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ON THE GENERIC BOUNDARIES WITHIN THE MARINE INTERSTITIAL LATIREMIDAE (COPEPODA: HARPACTICOIDA)

BY RONY HUYS¹ & HELMUT KUNZ²

1) Marine Biology Section, Institute of Zoology, State University of Gent,
K. L. Ledeganckstraat 35, B-9000 Gent, Belgium.
2) Im Allmat 8, D-6601 Ricchmichain, Federal Benyblic of Cormons

²) Im Allmet 8. D-6601 Bischmisheim, Federal Republic of Germany.

SUMMARY

Character analysis of the various species of the marine interstitial family Latiremidae revealed that they should be placed in at least three genera instead of the single genus Delamarella Chappuis. The original type genus Latiremus Božić is reinstated and comprises L. eximius only. The mediterranean genus Delamarella includes D. arenicola, D. karamani and D. galateae; the latter two probably constitute a separate taxon. D. phyllosetosa is removed from the genus Delamarella and is considered the type species of a new genus Arbutifera. The significance of characters such as the incorporation of the first pedigerous somite, the fusion of the genital somites and the antennal segmentation is stressed. Two main evolutionary lineages are recognized within the Latiremidae. Latiremus and Arbutifera are linked on the basis of the fine morphology of the lateral caudal rami setae.

RÉSUMÉ

Une analyse des caractères des espèces de la famille interstitielle-marine des Latiremidae, montre que celles-ci doivent être groupées en un minimum de 3 genres, et non dans le seul genre Delamarella Chappuis. Le genre-type originel Latiremus Božić est re-institué; il comprend seulement L. eximius. Le genre méditerranéen Delamarella comprend D. arenicola, D. karamani et D. galateae, mais ces deux dernières espèces constituent probablement un taxon indépendant. D. phyllosetosa est retiré du genre Delamarella et considéré comme espèce-type du genre nouveau Arbutifera. On souligne la signification de caractères tels que l'incorporation du 1er somite pédigère, la fusion des somites génitaux et la segmentation de l'antenne. On reconnaît l'existence de deux lignées évolutives principales au sein des Latiremidae. Latiremus et Arbutifera sont considérés comme étroitement apparentés, ceci étant fondé sur la morphologie fine des soies latérales des branches caudales.

INTRODUCTION

In the several years since the original description of *Delamarella arenicola* from a sandy beach in Roussillon, France by Chappuis (1953, 1954a) the newly erected family, the Latiremidae, has received only little attention. For the most part this has taken the form of evaluations of the gross morphology of the various species and attempts to place them in Lang's taxonomic hierarchy of the Harpacticoida. All latiremids are genuinely mesopsammic, and many of the morphological traits that unify them can be attributed to life in the interstitial habitat, i.e. swimming and crawling within the lacunae between the sand

grains with no, or negligible, disturbance to the arcade structure of the sediment (Wells, 1986).

Chappuis, in a series of papers (1953, 1954a-b), considered *D. arenicola* to be a *species incerta sedis* because of the atypical modifications in the male P4. Shortly after the description of the type species, Petkovski (1957) reported the discovery of a second species from the Yugoslavian coast, *D. karamani*, however, no new evidence was presented on affinities. Božić (1969), apparently unaware of the existence of the genus *Delamarella*, described the closely related species *Latiremus eximius* from La Réunion. The author also regarded the male P4 exopod as the stumbling block to incorporate the genus *Latiremus* in one of the established families and for that reason he proposed, although with some reservations, the monotypic family Latiremidae. Cottarelli (1971), who in turn had overlooked Božić's (1969) paper, added a third mediterranean species to the genus *Delamarella*, *D. galateae*, whilst Apostolov (1969) published the second record of *D. karamani* from the Bulgarian Black Sea coast.

