

Cladistic revision of talitroidean amphipods (Crustacea, Gammaridea), with a proposal of a new classification

CRISTIANA S. SEREJO

Accepted: 8 December 2003

Serejo, C. S. (2004). Cladistic revision of talitroidean amphipods (Crustacea, Gammaridea), with a proposal of a new classification. — *Zoologica Scripta*, 33, 551–586.

This paper reports the results of a cladistic analysis of the Talitroidea s.l., which includes about 400 species, in 96 genera distributed in 10 families. The analysis was performed using PAUP and was based on a character matrix of 34 terminal taxa and 43 morphological characters. Four most parsimonious trees were obtained with 175 steps (CI = 0.617, RI = 0.736). A strict consensus tree was calculated and the following general conclusions were reached. The superfamily Talitroidea is elevated herein as infraorder Talitrida, which is subdivided into three main branches: a small clade formed by *Kuria* and *Micropythia* (the Kurioidae), and two larger groups maintained as distinct superfamilies (Phliantoidae, including six families, and Talitroidea s.s., including four). Within the Talitroidea s.s., the following taxonomic changes are proposed: Hyalellidae and Najnidae are synonymized with Dogielinotidae, and treated as subfamilies; a new family rank is proposed for the Chiltoniinae.

Cristiana S. Serejo, Museu Nacional/UFRJ, Quinta da Boa Vista s/n, 20940–040, Rio de Janeiro, RJ, Brazil. E-mail: csserejo@acd.ufrj.br

Introduction

The talitroideans include amphipods ranging in length from 3 to 30 mm, and are widely distributed in the tropics and subtropics. In marine and estuarine environments, they are usually found in shallow water, intertidally or even in the supra-littoral zone. Some groups have also colonized freshwater and forest litter. According to Barnard & Karaman (1991), Bousfield (1996), and the recent revision of Bousfield & Hendrycks (2002) they comprise c. 400 species distributed in 96 genera in 10 families (Table 1). Half of the genera are included in the semiterrestrial and terrestrial Talitridae, indicating a strong adaptive radiation of the group in this habitat.

The first modern revision of the group was performed by Bulychева (1957), who raised Talitridae s.l. to superfamily status (Talitroidea) and created two new families, Hyalidae and Hyalellidae, retaining Talitridae s.s. as a valid family. This classification is currently in use, although it has received some criticism, considering that the main division of the families is not morphological and indeed to some extent deals with the ecology of the organisms (Barnard 1969, 1972a). Using this ecological approach, Bulychева (1957) divided the Talitroidea into three families:

(1) Hyalidae, exclusively marine and considered as basal within the group's evolution. They include *Parhyale* Stebbing, 1897, *Hyale* Rathke, 1837, *Allorchestes* Dana, 1849, *Ceina* Della Valle, 1893 and *Najna* Derzhavin, 1937.

Table 1 Talitroidean classification following Barnard & Karaman (1991), Bousfield (1996) and Bousfield & Hendrycks (2002)

Superfamily Talitroidea Rafinesque, 1815
Family Ceinidae Barnard, 1972
Family Dogielinotidae Gurjanova, 1953
Family Eophlinatidae Sheard, 1936
Family Hyalellidae Bulychева, 1957
Subfamily Chiltoniinae Barnard, 1972
Subfamily Hyalellinae Bulychева, 1957
Family Hyalidae Bulychева, 1957
Subfamily Hyachelinae Bousfield & Hendrycks, 2002
Subfamily Hyalinae Bulychева, 1957
Subfamily Kuriinae Barnard, 1964
Family Najnidae Barnard, 1972
Family Phliantidae Stebbing, 1899
Family Plioplateidae Barnard, 1978
Family Talitridae Rafinesque, 1815
Family Temnophliantidae Griffiths, 1975

(2) Hyalellidae, which live mainly in freshwater habitats. They include *Chiltonia* Stebbing, 1899, *Hyalella* Smith, 1874 and *Parhyalella* Kunkel, 1910 (which, exceptionally, is found in marine and brackish environments).

(3) Talitridae s.s., confined to semiterrestrial or terrestrial habitats. They include *Orchestia* Leach, 1814, *Orchestoidea*, Nicolet, 1849, *Talitrus* Latreille, 1802 and *Talorchestia* Dana, 1852.

Since this first revision of the Talitroidea, new taxa have been included and several genera rearranged in the families. Barnard (1969) agreed to some extent with Bulycheva's (1957) classification, but noted the difficulties in separating the three proposed families using morphological characters: 'morphologically it is impossible strictly and qualitatively to separate the terrestrial Talitridae from the concepts of the other two families'. However, he retained Talitridae *s.l.*, including Hyalinae, Hyaellinae and Talitrinae as subfamilies.

Later, Barnard (1972b) created the Ceinidae to include *Ceina* and certain other genera. In the same year, based on material from New Zealand, he (Barnard 1972a) rearranged other genera and erected Najnidae to include *Najna*, as he had suggested previously (Barnard 1969). Barnard (1972a) maintained Hyalinae and Hyaellinae as subfamilies within Talitridae. Ceinidae was divided into two subfamilies: (1) Chiltoniinae, including *Chiltonia* Stebbing, 1899, *Afrochiltonia* K.H. Barnard, 1955 and *Austrochiltonia* Hurley, 1958; (2) Ceininae, including *Ceina*, *Taihapa* Barnard, 1972 and *Waitomo* Barnard, 1972. The Chiltoniinae, previously allocated to the Hyaellidae, were transferred to Ceinidae based on the lack of a ramus on uropod 3. Dogielinotidae, Kuriidae, Eophliantidae and Phliantidae were also included within the Talitroidea, based on diagnostic characters of the superfamily such as the absence of a mandibular palp, and uniramous uropod 3.

Bousfield (1978) criticized Barnard's (1972a) revision, but did not suggest a new classification, only revalidating the classification of Bulycheva (1957). Hyalidae, Hyaellidae and Talitridae *s.s.* were again given family status, and the Temnophliantidae were also included as part of Talitroidea.

Barnard & Karaman (1991) published a world revision of the marine gammarideans, including a key for the Talitroidea families, and added Plioplateidae to the 10 previously proposed for the group. The chiltoniines were once more included as part of the Ceinidae, as proposed previously by Barnard (1972a). However, the presence of cuticular pits was also used as a diagnostic character for Ceinidae. *Hyachelia* Barnard, 1967, ascribed initially to the Hyalidae (Barnard 1967), was considered as a member of the Ceinidae mainly because of the lack of a ramus on uropod 3. Hyalidae was thus composed of nine genera: *Allorchestes*, *Hyale*, *Insula*, *Lelehua*, *Microphythia*, *Neobule*, *Parallorchestes*, *Parhyale* and *Parhyalella*.

Five years later, Bousfield (1996) proposed a classification for the Hyaellidae. Following his previous work (Bousfield 1964, 1978, 1982a), the Chiltoniinae were included within the Hyaellidae as one of two subfamilies. The other subfamily, Hyaellinae, included the freshwater *Hyalella* (divided into three subgenera), and the marine *Allorchestes*, *Insula* and *Parhyalella*, transferred from Hyalidae. Lazo-Wasem & Gable (2001) revised *Parhyalella*, re-establishing *Exhyalella* Stebbing, 1917 and describing a new genus, *Marinohyalella*. These three genera were maintained within the Hyalidae, following the

pragmatic ecological decision to place them with the marine hyalids. Recently, Bousfield & Hendrycks (2002) proposed a revision of the Hyalidae based on the North Pacific fauna including three subfamilies: Hyacheliinae, Hyalinae and Kuriinae. These authors also revised the large *Hyale* genus, proposing five new genera.

Barnard (1972a) allocated Kuriidae, Eophliantidae and Phliantidae to the Talitroidea *s.l.* Later, Temnophliantidae and Plioplateidae were also included. A brief history of these families follows.

Stebbing (1899) included five genera in his classification of the Phliantidae: *Phlias* Guérin, 1836, *Iphinotus* Stebbing, 1899, *Iphiplateia* Stebbing, 1899, *Pereionotus* Bate & Westwood, 1863 and *Bircenna* Chilton, 1884. He characterized this family based on common characters found in other talitroideans, including: lack of accessory flagellum; lower lip lacking inner lobe; lack of mandibular palp; maxilla 1 with vestigial palp; gnathopods simple or weakly subchelate and pleopods laterally produced in two or more pairs.

Later, Walker & Scott (1903) described *Kuria longimanus* and discussed its similarity with *Bircenna*; however, they maintained this taxon as *incertae sedis*. Later, Stebbing (1906) included *Kuria* and *Palimnotus* Stebbing, 1900 in the Phliantidae.

Sheard (1936) divided the Phliantidae into two subfamilies, based primarily on the structure of the telson: (1) Eophliantinae, with a cleft telson, including *Bircenna*, *Kuria* and the new genus *Eophliantis*; (2) Phliantinae, with an entire telson, including *Iphinotus*, *Iphiplateia*, *Phlias*, *Pereionotus*, *Palimnotus*, *Plioplateia* K.H. Barnard, 1916, *Quasimodia* Sheard, 1936, and *Temnophlias* K.H. Barnard, 1916.

Nicholls (1939) elevated Phliantinae to family status (with 10 genera), characterizing it as having the telson entire and the body depressed dorso-ventrally. He also created the family Prophliantidae, which included Eophliantinae (*Ceina*, *Cylindryllioides* Nicholls 1938, *Biancolina* Della Valle, 1893, *Wandelia* Chevreux, 1906 and the new genus *Prophlias*). The Prophliantidae were characterized as having an emarginate or cleft telson and cylindrical body.

The classification of Prophliantidae proposed by Nicholls (1939) was not generally accepted. Gurjanova (1958) elevated the Eophliantidae to family status, including genera with a cylindrical body (*Bircenna*, *Biancolina*, *Eophliantis*, *Cylindryllioides*, *Wandelia* and *Amphitholina* Ruffo, 1953). Prophliantidae was maintained, but included only *Prophlias*, *Ceina*, *Najna* and *Kuria*. Barnard (1964) revised these families. He supported the genera cited by Gurjanova (1958) for Eophliantidae, and also included *Ceinina*. Within the Prophliantidae he maintained *Prophlias* and included *Haustoriopsis* Schellenberg, 1938. He also identified the Prophliantidae as a divergent evolutionary line from the other families, because of their fused urosomites and biramous uropod 3. Phliantidae was revised, including the genera listed by Sheard (1936): *Pariphinotus*,

Heterophlias Shoemaker, 1933 and *Ceina*. Barnard (1964) also noted the necessity for a redescription of the type genus *Phlias*, in order to elucidate taxonomic problems within the group and improve the characterization of the family diagnosis. *Najna* was maintained within Talitridae s.l., while *Kuria* was transferred to the new family Kuriidae. Subsequently, the Prophliantidae fide Barnard (1964) were transferred to Dexaminidae with subfamily status, being definitely separated from the Talitroidea s.l. (Barnard 1970a, 1972a). Recently, Bousfield & Hendrycks (2002) transferred Kuriidae to Hyalidae with subfamily status.

Biancolina has a cylindrical body, apparently an adaptation to its life-style as a kelp burrower. For this reason, it was first included within the Eophliantidae (Gurjanova 1958; Barnard 1964, 1969). In his study of the New Zealand marine gammarids, Barnard (1972a) discussed reasons for removing *Biancolina* from Eophliantidae, and created a new family for it, Biancolinidae. The characteristics which Barnard (1972a) used to exclude *Biancolina* from the Eophliantidae and even from the Talitroidea were as follows: inner ramus of maxilliped short, not reaching the distal margin of outer ramus bearing long fine or stout setae; distal portion of pereopods 3–5 very thin; and (mainly) the retention of the plesiomorphic biramous uropod 3. In the same work, Barnard reassigned *Amphitholina* Ruffo, 1953 from Eophliantidae to Ampithoidae.

The monotypic *Temnophlias*, endemic to South Africa, was initially described by K. H. Barnard (1916) as belonging to the Phliantidae, in view of the dorso-ventrally depressed body, reduced mouthparts and deeply lobated peduncle of pleopods 1–3. J. L. Barnard (1969, 1972a) discussed the position of *Temnophlias* as part of the Phliantidae, and indicated important differences such as: reduction of coxae and the presence of pleura on the pereon, an autapomorphy for *Temnophlias*. Griffiths (1975) allocated *Temnophlias* to a separate family (Temnophliantidae) based on the following characters: presence of pleura on the pereon, palp of maxilliped bi-articulate, and uniramous uropod 1.

Similarly to *Temnophlias*, *Plioplateia* was also described from South Africa and was initially allocated to the Phliantidae because of its body shape (K. H. Barnard 1916). However, several differential characters led Barnard (1978) to allocate *Plioplateia* to its own family, the Plioplateidae.

Talitroideans are an abundant and diverse group of amphipods with a worldwide distribution. Like other amphipods, they play an important role in the food chain. They are mainly detritivores in marine, freshwater and terrestrial habitats, and serve as food for many fishes and birds. Despite being such important inhabitants of the benthos, amphipods have been the subjects of few cladistic studies (e.g. Watling & Thurston 1989; Kim & Kim 1993; Berge *et al.* 2000; Myers & Lowry 2003). The present study is a first step toward an evolutionary understanding of this group of amphipods using cladistic methods; it also proposes a new classification.

Materials and methods

Specimens included in the phylogenetic analysis were obtained from a number of institutions (listed in Table 2).

Cladistic methodology

The cladistic methodology used in this study is based on the theory proposed initially by Hennig (1966), and which has been widely discussed in the literature (e.g. Brook & McLennan 1991; Wiens 2000).

To obtain the morphological characters, a species of each genus was chosen, preferably the type species when available. Each species chosen represents a terminal taxon. In genera such as *Allorchestes*, *Hyaella* and the *Hyale* complex, more than one species was included in the analysis. Representatives of all 10 talitroidean families were treated, emphasizing the Hyalidae and Hyaellidae, where most genera were included, and excluding *Neobule*, *Afrochiltonia* and *Phreatochiltonia*. *Neobule* is an obscure genus, not currently recognized and was therefore not included in the analysis (Table 2).

The genera *Kuria* and *Insula* are monotypic, their species recorded only by Walker & Scott (1903) and Kunkel (1910), respectively. Material of these genera was not observed; both taxa were treated in the analysis based on information from the literature.

Character matrix and outgroup

A character matrix was developed with 34 terminal taxa and 43 morphological characters (Table 3). Two characters were from general aspects of the body, 18 from the head (including antennae and mouthparts), 18 from the thorax (including coxae, pereopods and oostegites), and five from the abdomen. The characters were obtained by detailed observation of the material and also from published data.

Characters dealing with reductions, which are quite common within Talitroidea s.l., were included in order to observe their relevance *a posteriori*. This same principle was followed in relation to the less informative characters, which could help in the resolution of the final topology.

The polarization of the characters was done with outgroup comparison. The relation between ingroup and outgroup was not constrained, which allowed the monophyly of the ingroup to be tested (Nixon & Carpenter 1993). Considering the absence of studies of phylogeny within the Talitrida, there was no suggestion in the literature for an outgroup. Nevertheless, *Gammarus* was chosen to root the trees, as it is considered a basal genus in the evolution of the Gammaridea (Barnard 1969). Two more genera were included as outgroups: *Beaudettia*, considered an intermediate form between Gammaridae and Talitroidea s.l. (Barnard & Karaman 1991), and *Biancolina*, which was classified within the Eophliantidae and considered close to the Talitroidea s.l. (Barnard 1972a).

Table 2 Species examined and included in the character matrix. Locality and institution number are provided for each species. –, Taxa were not observed (type material probably lost) and the morphological characters were obtained from the literature. Abbreviations: AM, Australian Museum; CMNC, Canadian Museum of Nature; ZMC, Zoologiske Museum, Copenhagen; MCVR, Museo Civico di Storia Naturale Verona; MNHN, Museum National d'Histoire Naturelle; MNRJ, Museu Nacional/Universidade Federal do Rio de Janeiro; SAM, South African Museum; USNM, National Museum of Natural History (Smithsonian Institution)

Taxa	Locality	Institution
OUTGROUPS		
Family Beaudetiidae		
<i>Beaudettia palmeri</i> Barnard, 1965	Marshall Engebi Islands, Eniwetok Atoll, North Pacific (holotype and paratype)	USNM 108985, 107572
Family Gammaridae		
<i>Gammarus</i> sp.	Copenhagen, Denmark	MNRJ 10667
INGROUPS		
Family Biancolinidae		
<i>Biancolina</i> sp.	Bare Island, Botany Bay, NSW, Australia	AM P42974
Family Ceinidae		
<i>Ceina egregia</i> (Chilton, 1883)	Off Strathmore, Eve Bay, North Island, New Zealand	USNM 149376
Family Dogielinotidae		
<i>Dogielinoides golikovi</i> (Kudrjaschov, 1979)	Kuril Island, Shikhotan, Russia	CMNC 1999–0031
<i>Probosciniotus loquax</i> (Barnard, 1967)	Clam Beach, California, USA	USNM 261441
Family Eopliantidae		
<i>Bircenna fulva</i> (Chilton, 1884)	Off Strathmore, Eve Bay, North Wellington, New Zealand	USNM 149374
Family Hyalellidae		
Subfamily Chiltoniinae		
<i>Austrochiltonia australis</i> (Sayce, 1901)	38°19' S, 141°28' E, Victoria, Australia, G. Poore leg.	MNRJ 12956
<i>Chiltonia enderbiensis</i> Hurley, 1954	Auckland Island, New Zealand	ZMC CRU 3079
Subfamily Hyalellinae		
<i>Hyalella azteca</i> (Saussure, 1858)	Guadaloupe, Leeward Island, Caribbean Sea	USNM 151247
<i>Hyalella</i> cf. <i>pernix</i> Moreira, 1903	Jacaré-piá Lagoon, Saquarema, RJ, Brazil	MNRJ 9923
<i>Insula antennulella</i> * Kunkel, 1910	Bermuda	–
<i>Parhyalella pietschmanni</i> Schellenberg, 1938	Hamil Island, Red Sea	MCVR (not numbered)
Family Hyalidae		
Subfamily Hyachelinae		
<i>Hyachelia tortugae</i> Barnard, 1967	Porto Nuñez, Santa Cruz, Galapagos Islands	USNM 111528
Subfamily Hyalinae		
<i>Apohyale media</i> (Dana, 1853)	Guarapari, Espírito Santo, Brazil	MNRJ 4564
<i>Apohyale wakabarae</i> (Serejo, 1999)	Trinta Reis da Barra Island, Rio de Janeiro, Brazil	MNRJ 12767 (Holotype), 12768, 12781
<i>Hyale nigra</i> (Haswell, 1879)	Itaipú Beach, Rio de Janeiro, Brazil	MNRJ 12781
<i>Hyale pontica</i> Rathke, 1837	Morocco, East Atlantic	MCVR (not numbered)
<i>Serejohyale spinidactyla</i> (Chevreux, 1939)	Canary Islands	MNHN-Am 5106 (lectotype), 5122 (paralectotype)
<i>Lelehua waimea</i> (Barnard, 1970)	Oahu, Hawaii, USA	USNM 151345
<i>Parallorchestes ochotensis</i> (Brandt, 1851)	South-east of Farallon Islands, California, USA	CAS 003443
<i>Parhyale fascigera</i> Stebbing, 1897	St. Thomas, Caribbean Sea	ZMC CRU 6408
Subfamily Kuriinae		
<i>Kuria longimanus</i> * Walker & Scott, 1903	Sokotra and Abd-el-Kuri Islands, Arabian Sea, Indian Ocean	–
<i>Micropythia carinata</i> (Bate, 1862)	Morocco, Mediterranean Sea	MCVR not numbered
Family Najnidae		
<i>Najna kitamati</i> Barnard, 1979	Shelf of Point Conception, California, USA	USNM 106861
Family Phliantidae		
<i>Ipheplateia whiteleggei</i> Stebbing, 1899	Madang, New Guinea	USNM 184222
Family Plioplateidae		
<i>Plioplateia triquetra</i> K.H. Barnard, 1916	South Africa	SAM A15593
Family Talitridae		
<i>Chelorchestia darwini</i> (Müller, 1864)	Baía de Paranaguá, Paraná, Brazil	MNRJ 17000
<i>Orchestia gammarellus</i> (Pallas, 1766)	Het Zwin, Holland	USNM 138961
<i>Protorchestia nitida</i> (Dana, 1852)	Hoste Island, Magellan's Province, Chile	CMNC 1981–0589
<i>Talitrus saltator</i> (Montagu, 1808)	Oxwich Bay, Glamorganshire, UK	USNM 120463
Family Temnophliantidae		
<i>Temnophilias capensis</i> K.H. Barnard, 1916	Buffels River, west coast of South Africa	SAM A10308

Table 3 Character matrix with 34 terminal taxa and 43 morphological characters used in the analysis. Terminal taxa are ordered as they emerged in the consensus analysis. Numerals 0–7 represent the character states listed and discussed in the results; '?' missing data or no applicable character.

Taxon	1111111111222222222233333333334444	12345678901234567890123456789012345678901234567890123
<i>Gammarus</i> sp.	000	
<i>Beaudettia palmeri</i>	000000011510100011000100011000000450000130	
<i>Ceina egregia</i>	102101210110302?010000000040000001201200410	
<i>Plioplateia triquetra</i>	220103511420301210204310010000000120120040	
<i>Biancolina</i> sp.	010103111220202?010000102100200001451210020	
<i>Bircenna fulva</i>	010104110610202?010013202130200001501120400	
<i>Iphiplateia whiteleggei</i>	0211053103?1?12?210000003130300001334511430	
<i>Temnophilus capensis</i>	0221054101?1?12?210200103100300001145611430	
<i>Allorchestes angusta</i>	0021120101101012010000010011020001112100310	
<i>Allorchestes compressa</i>	0021120101101012010000010011020001112100310	
<i>Parhyalella pietschmanni</i>	002112010110102?010000010011020001112100330	
<i>Dogielinoides golikovi</i>	0021010101101012010000010011021101112100310	
<i>Probosciniotus loquax</i>	0021010101101012010000010011021101112100310	
<i>Najna kitamati</i>	0011031101101012010030000101020001112100330	
<i>Insula antenulella</i>	002107?010?101?120?00?00?0100?????????????330	
<i>Hyalella</i> cf. <i>pemix</i>	0021010101101012010000000011010011112100330	
<i>Hyalella azteca</i>	0021010101101012010000000011010011112100330	
<i>Hyachella tortugae</i>	00210101011010120101000000100100011123700400	
<i>Parhyale fascigera</i>	0021010101101011010000110010020001111400200	
<i>Lelehua waimea</i>	0021010101101011010000110010011001101400300	
<i>Hyale pontica</i>	0021020101101011010000110010010001101400300	
<i>Hyale niger</i>	0021020101101011010000110010010001101400300	
<i>Parallorchestes ochotensis</i>	0021020101101001010000110011010001101200200	
<i>Apoehale media</i>	00210201011010110100000110010010001112300300	
<i>Serejohale spinidactyla</i>	0021020101101011010000110010010001112300300	
<i>Apoehale wakabarae</i>	0021020101101011010000110010010001112300300	
<i>Chiltonia enderbiensis</i>	000101010110102?010000020020000011112300430	
<i>Austrochiltonia australis</i>	000101010110102?010000000200000101112300330	
<i>Protorchestia nitida</i>	0031110101101012010021120010400001201200331	
<i>Orchestia gammarellus</i>	0031110101101012010121120010400000201200321	
<i>Talitrus saltator</i>	003111010110101201012112330400100201200321	
<i>Chelorchestia darwinii</i>	0031100101101012010121120040400000201200321	
<i>Micropythia carinata</i>	0001010101101011010000021100101001201000300	
<i>Kuria longimanus</i>	00010?01?????????000000?????1010?????????3300	

Parsimony analysis

Cladistic data were compiled in MacClade 3.0 (Maddison & Maddison 1992) while the general heuristic search option of PAUP 3.1. (Swofford 1993) was used to identify the most parsimonious hypothesis of relationship. Unordered and equally weighted character states were used. To produce a final topology, a strict consensus tree was calculated, which summarized all the information obtained in the fundamental trees. Assessment of support for individual nodes was calculated using Bremer (1994) support.

