifically in the Darwinulidae, has for a long time been rather confused, but recently some order has been restored by SOHN (1987, 1988). The early nomenclatorial confusion around the type species of the genus *Darwinula* (and thus of the entire group) is briefly summarized above, but was extensively discussed by SOHN (1987: 150-152), who has also designated a lectotype from the collections in the Hancock Museum (Newcastle-upon-Tyne), thus making Somerton Broad (Norfolk, England) the type locality. The type series on which the original description was based, indeed consisted of material from several localities, so that an unequivocal designation was needed.

Within the Darwinulocopina, only one superfamily, the Darwinuloidea BRADY & NORMAN, 1889, is recognized. SOHN (1987) listed 6 families in this group, but later (1988) synonymized Microdarwinulidae KASHEVAROVA & NEUSTRUEVA, 1982 with the Darwinulidae BRADY & NORMAN, 1889; he then also explicitly cited Suchonellininae KUKHTINOV, 1985 (written with subfamilial name ending) as a synonym of Darwinulidae. Of the five families thus left, one is unnamed (containing the marine Middle Ordovician genus *Predarwinula* JIANG, 1978), one did not survive the Permian-Triassic extinction (Darwinuloididae MOLOSTOVSKAJA, 1980) and two were greatly reduced by the same extinction and fully disappeared at the end of the Triassic (Suchonellidae MISCHINA, 1972 and Panxianidae WANG, 1980). The Darwinulidae are thus the only survivors of the lineage since the Jurassic. SOHN (1988) recognized three genera in this group: *Darwinula* s.s. and *Microdarwinula* DANIELOPOL, 1968 with Recent representatives and the late Triassic *Paradarwinula* KOZUR, 1970. Two fossil genera, *Neudarwinula* MISCHINA, 1972 (Late Permian) and *Dictyodarwinula* JIANG, 1983 (upper Triassic) are surpisingly maintained as subgenera of *Darwinula* only.

We can thus conclude that the largest supra-generic diversity occurred in the Palaeozoic, while the post-Triassic fauna in this lineage is represented by one family and two genera only. According to SOHN (1987), more than 250 species, of Carboniferous to Holocene age, have been referred to *Darwinula* s.s., although several have meanwhile been lodged in other genera and families. KEMPF

(1980), however, already listed not less than 350 different species and subspecies at some stage referred to the genus *Darwinula* and another 180 species in the update of his list (KEMPF, 1995). SOHN (*loc. cit.*) furthermore listed 25 described and one undescribed Recent species and subspecies in this genus (*D. dicastrii* LÖFFLER, 1966 was not mentioned). Twenty-two described Recent species are retained here worldwide, while evidence for at least another 7 extant taxa exists. There is only one extant species in the genus *Microdarwinula*. It is thus clear that the relatively extensive fossil record, more than 500 (sub-) species, most of which are furthermore pre-Jurassic, is in sharp contrast with the paucity of post-Jurassic and extant specific diversity. It is true that Recent species of *Darwinula* occur in a variety of habitats (high mountain lakes, rivers, bogs, springs, interstitial aquifers, etc.) (SOHN, 1987, DANIELOPOL, 1980), but only one species, *Darwinula stevensoni* can truly be termed successful, as it has a global distribution, occurs in a variety of habitats and is seldom rare. Other species are rare to very rare and generally occur in marginal habitats in low densities. SOHN's (1987) statement that the 'darwinulid group' is highly successful, thus largely refers to pre-Jurassic situations and is disputable with regard to extant diversity. Looking at the diversity of non-marine ostracods as a whole, the Darwinulocopina, being one of three Recent non-marine infraorders, comprise only 1% of the extant specific diversity in Europe (LÖFFLER & DANIELOPOL, 1978) and about 2% in both Africa and South America (MARTENS, in press). In spite of the fact that the Darwinulocopina have managed to persist since the Carboniferous (c. 360 Ma), they constitute to date only a marginal fraction of the extant non-marine ostracod fauna. It is important to note, however, that this decrease in diversity of the Darwinulidae is not only relative, and due to the explosive radiation of the Cypridocopina in non-marine habitats since the lower Jurassic (WHATLEY, 1988, 1990a, b), but also represents a genuine (absolute) decrease in specific and supra-specific diversity.