It was only in the late seventies that several authors (Bodin, 1975, 1976; Wells, 1976, 1978; Kunz, 1977) — and almost simultaneously — recognized the undeniable relationship between Delamarella and Latiremus. Wells (1976) preferred to regard them as distinct genera, pending a thorough reexamination. Bodin (1975) and Kunz (1977), on the contrary, considered them congeneric and re-allocated L. eximius to the genus Delamarella. This resulted in a somewhat dubious situation as the generic name on which the family name was based was rejected as a junior synonym, but as this nomenclatural change happened only after 1960, the family-group name is not to be replaced (ICZN, 3rd ed.: Art. 40, p. 81). Finally, Božić (1978) also supported this re-allocation by comparison of the setation and segmentation of the antennula and P1-P4 and of the structure of the P5 and the anal operculum. Although we admit that these appendages do not show a great deal of variability, it is undoubtedly clear that the diagnosis of Delamarella has broadened considerably by incorporating L. eximius. This is best exemplified when one takes into consideration characters of major importance such as the segmentation of the antenna (basis vs. allobasis), the incorporation of the first pedigerous somite, the separation of the female genital somite and the structure of the genital complex. The recent discovery of the Namibian species D. phyllosetosa (Kunz, 1984) further increased the intrageneric variability and forced us to re-examine the generic boundaries with the Latiremidae.

MATERIAL AND METHODS

All figures have been prepared using a camera lucida on a Leitz Dialux 20 interference microscope. The terminology is adopted from Lang (1948, 1965) except for (1) the terms pars incisiva, pars molaris and lacinia mobilis which are omitted in the description of the mandibular gnathobasis (Mielke, 1984), (2) the segmental composition of the mandible and maxilliped which are followed according to Boxshall (1985: pp. 341-345). The terminology of Huys (1988a) for the caudal ramus structure is used.

SYSTEMATICS AND DISCUSSION

Family Latiremidae Božić, 1969

Diagnosis. — Habitus cylindrical, no distinct separation between prosome and urosome. P1-bearing somite either free or fused to cephalosome. Genital somite in female either completely free or fused dorsally with first abdominal somite. Abdominal somites with spinular ornamentation ventrally. Anal somite with well developed posteriorly located anal operculum. Caudal rami short, often concealed beneath anal operculum; furnished with 6 setae, anterolateral accessory seta (I) absent.

Rostrum diminutive, fused with cephalosoma, without sensillae. Nauplius eye absent. Antennula with smooth setae (except for plumose seta on segment I), 4th segment with aesthetasc; 8- or 9-segmented in female, subchirocer in male. Antenna with inner seta on both basis and proximal endopod segment (or allobasis with 2 inner setae); exopod 1-segmented, with 1 apical and 3 lateral setae. Mandible with reduced palp; basis with 3 setae; endopod 1-segmented with 2 lateral and 5 terminal setae; exopod absent. Maxillula with well developed praecoxal arthrite; coxa without epipodite; endo- and exopod 1-segmented. Maxilla with 1 endite on praecoxa and 2 endites on coxa; basal endite not produced into a claw; endopod indistinctly 2-segmented. Maxilliped prehensile; with syncoxa, basis and 1-segmented endopod bearing claw and up to 3 setae.

Swimming legs with well developed intercoxal sclerites. P1 with 2- or 3-segmented exopod; endopod 2-segmented with distal segment shortest, bearing 1 subapical long seta and 1 apical geniculate claw. Rami of P2-P4 typically 3-segmented (except endopod P4 of *D. arenicola*). Rami of P5 forming a broad common plate in both sexes. Female genital complex simple, without vestige of P6. Male P6 represented by 2 setae.

Sexual dimorphism in antennula, P4 (both rami), P5, P6 and in genital segmentation. Male P4 with transversely expanded exopod and modified setae on (2nd and) 3rd segments; endopod without inner seta on 1st segment.

Marine interstitial.

Type genus: Latiremus Božić, 1969 Other genera: Delamarella Chappuis, 1953; Arbutifera gen. nov.

Genus Laterimus Božić, 1969

Diagnosis. — Latiremidae. P1-bearing somite completely incorporated in cephalosome forming a cephalothorax. Genital somite and first abdominal somite entirely free in both sexes. All postgenital somites with transverse spinular rows along the ventral side. Seminal receptacles of female clearly separated from each other. Anal operculum densely fringed but without spinules. Caudal rami almost completely exposed; setae IV and V well

developed; setae II and III spiniform, bearing a flagellum near the tip. Antennula 8-segmented in female; 9- or 10-segmented in male. Antenna with basis and proximal endoped segment separated. Maxilliped with 1 seta on syncoxa; endopod bearing 1 claw and 2 setae. P1 exopod 3-segmented; proximal endopod segment at least twice as long as broad, with inner subdistal seta. P4 endopod 3-segmented; distal segment with 2 setae. Setae of P5 not modified; exopodal lobe with 3 bipinnate spines and 1 smooth seta in female, with 3 bipinnate spines in male. Distal exopod segment of male P4 with 3 setae and 1 strong spine.