Results

Several characters appearing in this analysis are currently used by other workers. However, details of the mouthparts and oostegites, which are not normally used in the taxonomy of the group, are also included. The character matrix includes 34 terminal taxa and 43 morphological characters (Table 3). Of the latter, 30 are multistate and 13 are binary.

As a result of the parsimony analysis, four fundamental trees were recognized with 175 steps each (CI = 0.61, RI = 0.73). From these a consensus tree was calculated (175 steps) (Fig. 1), which provides the basis for phylogenetic discussion and modification of the classification of the group. The trees were rooted on the outgroup *Gammarus* and *Beaudettia* is also maintained as an outgroup. *Biancolina*, included initially as an outgroup, subsequently emerged as an ingroup during the analysis and is discussed in this position. Aspects of the polarization of the characters are also discussed, based on the consensus tree.

Description and polarization of characters

Body

1 Body surface: (1) lacking cuticular pits; (2) cuticular pits, type a; (3) cuticular pits, type b. Barnard & Karaman (1991), in addition to using the absence of ramus on uropod 3 as a diagnostic character for the Ceinidae, stated that members of this family (Chiltoniinae + other genera) have cuticular

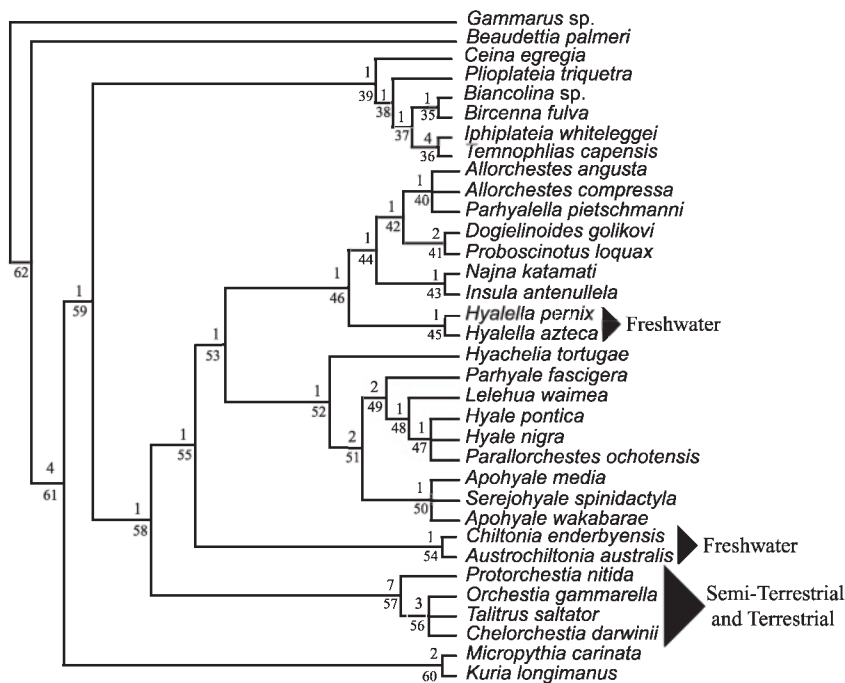


Fig. 1 Strict consensus cladogram (175 steps) calculated from the four fundamental trees. Numbers of nodes are included under each branch, the Bremer support above. Groups who have colonized freshwater and terrestrial habitats are marked.

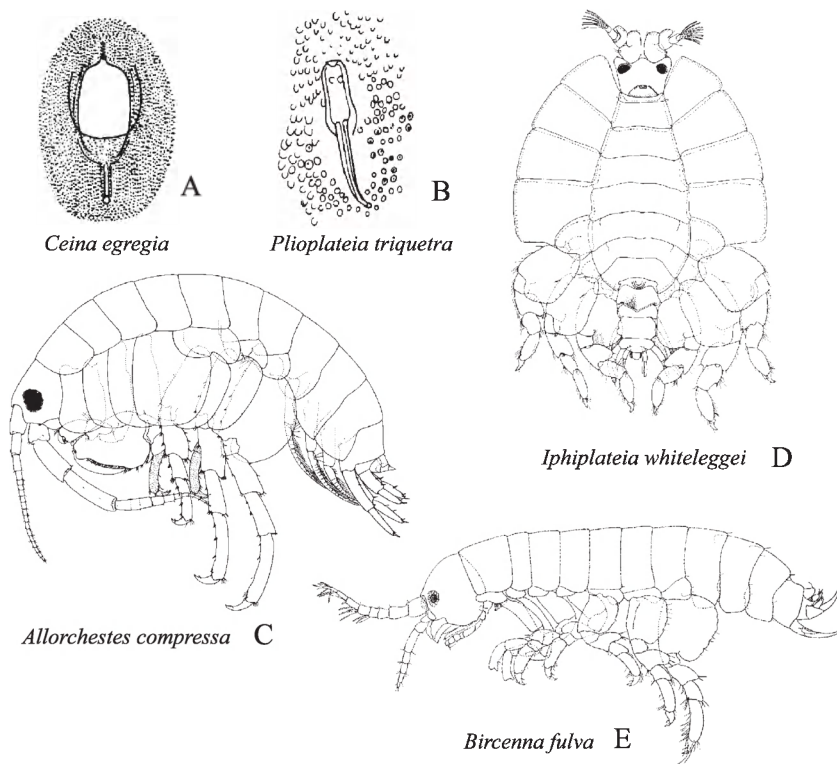


Fig. 2 A–E. —A, B. Cuticular pits, types A and B, respectively. —C–E: variation of body form within Talitrida. —C. Laterally compressed. —D. Dorso-ventrally compressed. —E. Cylindrical. Figures redrawn: A, E from Barnard (1972a), B from Barnard (1978), C from Barnard (1974b), D from Barnard (1981).

pits. Examination of species of *Austrochiltonia*, *Chiltonia* and *Hyachelia* showed that these taxa have a textured body surface, but lack the cuticular pits observed in *Ceina* (Fig. 2A). *Plioplateia* also has concavities (Fig. 2B), but these structures are different

from those of *Ceina* (Barnard 1978). The presence of cuticular pits was not informative in the analysis, but this structure can be better observed with an electronic microscope, and thus treated as an important taxonomic feature.

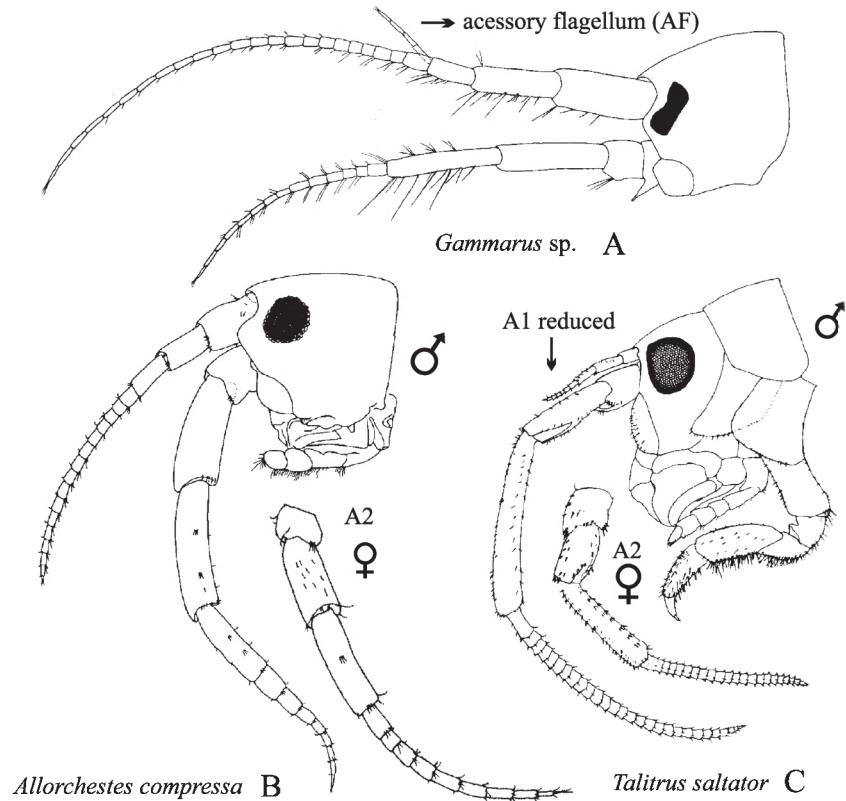


Fig. 3 A–C. Accessory flagellum (AF), length ratio of antennae A1/A2, and sexual dimorphism of A2. —A. AF present, A1 larger than A2, lack of sexual dimorphism. —B & C. AF absent, A1 smaller than A2, with sexual dimorphism. B redrawn from Barnard (1974b), C from Bousfield (1982b).

2 Body shape: (0) laterally compressed; (1) cylindrical; (2) dorso-ventrally compressed. The basic body shape of the gammarids is laterally compressed (Fig. 2C), the state observed in the majority of the groups. However, a variation of this pattern in some families within the Talitrida was observed. The body may be dorso-ventrally compressed (Fig. 2D), similar to the isopod body shape, as seen in Phliantidae, Temnophliantidae and Plioplateidae. In *Bircenna* (Eophliantidae) and *Biancolina* (Biancolinidae) the body is cylindrical (Fig. 2E), possibly as an adaptation to the habit of burrowing into algae.

Head

3 Ratio of length of antenna 1 to antenna 2 (A1/A2): (0) A1 longer than A2; (1) A1 equal in length to A2; (2) A1 shorter than A2, but longer than peduncle of A2; (3) A1 shorter than A2, but shorter than peduncle of A2. State 0 (S0) is the plesiomorphic condition (Fig. 3A), found in the outgroup and among the Talitrida in *Kuria*, *Bircenna*, *Plioplateia*, *Austrochiltonia* and *Chiltonia*. S1 occurred independently in *Iphiplateia* and *Najna*. S2 (Fig. 3B) is the apomorphic condition found in Hyalinae (clade 51), while S3 (Fig. 3C) is the apomorphic condition found in Talitridae (clade 57).

4 Accessory flagellum: (0) present; (1) absent. This may be uni- or multiarticulate and is inserted, when present, on the

end of the peduncle of A1 (Fig. 3A). Its presence/absence was discussed by Barnard (1974a), who considered some families, where it is well developed, closer to the basal plan of the gammarideans.

5 Sexual dimorphism in peduncle of A2: (0) absent; (1) present. In some gammaridean groups the male waits for the female to undergo the nuptial moult before copulation (mate-guarding). These males are known as carriers or attenders. Sexual dimorphism, more common and distinct in these groups, consists of the increased size of the male gnathopod 2, which functions to hold or even defend the partner before copulation. In some groups, A2 also presents modifications, generally increasing in size. The majority of the Talitrida show mate-guarding behaviour, i.e. the male grasps the female's dorsum or lateral plates and holds her until she moults (Conlan 1991). The increased size of gnathopod 2 and A2 in males may reflect an increase of sensory capacity and a more aggressive behaviour. Sexual dimorphism of A2 is apomorphic, occurring in *Allorchestes* (Fig. 3B), *Parhyalella*, and all Talitridae (Fig. 3C).

Mouthparts

Mandible

6 Dentition of left lacinia mobilis: (0) four teeth; (1) five teeth; (2) six teeth; (3) eight teeth; (4) reduced, bifid; (5)

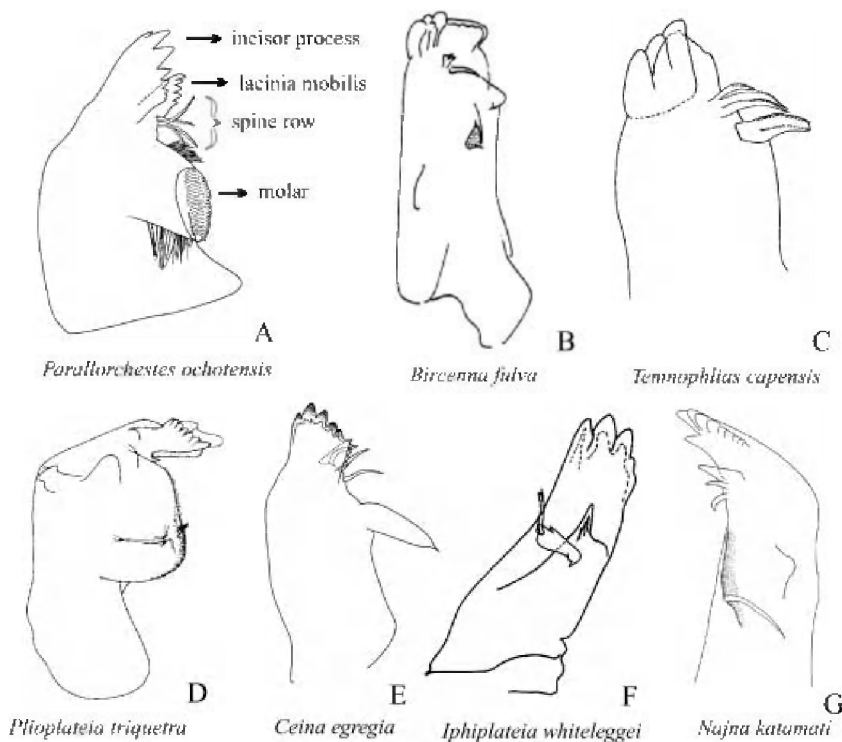


Fig. 4 A–G. Dentition of left lacinia mobilis and variation of mandibular molar. —A. Five teeth, molar triturate. —B. Reduced to 1–2 spines, molar vestigial. —C. Lacinia absent, molar laminar. —D. Seven teeth, molar weakly triturate and very large. —E. Five teeth, molar cone-shaped. —F. Lacinia absent, molar rod-shaped. —G. Molar absent. B, D and F redrawn from Barnard (1972a, 1978, 1981) respectively.

absent. The lacinia mobilis is a movable plate located near the base of the incisor process of the mandible (Fig. 4A). Present in the adult forms of Peracarida, it has been considered one of its synapomorphies. However, Hessler & Watling (1999) questioned the validity of this synapomorphy for Peracarida, as some juvenile decapods seem to present a homologous structure. Normally both mandibles have a lacinia, but as a rule there are differences between the left and the right mandibles, the left one being larger, stronger and generally more dentate in most amphipods (Dahl & Hessler 1982). Bousfield (1982b, 1984) first used the dentition of the left lacinia mobilis as a taxonomic character to separate some groups within the Talitridae. S0 is the plesiomorphic condition, as it is found in both outgroups (*Gammarus* and *Beaudettia*). S1 (Fig. 4A) is a synapomorphy for Talitrida, but changes may occur within the group. In Talitroidea s.s. (clade 58), there are four teeth in *Chelorchestia* and many hyalid species (clades 50 and 47); in clade 40 there are six. S4 (Fig. 4B) occurs in *Bircenna*, S5 (Fig. 4C) in *Iphioplateia* and *Temnophlias* and S3 (Fig. 4D) in *Biancolina* and *Plioplateia*.

7 Mandibular molar: (0) well-developed, triturate; (1) vestigial or lacking; (2) modified as a cone; (3) modified as a rod; (4) laminar; (5) weakly triturate. S0 is plesiomorphic in the outgroup and in most Talitrida (Fig. 4A). Reduction and modification has occurred several times in various genera. In *Bircenna* and *Najna*, the molar is vestigial (Fig. 4B,G), in

Temnophlias laminar (Fig. 4C), in *Plioplateia* large although weakly triturate (Fig. 4D), in *Ceina* modified into a cone (Fig. 4E), and in *Iphioplateia* rod-shaped (Fig. 4F). The different states of the molar, with the exception of S1, were not informative in the analysis as they are autapomorphies of each taxon. However, molar shape remains an important taxonomic character for future cladistic studies.

8 Palp of mandible: (0) present; (1) absent. The presence of a 3-articulate mandibular palp is the plesiomorphic state found in the outgroup *Gammarus*. One of the characters that suggests that *Beaudettia* is the sister-group of Talitrida (others are discussed below) is the loss of the mandibular palp, which has been considered a synapomorphy (Bousfield 1978; Barnard & Karaman 1991). Considering *Beaudettia* as the outgroup, this synapomorphy appears in clade 62 (*Beaudettia* + Talitrida).

Lower lip

9 Inner lobe of lower lip: (0) present; (1) absent. In Gammaridea, the basic plan is the lower lip bearing an outer and an inner lobe. The loss of the latter has been considered a diagnostic character for Talitrida. However, it is also absent in the outgroup *Gammarus* (Fig. 5A), so the loss is plesiomorphic for Talitrida. The other outgroup, *Beaudettia*, has an inner lobe (Fig. 5B). Within Talitrida, an inner lobe occurs only in *Biancolina* and *Plioplateia* (Fig. 5C,D).

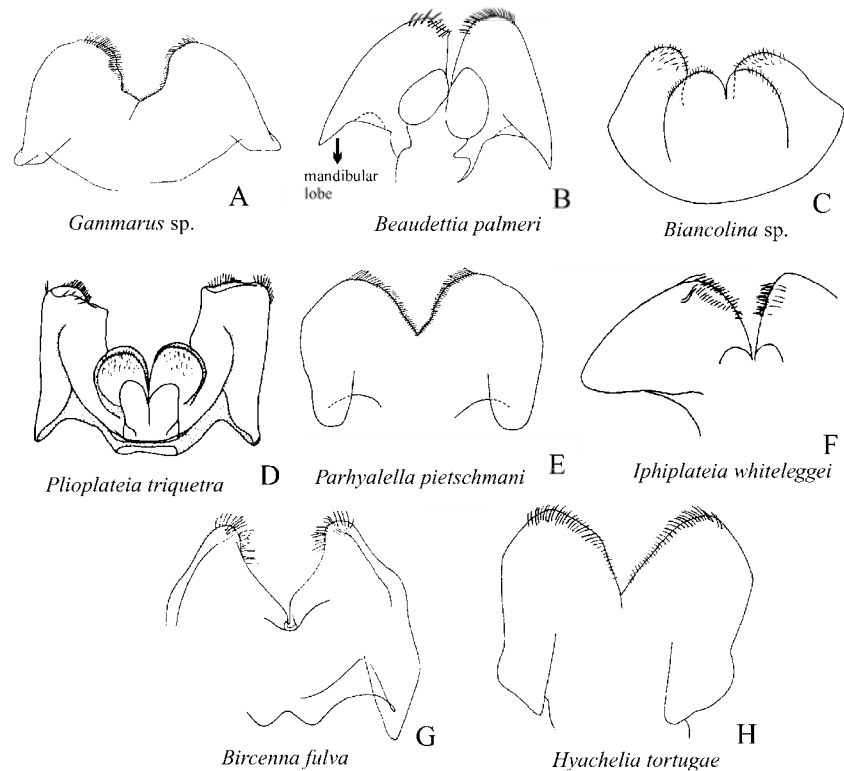


Fig. 5 A–H. Inner lobe of lower lip: absent in A, E–H, present in B–D. Shape of outer lobe. —A. Lateral, apical margin rounded. —B. Pointed, apical margin rounded. —C. Absent (form c). —D. Lateral, apical margin truncated. —E. Both lobes and apical margin rounded. —F. Absent (form d). —G. Lobe and apical margin narrowing distally. —H. Convex laterally, apical margin rounded. B, D, F and G redrawn from Barnard (1965, 1978, 1981, 1972a) respectively.

10 Shape of outer lobe of lower lip: (0) mandibular lobe lateral, form a; (1) apical margin and mandibular lobe rounded, form b; (2) without mandibular lobe, form c; (3) without mandibular lobe, form d; (4) apical margin truncated, form e; (5) mandibular lobes pointed, form f; (6) apical margin and mandibular lobe tapering distally, form g; (7) apical margin rounded and mandibular lobe lobate, form h. The outer lobe of the lower lip assumed different shapes in the taxa, being one of the most variable multistate characters observed. The state in the outgroups varies: S0 in *Gammarus* (Fig. 5A), S5 in *Beaudettia* (Fig. 5B). S1 (Fig. 5E) is a synapomorphy for Talitrida (clade 61). However, some modifications occurred as autapomorphies of some terminal taxa: S2 for *Biancolina* (Fig. 5C), S3 for *Iphiplateia* (Fig. 5F), S6 for *Bircenna* (Fig. 5G) and S7 for *Hyachelia* (Fig. 5H). In *Plioplateia* the distal margin is truncated (Fig. 5D).

Maxilla 1

11 Shape of inner lobe of maxilla 1: (0) large, foliaceous; (1) slender, rod-shaped; (2) linguiform. The plesiomorphic condition, found in *Gammarus*, is S0 (Fig. 6A). S1 is shared between *Beaudettia* (Fig. 6B) and the other Talitrida (clade 62), while S2 appeared independently in *Biancolina* and *Plioplateia* (Fig. 6C).

12 Inner lobe of maxilla 1: (0) present; (1) absent. S0 is the plesiomorphic condition, while S1 is a synapomorphy of *Iphiplateia* and *Temnophlias* (clade 34) (Fig. 6D).