MORPHOLOGICAL UNIFORMITY

From the results presented above and the foregoing discussion, it appears that this lineage not only presents low supra-specific and specific (extant) diversity, but also neglectable morphological variability in at least one of its species. The distinction between species in *Darwinula* relies on combinations of small structural differences only (number and shape of internal teeth in LV, presence and shape of ventral keel in RV) and that overall morphology in the genus is very uniformous. Within one species then, *Darwinula stevensoni* in this case, there are almost no morphological differences between geographically and ecologically significantly different populations: the latitudinal gradient and the ecological differences (temperature, salinity) are only reflected in differences in size, almost not in shape of carapace, while all soft parts are absolutely identical, with the exception of one

teratological specimen. When this is compared to differences in shape of valves in for example *Eucypris virens* (TÉTART 1982; BALTANAS et al. in prep.) or in differences in natatory setae on A2 in species of *Herpetocypris* (GONZALEZ et al., in prep), the morphological uniformity in *D. stevensoni* is truly astonishing.

How, then, should one interpret the teratological female from Lake Montorfano, which has aberrant Mx2 palps only, and no special morphology in any other of the soft parts or valves? We here deem these aberrations to be epigenetic, rather than genetically induced, for example a as a consequence of problems experienced during one of the 9 moults in this particular specimen. This hypothesis can be falsified by checking long series of specimens from this population.

THE ELUSIVE MALES

BUTLIN & GRIFFITHS (1993) and JUDSON & NORMARK (1996) consider *Darwinula* as an ancient asexual, i.e. as one of the few lineages which has persisted without sexual reproduction for a considerable time, in spite of assumed theoretical impossibilities (see introduction). According to BUTLIN & GRIFFITH (*loc. cit.*), the Darwinuloidea have been asexual for at least 70 Ma and this is a conservative estimate, as only few putative males have been cited since the Permian (c. 250 Ma) (SCHOEN et al. 1996). From recent fauna's, putative males of *D. stevensoni* have been reported twice. In their original description of *D. stevensoni*, BRADY & ROBERTSON (1870) (see also BRADY & NORMAN, 1889) reported and even illustrated hemipenes and carapace of a male of this species. TURNER (1895) reported a male of *D. improvisa* (a synonym of *D. stevensoni*) from North America, but only illustrated the A1 and T2 of this presumed male. Since then, researchers have intensively looked for males in this lineage (for example RANTA, 1979 and McGREGOR, 1969) but without any success.

The record of TURNER (*loc. cit.*) cannot be validated on the evidence provided. The illustrations of BRADY & ROBERTSON (1870) and BRADY & NORMAN (1889), however, constitute more solid evidence. The illustration of the carapace in dorsal view indeed shows that it is more laterally compressed, which could be related to the absence of a brooding chamber in this specimen. The drawing of the hemipenis is difficult to interpret, although MADDOCKS (1973) compared it to the morphology of the hemipenes in *Saipanetta*. It seems that at least the male found by BRADY & ROBERTSON (1870) cannot be disgarded. How, then, should this be interpreted?

Asexual and sexual reproduction are two extremes, whith several possible intermediates. Single gender reproduction can also be automictic, i.e. with internal meiosis, in stead of apomictic (without meiosis). Cyclic reproduction, like in Cladocera, can occur, while both reproductive modes can exist in different populations of the same species, or can even occur sympatrically (CHAPLIN, 1993). In all of these cases, instances of sexual reproduction or at least

of meiosis are incorporated into the general reproductive strategy.

A final possibility is the so-called single-male (or rare male) occurrence, repeatedly reported for *Limnocythere inopinata* (GEIGER, unpubl.), where single male individuals occur amongst thousands of parthenogenetic females. Although seemingly exciting at first, the importance of such males must not be over-estimated. Such single-male populations cannot be considered bisexual, as the functionality of these males is doubtful and their impact on a population and meta-population level is at best marginal. More likely, however, such males are non-functional relicts or attavisms, only useful from a morphological-taxonomical point of view, and of little importance for the reproductive strategies. Further discussions on rare-male occurrences in non-marine ostracods will be presented elsewhere, but in conclusion we here consider that the reports on the male(s) of *Darwinula stevensoni*, if at all valid, deal with such rare-male occurrences, with no conceivable impact on reproductive strategy in this lineage.

CONCLUSION: EVOLUTIONARY STRATEGY

Taking into account the combination of low post-Jurassic diversity in the Darwinulocopina at all taxonomic levels low inter- and intra-specific morphological variability and the fact that they are ancient asexuals, the *Darwinula*-paradox is not concerned with reasons behind the low diversity in this group, but with the fact that it managed to persist at all for such a long time. The Darwinulocopina are therefore of interest, not so much from an ecological point of view, but for their aberrant evolutionary strategy. All of the above, combined with the wide ecological tolerance of for example *Darwinula stevensoni* (GRIFFITH & BUTLIN, 1994), seems to indicate that at least this species has developed a conservative, multi-purpose phenotype. The genetic bases of this hypothesis will be discussed elsewhere.

Acknowledgements

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