Type and unique species: Latiremus eximius Božić, 1969 (by monotypy).

Remarks. — It is obvious that L. eximius cannot be included in the genus Delamarella because of the 4-segmented prosome. The state of the first pedigerous somite is a character that has served to distinguish genera in other families as well (Canuellidae, Cerviniidae); however, none of the authors postdating Božić (1969) has given this major character the attention it obviously deserves. The completely separated female genital somite is shared with the new genus Arbutifera, however, Latiremus differs in the segmentation of the antennula. The distal antennular segment in the latter is equivalent to segments VIII and IX of A. phyllosetosa. An interesting feature, thus far found only in L. eximius, is the presence of a distinct praecoxa and coxa in the maxilla. In all other latiremids and most harpacticoids these elements are fused into a syncoxa. Within the harpacticoids a 3-segmented maxillar protopod is further also exhibited by most Canuellidae (however with 2 distinct endites on the praecoxa), and represents a character retained from the common ancestral copepod stock. Thus far, the genus Latiremus is restricted to the East African coast of the Indian Ocean (La Réunion), but a pan-tropical distribution pattern might be more likely. Re-examination of L. eximius was impossible as Božić never deposited material in the "Muséum national d'Histoire naturelle" of Paris (Forest, Gourbault, pers. comm.).

Genus Delamarella Chappuis, 1969

Diagnosis. — Latiremidae. P1-bearing somite partially incorporated in cephalosome; anterior part concealed beneath dorsal cephalic shield. Genital somite and first abdominal somite fused dorsally in female. All postgenital somites with transverse spinular rows along the ventral side. Seminal receptacles of female closely set to each other. Anal operculum provided with 10-15 spinules. Caudal rami often concealed beneath anal operculum; setae IV and V well developed; setae II and III spiniform, not bearing a flagellum near the tip. Antennula 8- or 9-segmented in female; 8(?)-segmented in male. Antenna with basis and proximal endopod segment fused into allobasis. Maxilliped with 1 seta on syncoxa; endopod bearing 1 claw and 2-3 setae. P1 exopod 2-

segmented; proximal endopod segment at least twice as long as broad, without inner subdistal seta. P4 endopod 2- or 3-segmented; distal segment with 2 setae. Middle seta of endopodal lobe of P5 with strips of serrated membrane; exopodal lobe with 3 bipinnate/serrate spines and 1 smooth seta in both sexes. Distal exopod segment of male P4 with 3 setae and at least 2 strong blunt processes.

Type species: Delamarella arenicola Chappuis, 1953 (by monotypy). Other species: D. karamani Petkovski, 1957; D. galateae Cottarelli, 1971

Remarks. — Cottarelli (1971) mentioned sexual dimorphism in the caudal rami of D. galateae, viz. the presence of a ventral tubercle in the male. It is possible that this structure represents a modified secretory pore as a circular cup-shaped pore was found in exactly the same position in A. phyllosetosa. This type of cryptic sexual dimorphism is not reported for the other congeners. Character analysis reveals that D. arenicola represents the most advanced member of the Latiremidae and its isolated position has already been pointed out by Cottarelli (1971) and Kunz (1984). The 2-segmented P4 endopod and the 8-segmented antennula are unique characters for the species; the latter character is not homologous with the state found in L. eximius because the plane of fusion (between segments VI and VII) is different. Since Chappuis (1953, 1954a) did not mention the condition of the first pediger, it might be completely incorporated in the cephalosome; this eventually would constitute a third apomorphy. On the basis of these characters we were inclined to consider the karamani-galateae grouping to be a separate genus, however, since this lineage cannot be supported by any autapomorphies, the proposed subdivision is obviously premature. None of the three species was re-examined as neither the type material nor other specimens could be obtained. The types of D. karamani were destroyed during an earthquake (Petkovski, pers. comm.). Chappuis' material of D. arenicola was lost shortly after the original description (Rouch, pers. comm.). Requests to Prof. Dr. V. Cottarelli to borrow the types of D. galateae remained unanswered. The geographical distribution of Delamarella is confined to the Mediterranean with records in France, Spain, Algeria, Italy and Yugoslavia. Apostolov's (1969) find of D. karamani near Varna is the sole Black Sea record for the genus.