13 Setal formula of the inner lobe of maxilla 1: (0) with row of marginal setae; (1) with two distal setae; (2) with one seta; (3) lacking seta. In addition to its shape, the inner lobe of maxilla 1 varies in the setal formula. S0 is the plesiomorphic condition, found in *Gammarus* (Fig. 6A). S1 is a synapomorphy of clade 62. Maxilla 1 of *Beaudettia* (Fig. 6B), with inner lobe bearing two setae, the pattern also observed in Talitrida, differs from Barnard's illustration (Barnard 1965: 515, fig. 20J), which depicts five setae. The similar structure of the inner lobe in *Beaudettia* and Talitrida strengthens the hypothesis that *Beaudettia* may be a link between Gammaridae and Talitrida, and the possible sister-group of the latter. S2 is a synapomorphy of clade 35 (*Bircenna* + *Biancolina*), while S3 has occurred independently in *Ceina* and *Plioplateia* (Fig. 6C). **14** Distal setal-teeth on the outer lobe of maxilla 1: (0) 8–10; (1) five. S0 is the plesiomorphic condition. Modification of this pattern was observed in clade 35 (*Iphiplateia* + *Temnophlias*), where the number of stout setae was reduced to five setal-teeth (Fig. 6D).

15 Palp of maxilla 1: (0) bi-articulate; (1) uni-articulate; (2) vestigial or absent. S0 is the plesiomorphic condition, present in outgroups *Gammarus* and *Beaudettia* (Fig. 6A,B). S1 is a synapomorphy of Talitrida (Fig. 6C,E,F). Within Talitrida, many taxa have lost the palp independently. In the Phliantoidea (clade 39), this occurred in *Ceina* (Fig. 6G) and on node 37. *Plioplateia* has a uni-articulate palp (Fig. 6C). Within clade

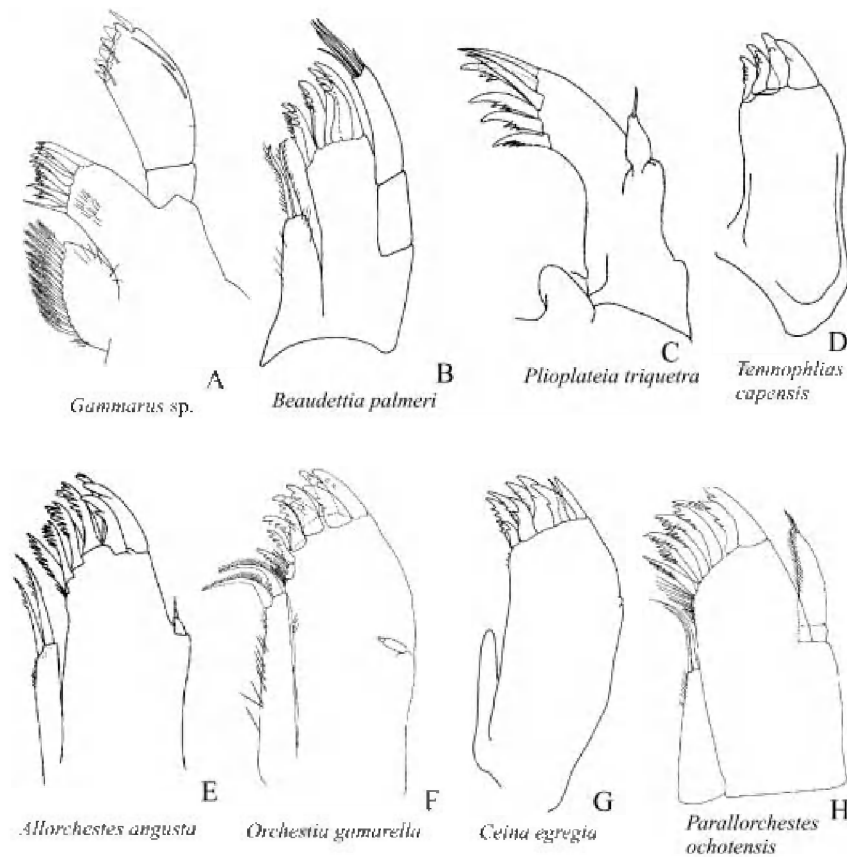


Fig. 6 A–D. Shape of maxilla 1 inner lobe. —A. foliaceous; —B. slender, rod-shaped; —C. linguiform; —D. inner lobe absent. A–C: setae on maxilla 1 inner lobe. —A. with row of setae; —B. with two setae; —C. lacking setae. A–H: distal setal-teeth on maxilla 1 outer lobe. A–C, E–H, with 8–10 setal-teeth, —D. with five setal-teeth. A–H: articulation of maxilla 1 palp. A, B, H, bi-articulate; C, E, F, uni-articulate; D, G, absent. A, B, E, F, H: length of maxilla 1 palp. A, B, reaching half-way or more along the length of the setal-teeth of outer lobe; E, F, reduced, not reaching the base of the setal-teeth of outer lobe; H, reaching the base of setal-teeth of outer lobe. C and E redrawn from Barnard (1978, 1979) respectively.

55, the palp is lost in the Chiltoniinae (clade 54) and in *Parhyalella*, independently. *Parallorchestes* is unique within Talitrida in showing a reversion to S0 (Fig. 6H); however, the articulation is weakly delimited and in some cases doubtful, which can cause confusion in the identification of this genus. Some authors described this palp in Talitridae *s.l.* (Barnard 1969) and *s.s.*, and *Hyaella* (Bousfield 1982b, 1996), as bi-articulate. Comparing its morphology within the Talitrida, it was observed that what had been considered to be a second article is either a distal slender seta, as seen in *Allorchestes* (Fig. 6E), or a robust seta, as commonly found in species of Talitridae *s.s.* (Fig. 6F). Therefore, the palp of maxilla 1 is considered as uni-articulate for those taxa mentioned above.

16 Length of palp of maxilla 1: (0) reaching half or more the length of the setal-teeth of the outer lobe; (1) reaching the base of the setal-teeth of the outer lobe; (2) reduced, not reaching the base of the setal-teeth of the outer lobe. The palp is long in the plesiomorphic form, surpassing the base of the setal-teeth of the outer lobe, a condition found in *Gammarus* and *Beaudettia* (Fig. 6A,B). S1 (Fig. 6H) is a synapomorphy of clade 51. *Micropythia* also has S1, which is homoplastic in the analysis, as this taxon remained outside clade 51. S2 (Fig. 6C,E,F) appears as a synapomorphy on node 59.

Maxilla 2

17 Maxilla 2: ratio of width between inner lobe (IL) and outer lobe (OL): (0) OL and IL similar in width; (1) OL stouter than IL; (2) OL thinner than IL. Maxilla 2 has two lobes that are subequal in width in its plesiomorphic form (Fig. 7A,B). The variation of lobe width occurred independently in *Biancolina* and *Plioplateia*, where OL is stouter than IL (Fig. 7C), and as a synapomorphy of *Iphiplateia* and *Tennophlias* (clade 36), where it is thinner (Fig. 7D,E).

18 Enlarged proximal seta on inner lobe of maxilla 2: (0) absent; (1) present. *Gammarus* does not have an enlarged proximal seta, but rather a row of plumose medial setae, which is the plesiomorphic state (Fig. 7A). S1 is a synapomorphy of clade 62 (*Beaudettia* + Talitrida); the seta may be plumose (Fig. 7B), the most common condition, spiniform, or serrate on both margins (Fig. 7D), or bi- or uni-pectinate (Fig. 7E). However, these states were not included in the analysis, only illustrated. Careful observation of these setae is necessary. Within Talitrida, only *Biancolina* and *Plioplateia* (Fig. 7C) did not have an enlarged seta.

Maxilliped

19 Distal margin of maxilliped inner lobe: (0) with three short triangular stout setae; (1) with 2–3 long setae; (2) with

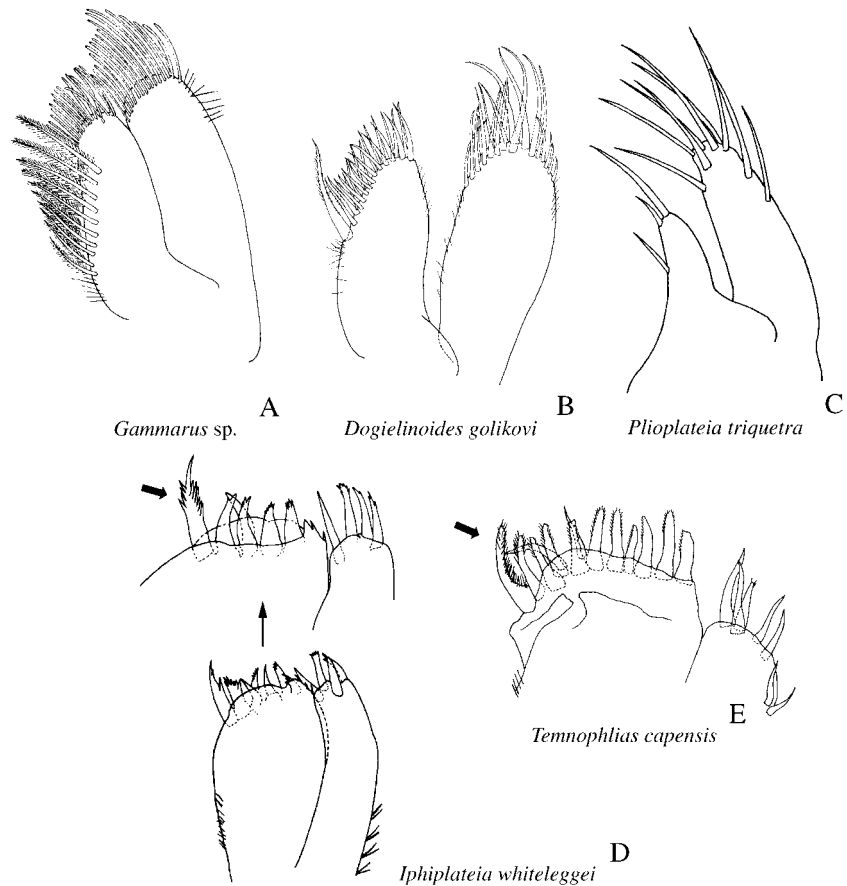


Fig. 7 A–E. Length ratio of outer lobe (OL) and inner lobe (IL) of maxilla 2. —A, B. OL subequal to IL. —C. OL stouter than IL. —D, E. OL thinner than IL. A–D: enlarged proximal seta on inner lobe. A, C, absent. B, D, present. D redrawn from Barnard (1981).

1–2 slender stout setae. The Gammaridea have a pair of maxillipeds fused at the base, each with an outer and an inner lobe. S0 is the plesiomorphic condition, S1 is homoplastic, occurring in *Beaudettia* and *Biancolina*, and S2 is an autapomorphy of *Plioplateia*. This character was not informative in the formation of groups in the analysis.

20 Article 4 of maxilliped palp: (0) well-developed; (1) reduced; (2) absent. The maxilliped palp has four well-developed articles in its plesiomorphic form (Fig. 8A,B). Article 4, also called the dactylus, may be reduced, as observed in *Hyachelia* and on clade 56 (Fig. 8C,D). Within the Talitridae, only the basal taxa retain a well-developed palp, as seen in *Protorchestia* (Fig. 8B). The tendency in the evolution of the dactylus in Talitridae is toward S1 or S2 (Hurley 1968), probably as an adaptation to the change of feeding behaviour in these animals. In *Temnophlias*, articles 3 and 4 are absent (Fig. 8E).

Pereon

Coxal plates

Amphipods have seven pairs of pereopods. Each pereopod has seven articles, the first two from the protopodite and the

remaining five from the endopodite. The first article is called the coxa. Coxal plates, normally called coxae, are outer lateral projections of the coxa directed ventrally, which play an important role in the functional model of the amphipods (Dahl 1977). The coxae were examined as to shape, length, and ratio of length/size.

21 Shape of coxae 1–4: (0) all rectangular; (1) all irregular; (2) coxa 1 subtriangular, coxae 2–4 rectangular; (3) coxae 1–3 pyriform, coxa 4 rectangular; (4) coxae 1–4 rectangular and concave distally. These coxae vary most in shape, and are very important in the taxonomy of the gammarideans. The option to treat all four coxae together as a character was chosen, because a defined pattern between the taxa was noted. In many groups, this change in structure seems to be directly correlated with lifestyle. S0 is the plesiomorphic condition (Fig. 9A,F), found in the outgroups and in the majority of the Talitrida. S1 (Fig. 9B) is an autapomorphy of *Bircenna*, a genus representing the Eophliantidae. Eophliantids are algal burrowers, which seems to be the determinant for variation of shape, reduction of the coxae, and consequently of the ventral channel (Barnard & Karaman 1991). S2 (Fig. 9C) is a synapomorphy of Talitridae (clade 57), S3 (Fig. 9D) an

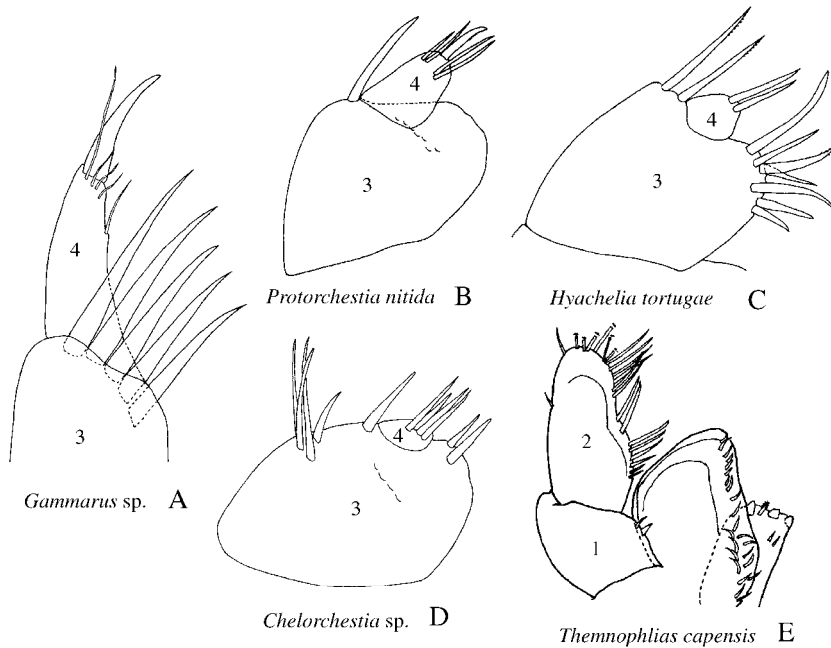


Fig. 8 A–E. Variation in article 4 of palp of maxilliped (setae omitted). —A, B. Well-developed. —C, D. Reduced. —E. Absent.

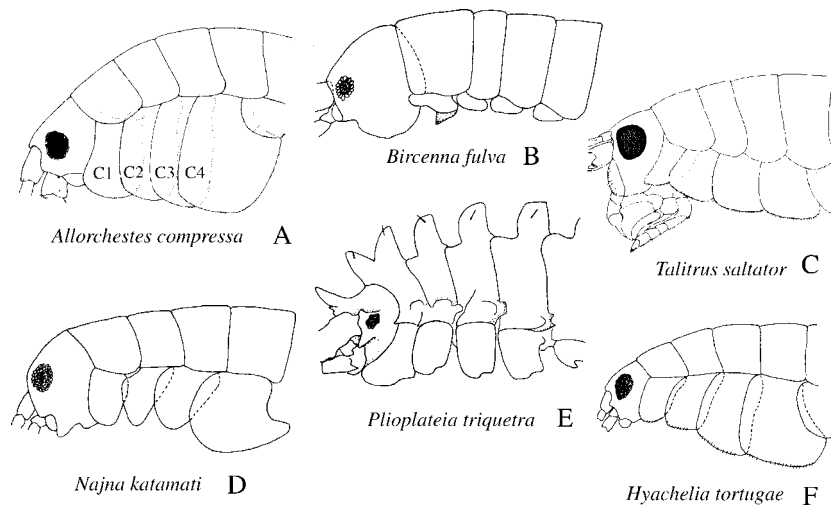


Fig. 9 A–F. Shape of coxae (C) 1–4. —A, F. rectangular; —B. irregular; —C. coxa 1 sub-triangular, coxae 2–4 rectangular; —D. coxae 1–3 pyriform, coxa 4 rectangular; —E. concave distally. A–F: length of coxae 1–4. A, D. sub-equal; B, E. coxa 1 longer than coxae 2–4; C. coxa 1 shorter than coxae 2–4; F. coxae 1–2 shorter than coxae 3–4. A–C: ratio size/length of coxae 2–3. A, 1.5× longer than wide; B, wider than long; C, about as long as wide. A, B, D, E, F redrawn from Barnard (1974b, 1972a, 1962, 1978, 1967) C from Bousfield (1982b), respectively.

autapomorphy of *Najna* and S4 (Fig. 9E) is exclusive to *Plioplateia*.

22 Length of coxae 1–4: (0) subequal in length; (1) coxa 1 smaller than coxae 2–4; (2) coxae 1–2 smaller than coxae 3–4; (3) coxa 1 larger than coxae 2–4. These coxae vary in length, a character which may or may not be associated with shape. S0 (Fig. 9A) is the plesiomorphic state found in the outgroup and in the majority of the Talitrida. Modifications were found in Talitridae (clade 57), where coxa 1 is smaller than the others (Fig. 9C), a character used in Bousfield's (1982b) classification. S2 (Fig. 9F) is an autapomorphy of *Hyachelia*, and S3 (Fig. 9B,E) has occurred independently in *Bircenna* and *Plioplateia*.

23 Size/length ratio of coxae 2–3: (0) 1.5 times longer than wide; (1) about as long as wide; (2) 1.5 times wider than long. S0 is the plesiomorphic condition (Fig. 9A). This character has not yet been used in Talitrida systematics, but has interesting patterns within the Talitroidea (clade 58), where S1 defines Talitridae (clade 57) and clade 51, independently (Fig. 9C). S2 is an autapomorphy of *Bircenna* (Fig. 9B).

24 Postero-lateral processes on coxae 1–3: (0) absent; (1) present on coxae 1–3; (2) absent on coxa 1, present on coxae 2–3. Some groups of Talitrida have coxae 1–3 or 2–3 with acute or rounded posterior processes. Bousfield (1996) used this character to separate Hyaellidae from the Hyalidae. Analysing this character carefully, it was observed that

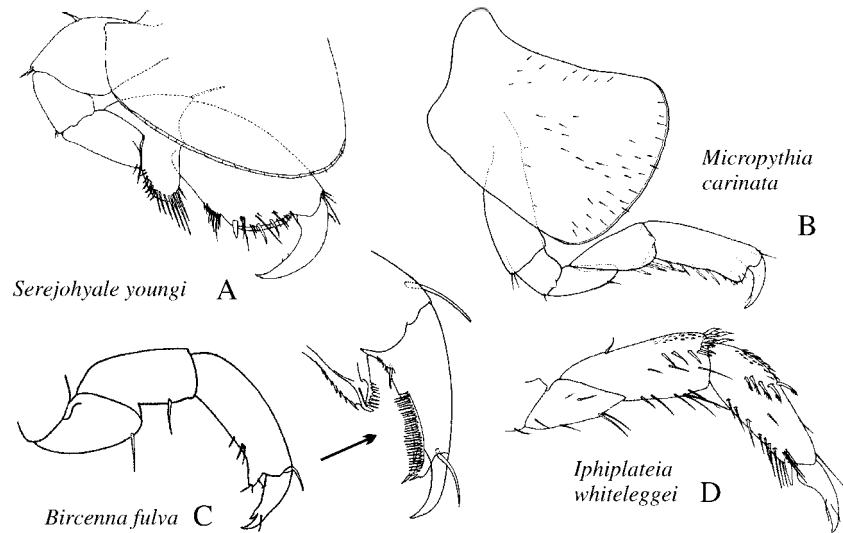


Fig. 10 A–D. Male gnathopod 1. —A. Subchelate. —B. Almost subchelate. —C. Parachelate. —D. Simple. B redrawn from Krapp-Schickel (1972), C and D from Barnard (1972a, 1981) respectively.

Chiltonia, considered to be a hyalellid by Bousfield (1996), presented acute processes on coxae 2–3, and within *Hyale* (Hyalidae), there exist two states (weak and developed). Therefore, it was decided to use only presence or absence of the processes on the coxae. S0 is the plesiomorphic condition (Fig. 9B,D–F); S1 occurred independently in clades 42 (Fig. 9A) and 51 and S2 in *Micropythia*. S2 is a homoplastic character that is also synapomorphic for Talitridae (clade 57) (Fig. 9C) and occurred independently in *Chiltonia*.

Gnathopods 1 and 2

25 Male gnathopod 1: (0) subchelate; (1) almost parachelate; (2) parachelate; (3) simple. S0 is the plesiomorphic condition, as seen in the majority of the Talitrida (Fig. 10A). Modifications were observed in *Micropythia*, where gnathopod 1 is almost parachelate (Fig. 10B), an intermediate condition between subchelate and parachelate. The term ‘parachelate’ was created by Nicholls (1939) to designate the prehensile condition of the gnathopods, where the palm is very reduced, and the dactylus greatly overreaches the palm. S2 (Fig. 10C) is a synapomorphy of clade 35 (*Bircenna* + *Biancolina*), while S3 (Fig. 10D) is a synapomorphy of clade 36 (*Iphiplateia* + *Temnophlias*), a homoplastic character, which also occurs in *Talitrus*.

26 Male gnathopod 2: (0) strongly subchelate, with sexual dimorphism; (1) subchelate, but not modified, similar to the female. The Talitrida belong to the group where the males mate-guard (Conlan 1991). In this group, the male gnathopod 2 is larger and modified in relation to gnathopod 1, assuming differentiated forms that are used to grasp sexually receptive females. S0 is the plesiomorphic condition (Fig. 11A,B). However, within Talitrida, some groups have independently lost this sexual dimorphism, as observed in *Micropythia* (Fig. 11C,D), *Najna*, *Talitrus*, and clade 38. Within Talitridae, the

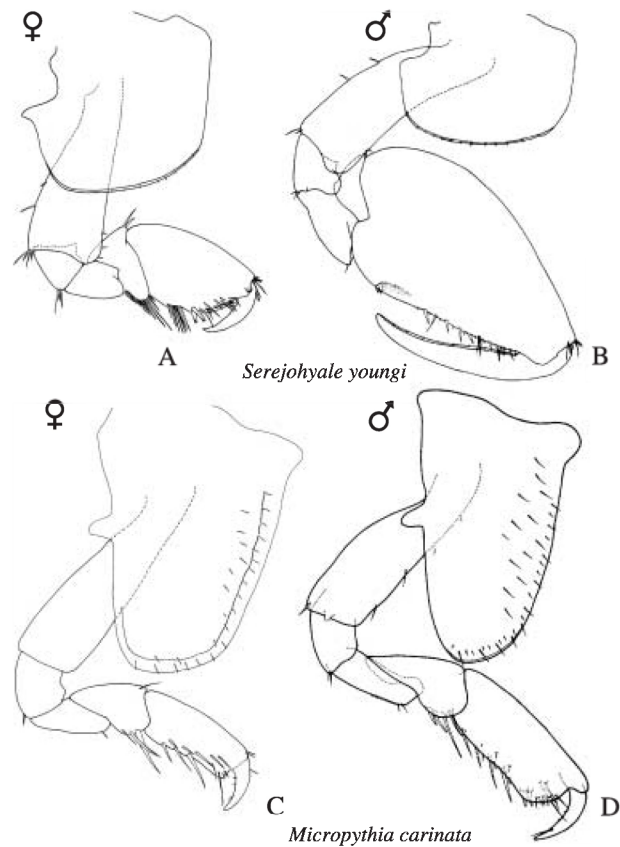


Fig. 11 A–D. Sexual dimorphism on gnathopod 2. —A. Female. —B. Male with sexual dimorphism. —C. Female. —D. Male lacking sexual dimorphism. D redrawn from Krapp-Schickel (1972).

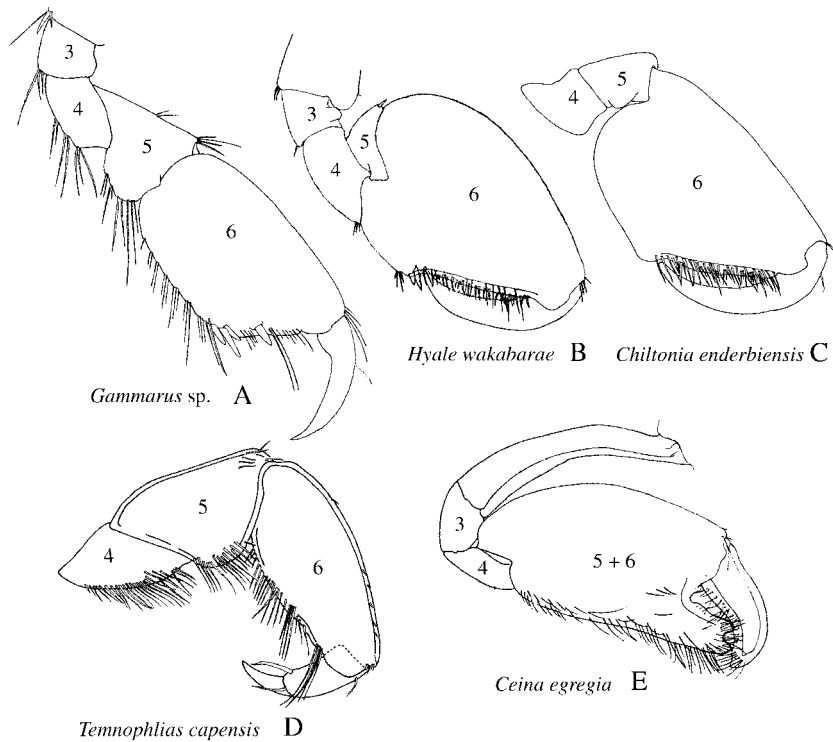


Fig. 12 A–E. Shape variation on carpus (article 5) of gnathopod 2 on adult males. —A. Triangular, well-developed. —B. Triangular, reduced. —C. Rectangular, reduced. —D. Trapezoid. —E. Indistinct (fused to propodus; redrawn from Barnard 1972a).

loss of sexual dimorphism occurs in some groups, and seems to be caused by neoteny (Matsuda 1982; Friend & Richardson 1986). Where there is sexual dimorphism the male gnathopod 2 passes through a mitten-shaped form identical to that found in the female, before reaching the mature adult form (Fig. 13A–D).

27 Shape of carpus of male gnathopod 2: (0) triangular, well-developed; (1) triangular, reduced; (2) rectangular, reduced; (3) trapezoid. The male gnathopod 2 carpus varies in shape and in the presence or absence of a posterior lobe. The plesiomorphic condition in the Talitrida is S0, found in *Gammarus* (Fig. 12A); this appears independently in taxa lacking sexual dimorphism such as *Micropolybia*, *Plioplateia*, *Biancolina*, *Temnophlias*, and *Najna*. S1 (Fig. 12B) is a synapomorphy of the Talitroidea (clade 58). Modifications occur on node 56, which has S2 (Fig. 12C); *Talitrus* and *Temnophlias* (Fig. 12D) have S3. In adult *Chelorchestia* and *Ceina* (Fig. 12E) the carpus is fused to the propodus and was not used in the analysis.

28 Carpus of male gnathopod 2: (0) posterior carpal lobe absent; (1) posterior carpal lobe present. This was discarded by Barnard (1974b: 42) as a generic character within Hyalidae, because he confirmed that variation of this structure occurs during the development of *Hyale* and *Parhyale* species (Shoemaker 1956; Stock 1987). In juvenile males of some *Hyale*, *Parhyale* (Fig. 14E–G) or even in *Ceina egregia* (Ceinidae) (Fig. 14I), the lobe is developed, but as the

animal grows it becomes reduced or may even disappear in just one moult. Therefore, in adult males the carpus assumes a triangular shape, without any trace of a lobe (Fig. 14H) or may simply be fused to the propodus (Fig. 14J) (Shoemaker 1956; Barnard 1974b). Although the ontogenetic processes of the hyalids and ceinids indicate the contrary, the analysis showed that the plesiomorphic form in the evolution of the group is S0 (Fig. 15A). S1 (Fig. 15B) is a synapomorphy which defines clade 46; among the Hyalidae (clade 52), it occurs as a homoplasy in *Parallorchestes*. In most species of *Hyale* and *Parhyale* the lobe is absent, but in *Parhyale plumicornis* (Heller, 1866) it is retained in adults (Krapp-Schickel 1974), assuming a similar form to that seen in *Parallorchestes*.

29 Shape of female gnathopod 2: (0) subchelate; (1) almost parachelate; (2) parachelate; (3) simple; (4) mitten-shaped. In a similar fashion to the male gnathopod 1, the shape of the female gnathopod 2 also varies in the dactylus/propodus articulation. S0 is the plesiomorphic condition (Fig. 15A); modifications include S1 in *Micropolybia* and *Kuria* (Fig. 15B,C), S2 in *Biancolina* and *Bircenna* (Fig. 15D), and S3 in *Iphiplateia* and *Temnophlias*. The gnathopod 2 is similar in shape to gnathopod 1 in most taxa; an exception is found in Talitridae (clade 57), where gnathopod 2 is mitten-shaped, a synapomorphy of the group (Fig. 15E).

30 Carpal lobe on female gnathopod 2: (0) absent; (1) reaching up to $\frac{1}{4}$ of propodus posterior margin; (2) reaching

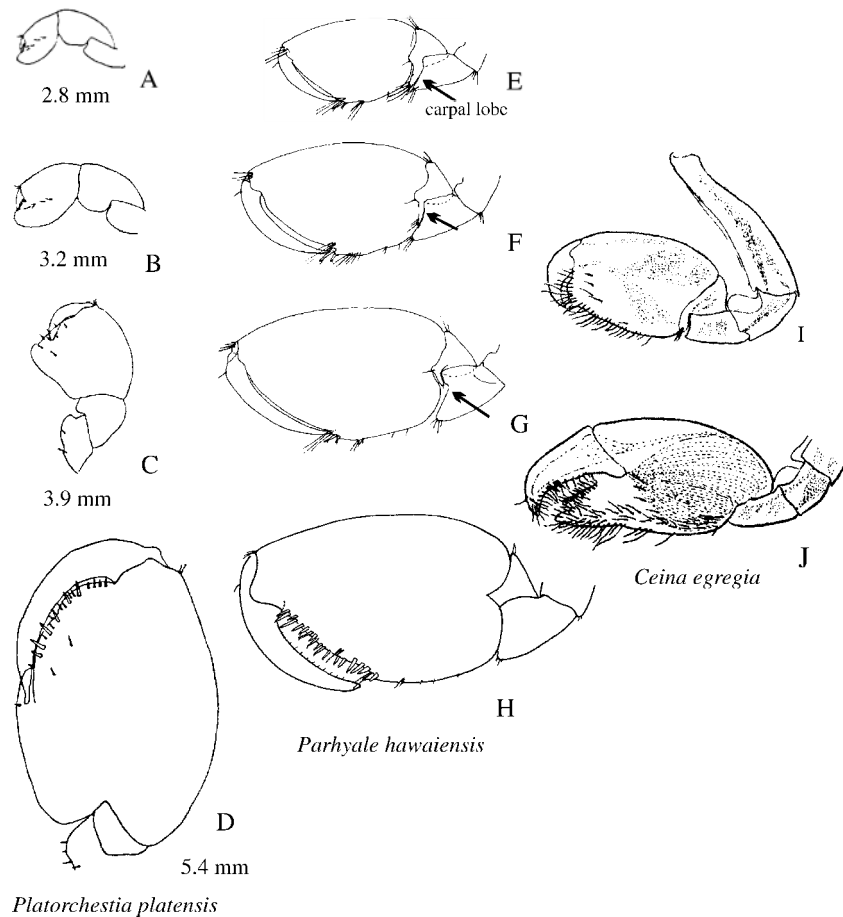


Fig. 13 A–J. Development stages of male gnathopod 2. —A, B. Juvenile mitten-shaped stages of *Platorchestia platensis* (Kroyer). —C. Intermediate form. —D. Adult form, convergent to the pattern seen in *Parhyale hawaiiensis*. E–G: juvenile forms of *P. hawaiiensis* with carpal lobe well-developed. —H. Adult form lacking carpal lobe. —I. Stage of *Ceina egregia* with carpal lobe. —J. Adult form lacking carpal lobe and with carpus indistinct, fused to propodus. A–D redrawn from Morino (1981), E–G from Stock (1987) and I–J from Chilton (1919).

$\frac{1}{2}$ or more of propodus posterior margin. As in males, this lobe is important for understanding the evolution of the Talitrida. S0 is the plesiomorphic condition (Fig. 16A), S1 occurs in clade 53 (Fig. 16B,C) and S2 defines clade 44 (Fig. 16D), occurring as a homoplasy in *Parhyale* (Fig. 16E).

Pereopods

31 Article 4 of pereopods 5–6: (0) not expanded; (1) expanded. S1 occurred independently in *Micropythia*, *Lelebuia* and as a synapomorphy of clade 41 (*Dogielinoides* + *Probosciniotus*).

32 Pereopods 3–7 (0) with few stout setae; (1) with many stout setae. S0 is the plesiomorphic condition. Pereopods with many stout setae, and in some cases also with slender setae, are called fossorial, a typical modification for the burrowing habit (Barnard & Karaman 1991). S1 occurred independently in *Austrochiltonia* and *Talitrus*. The burrowing habit in *Austrochiltonia* has not been reported in the literature. However, *Talitrus* is considered a sandhopper, a talitrid group known to have the capacity of burrowing in sands of the supra-littoral zone of beaches; these sandhoppers were also called substrate-modifiers by MacIntyre (1963). Pereopods

3–7 with many stout and slender setae appeared as a homoplasy on clade 39 (*Dogielinoides* + *Probosciniotus*), a group which belongs to Dogielinotidae. This group is unique in the Talitrida, its members spending their entire lives in soft bottoms, being sand-burrowing in the shallow infra-littoral.

33 Sternal branchiae: (0) absent; (1) present. The sternal branchiae usually occur on the medial or posterior part of the sternum on thorax segments 2–7 (Barnard & Barnard 1983: 47). They appeared independently in several groups of freshwater gammarids and function in the osmotic regulation of these animals. The two *Hyalella* species included in the analysis have sternal branchiae, but within Chiltoniinae only *Chiltonia enderbiensis* has developed this structure.

Oostegites

Found only in females, oostegites are coxal endites fixed on the inner side of coxae 2–5 (or 3–4 in Caprelliidea), that form the brood pouch that encloses the eggs. In young females, the oostegites are single buds. In adult forms, they assume a diverse lamellar shape, and are interlocked by their marginal setae to enclose the pouch. The oostegites have also been considered one of the synapomorphies of the Peracarida.

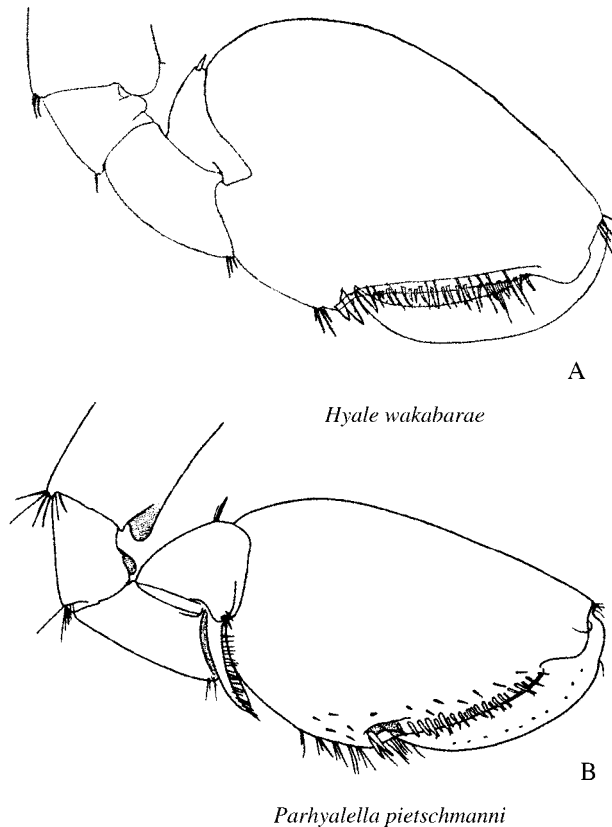


Fig. 14 A, B. Carpal lobe of adult male gnathopod 2. —A. Lacking lobe. —B. With lobe. B redrawn from Barnard (1970b).

Oostegites are practically unused in amphipod taxonomy. Only a few recent papers have described and illustrated these structures. The oostegite shapes of all terminal taxa were observed and included in the analysis, showing that these structures not only have taxonomic importance, but also provide much evolutionary information within the Talitrida.

The evolution of the shape and type of setae on the oostegites seems to be directly related to environmental factors, or even to the reproductive strategy of the animal (Steele 1991). Leite *et al.* (1986) examined the oostegites of several amphipod families, dividing them into two groups based only on the type, size and quantity of setae. More recently, Steele (1991) discussed the relevance of the oostegites as a diagnostic character and classified them in two categories: (1) broad, with relatively short marginal setae, suggested as the basal form, because it is found in other Peracarida and (2) narrow, with long setae, a form which seems to be unique to amphipods. However, these two morphotypes do not always appear to be homogeneous. Both broad and narrow oostegites were observed in the same species, such as in *Gammarus* sp. and *Biancolina* sp. (Figs 17A,E,H,L and 19D,H,M,Q). Setal length also showed wide variability and was not included in the analysis.

Variations in the types of setae and shape of oostegites in Talitrida were analysed, yielding relevant and original results for the evolution of the group.

34 Oostegite setae: (0) non curl-tipped; (1) curl-tipped. S0 is the plesiomorphic condition in the group, found in *Gammarus* and *Beaudettia* (Fig. 17A,D,E,H,L). S1 (Figs 17B,F,I,M, 18A,B,D–F,H–J,M–O,Q and 19A–Q) is the only apomorphy for Talitrida which is not a reduction or missing structure as are the other apomorphies discussed for the group. S1 is a character already known for several Talitrida, although it was never used as a synapomorphy for the group. The reversion to S0 was observed only within clade 56 (Fig. 17C,G,J,N), a derived group of Talitridae (clade 57). *Protorchestia*, a genus considered basal within Talitridae (Bousfield 1982b), maintained the curl-tipped setae.

35 Shape of oostegite 2: (0) half-moon; (1) triangular; (2) oval; (3) concave distally; (4) digitiform; (5) paddle-shaped. The plesiomorphic state, found in *Gammarus* (Fig. 17A), is S0; S2 (Fig. 17C) appeared as an evolutionary novelty on node 61, occurring in *Ceina*, *Pliopluteia*, *Microphythia*, and in Talitridae (clade 57). The transformation to S1 (Figs 17B, 18C,D) is a synapomorphy of clade 55 and also occurs independently in *Tennophlias* (Fig. 19B). S2 occurs in *Microphythia* (Fig. 19C), while S4 is homoplastic, occurring in *Beaudettia* and *Biancolina* independently (Figs 17D, 19D). S5 (Fig. 18A) and S3 (Fig. 18B) are autapomorphies of *Bircenna* and *Iphiplateia*, respectively.

36 Shape of oostegite 3: (0) oval; (1) rectangular; (2) bell-shaped; (3) concave distally; (4) trapezoid; (5) digitiform. The basal state in the evolution of the group is S0, which occurs in *Gammarus* (Fig. 17E) and in several other groups. S1 is a synapomorphy of clade 55 (Figs 17E, 18G). A reversal to S0 is found on node 48 (Fig. 18H). S3 (Fig. 18F), S2 (Fig. 19E), and S4 (Fig. 19F), are autapomorphies of *Iphiplateia*, *Hyachelia* and *Tennophlias*, respectively. S5 is homoplastic, occurring in *Beaudettia* and *Biancolina*.

37 Shape of oostegite 4: (0) digitiform; (1) oval; (2) rectangular; (3) boot-shaped; (4) concave distally; (5) trapezoid. S0 is the plesiomorphic condition (Fig. 17H), S1 a synapomorphy of Talitrida (Fig. 17J). Transformation to S2 occurs on node 55 (Figs 17I, 18L), with a reversal to S1 on node 49 (Fig. 18M). S4 (Fig. 18J), S3 (Fig. 19I) and S5 (Fig. 19J) are autapomorphies of *Iphiplateia*, *Hyachelia* and *Tennophlias*, respectively.

38 Shape of oostegite 5: (0) digitiform; (1) rectangular; (2) oval; (3) foliaceous; (4) boomerang; (5) concave distally; (6) arrow-shaped; (7) triangular. Several states of this character are autapomorphies of some taxa, although some patterns were observed to be important in the formation of certain clades. S0 is the plesiomorphic condition, found in *Gammarus* (Fig. 17L), *Beaudettia* and *Microphythia* (Fig. 19P). On node 59, modification to S2 occurs. S1, S5 and S6 are autapomorphies of *Bircenna*, *Iphiplateia* and *Tennophlias*, respectively, within clade 37 (Figs 18N,O, 19O). S3 (Fig. 17M) appears on node 55 but is modified within this group. In clade 46 the shape is S1

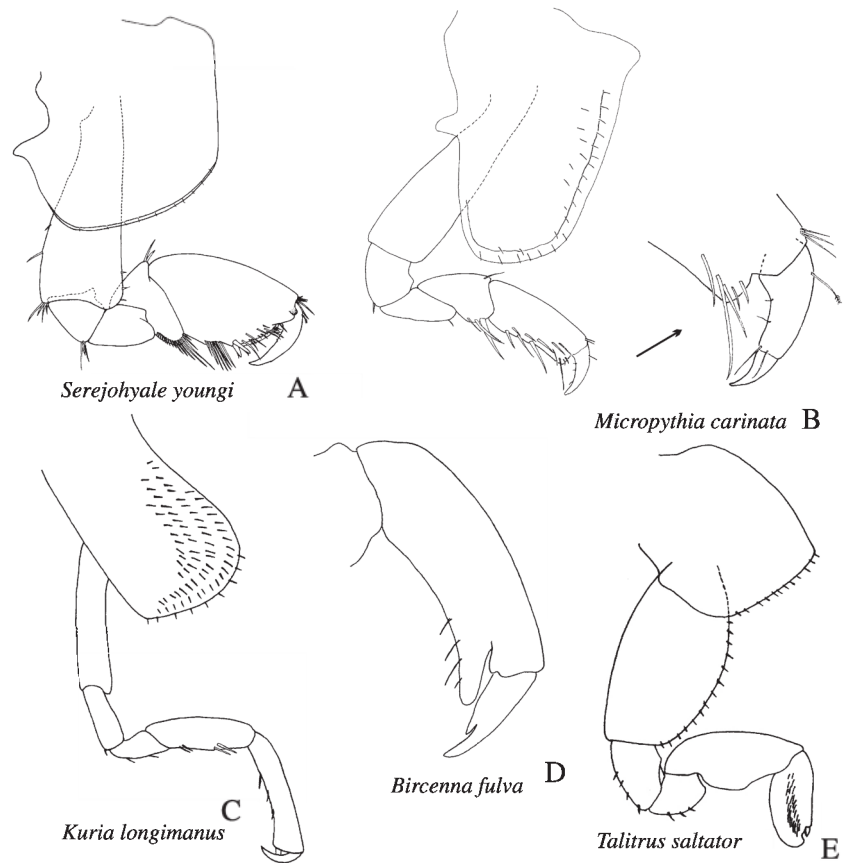


Fig. 15 A–E. Shape of female gnathopod 2. —A. Subchelate. —B, C. Almost parachelate. —D. Parachelate. —E. Mitten-shaped. C redrawn from Walker & Scott (1903), D from Sheard (1936), E from Bousfield (1982b).

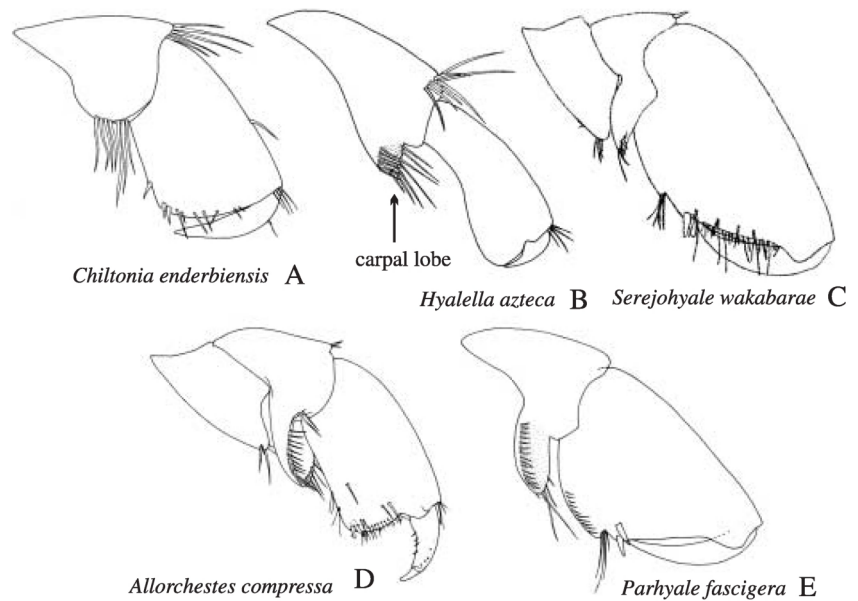


Fig. 16 A–E. Carpal lobe of female gnathopod 2. —A. Absent. —B, C. Present, reaching up to $\frac{1}{4}$ of posterior margin. —D, E. Present, reaching $\frac{1}{2}$ or more of posterior margin. D redrawn from Barnard (1974b).