Genus Arbutifera gen. nov.

Diagnosis. — Latiremidae. P1-bearing somite not incorporated in cephalosome; fully exposed. Genital somite and first abdominal somite entirely free in both sexes. Anal somite only with transverse spinular rows along the ventral side. Seminal receptacles of female closely set to each other. Anal operculum strongly developed, serrated along the posterior margin. Posterior half of caudal rami exposed; setae IV and V strongly reduced; setae II and III

short, extremely swollen and densely covered with fine spinules, bearing a flagellum near the tip. Antennula 9-segmented in female. Antenna with basis and proximal endopod segment separated. Maxilliped with 1 seta on syncoxa; endopod bearing 1 claw and 2 setae. P1 exopod 3-segmented; proximal endopod segment nearly as long as broad, with inner subdistal seta. P4 endopod 3-segmented; distal segment with 1 bipinnate spine. Almost all setae of P5 modified; exopodal lobe with 2 serrated spines and 2 smooth setae in female.

Etymology. — The generic name is derived from the Latin *arbutum*, meaning strawberry and *ferre*, meaning to carry, and alludes to the shape of the lateral setae of the caudal rami. Gender: feminine.

Type and unique species: Arbutifera phyllosetosa (Kunz, 1984) comb. nov.

Arbutifera phyllosetosa (Kunz, 1984) comb. nov. Syn. Delamarella phyllosetosa: Kunz (1984), p. 54, figs. 1-2.

Redescription. — Material examined: holotype female dissected and mounted on 4 slides, deposited in the Zoologisches Museum, University of Hamburg under no. K 32588a-d.

FEMALE. Body length about 380 µm, rostrum and caudal rami included (according to Kunz, 1984). Rostrum small, fused to dorsal cephalic shield, without sensillae. First pedigerous somite fully exposed, not fused to cephalosome. Genital somite completely separated from first abdominal somite (fig. 2A); genital complex very weakly developed, no trace of P6, seminal receptacles closely set to each other (fig. 1F). Hyaline frill of urosomites almost plain, finely striated (fig. 2A). Anal somite furnished ventrally with 3 sets of fine spinules in anterior half; rear edge with spinular row midventrally, distinctly serrated dorsolaterally (figs. 2A-C). Anal operculum located posteriorly, semicircular in shape, serrated. A spinular row is discernible beneath the anal operculum. Other abdominal somites without distinct ornamentation. Caudal rami (figs. 2B-C) in part covered by anal operculum; short, tapering posteriorly, dorsal surface armed with an oblique spinular row; furnished with 6 setae: anterolateral (III) setae bulb-shaped and densely covered with minute spinules, provided with a flagellum near the apex, seta III also with numerous hair-like filaments along the inner margin; outer (IV) and inner terminal (V) setae broken, but presumably strongly reduced; terminal accessory seta (VI) short and bare, accompanied by some fine spinules at the base; dorsal seta (VII) plumose and tri-articulated at the base.

Antennula (fig. 1A) short, 9-segmented, directed laterally; first segment shorter than wide, furnished with 1 outer plumose seta; segments 2 and 3 armed with 9 and 4 bare setae, respectively; segment 4 with 1 inner seta, distal corner produced into a distinct process bearing a slender seta and a short