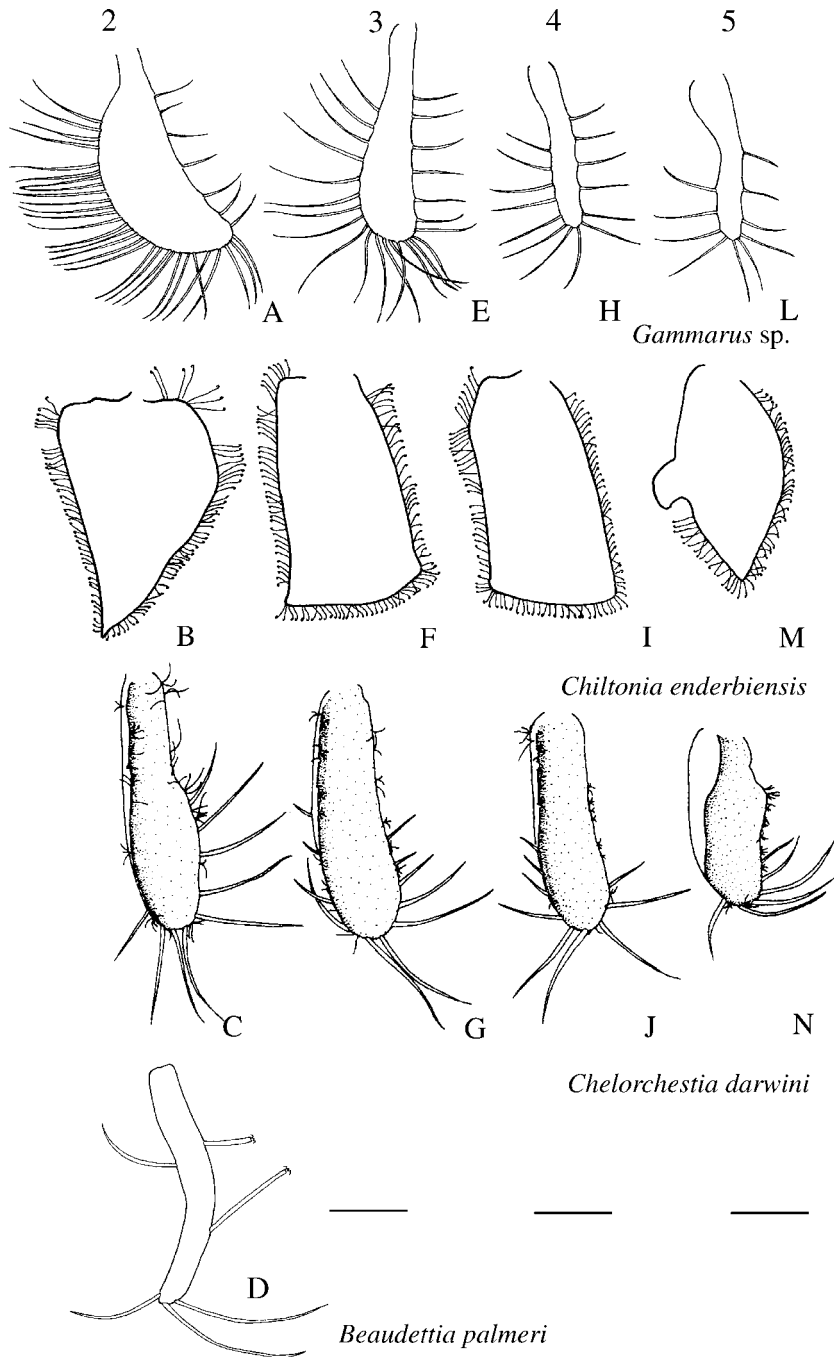


Fig. 17 A–D. Shape of oostegite 2. —A. Half-moon. —B. Triangular. —C. Oval. —D. Digitiform. E–G: shape of oostegite 3. —E. Oval. —F. Rectangular. —G. Oval. H–J: shape of oostegite 4. —H. Digitiform. —I. Rectangular. —J. Oval. L–N: shape of oostegite 5. —L. Digitiform. —M. Foliaceous. —N. Oval.

and in clade 49 it is S4 (Fig. 18Q). S7 is an autapomorphy of *Hyachelia* (Fig. 19N). In *Parallorchestes* the shape reverses to S2.

Pleon

Pleopods 2–3

Morphological variation of the pleopods is not very common within the Gammaridea, and for this reason has been little used in the systematics of the group.

39 Peduncle of pleopod 2: (0) 1.5 times longer than broad; (1) about as long as broad; (2) 1.5 times broader than long. S0 is the plesiomorphic condition (Fig. 20A). The modification for S1 was observed in clade 37 (Fig. 20B). Within clade 37, S2 occurs only in *Bircenna* (Fig. 20C).

40 Peduncle of pleopod 3: (0) without inner lobe; (1) with inner lobe. The presence of lobes on the pleopods was used initially as one of the characters to define Phliantidae

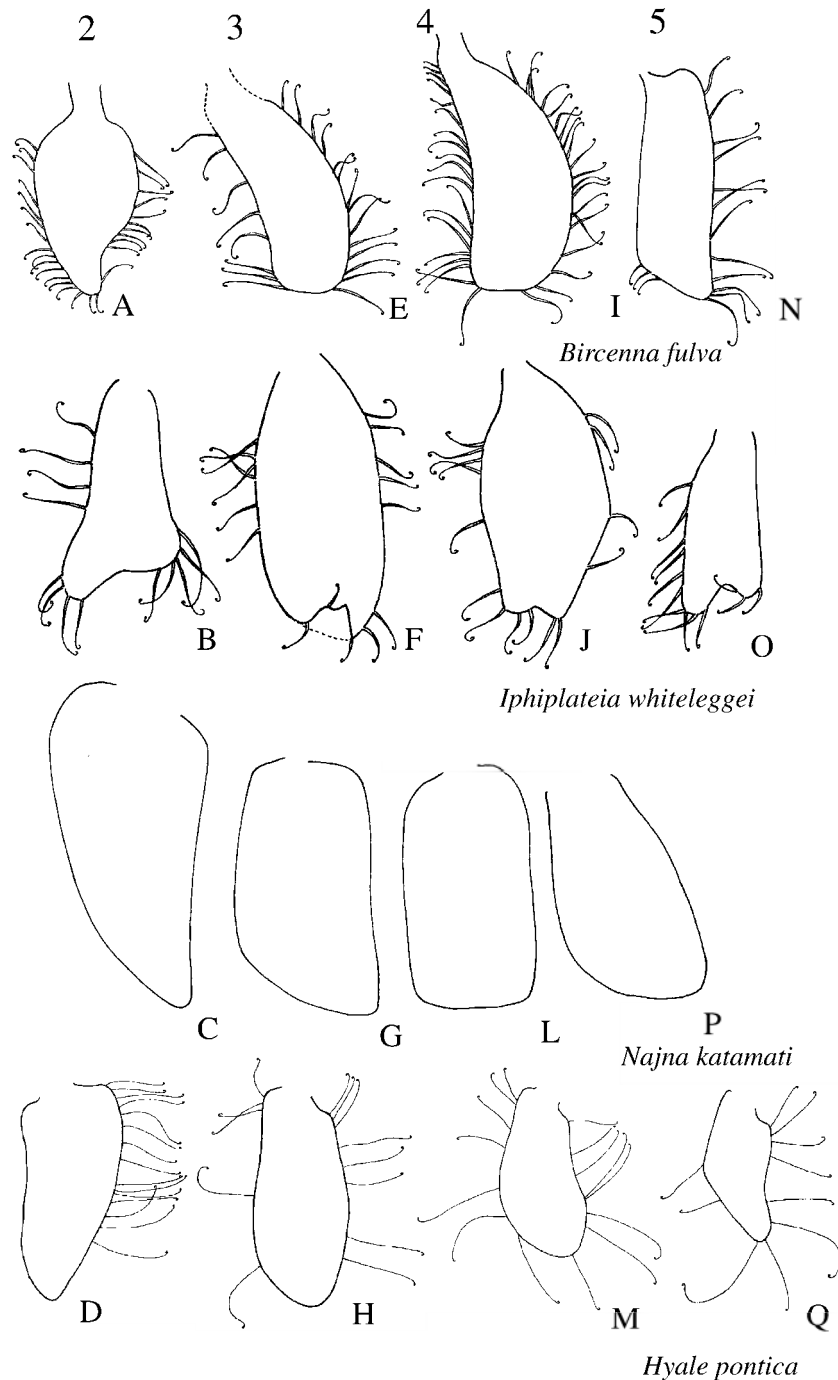


Fig. 18 A–D. Shape of oostegite 2. —A. Paddle. —B. Concave distally. —C, D. Triangular. E–H: shape of oostegite 3. —E, H, Oval. —F. Concave distally. —G. Rectangular. I–M: shape of oostegite 4. —I, M. Oval. —J. Concave distally. —L. Rectangular. N–Q: shape of oostegite 5. —N, P. Rectangular. —O. Concave distally. —Q. Boomerang-shaped.

(Stebbing 1899). S1 (Fig. 20D) is a synapomorphy of clade 36 (*Iphiplateia* + *Temnoplbas*).

Uropod 3

41 Rami of uropod 3: (0) rami well developed; (1) outer ramus developed and inner ramus surpassing half of outer ramus; (2) outer ramus developed and inner ramus not

reaching half of outer ramus; (3) with one ramus; (4) lacking rami. S0 is the plesiomorphic form observed in *Gammarus* (Fig. 21A). S1 is an autapomorphy of *Beaudettia* (Fig. 21B), and appears to be intermediate between the outgroup *Gammarus* and the Talitrida. S3 is a synapomorphy of Talitrida (clade 62) (Fig. 21C). However, modification occurs within the group. Within the Talitroidea (clade 58), S2

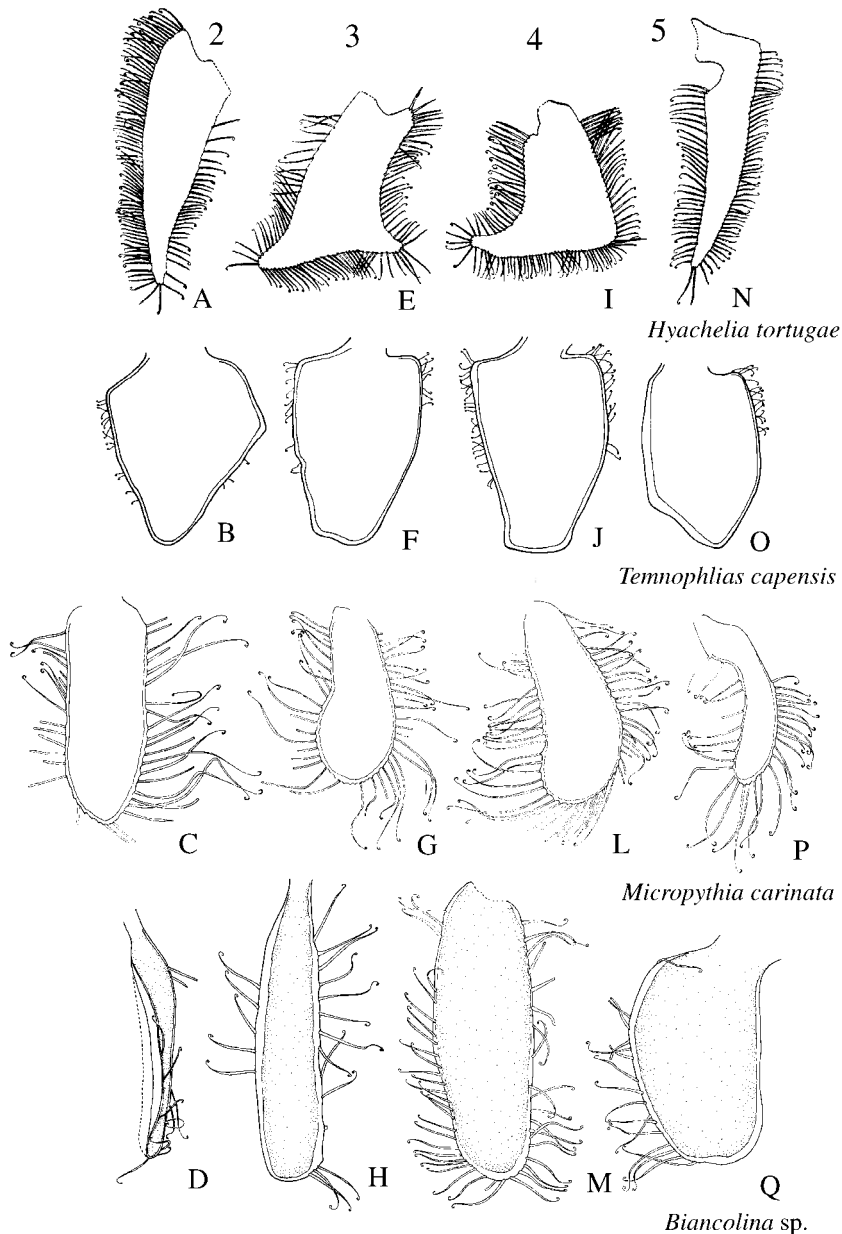


Fig. 19 A–D. Shape of oostegite 2. —A, B. Triangular. —C. Oval. —D. Digitiform. E–H: shape of oostegite 3. —E. Bell-shaped. —F. Trapezoid. —G, H. Oval. I–M: shape of oostegite 4. —I. Boot-shaped. —J. Trapezoid. —L, M. Oval. N–Q: shape of oostegite 5. —N. Triangular. —O. Arrow-shaped. —P. Digitiform. —Q. Oval. A, E, I, N, redrawn from Barnard (1967).

(Fig. 21D) appeared independently in two Hyalidae genera, *Parhyale* and *Parallorchestes*. In *Chiltonia* and *Hyachelia* the rami are absent. Within the Phliantoidea (clade 39) the rami are absent (Fig. 21E), with a reversal to the plesiomorphic biramous state in *Biancolina*.

Telson

42 Telson type: (0) cleft to the base; (1) cleft until half length or less; (2) emarginate; (3) entire. The discussion of the basal form of the telson in Gammaridea is still active, as the basal plan within the group is still uncertain. Following the hypothesis that the Corophiidae is the basal form in

gammaridean evolution, the entire fleshy telson would be the plesiomorphic state (Barnard 1974a; Barnard & Barnard 1983). Considering the Gammaridae as the basal plan, a totally cleft flat telson would be the plesiomorphic pattern (Barnard 1969, 1974a). Bousfield & Shih (1994) supported the hypothesis of an ancestral swimmer for the Amphipoda, and also assumed the cleft telson as basal, suggesting that the entire form is a consequence of the fusion of the two primary lobes of the cleft telson. In the present study, *Gammarus* sp. (Gammaridae) was used to root the tree, S0 being considered plesiomorphic (Fig. 22A). However, the notch in the telson is variable in size, and the states referred to this notch were very

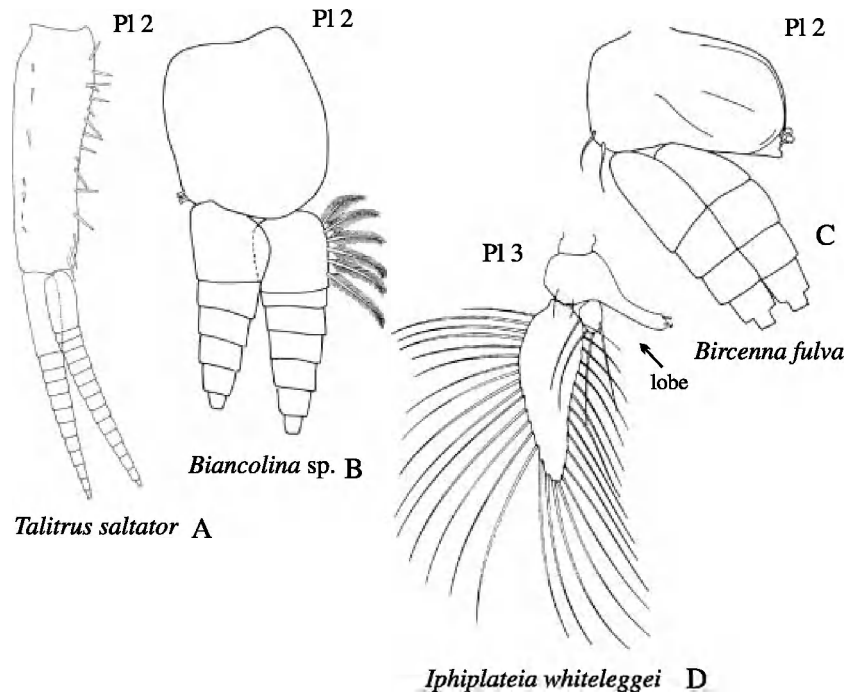


Fig. 20 A–C. Peduncle of pleopod 2 (Pl 2). —A. 1.5× longer than wide. —B. As long as wide. —C. 1.5× as wide as long. —D. Peduncle of pleopod 3 (Pl 3), with inner lobe. Setae of rami omitted in A–C. D redrawn from Barnard (1981).

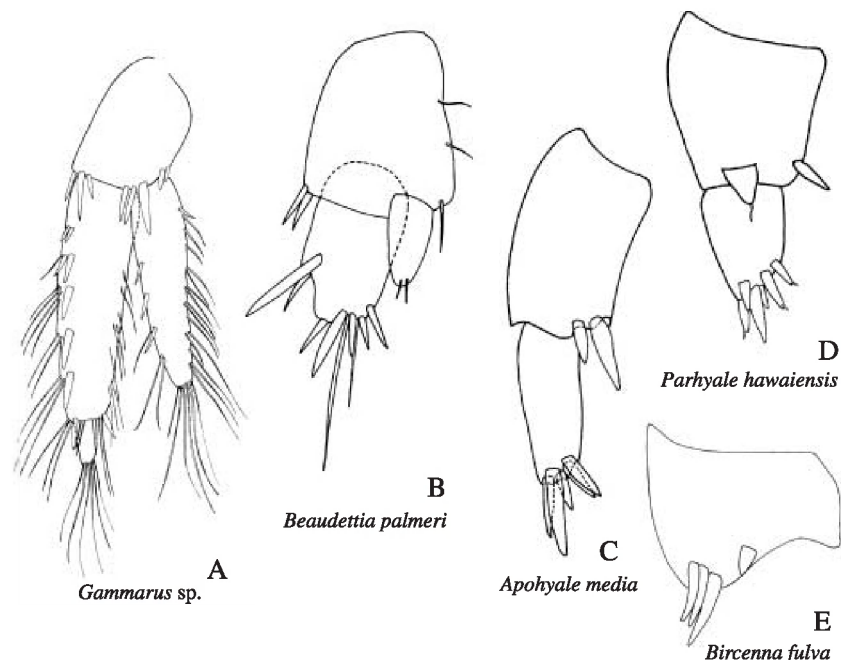


Fig. 21 A–E. Rami of uropod 3. —A. With two well-developed rami. —B. Inner ramus slightly longer than $\frac{1}{2}$ of outer ramus. —C. With one ramus. —D. Inner ramus reduced, not reaching $\frac{1}{2}$ length of outer ramus. —E. Lacking rami. B redrawn from Barnard (1965).

homoplastic within the analysis. In *Beaudettia* and on node 58 (Talitroidea) the telson is entire (Fig. 22B,C). Modifications occur on node 56, where the telson is emarginate (Fig. 22D). On node 52 there is a reversion to S0 (Fig. 22E,F) and on node 42 there is a modification to S1 (Fig. 22G). In *Parhyalella*, the telson reverts to S3. Within the Phliantoidea

(clade 39), the shape of the telson varies widely, being weakly informative for the formation of the groups: in *Ceina*, the telson is S1 (Fig. 22H); it reverts to S0 in *Phlioplateia* (Fig. 22I) and *Bircenna* (Fig. 22J) independently; S3 is a synapomorphy of clade 36, and S2 appears isolated in *Biancolina* (Fig. 22K).

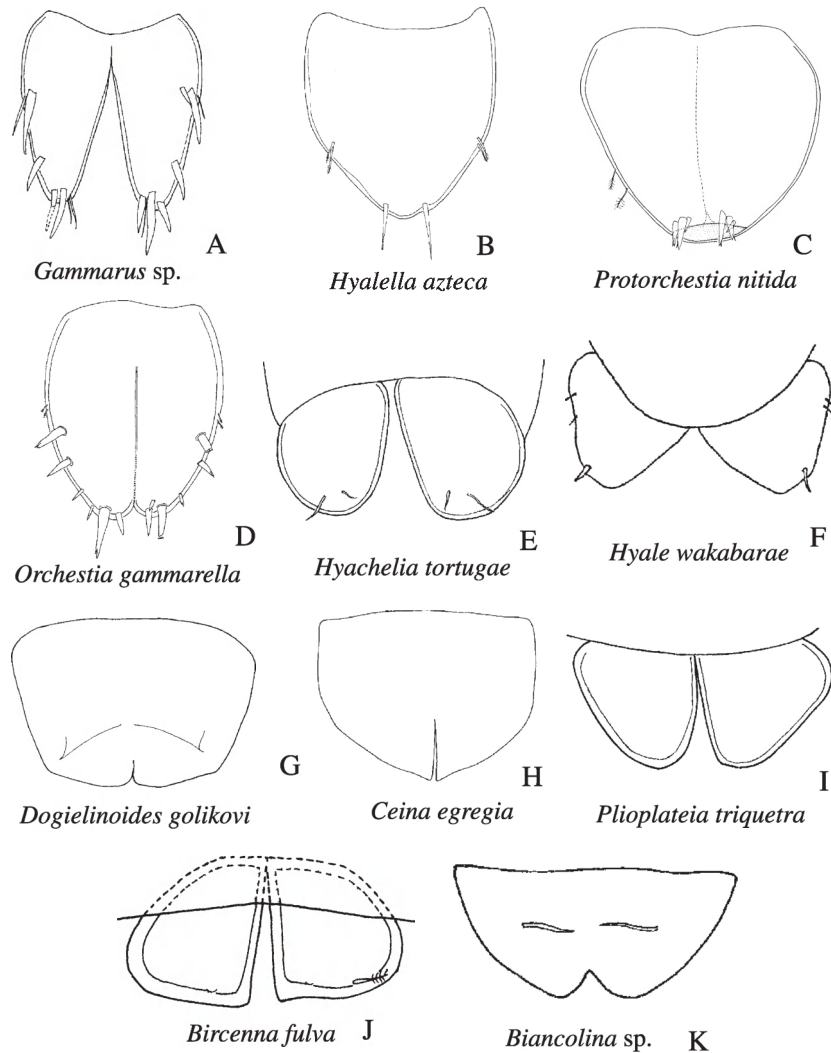


Fig. 22 A–K. Notch variation of telson. —A, E, F, I, J. Cleft to the base. —B, C. Entire. —D, K. Emarginate. —G, H. Cleft until half-way or less. —C, D. Median line on telson present.