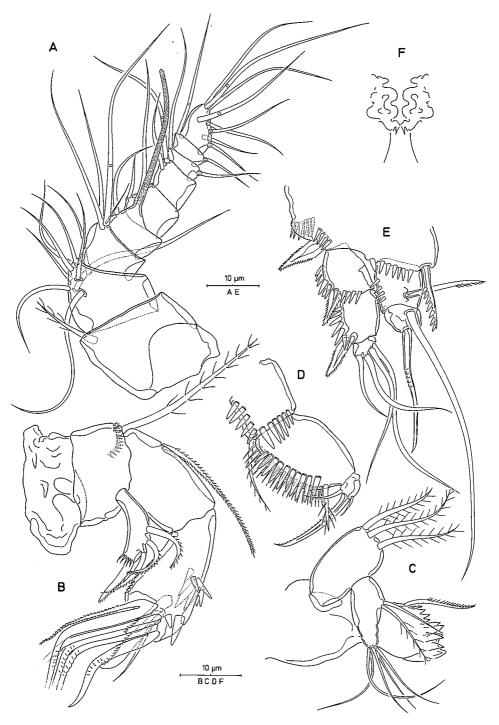


Fig. 1. Arbutifera phyllosetosa (Kunz, 1984) comb. nov., female: A, antennula; B, antenna; C, mandible; D, maxilliped; E, P1; F, genital complex.

aesthetasc; segments 5 and 6 with 1 and 2 inner setae, respectively; segments 8 and 9 with 1 inner and 1 outer (bi-articulated) seta; distal segment bearing 3 simple, 3 bi-articulated and 2 geniculate setae.

Antenna (fig. 1B) short, robust; coxa not well defined, unarmed; basis twice as wide as long, with spinular row and bipinnate seta near outer corner; exopod 1-segmented, slightly recurved, bearing 3 unipinnate setae laterally and 1 spine at the tip; endopod 2-segmented, proximal segment with bipinnate seta in anterior half, segment 2 with 1 slender seta, 2 pinnate claws and 5 geniculate setae (the outermost of which being fused at the base with slender pinnate seta).

Mandible (fig. 1C) with well developed gnathobase; palp uniramous; basis with 3 inner plumose setae; endopodite 1-segmented, with 2 lateral and 5 terminal setae, apical part thin-walled; exopod wanting.

Maxillula and maxilla damaged during dissection.

Maxilliped (fig. 1D) prehensile; praecoxa and coxa fused into a syncoxa, armed with strong spinules along the distal and inner margins, bearing 1 plumose seta; basis with pinnate seta, inner margin adorned with anterior row of strong spinules and posterior row of fine setules; endopod 1-segmented, armed with a finely spinulated claw and 2 short bare setae.

P1 (fig. 1E). Basis armed with a strong bipinnate spine at the outer distal corner and an inner unipinnate spine. Exopod 3-segmented; segments 1 and 2 with outer bipinnate spine and covered with coarse spinules along the outer and distal margins, no setae along the inner side; segment 3 small, provided with 4 slender setae of different lengths. Endopod 2-segmented; proximal segment squarish, outer margin spinulose, with inner subdistal seta; distal segment with apical geniculate claw and subdistal very long, bare seta.

Seta and spine formula of P2-P3 see table I.

Table I
Seta and spine formula of Arbutifera phyllosetosa comb. nov.

	Exopod	Endopod
P1 P2 P3 P4	0.0.211 0.1.121 0.1.121 0.0.121	- 1.110 1.1.020 1.1.020 1.0.010
1 7	0.0.141	1.0.010

P4 (fig. 2D). Basis covered with spinular rows on the posterior and anterior surfaces, furnished with a plumose seta standing on a sub-cylindrical process along the outer margin. Exopod 3-segmented; segments 1 and 2 with a strong, blunt, unipinnate spine at the outer subdistal corner, outer and distal margins

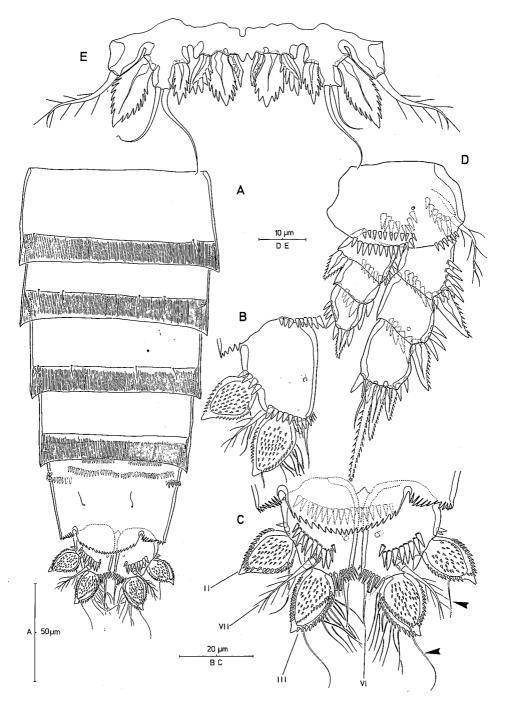


Fig. 2. Arbutifera phyllosetosa (Kunz, 1984) comb. nov., female: A, urosome (excluding P5-bearing somite), dorsal view; B, caudal ramus, ventral view; C, caudal rami and posterior part of anal somite, dorsal view (arrows indicate articulating flagellum on setae II and III); D, P4, posterior view; E, 5th pair of legs.