43 Median line of telson: (0) absent; (1) present. S1 (Fig. 22C,D) is a synapomorphy of the Talitridae. The median line has not been mentioned in the literature as a diagnostic character for this group. It may represent the suture of a primary cleft telson transformed to an entire state by the fusion of both lobes.

Discussion

The present analysis has provided data to propose a new classification for the Talitroidea *s.l.* Based on the testable cladistic method and following some suggestions of Lowry (in litt.), who is also treating the corophiideans as an infraorder (Myers & Lowry 2003), some modifications to the systematics of the group are proposed (Fig. 23 and Table 4).

The most relevant synapomorphies of each clade are analysed and compared with available data from the literature. The optimization of some characters varies according to

whether the ACCTRAN or DELTRAN method is used (Swofford 1993). These ambiguous characters, with a few exceptions, were not included in the final topology.

Monophyly of the Talitrida

The monophyly of the Talitrida was confirmed based on characters previously mentioned in the literature, as well as additional synapomorphies revealed in the analysis (Fig. 24).

The classical diagnosis of Talitrida (Barnard 1969, 1972a; Barnard & Karaman 1991) is based only on characters related to absences and reductions, i.e.: (1) accessory flagellum absent; (2) mandibular palp absent; (3) inner lobe of lower lip absent, and (4) uropod 3 essentially uniramous. The analysis showed that accessory flagellum absent [4(1)] and uropod 3 uniramous [(41(3))] are synapomorphies of Talitrida. 'Inner lobe of lower lip absent' [9(1)] was optimized as plesiomorphic as this state is found in the outgroup *Gammarus*. Uropod

Table 4 Proposed new classification for the superfamily Talitroidea *s.l.* based on the consensus tree (Fig. 23). Talitroidea is herein erected to infraorder Talitrida, including three superfamilies, 11 families and 96 genera.

Infraorder Talitrida Rafinesque, 1815 **stat. nov.**
 Superfamily Kurioidae Barnard, 1964 **stat. nov.**
 Family Kuriidae Barnard, 1964
Kuria Walker & Scott, 1903
Micropythia Krapp-Schickel, 1972
 Superfamily Phliantoidea Stebbing, 1899
 Family Biancolinidae Barnard, 1972a
Biancolina Della Valle, 1893
 Family Ceinidae Barnard, 1972
Ceina Della Valle, 1893
Taihape Barnard, 1972
Waitomo Barnard, 1972
 Family Eophlinatidae Sheard, 1936
Bircenna Chilton, 1884
Ceinina Stephensen, 1933
Cylindryllioides Nicholls, 1938
Eophliantis Sheard, 1936
Lignophliantis Barnard, 1969
Wandelia Chevreux, 1906
 Family Phliantidae Stebbing, 1899
Gabophilias Barnard, 1972
Iphinosus Stebbing, 1899
Iphiplateia Stebbing, 1899
Pariphinosus Kunkel, 1910
Pereionotus Bate & Westwood, 1863
Phlias Guerin, 1836
Quasimodia Sheard, 1936
 Family Plioplateidae Barnard, 1978
Plioplateia Barnard, 1916
 Family Temnophliantidae Griffiths, 1975
Hystriphlias Barnard & Karaman, 1987
Temnophlias Barnard, 1916
 Superfamily Talitroidea *s.s.*
 Family Chiltoniidae Barnard, 1972a
Afrochiltonia Barnard, 1955
Austrochiltonia Hurley, 1958
Chiltonia Stebbing, 1899
Phreatochiltonia Zeidler, 1991
 Family Dogielinotidae Gurjanova, 1953
 Subfamily Dogielinotinae Gurjanova, 1953
Allorchestes Dana, 1849
Dogielinoides Bousfield, 1982
Dogielinotus Gurjanova, 1953
Eohaustorioides Bousfield & Tzvetkova, 1982
Exhyalella Stebbing, 1917
Haustorioides Oldevig, 1958
Marinohyalella Lazo-Wasem & Gable, 2001
Parhyalella Kunkel, 1910
Probosciniotus Bousfield, 1982
 Subfamily Hyalellinae Bulychева, 1957
Hyalella (*Austrohyalella*) Bousfield, 1996
Hyalella (*Hyalella*) Smith, 1874
Hyalella (*Mesohyalella*) Bousfield, 1996
 Subfamily Najniinae Barnard, 1972
Insula Kunkel, 1910
Najna Derzhavin, 1937
 Family Hyalidae Bulychева, 1957
 Subfamily Hyacheliinae Bousfield & Hendrycks, 2002
Hyachelia Barnard, 1967

Subfamily Hyalinae Bulychева, 1957
Apohyale Bousfield & Hendrycks 2002
Hyale Rathke, 1837
Lelehua Barnard, 1970
Neobule Haswell, 1879
Parallorchestes Shoemaker, 1941
Parhyale Stebbing, 1897
Protohyale (*Boreohyale*) Bousfield & Hendrycks, 2002
Protohyale (*Diplohyale*) Bousfield & Hendrycks, 2002
Protohyale (*Leptohyale*) Bousfield & Hendrycks, 2002
Protohyale (*Protohyale*) Bousfield & Hendrycks, 2002
Ptilohyale Bousfield & Hendrycks, 2002
Ruffohyale Bousfield & Hendrycks, 2002
Serejohyale Bousfield & Hendrycks, 2002
 Family Talitridae Raphinesque, 1815
Agilestia Friend, 1982
Americorchestia Bousfield, 1991
Arcitalitrus Hurley, 1975
Austrotroides Friend, 1982
Bousfieldia Chou & Lee, 1996
Brevitalitrus Bousfield, 1971
Caribitroides (*Caribitroides*) Bousfield, 1984
Caribitroides (*Mexitroides*) Lindeman, 1990
Cariborchestia Smith, 1998
Cerrorchestia Lindeman, 1990
Chelorchestia Bousfield, 1984
Chiltonorchestia Bousfield, 1984
Chroestia Marsden & Fenwick, 1984
Eorchestia Bousfield, 1984
Floresorchestia Bousfield, 1984
Hawaiorchestia Bousfield, 1984
Kanikania Duncan, 1994
Keratroides Hurley, 1975
Macarorchestia Stock, 1989
Makawe Duncan, 1994
Megalorchestia Brandt, 1851
Microrchestia Bousfield, 1984
Mysticotalitrus Hurley, 1975
Neorchestia Friend, 1987
Orchestia Leach, 1814
Orchestiella Friend, 1987
Orchestoidea Nicolet, 1849
Paciforchestia Bousfield, 1982
Palmorchestia Stock & Martin, 1988
Parorchestia Stebbing, 1899
Platorchestia Bousfield, 1982
Protaustrotroides Bousfield, 1984
Protorchestia Bousfield, 1982
Pseudorchestoidea Bousfield, 1982
Puhuruhuru Duncan, 1994
Sinorchestia Miyamoto & Morino, 1999
Spelaeorchestia Bousfield & Howarth, 1976
Talitriator Methuen, 1913
Talitroides Bonnier, 1898
Talitrus Latreille, 1802
Talorchestia Dana, 1852
Tara Duncan, 1994
Tasmanorchestia Friend, 1987
Tethorchestia Bousfield, 1984
Transorchestia Bousfield, 1982
Traskorchestia Bousfield, 1982
Trinorchestia Bousfield, 1982
Ulorchestia Bousfield, 1984
Waematau Duncan, 1994

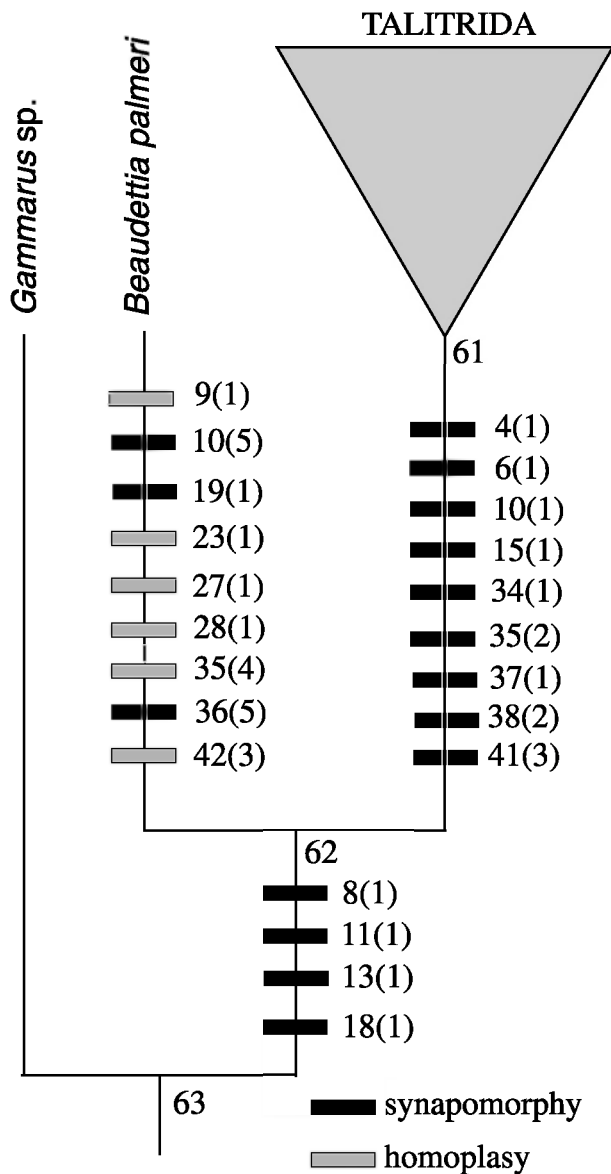


Fig. 24 Relationship between the outgroup *Beaudettia* with Talitrida and the monophyly of Talitrida.

she (Krapp-Schickel 1976) renamed it *Micropythia* because of the homonymy of *Pythia* with a mollusc genus. *Micropythia carinata* was always maintained within Talitroidea s.s. (clade 58), so it is curious that it separated from Talitroidea in the analysis.

Almost all the apomorphies present on nodes 57, 56, 53 and 51 did not occur in *M. carinata*, which has a digitiform [38(0)] and not oval [38(2)] oostegite 5 as on node 57. The adult male gnathopod 2 is not modified, and the carpus is well-developed and triangular [27(0)]. This is different from the state in clade 56, where the carpus is reduced and triangular [27(1)]. Oostegite 2 is oval [35(2)], but in all the taxa of

clade 53 it is triangular [35(1)]. Antenna (A) 1 is equal to or longer than A2 (in clade 53, A1 is shorter than A2, although it is longer than the A2 peduncle).

The results of the present analysis suggest that *M. carinata* does not share a common ancestor with the other hyalid genera. Basically, two characters have been used in the literature to include *M. carinata* within Hyalidae (Barnard & Karaman 1991): the deeply cleft telson [42(0)], which is homoplastic in the evolution of Talitrida, and the palp of maxilla 1, also homoplastic, which reaches the setal-teeth of the outer lobe [(16)1].

Kuria longimanus is unique within Kuriidae and was recorded only once in two females from Abd-el-Kuri Island in the Arabian Sea (Walker & Scott 1903). The type material of this species was not found and is possibly lost. As a result, the data for this taxon were obtained from the literature (Walker & Scott 1903; Barnard & Karaman 1991). Clade 60 is defined by two synapomorphies: female gnathopod 2 almost parachelate [29(1)] (Fig. 15B,C) and article 4 of pereopods 5–6 expanded. The almost parachelate pattern of the gnathopods is similar to the parachelate form found in *Bircenna* (Fig. 15D). The palm is short and transverse with dactylus long, surpassing the palm; there is no process on the palm that suggests a parachelate form.

The structures of the gnathopods and urosome led Stebbing (1906) to include *K. longimanus* in Phliantidae, near *Bircenna*. Chilton (1909) redescribed the telson of *Bircenna* as cleft to the base (similar to that found in *Kuria*), suggesting that the position of *Kuria* is very close to *Bircenna* within the Phliantidae. Sheard (1936) divided the Phliantidae into two subfamilies, maintaining *Kuria*, *Bircenna*, and *Eophliantis* in Eophliantinae, which would later be elevated to family status (Gurjanova 1958). Later, *K. longimanus* was allocated to the Kuriidae (Barnard 1964: 69).

The present analysis showed that *Kuria* is related neither to *Bircenna* nor to the Phliantoidea. However, it is necessary to find more material of *K. longimanus* in order to provide a better redescription of this taxon. Detailed knowledge of its morphological characters would give us a better understanding of its position within the Talitrida.

The Talitroidea s.s. (clade 58)

The Talitroidea s.s. are restricted to clade 58 (Fig. 25). The characters used in the literature to define what was called Talitridae s.l. were as follows: A1 usually shorter than A2; accessory flagellum absent; mandibular palp absent; inner lobe of maxilla slender with two distal plumose setae; inner lobe of maxilla 2 with one differentiated seta; and uropod 3 essentially uniramous (Stebbing 1906; Bulycheva 1957; Barnard 1969). However, all these characters, with the exception of the first, which defines clade 53, appear as synapomorphies at a more basal level of the topology, characterizing clade 62

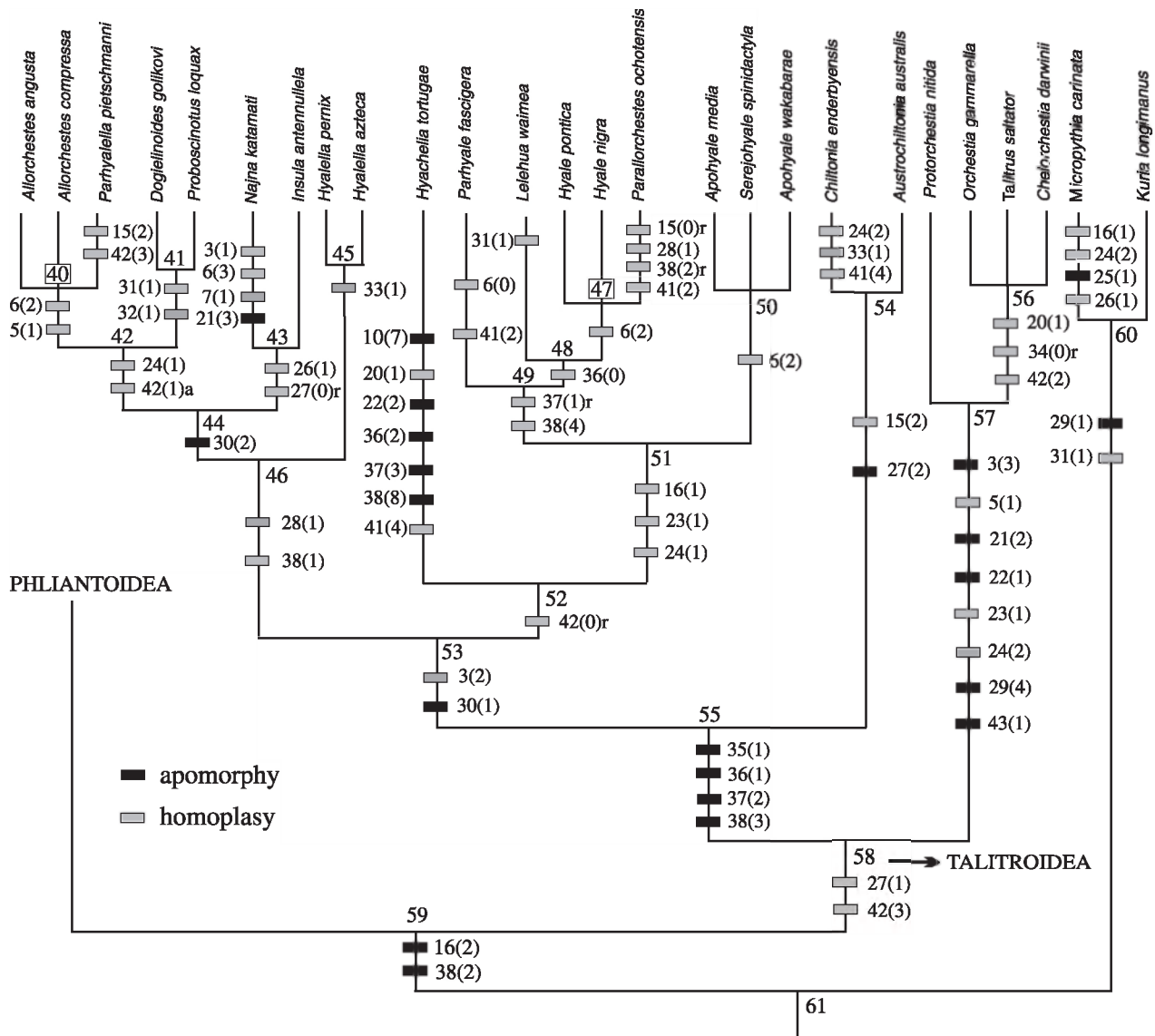


Fig. 25 Detail of the strict consensus cladogram, defining clade 59, the Kurioidae (clade 60), the Talitroidae (clade 58) and subgroups. Abbreviations: a, optimization ACCTRAN; r, reversion.

(*Beaudettia* + Talitridae) or clade 61 (Talitridae). In the analysis, there are two synapomorphies characterizing clade 58: adult male gnathopod 2 with carpus triangular and reduced [27(1)] (Fig. 12B) and telson entire [42(3)]. The first character seems to be directly related to the modification of the gnathopod for carrying and defending the animal's mate (mate-guarding), which results in an increase in propodus size and subsequent reduction of the carpus. With the exception of *Najna* and *Insula*, all the taxa of this clade have the gnathopod 2 increased, with carpus triangular and reduced or rectangular and reduced as in the Chiltoniidae (Fig. 12C). Within the Phliantoidae, the carpus assumes different forms but is never

triangular and reduced, as observed in clade 58. However, *Ceima* has the carpus triangular and reduced in its juvenile form, and fused to the propodus in adults (Fig. 13I,J). The entire telson appears as a synapomorphy of node 58, but there are modifications within the group for the state cleft until half length [42(1)] on node 42, and a reversal on node 52 (Hyalidae) to the state cleft until base [42(0)].

The Talitridae s.s. (clade 57)

The family Talitridae represents the only lineage of amphipods to have invaded the terrestrial habitat. Apparently correlated with this change of environment, a series of structural

modifications appeared, some of them novelties for the group. However, there is a gradient in the invasion of the terrestrial habitat, from the forms called semiterrestrial, that live on the supra-littoral of beaches (beach- and sandhoppers), to the true terrestrial forms (landhoppers), which live in forests (Hurley 1959). According to this gradient, there are two levels of change in the environment, the first related to the exit from water, and the second to the conquest of the terrestrial environment. The event of leaving the aquatic milieu includes all Talitridae, a clade which was defined in the analysis by eight synapomorphies: (1) A1 reduced, and smaller than peduncle of A2 [3(3)]; (2) presence of sexual dimorphism in peduncle of A2 [5(1)]; (3) coxa 1 subtriangular, and coxae 2–4 rectangular [21(1)]; (4) coxa 1 smaller than coxae 2–4 [22(1)]; (5) ratio size/length of coxae 2–3 approximately as long as wide [23(1)]; (6) latero-posterior processes absent on coxa 1 and present on coxae 2–3 [24(2)]; (7) female gnathopod 2 mitten-shaped [29(4)]; and (8) telson with median line [43(1)].

Bulycheva (1957) discussed some morphological aspects of the group related to the colonization of the terrestrial habitat: reduction of the urosome to develop the ability to jump; reduction of A1; and modifications in the pleopods and branchiae. However, a criticism of Bulycheva's classification was the lack of a precise diagnosis of the three families proposed (Hyalidae, Hyalellidae and Talitridae *s.s.*) as stated by Barnard (1969). Bousfield (1982b, 1984), who revised the group with material from the north-eastern Pacific, defined the Talitridae based on synapomorphies 1–4 and 6–7 listed above. The sexual dimorphism of A2 was used as a diagnostic character. However, there is variation within the group. The ratio size/length of coxae 1–4 and the presence of the median line on the telson have not yet been used to define Talitridae. Coxae as long as wide is a homoplastic character [23(1)] (Fig. 9C), occurring also in Hyalidae, but this is very different from the pattern observed in clade 44, where the coxae are much longer than wide [23(0)] (Fig. 9A). The median line of the telson is clear (Fig. 22C,D) and seems to represent the suture of a prior plesiomorphic cleft telson.

The second change within the group is the invasion of land by the Talitridae. Friend & Richardson (1986) described a tendency toward modification of some structures in those talitrids which colonized the forest: reduction of pleopods, increase of the branchial surface, and loss of sexual dimorphism in the male gnathopod 2. This last character was previously observed in *Talitrus saltator* [26(1)], although this species still lives in the supra-littoral zone.

Clade 56 is defined by article 4 of maxilliped reduced [20(1)]; oostegites setae not curl-tipped [34(0)]; and telson emarginate distally [42(2)]. The first was used and discussed by Bousfield (1982b) as a diagnostic character and is a clear tendency in the evolution of the group, probably related to

the change in food habit. The reversion to a no curl-tip state on the oostegites seems to be unique within Talitrida, and there is no apparent explanation for this fact. Only the basal forms of Talitridae maintained the curl-tipped setae, as observed in *Protorchestia* and other palustral species.

Clade 55

Clade 55 unites the Chiltoniidae (*Chiltonia* + *Austrochiltonia*) with clade 53, which is larger, including species of Dogieli-notidae *s.l.* and Hyalidae, including *Hyachelia* (Fig. 25). Clade 55 was characterized by the presence of four apomorphies related to the oostegites: oostegite 2 triangular [35(1)], oostegites 3 and 4 rectangular [36(1), 37(2)], and oostegite 5 foliaceous [38(3)]. Bousfield (1996) previously used the shape of the oostegites as a diagnostic character for Hyalellidae when he said: 'brood plates large, subtriangular, with numerous marginal, short hook-tipped setae'. However, this statement suggests that all oostegites are subtriangular, which is not the case. Separating each oostegite as an independent character, it was observed that the triangular state of oostegite 2 [35(1)] is plesiomorphic to the Hyalellidae. Bousfield (1996) used eight characters to define Hyalellidae. However, most of these included more than one state, which makes it impossible to define the synapomorphies of the group. These characters would be: palp of maxilla 1 minute or absent; coxae 1–3 with weak or lacking posterior processes; carpal lobe of male gnathopod 2 variable or lacking; telson entire or distally cleft. The few characters listed with one state are either plesiomorphic for the group (A1 longer than A2, maxilliped dactylate, oostegites subtriangular) or are exclusive to the freshwater species (presence of sternal branchiae).

The characters used by Bousfield (1996) were included in the present analysis, but coding the states separately results in a different topology. Analysing the position of clade 54 independently, I noted that it appeared early in the evolution of the group, not forming a monophyletic clade with *Hyalella* and other taxa of the family, a distinct sister-group represented by clade 53. Chiltoniidae (clade 54) was defined by the absence of the palp on maxilla 1 [15(2)] and the carpus of male gnathopod 2 rectangular and reduced [27(2)]. The characters A1 longer than A2 and absence of lobes on the carpus of female gnathopod 2 helped decide the final position of this clade.