armed with strong spinules; distal margin of segment 3 covered with strong spinules, bearing 3 pinnate spines of different lengths and 1 slender seta. Endopod 3-segmented; segment 1 expanded, having a short bipinnate spine at the inner subdistal corner; segment 2 without any spines or setae, but with blunt spinules along the distal edge; segment 3 tapering distally, armed with several spinules and 1 apical spine.

P5 (fig. 2E). Fifth pair of legs fused medially; baseoendopod and exopod forming a common plate; basal seta plumose and standing on a prominent process; margin of exopodal lobe stepped, armed with 2 strong serrated spines and 2 medial slender setae; endopodal lobe less pronounced, bearing a strong, serrated spine medially and 2 short unipinnate spines.

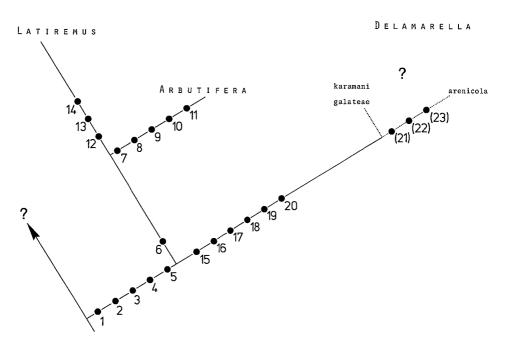
MALE. Unknown.

Remarks. — Arbutifera gen. nov. is unique amongst Latiremidae in the combined presence of a separated genital somite in the female and of the free first pedigerous somite. The 3-segmented exopod P1 and the antennal allobasis are shared with Latiremus but the latter lacks the modified spines on the P5 and the caudal rami.

PHYLOGENY

Latiremidae exhibit a mosaic of unusual plesiomorphies and unique derived character states. Of the former the 5-segmented prosome is of major significance, because it serves to distinguish Latiremus from Delamarella. Except for the siphonostomatoids, all copepod orders primitively exhibit the free condition of the first pedigerous somite. In contrast to most other orders this character is rather unusual amongst harpacticoids and is found only in Canuellidae, Chappuisiidae, Phyllognathopodidae and in the families of the Cervinioidea (Huys, 1988b). The female genital somite displays the basic condition, viz. completely separated from the first abdominal somite. This ancestral state is commonly found in Platycopioida, Misophrioida, Cyclopoida and Poecilostomatoida but is to our knowledge almost unique for the harpacticoids. It is further also found in an undescribed tetragonicipitid (Huys, unpubl.). The 3-segmented protopod of the maxilla is also atypical and indicates that the Latiremidae diverged early from the common harpacticoid stem.

Although it is at present a hard task to determine the exact outgroup of the family, at least some of the autapomorphies can be defined with certainty because of their advanced facies and because they are primitively absent in other families. The peculiar sexual dimorphism in the P4 exopod is the most important apomorphy for the family. The significance of this character was interpreted incorrectly by Božić (1978) because he used it as good evidence for lumping all the Latiremidae into a single genus. The complex male P4 justifies



LATIREMIDAE-

Fig. 3. Cladogram depicting the phylogenetic relationships of the latiremid genera. Brackets refer to potential apomorphies if the karamani-galateae complex turns out to be a monophyletic taxon. Synapomorphies are: (1) sexual dimorphism of P4, (2) loss of exopod mandible, (3) reduction of the female genital complex (loss P6), (4) 2-segmented endopod P1, (5) fusion of rami of P5, (6) caudal rami setae II and III with flagellum, (7) modified serrated spines of P5, (8) bulb-shaped setae II and III of caudal rami and reduction of setae IV and V, (9) reduction of abdominal ornamentation, (10) blunt spines on P4, 3rd endopod segment with 1 seta, (11) serrated anal operculum, (12) 8-segmented antennula (fusion of VIII and IX), (13) loss of spine maxillipedal basis, (14) 4-segmented prosome, (15) partial incorporation of 1st pedigerous somite, (16) antenna with allobasis, (17) exopod P1 2-segmented, (18) proximal endopod segment P1 without inner seta, (19) genital and 1st abdominal somite fused dorsally in female, (20) spinulose anal operculum, (21) 8-segmented antennula (fusion of VI and VII), (22) endopod P4 2-segmented, (23) P1 fused to cephalosome.