Differing from the hypotheses of Bulycheva (1957) and Bousfield (1996), Barnard (1972a) included the chiltoniids within the Ceinidae, basing his classification on the loss of rami on uropod 3, a character which appears independently in both groups in the analysis. In Chiltoniidae this occurred only in *Chiltonia* [41(4)]; *Austrochiltonia* maintained the uniramous state characteristic of Talitrida, suggesting that the optimization on node 54 is the uniramous state [41(3)] (the plesiomorphic state for the group), with subsequent loss

in *Chiltonia*. The presence of cuticular pits was another character used by Barnard & Karaman (1991) to unite the chiltoniids with Ceinidae. However, in the first group, the presence of true pits as seen in *Ceina* was not observed. The body surface of *Chiltonia* is textured, but lacks well-defined pits.

Clade 53

Clade 53 has two monophyletic clades: (1) Dogielinotidae *s.l.* (clade 46), including Dogielinotinae, Hyalellinae and Najniinae, and (2) Hyalidae (clade 52), including Hyalinae and Hyacheliinae. The clade is defined by two synapomorphies: A1 shorter than A2, but longer than peduncle [3(2)], and carpal lobe of female gnathopod 2 reduced [30(1)].

The monophyly of Hyalidae was established in the analysis, but with fewer genera than described in the literature, indicating that Hyalidae *sensu* Barnard & Karaman (1991) and *sensu* Bousfield (1996) is polyphyletic (Fig. 25). Barnard & Karaman (1991) included nine genera in Hyalidae — *Allorchestes*, *Hyale*, *Insula*, *Lelehua*, *Micropythia*, *Neobule*, *Parallorchestes*, *Parhyale* and *Parhyalella* — and diagnosed the group with the same characters that were used to define Talitrida (palp of mandible absent, uropod 3 uniramous, and telson variously cleft), which are obviously plesiomorphic for the family. Bousfield (1996) transferred *Allorchestes*, *Insula* and *Parhyalella* from Hyalidae to Hyalellidae. The characterization of Hyalidae was formulated based on comparison to the Hyalellinae diagnosis, being subjective, as the author did not specify the states of some characters. Recently, Bousfield & Hendrycks (2002) revised and defined Hyalidae more closely, including two subfamilies, Hyacheliinae and Kuriinae.

The present topology defines Hyalidae as *Apohyale*, *Hyale*, *Lelehua*, *Parhyale*, *Parallorchestes*, *Hyachelia* and *Serejohyale*, removing *Allorchestes*, *Insula* and *Parhyalella* (which are part of clade 44) as proposed by Bousfield (1996). However, *Micropythia* and *Kuria* are not related to Hyalidae, as already discussed, while *Hyachelia* is part of this clade, which agrees with Bousfield & Hendrycks' (2002) classification. Defining Hyalidae in the analysis, we have the telson cleft to the base [42(0)]. The male gnathopod 2 with carpus triangular and reduced and lacking lobe [27(1)] was used as diagnostic for the Hyalidae by Bousfield & Hendrycks (2002), but appears on node 58, being plesiomorphic at this level of the analysis.

Hyachelia diverged early in the evolution of the group, appearing separately as a sister-group of clade 51. This genus was initially included in Hyalidae (Barnard 1967) and was later transferred to Ceinidae, as it lacks rami on uropod 3 (Barnard & Karaman 1991). The analysis indicated that it shares a common ancestor with Hyalidae, as proposed previously, being distant from *Ceina* (Ceinidae), which belongs to the Phliantoidea. *Hyachelia tortugae* Barnard, 1967, the only species in this genus, has an uncommon habit within the

gammarids, as commensal in the buccal cavity of turtles, specifically found on *Chelonia mydas* (Linnaeus, 1758) in the Galapagos Islands (Barnard 1967). Possibly because of this commensal habit, *H. tortugae* diverged early from the ancestor shared with the other hyalids, showing a series of autapomorphies: article 4 of maxilliped reduced [20(1)]; coxae 1–2 smaller than coxae 3–4 [22(2)]; oostegite 3 bell-shaped [36(2)]; oostegite 4 boot-shaped [37(3)]; oostegite 5 triangular and slender [38 (8)], and loss of rami on uropod 3 [41(4)].

Clade 51 includes the other hyalid genera (*Apohyale*, *Hyale*, *Lelehua*, *Parhyale*, *Parallorchestes* and *Serejohyale*), and is defined by the following synapomorphies: palp of maxilla 1 uniarticulate, reaching the base of setal-teeth of outer lobe [16(1)]; coxae 2–4 about as long as wide [23(1)]; and coxae 1–3 with posterior processes [24(1)]. The types of posterior process on coxae 1–3 were not included in the analysis, because they varied within the genera.

The genus *Neobule* includes three species, all of them found and described only in the past century, with sparse descriptions (Barnard & Karaman 1991). Taking this into account, and considering that this taxon would have many question marks within the character matrix, it was not included in the analysis.

There are two important aspects concerning the hyalids which remain to be discussed. One is the distance between *Parhyale* and *Parallorchestes* in the analysis. *Parallorchestes* was created by Shoemaker (1941) based on the articulation of the maxilla 1 palp, which is biramous, and the presence of a carpal lobe on male gnathopod 2. Barnard (1974a, 1979) disregarded the latter as a generic character, as it is known that this structure varies during the life-cycle of some hyalid species (Fig. 14E–H). Thus, the variation between these genera would be based solely on the articulation of the maxilla 1 palp, which is sometimes difficult to define in *Parallorchestes* and is absent in *Parhyale*. Based on these ideas, Stock (1987) considered the differences between these genera insufficient, suggesting that they are synonyms, an opinion previously defended by Bulycheva (1957).

The present analysis did not corroborate the synonymy of *Parhyale* and *Parallorchestes*. Both have the inner scale-like ramus of uropod 3 [42(2)] (Fig. 22D), a character which would suggest a common ancestry, but is homoplastic in the analysis. The shape of oostegites 3–5 was the determining factor. On node 49, oostegite 4 is oval [37(1)] while oostegite 5 has a boomerang shape [38(4)]. On node 48 occurs a modification to the shape of oostegite 3 [36(0)], which is rectangular in *Parhyale* [36(1)]. Another difference occurs on node 47, where the left lacinia mobilis has six teeth [6(2)], but five in *Parhyale* [6(0)]. In addition to these characters, the oval shape of oostegite 5 [38(2)], the presence of a carpal lobe in adult male gnathopod 2 [28(1)] and bi-articular palp of maxilla 1 [15(0)] suggest that *Parallorchestes* is not a synonym of *Parhyale*.

The second important aspect is the paraphyly of *Hyale*. Five species of the *Hyale* group, which form two distinct subgroups, were included. Clade 50 maintains the plesiomorphic states oostegite 4 rectangular [37(2)] and oostegite 5 foliaceous [38(3)]. In clade 49, containing *H. pontica* and *H. nigra*, oostegite 4 is oval [37(1)] and oostegite 5 has a boomerang shape [38(4)]. Bousfield (1981) phenetically analysed *Parhyale*, *Parallorchestes* and several *Hyale* species, presenting a quite similar result to the present topology. In his phenogram, *Parhyale* and *Parallorchestes* emerged as distinct groups and *Hyale* appeared as polyphyletic. Bousfield & Hendrycks (2002) presented a revision of the hyalid species from the north Pacific region based on phenetic methods, splitting *Hyale* into five separate genera. In the present analysis, the two species designated as *Apohyale* (*A. media* and *A. wakabarae*) emerged as a monophyletic group with *Serejohyale spinidactyla*. *Hyale pontica*, which is the type species of the genus, emerged as the sister taxon of *H. nigra*. However, few species were treated. The *Hyale* complex is quite a large group (about 110 species) that requires more detailed and wide-ranging study in order to make confident conclusions concerning its phylogenetic relationships.

Analysing clade 46, *Allorchestes*, *Hyaella*, *Insula* and *Parhyalella* do not form a monophyletic group as proposed by Bousfield (1996). Bousfield (1996) defined Hyaellinae based on the following characters: A1 usually smaller than A2, antero-ventral margin of female pereon segment 2 with a copulatory notch, and male gnathopod 2 with a distinct carpal lobe. Analysing the distribution of these characters in the cladogram, it was seen that the first [3(2)] is a synapomorphy of clade 53; the notch was not apparent in females of *Allorchestes*, *Parhyalella* and *Hyaella*, so it was not used in this analysis; and the third is really a synapomorphy of clade 46, which includes other taxa besides those mentioned by Bousfield (1996). Another character which defines clade 46 is the rectangular shape of the oostegite [38(1)]. The state 'reduced palp of maxilla 1' present in clade 46 (the palp is absent in *Parhyalella*) and used to define Hyaellidae *sensu* Bousfield (1996), appears at a more basal level of the tree, as a synapomorphy of clade 59, being plesiomorphic for clade 46.

The presence of a well-developed carpal lobe on the female gnathopod 2, reaching half or more of the posterior margin of the propodus [30(2)] (Fig. 17D) defines clade 44. The other taxa of clade 53 (including *Hyaella*) have a short carpal lobe [30(1)], with the exception of *Parhyale*, where it is long. For *Insula*, the female is not known.

Najna and *Insula* form clade 43, which is defined by two synapomorphies: male gnathopod 2 lacking sexual dimorphism [26(1)] and gnathopod 2 carpus triangular and developed [27(0)]. The data for *Insula* were obtained from the literature (Kunkel 1910; Barnard & Karaman 1991), which led to a series of question marks on the character matrix.

Najna has several autapomorphies probably related to the inquilinous habit of algae burrowing: A1 equal in length to A2 [3(1)]; left lacinia mobilis with eight teeth [6(3)]; mandibular molar absent [7(2)]; and coxae 1–3 pyriform, with coxa 4 rectangular [21(3)].

Clade 41 includes the species which are sand-burrowing and have adaptations for colonizing this habitat, i.e. fossorial pereopods and antennae. This clade forms a monophyletic group with *Allorchestes* and *Parhyalella* (clade 42). It is possible that the taxa of clade 42 evolved from a common ancestor with a similar habit to *Allorchestes*, which inhabits the sublittoral and intertidal regions of beaches and tends to have a semifossorial habit (Bousfield 1981). Clade 42 is defined using the following synapomorphies: presence of posterior processes on coxae 1–2 [24(1)] (absent in *Hyaella*) and telson cleft until half or less [42(1)] (Fig. 24G). The cleft telson, however, reverts to the entire state in *Parhyalella* [42(3)]. Barnard & Karaman (1991) and Lazo-Wasem & Gable (2001) employed an ecological approach, leaving *Parhyalella* (a marine genus) and the other two genera recently revalidated and described by the latter authors (*Exhyalella* and *Marinohyalella*) in the marine Hyalidae. In this analysis, *Parhyalella* appears as the sister-group of *Allorchestes* because of two synapomorphies: lacinia mobilis with six teeth [6(2)] and sexual dimorphism of A2, where the males have an enlarged peduncle [5(1)].

It is not rare to see traditional evolutionary studies where apparently more derived groups, with many autapomorphies, are separated into distinct clades, without taking into account the synapomorphies which unite these groups within a larger clade. This could be observed in dogielinotids and najnids, which are groups relatively modified from the basal plan of Hyalidae–Hyaellidae, but which share some synapomorphies with *Allorchestes*, *Parhyalella* and *Hyaella*, and should be maintained together within clade 46.

Superfamily Phliantoidea

The monophyly of the Phliantoidea (clade 39), which included genera of six different families (Ceinidae, Biancolinidae, Eophliantidae, Phliantidae, Plioplateidae and Temnophliantidae), was clear (Fig. 26). Specimens of only one genus for each family were included in the analysis, the initial aim of which was to test the monophyly of Talitrida. For this reason, no formal alteration on the classification of this group is proposed; more taxa need to be included in future studies. Despite the lack of phylogenetic studies on this group, some authors have discussed the evolutionary aspects of these families (Barnard 1964, 1972a,b, 1978), which are compared below with the results of this analysis.

Following the pattern of Talitrida, a tendency toward reduction in or loss of appendages was observed. Two characters defined clade 39. The first is the absence of setae on the inner

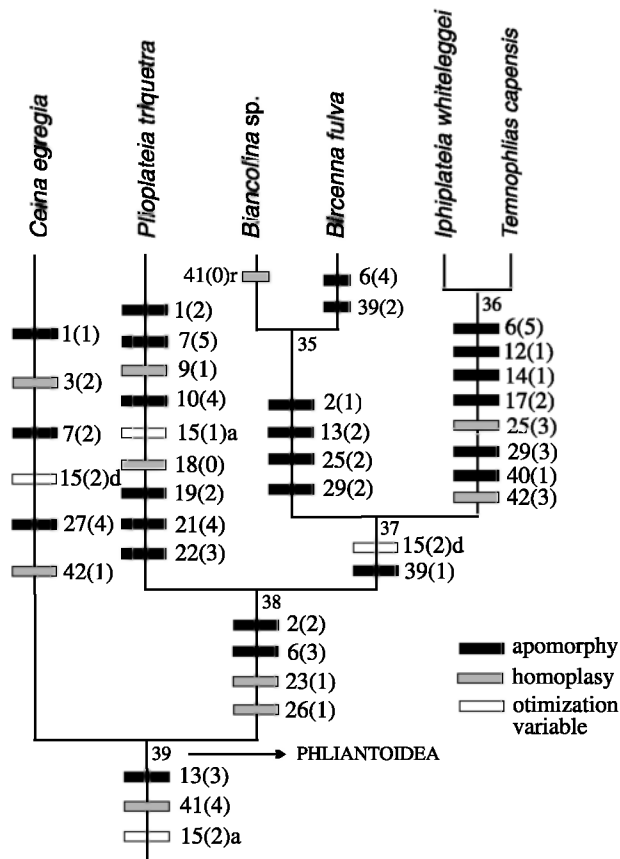


Fig. 26 Detail of the strict consensus cladogram, defining the monophyly of the Phliantoidea and subgroups. Abbreviations: a, optimization ACCTRAN; d, DELTRAN; r, reversion.

lobe of maxilla 1 [13(3)], maintained in *Ceina* and *Plioplateia* (Fig. 7C,G). Transformation occurs in clade 35 to the state with one seta [13(2)], and is not informative for clade 36, where the inner lobe is absent. It is interesting to note that none of these taxa have the state with two setae (Fig. 7B,E,F,H), characteristic of the other Talitrida groups. The second synapomorphy is the absence of rami on uropod 3 [41(4)]. There is a reversion in *Biancolina*, where uropod 3 has two well-developed rami. Using the optimization ACCTRAN (Swofford 1993), the absence of a maxilla 1 palp [15(2)] also could be used as an apomorphy of the group, with later reversion in *Plioplateia* to an uniarticulate state. However, as the basal state is uniarticulate (synapomorphy for node 61), I prefer the DELTRAN optimization, where the uniarticulate state is maintained on node 39, with loss of the palp occurring independently in *Ceina* and clade 37.

Barnard (1972b) suggested an evolutionary line from Hyalidae, to an intermediate form represented by the Ceinidae, culminating in the Phliantidae. The analysis indicates that *Ceina* is the sister-group of clade 38 (Phliantidae + Temnophliantidae + Eophliantidae + Biancolinidae), indicating a

proximity of Ceinidae not only to Phliantidae, but also to the other families of clade 38. On node 38, the dorso-ventral body shape appears [2(2)]. Still defining clade 38, gnathopod 2 is not modified, lacking sexual dimorphism [26(1)] and the coxae are as long as wide [23(1)]. Only in clade 37 is there a modification of pleopod 2, in that the peduncle is expanded, being as long as it is wide [39(1)] (Fig. 21B). *Bircenna* showed the maximum state of expansion of the pleopod peduncle, being wider than long [39(2)] (Fig. 21C).

Structural modifications of the pleopods are not common in gammaridean evolution, which led Stebbing (1899) to unite *Bircenna* with other Phliantidae based on pleopod modification. However, there are two types of modification that may occur together or not. The first is a widened peduncle, that assumes a more or less square shape. The second occurs only in clade 36 (*Iphiplateia* + *Temnophlias*), where the peduncle, as well as being expanded, has a well-developed latero-medial lobe [40(1)] (Fig. 21D), which appears on one or all of the pleopods. There is usually a gradient, with size of the lobe increasing from pleopod 1 to pleopod 3. *Plioplateia*, which was formerly considered as a phliantid, has the pleopod peduncles not expanded or lobate. This character, together with several other autapomorphies of this group (Fig. 26), suggests that Plioplateidae diverged early from a common sister taxon of clade 37.

In clade 36, *Temnophlias* appears as the sister-group of *Iphiplateia*, sharing several synapomorphies: left lacinia mobilis absent [6(5)]; inner lobe of maxilla 1 absent [12(1)]; outer lobe of maxilla 1 with five weakly dentate setal-teeth [14(1)]; outer lobe of maxilla 2 thinner than inner lobe [17(2)]; peduncle of pleopod 3 with inner lobe [40(1)]; and telson entire [43(3)]. The inclusion of *Temnophlias* in Phliantidae was suggested previously in the literature (K. H. Barnard 1916, J. L. Barnard 1964, 1969; Sheard 1936). However, autapomorphies of the group such as presence of pleurae on the pereon, palp of maxilliped bi-articulate, and uropod 1 uniramous, led Griffiths (1975) to separate this genus into a separate family, the Temnophliantidae.

The sister-group of clade 36 is clade 35, represented by *Biancolina* (Biancolinidae) + *Bircenna* (Eophliantidae). Clade 35 is sustained by the cylindrical shape of the body [2(1)] (Fig. 3E) and parachelate male gnathopod 1 [25(2)] (Fig. 11C) and female gnathopod 2 [29(2)] (Fig. 16D).

In contrast, Barnard (1972a, Barnard & Karaman 1991) supported the idea that *Biancolina* evolved independently from the Eophliantidae or even from the Talitrida. The main argument for this decision was the presence of a well-developed biramous uropod 3 in *Biancolina*.

Aspects of the talitrid invasion of land and freshwater habitats

The analysis indicates that the terrestrial talitrids originated from a marine ancestor, possibly one that lived in the

intertidal zone (Fig. 1). It is reasonable to postulate that the colonization of the supra-littoral by the intertidal species occurred repeatedly, as the migration across the tide line is directly related to the tidal cycle. Similarly, the invasion of the terrestrial habitat may have been accomplished by supra-littoral forms (beach and sand-hoppers) (Matsuda 1982). In tropical zones, it is common to have forests going down to the sea level, facilitating colonization of the forest by supra-littoral species. Hurley (1968) defended the hypothesis that the terrestrial talitrids evolved directly from the supra-littoral species, colonizing the forest litter from the supra-littoral, without a passage through fresh water. Duncan (1985) defended the hypothesis of a terrestrial colonization from proto-supra-littoral species, which inhabit salt-marsh environments and would be better preadapted to the hypohaline habitat of the forests.

Bulycheva (1957) suggested that the basal forms of the group are the marine hyalids. From these the terrestrial talitrids and then the freshwater species would have evolved (chiltoniids and *Hyaletta*). The invasion of freshwater would thus be secondary, from a terrestrial form, but unique within the group. Bousfield (1964, 1982a) suggested that the chiltoniids share a common ancestor with *Hyaletta*, with only one invasion of the freshwater habitat within the Talitrida. On the other hand, Barnard (1972a) held that two freshwater invasions occurred independently, as he considered the chiltoniids to be part of the marine Ceinidae.

The results of the present analysis indicate two freshwater invasions by a marine ancestor. The first was by the Chiltoniidae, which inhabits rivers and lakes of Australia, New Zealand and Africa, and appears as a sister-group of clade 53, being independent from the Ceinidae. The second would be by *Hyaletta*, a genus endemic to the Americas which shares a common ancestor with *Dogielinoides*, *Probosciniotus*, *Allorchestes*, *Parhyalella*, *Insula* and *Najna* (clade 46), but not with the Chiltoniidae.

Proposed new classification

Based on the strict consensus tree, a new classification of the Talitroidea *s.l.* is proposed, which is now erected as an infraorder, including three superfamilies, 11 families and 96 genera (Fig. 23 and Table 4). Minor modifications are proposed to clade 39 (Phliantoidea), as few genera from these families were included in the analysis.

For a better understanding of the groups a short diagnosis of each family and subfamily is given, based on the synapomorphies found in the analysis as well as other relevant characters for the groups.

Infraorder Talitrida Rafinesque, 1815

Diagnosis. Body shape variable, being laterally compressed, dorso-ventrally depressed or cylindrical. Mandible lacking

palp, molar triturative (most groups), modified or absent. Lower lip usually lacking inner lobe. Maxilla 1: inner lobe rod-shaped (most groups) or linguiform, usually with two distal plumose setae; palp uni-articulate or absent (bi-articulate only in *Parallorchestes*). Maxilla 2 usually with a differentiated setae on inner lobe. Oostegites 2–5 with curl-tipped setae. Uropod 3 uniramous or lacking rami (with small scale-like inner ramus in *Parhyale* and *Parallorchestes* and biramous in Biancoliniidae). Telson deeply or partially cleft, emarginate or entire.

Superfamily composition. Kuriioidea Barnard, 1964 stat. nov.; Phliantoidea Stebbing, 1899 and Talitroidea Rafinesque, 1815.

Superfamily Kuriioidea Barnard, 1964, stat. nov.

Family. Kuriidae Barnard, 1964.

Diagnosis. Body laterally compressed. Antenna (A) 1 equal or longer than A2. Gnathopods 1 and 2 almost parachelate. Male gnathopod 2 without sexual dimorphism. Coxa 1 lacking postero-lateral process; coxae 2–3 with postero-lateral process (in *Microphythia*). Pereopods 5–6 with article 4 expanded. Oostegites 2–4 oval and oostegite 5 digitiform (in *Microphythia*). Urosomites 1–3 all coalesced (in *Kuria*). Uropod 3 uniramous. Telson cleft until base.

Type genus. *Kuria* Walker & Scott, 1903.

Remarks. *Kuria* is a monotypic genus (*K. longimanus*) described only from female specimens, which makes this group difficult to define. The description is based only on the original (Walker & Scott 1903); no more material of this species has ever been found.

Habitat. Marine, shallow water.

Superfamily Phliantoidea Stebbing, 1899

Family Biancoliniidae Barnard, 1972a.

Diagnosis. Body cylindrical, coxae medium to large. Mandible lacking molar, left lacinia mobilis with eight teeth. Lower lip, with inner lobe; outer lobe without mandibular lobes. Maxilla 1, inner lobe linguiform, with one distal seta; outer lobe with nine simple setal-teeth; palp absent. Maxilla 2, outer lobe wider than inner, which lacks modified seta. Distal margin of maxilliped inner plate with 2–3 long setae, no short triangular stout setae. Gnathopods 1–2 parachelate, lacking sexual dimorphism. Peduncle of pleopods expanded, as wide as long. Uropod 3 biramous. Telson varying from slightly incised to distinctly cleft.