the separate familial status of the latiremids and for that reason it is of equal importance to the facies of the P1 in the Laophontidae or the amphipod-like body shape of the Tegastidae. Other advanced characters are the loss of the mandibular exopod, the combined profound reduction in the genital complex and loss of the P6, the 2-segmented P1 endopod and its characteristic setation and the fusion of the rami of the P5 in both sexes.

Wells' (1978) suggestion that the affinities of the Latiremidae may lie with the Ameiridimorpha is not well grounded. Also Itô's (1974) statement that there probably exists "... a rough evolutional line arising from *Protolatiremus* to *Latiremus* and further to *Delamarella* ..." should be rejected altogether (Božić,

1978; Kunz, 1984). We even do not exclude the possibility that *Protolatiremus* represents a separate family but this needs further investigation.

Two main lineages can be recognized within the family (fig. 3). The Latiremus-Arbutifera grouping stands closest to the latiremid ancestor because of the presence of an antennal basis, the completely separated genital somite in the female, the 3-segmented exopod P1 and of the inner seta on the proximal endopod segment of P1. The apomorphic alternatives of all these characters are found in the sister group that comprises thus far only the genus Delamarella. All three Delamarella species exhibit an allobasis with 2 inner setae through fusion of the basis and the proximal endopod segment. The P1 displays a double autapomorphy, viz. the loss of the inner seta on the first endopod segment, and the 2-segmented condition of the exopod through fusion of the middle and distal segments. The genital and first abdominal somites in the female are fused dorsally yet remain distinct along the lateral and dorsal sides. This state is unusual amongst harpacticoids as an incompletely fused genital double somite is without exception caused by failure of dorsal (and lateral) fusion of the constituent somites.

Within the Latiremus-Arbutifera grouping, the latter genus is without doubt the most primitive because of the fully separated first pedigerous somite, the 9-segmented female antennula and the presence of a bipinnate spine on the maxillipedal basis. The latter character is probably also exhibited by D. karamani. The former character indicates that the partial incorporation of the P1-bearing somite represents a further apomorphy for Delamarella. In both D. karamani and D. galateae the anterior part of this somite is concealed beneath the dorsal shield of the cephalosome (Petkovski, 1957; Cottarelli, 1971); no information is available for D. arenicola, probably indicating that it is entirely integrated (Chappuis, 1954a).

Autapomorphies for Arbutifera are (1) the modified serrated spines of the fifth pair of legs, (2) the highly transformed lateral setae (II, III) of the caudal rami (and reduction of setae IV and V), (3) reduction in abdominal ornamentation, (4) the blunt spines on the P4 with only 1 spine on 3rd endopod segment, (5) the serrated anal operculum. The genus Latiremus can be defined on the basis of the 8-segmented female antennula, the 4-segmented prosome and the loss of the spine on the maxillipedal basis.

The monophyletic status of the *Latiremus-Arbutifera* complex is sustained by the detailed morphology of the caudal rami setae. In both genera the anteroand posterolateral setae are characterized by the presence of a slender flagellum along the inner margin. This minute structure, called "fin poil subapical" by Božić (1969), is definitely absent in all *Delamarella* species yet easily discernible on the bulb-shaped ramal setae of *A. phyllosetosa* (figs. 2B-C).

In addition to the apomorphies mentioned above, the genus *Delamarella* is characterized by the anal operculum bearing a variable number of spinules along its posterior margin. The finely fringed (aspinulose) operculum of *L*.

eximius suggests that the smooth condition was the ancestral one from which the serrated (aspinulose) state has been evolved secondarily in *Arbutifera*. The true spinulose operculum then can be regarded as a de novo formation for the *Delamarella* lineage.

KEY TO THE LATIREMID GENERA

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