Type genus. *Biancolina* Della Valle, 1893 (monotypic).

Habitat. Marine, shallow water. Probably burrowers into fleshy algae.

Family Ceinidae Barnard, 1972a

Diagnosis. Body laterally compressed, with cuticular pits. A1 longer or shorter than A2. Mandibular molar tritulative or cone-shaped (*Ceina*). Palp of maxilla 1 present (varying in size) or lacking in *Ceina*. Male gnathopod 2 sexually dimorphic (*Ceina*) or not. Coxae 1–4 lacking postero-lateral processes. Uropod 3 lacking rami. Telson partially cleft.

Type genus. *Ceina* DellaValle, 1893.

Remarks. The three genera within this family are quite heterogeneous in mouthpart morphology. Unfortunately, *Waitomo* and *Taihapa* were not available for this analysis, although it would be interesting to reexamine these two taxa in a future study to understand better their position within the Talitrida.

Habitat. Marine. *Waitomo manene* Barnard, 1972 was recorded from depths of between 860 and 1683 m off New Zealand (Barnard 1972a), being the only talitrid species to inhabit deep water.

Family Eopbiantidae Sheard, 1936

Diagnosis. Body cylindrical. Coxae small and usually discontinuous. Mandibular molar not tritulative, usually absent or spinose. Palp of maxilla 1 vestigial or absent. Gnathopods 1–2 slender, parachelate or subchelate, lacking sexual dimorphism. Urosomites 2–3 occasionally coalesced. Uropod 3 lacking ramus. Telson entire or cleft until base.

Type genus. *Bircenna* Chilton, 1884.

Habitat. Marine, shallow water.

Family Pbiantidae Stebbing, 1899

Diagnosis. Body depressed. Mandible, molar modified, usually styliform. Maxilla 1, inner lobe vestigial or absent; outer lobe with five setal-teeth weakly dentate, lacking palp. Maxilla 2, outer lobe thinner than inner lobe. Gnathopods simple or weakly subchelate. Anterior coxae more or less splayed and without posterior processes. Peduncle of pleopod 1 usually unexpanded, that of pleopod 2–3 expanded and lobate medially. Uropod 3 with 0–1 ramus. Telson entire.

Type genus. *Pblias* Guerin, 1836.

Habitat. Marine, shallow water.

Family Plioplateidae Barnard, 1978

Diagnosis. Body dorso-ventrally depressed, with cuticular pits. Mandibular molar large and weakly tritulative. Lower lip with inner lobe; outer lobe truncated distally. Maxilla 1, outer lobe with eight setal-teeth, five dentate and three simple and

slender; palp reduced, not reaching the setal-teeth of the outer lobe. Inner lobe of maxilla 2 lacking differentiate seta. Distal margin of maxilliped inner plate with 1–2 slender stout setae. Gnathopods subchelate. Male gnathopod 2 without sexual dimorphism, carpus triangular and well-developed. Coxae 1–4 rectangular and distally concave. Coxa 1 a little longer than coxae 2–4. Oostegites 2–5 similar, oval and with curl-tipped setae (seen in *P. triquetra*). Peduncle of pleopods 1–3 not expanded or lobate. Uropod 3 lacking ramus. Telson cleft until base, each lobe triangular.

Type genus. *Plioplateia* K. H. Barnard, 1916 (monotypic).

Habitat. Marine, shallow water (50–105 m).

Family Temnophliantidae Griffiths, 1975

Diagnosis. Body dorso-ventrally depressed. Mandibular molar weakly tritulative, laminar; left lacinia mobilis absent. Maxilla 1, inner lobe vestigial or absent; outer lobe with five setal-teeth weakly dentate, lacking palp. Maxilla 2, outer lobe thinner than inner lobe. Palp of maxilliped bi-articulate. Pereon with distinct pleura. Gnathopods 1–2 simple. Base of pereopods 5–7 slender. Pleon short and flexed under thorax. Peduncle of pleopods 1–3 lobate. Uropods 1–2 with inner ramus very reduced, vestigial. Telson entire.

Type genus. *Temnophlias* K. H. Barnard, 1916.

Remarks. Controversies relating to the description of uropod 1–2 were noted. Griffiths (1975) described the family and illustrated uropods 1 and 2 of *T. capensis* as uniramous. Barnard & Karaman (1991) maintained the family diagnosis as uropods 1–2 uniramous, as they did not re-examine local material. K. H. Barnard (1916), in the original description of this species, described uropod 1 as ‘with a short blunt tubercle probably representing the inner ramus’ and uropod 2 as ‘bearing a tubercle (representing a inner ramus)’. The material examined has a distinct projection beside the outer ramus, which is considered to be a reduced inner ramus as stated in Barnard (1916). Redescription (including illustrations) of *T. capensis* with material provided by the South African Museum is being prepared (Serejo, in prep.).

Habitat. Marine, shallow water.

Superfamily Talitroidea s.s. Rafinesque, 1815

Family Chiltoniidae Barnard, 1972a.

Diagnosis. Body laterally compressed. A1 longer than A2. Maxilla 1, inner lobe with 8–9 dentate setal-teeth, palp absent. Coxae 1–3 about 1.5 times longer than wide. Coxa 1 without postero-lateral processes; coxae 2–3 with or without

postero-lateral processes. Male gnathopod 2 with sexual dimorphism, carpus rectangular and reduced, without lobe. Female gnathopod 2 subchelate, carpus without lobe. Oostegites: 2 triangular, 3–4 rectangular and 5 variable. Uropod 3 uniramous or lacking rami. Sternal branchiae present or not. Telson entire.

Type genus. *Chiltonia* Stebbing, 1899.

Habitat. Freshwater.

Family Dogielinotidae Gurjanova, 1953

Talitridae — Stebbing 1906: 523 (part).

Dogielinotidae Gurjanova 1953: 233; Barnard & Karaman 1991: 276 (part).

Hyaellidae Bulycheva 1957: 173 (part); Bousfield 1982b: 270 (part); 1996: 177 (part).

Najnidae Barnard 1972a.

Diagnosis. Body laterally compressed. A1 shorter than A2. Maxilla 1 with palp very reduced, not reaching the base of stout setae of outer lobe, or absent (*Exhyaella* and *Parhyaella*). Coxae 1–4 about 1.5 times longer than wide (exception, *Najna*). Male gnathopod 2 with sexual dimorphism (exception, *Najna*), carpus with lobe. Carpus of female gnathopod 2 with lobe. Uropod 3 uniramous or without ramus. In species herein observed the oostegites are: 2 triangular, 3–5 rectangular. Telson entire or cleft up to half-way.

Type genus. *Dogielinotus* Gurjanova, 1953.

Subfamilies. Dogielinotinae Gurjanova, 1953; Hyaellinae Bulycheva, 1957; Najninae Barnard, 1972a.

Subfamily Dogielinotinae Gurjanova, 1953

Diagnosis. Coxa 1–4 with weak posterior processes. Female gnathopod 2 with long carpal lobe, reaching $\frac{1}{2}$ or more of the posterior margin. Telson cleft until half-way and rectangular or entire in *Exhyaella*, *Parhyaella* and *Marinohyaella*.

Remarks. *Dogielinoides*, *Dogielinotus*, *Eobaustorioides*, *Haustorioides* and *Probosciniotus* were classified alone as Dogielinotidae (Barnard & Karaman 1991). Species within these genera are typical sand-burrowers from the infralittoral zone. They differ from other species of the group in having spinose antennae and heavily setose and fossorial pereopods as an adaptation for burrowing.

Habitat. Marine, shallow water. Some species are sand-burrowers in sediment and others live among algae.

Subfamily Hyaellinae Bulycheva, 1957

Diagnosis. Coxae 1–4 without posterior processes. Female gnathopod with carpal lobe short, reaching maximum of $\frac{1}{4}$ of propodus posterior margin. Sternal branchiae present. Telson entire.

Type genus. *Hyaella* Smith, 1874 (monotypic).

Remarks. *Hyaella* is a freshwater genus with about 39 described species, and is endemic to the Americas. For keys to subgenera and species see Bousfield (1996).

Habitat. Freshwater.

Subfamily Najninae Barnard, 1972a

Diagnosis. Body more or less laterally compressed, cuticle smooth, no pits. Mandible with molar vestigial, replaced by 1–2 stout setae; left lacinia mobilis with eight teeth (in *Najna kitamati*). Coxae 1–3 pyriform, lacking postero-lateral processes. Male gnathopod 2 without sexual dimorphism, carpus triangular, well developed. Female gnathopod 2 with long carpal lobe, reaching almost $\frac{1}{2}$ of posterior margin. Uropod 3 minutely uniramous. Telson short, broad and entire.

Type genus. *Najna* Derzhavin, 1937.

Remarks. The general diagnosis of this subfamily is based mostly on *Najna*. Unfortunately, the type material of *Insula antennulella*, the only species of the genus, is unavailable. The slides are dried out and searches around Bermuda (type locality) did not yield further material (Lazo-Wasem & Gable 2001). In addition, descriptions were brief (and lacking in the case of females), making it difficult to characterize the group. Based on this information, and also corroborating the hypothesis of Barnard (1969) that *I. antennulella* should be considered a juvenile stage of *Hyale*, Lazo-Wasem & Gable (2001) recently suggested that this taxon should be disregarded. If so, *Najna* would be unique within clade 43, being a monotypic genus within this subfamily.

Habitat. Marine, shallow water.

Family Hyalidae Bulycheva, 1957

Diagnosis. Body laterally compressed. A1 longer than peduncle of A2 (but shorter than A2). A2 without sexual dimorphism. Mandibular molar triturative; left lacinia mobilis with 5–6 teeth. Male gnathopod 2 with sexual dimorphism, carpus triangular reduced, lacking lobe in adult forms (carpal lobe maintained in adults of *Parallorchestes*). Female gnathopod 2 with carpal lobe short, reaching maximum of $\frac{1}{4}$ of propodus posterior margin. Telson cleft until base.

Subfamilies. Hyacheliinae Bousfield & Hendrycks, 2002 and Hyalinae Bulychева, 1957.

Subfamily Hyacheliinae Bousfield & Hendrycks, 2002

Diagnosis. Lower lip with mandibular lobe laterally convex. Maxilla 1, palp uni-articulate and very reduced, not reaching base of setal-teeth of outer lobe. Article 4 of maxilliped palp reduced, not unguiform. Coxae 1–2 smaller than coxae 3–4, coxae 1–4 longer than wide, without posterior processes. Pereopods 3–7 prehensile. Oostegites: 2 triangular, 3 bell-shaped, 4 boot-shaped and 5 triangular. Uropod 3 lacking rami. Telson cleft until base, lobes distally rounded.

Type genus. *Hyachelia* Barnard, 1967 (monotypic).

Habitat. Marine. Ectoparasite in the buccal cavity of marine turtoises.

Subfamily Hyalinae Bulychева, 1957

Diagnosis. Lower lip with mandibular lobe normally rounded. Maxilla 1, palp uni-articulate and slightly reduced, reaching base of setal-teeth of outer lobe (*Parallorchestes* is bi-articulate). Article 4 of maxilliped palp well-developed, unguiform. Coxae 1–4 subequal in length and about as long as wide, with postero-lateral processes. Uropod 3 uniramous or with a small scale-like inner ramus in *Parhyale* and *Parallorchestes*. Telson cleft until base, lobes usually triangular in shape.

Type genus. *Hyale* Rathke, 1837.

Habitat. Marine, shallow water.

Family Talitridae Rafinesque, 1815

Diagnosis. Antenna 1 reduced, shorter than peduncle of antenna 2. Antenna 2 with sexual dimorphism in some genera. Mandibular molar tritulative; left lacinia mobilis with 4–6 teeth. Maxilla 1, palp uni-articulate and reduced, not reaching base of setal-teeth of outer lobe. Coxae 1–4 about as long as wide. Coxae 1 subtriangular and smaller than coxae 2–4. Coxae 2–3 with posterior processes. Male gnathopod 2 with sexual dimorphism, carpus triangular reduced and lacking lobe. Male gnathopod 2 without sexual dimorphism, mitten-shaped as in females. Female gnathopod 2 mitten-shaped, carpus trapezoid, lacking lobe. Telson emarginate or entire, with a distinct median line.

Type genus. *Talitrus* Latreille, 1802.

Habitat. Semi-terrestrial, supralittoral of beaches and mangrove areas. Terrestrial, forest litter.

Key to families of Talitridae

- 1 Body cylindrical (Fig. 2E). Mandibular molar absent or vestigial (Fig. 4B) 4
- 2 Body dorso-ventrally depressed (Fig. 2D). Mandibular molar not fully tritulative (Fig. 4C,D,F) 5
- 3 Body laterally compressed (Fig. 2C). Mandibular molar usually fully tritulative (Fig. 4A) (exception in *Ceina* (Fig. 4E), *Najna* (Fig. 4G) and *Taihape*) 7
- 4 Coxae 1–4 medium to large, about as long as wide. Uropod 3 biramous Biancolinidae
- 4' Coxae 1–4 small, wider than long (Fig. 9B). Uropod 3 lacking ramus (Fig. 21E) Eophliantidae
- 5 Pereon with lateral pleura. Palp of maxilliped bi-articulate (Fig. 8E) Temnophliantidae
- 5' Pereon without lateral pleura. Palp of maxilliped 3 or 4-articulate 6
- 6 Article 4 of maxilliped palp, when present, shorter than 2× length article 3. Some peduncle of pleopods expanded (Fig. 20D) Phliantidae
- 6' Article 4 of maxilliped palp always present, about 2× length article 3. Peduncle of pleopods not expanded Plioplateidae
- 7 Gnathopods 1–2 feeble, almost parachelate (Fig. 15B,C) Kuriidae
- 7' Gnathopods 1–2 subchelate or chelate 8
- 8 Antenna 1 reduced, shorter or equal to peduncle of antenna 2. Female and sometimes male gnathopod 2 mitten-shaped (Fig. 15E) Talitridae
- 8' Antenna 1 longer than peduncle of antenna 2. Female and male gnathopod 2 not mitten-shaped 9
- 9 Telson cleft until base (Fig. 22E,F) Hyalidae
- 9' Telson entire or cleft until half (Fig. 22G,H) 10
- 10 Carpus of adult male and female gnathopod 2 with lobe (Figs 14B, 16D) Dogielinotidae
- 10' Carpus of adult male and female gnathopod 2 lacking lobe (Fig. 16A) 11
- 11 Carpus of male gnathopod 2 rectangular reduced (Fig. 12C). Telson entire Chiltoniidae
- 11' Carpus of male gnathopod 2 fused to propodus (Fig. 12E) or subtriangular well-developed. Telson cleft until half Ceinidae

Key to subfamilies of Dogielinotidae

- 1 Carpal lobe of female gnathopod 2 reaching up to $\frac{1}{4}$ of propodus posterior margin (Fig. 16B) Hyaellinae
- 1' Carpal lobe of female gnathopod 2 reaching $\frac{1}{2}$ or more of propodus posterior margin (Fig. 16D) 2
- 2 Mandibular molar vestigial, replaced by 1–2 stout setae (Fig. 4G). Coxae 1–3 usually pyriform (Fig. 9D). Male gnathopod 2 not sexually dimorphic Najniinae

- 2' Mandibular molar fully tritulative (Fig. 4A). Coxae 1–3 rectangular (Fig. 9A).
Male gnathopod 2 sexually dimorphic.... Dogielinotinae

Key to subfamilies of Hyalidae

- 1 Coxae 1–2 shorter than coxae 3–4. Pereopods 3–7 prehensile. Uropod 3 lacking ramus..... Hyacheliinae
1' Coxae 1–4 about the same size. Pereopods 3–7 not prehensile. Uropod 3 uniramous or with a tiny scale-like inner ramus (Fig. 21C,D)..... Hyalinae

Acknowledgements

During the course of this 4-year PhD project a number of people made critical contributions to its development. Dr Carlos E. F. da Rocha (Universidade de São Paulo, USP) supervised my work, making valuable suggestions. Dr Paulo S. Young (Museu Nacional/UFRJ) discussed issues and participated intensively throughout. Dr Yoko Wakabara (Instituto Oceanográfico, USP) provided many bibliographic references. Dr Hélio Ricardo Silva (Universidade Rural do Rio de Janeiro) helped with the PAUP analysis. Dr Jim Lowry (Australian Museum) critically reviewed the manuscript, making several suggestions concerning the systematic revision. Dr Alastair Richardson (University of Tasmania) provided the translation of Bulycheva (1957). Dr Ed Bousfield (Canadian Museum of Nature) discussed several aspects of the evolution of the Talitroidea. Dr Janet Reid carefully corrected the language. Last but not least, I want to thank all the curators and researchers who kindly lent amphipod material for this study: Dr Anne Klitgaard (Zoölogisk Museum), Dr Bob Vansyoc (California Academy of Science), Mr Chad Walter and Dr Janet Reid (National Museum of Natural History, Smithsonian Institution), Dr Danielle Defaye (Muséum National d'Histoire Naturelle, Paris), Mrs Judith Price (Canadian Museum of Nature), Dr M. Merwe (South African Museum), Dr Penny Berents (Australian Museum) and Dr Sandro Ruffo (Museo Civico di Storia Naturale di Verona).

References

Barnard, K. H. (1916). Contributions to the crustacean fauna of South Africa. 5. The Amphipoda. *Annals of the South African Museum*, 15, 105–302.
Barnard, J. L. (1962). Benthic marine Amphipoda of Southern California: families Aoridae, Photidae, Ischyroceridae, Corophiidae, Podoceridae. *Pacific Naturalist*, 3, 1–72.
Barnard, J. L. (1964). Revision of some families, genera and species of gammaridean Amphipoda. *Crustaceana*, 7, 49–74.
Barnard, J. L. (1965). Marine Amphipoda of atolls in Micronesia. *Proceedings of the United States National Museum*, 117, 459–551.
Barnard, J. L. (1967). A new genus of Galapagan amphipod inhabiting the buccal cavity of the sea-turtle, *Chelonia mydas*. *Proceedings of the Symposium on Crustacea at Ernakulum, India*, 1, 119–125.
Barnard, J. L. (1969). The families and genera of marine gammaridean Amphipoda. *Bulletin of the United States National Museum*, 271, 1–535.

Barnard, J. L. (1970a). The identity of *Dexamonica* and *Prinassus* with a revision of Dexaminidae (Amphipoda). *Crustaceana*, 19, 161–180.
Barnard, J. L. (1970b). Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands. *Smithsonian Contributions to Zoology*, 34, 1–286.
Barnard, J. L. (1972a). The marine fauna of New Zealand: Algae living in littoral Gammaridea (Crustacea Amphipoda). *Memoir of the New Zealand Oceanographic Institute*, 62, 7–216.
Barnard, J. L. (1972b). Gammaridean Amphipoda of Australia, Part I. *Smithsonian Contribution to Zoology*, 103, 1–333.
Barnard, J. L. (1974a). Evolutionary patterns in Gammaridean Amphipoda. *Crustaceana*, 27, 137–146.
Barnard, J. L. (1974b). Gammaridean Amphipoda of Australia, Part II. *Smithsonian Contribution to Zoology*, 139, 1–148.
Barnard, J. L. (1978). Redescription of *Plioplateia* K. H. Barnard, a new genus of amphipod (Crustacea) from South Africa. *Annals of the South African Museum*, 77, 47–55.
Barnard, J. L. (1979). Littoral gammaridean Amphipoda from the Gulf of California and the Galapagos Islands. *Smithsonian Contribution to Zoology*, 271, 1–148.
Barnard, J. L. (1981). Redescription of *Iphioplateia whiteleggei*, a New Guinea marine amphipod (Crustacea). *Proceedings of the Biological Society of Washington*, 94, 1211–1218.
Barnard, J. L. & Barnard, C. M. (1983). *Fresh water Amphipoda of the world — I. Evolutionary patterns. II. Handbook and Bibliography*. Mt. Vernon, Virginia: Hayfield Associates.
Barnard, J. L. & Karaman, G. S. (1991). The families and genera of marine gammaridean Amphipoda (except marine gammaroids), Parts 1 and 2. *Records of the Australian Museum, Supplement*, 13, 1–866.
Bate, C. S. (1862). *Catalogue of the Specimens of Amphipodous Crustacea in the Collection of the British Museum*. London: British Museum, Natural History.
Berge, J., Boxshall, G. & Vader, W. (2000). Phylogenetic analysis of the Amphipoda, with special emphasis on the origin of the Stegocephalidae. *Polskie Archiwum Hydrobiologii*, 47, 379–400.
Bousfield, E. L. (1964). Insects of Campbell Island. Talitrid amphipod crustaceans. *Pacific Insects Monograph*, 7, 45–57.
Bousfield, E. L. (1978). A revised classification and phylogeny of amphipod crustaceans. *Transactions of the Royal Society of Canada*, 4, 343–390.
Bousfield, E. L. (1981). Evolution in North Pacific coastal marine amphipod crustaceans. In: G. Scudder & J. Reveal (Eds) *Evolution Today. Proceedings of the Second International Congress of Systematics and Evolutionary Biology*, pp. 69–89.
Bousfield, E. L. (1982a). The amphipod superfamily Talitroidea in the northeastern Pacific region: 3. Family Talitridae. Systematics and distributional ecology. *Publications in Biology Oceanography*, 11, 1–73.
Bousfield, E. L. (1982b). Amphipoda — Gammaridea. In: S. P. Parker (Ed.) *Synopsis and Classification of Living Organisms*, Vol. 2. (pp. 254–285). New York: McGraw-Hill.
Bousfield, E. L. (1984). Recent advances in the systematics and biogeography of landhoppers (Amphipoda: Talitridae) of the Indo-Pacific region. In: F. J. Radovsky, P. H. Raven & S. H. Sohier (Eds) *Biogeography of the Tropical Pacific. Bishop Museum Special Publications*, 72, 171–210.
Bousfield, E. L. (1996). A contribution to the reclassification of neotropical fresh water hyalellid amphipods (Crustacea: Gammaridea: Talitroidea). *Bollettino del Museo Civico di Storia Naturale, Verona*, 20, 175–224.
Bousfield, E. L. & Hendrycks, E. A. (2002). The talitroidean amphipod family Hyalidae revised, with emphasis on the North Pacific

- fauna: systematics and distributional ecology. *Amphipacifica*, 3 (3), 17–134.
- Bousfield, E. L. & Shih, C. T. (1994). The phyletic classification of amphipod crustaceans: problems in resolution. *Amphipacifica*, 1 (3), 76–134.
- Bremer, K. (1994). Branch support and tree stability. *Cladistics*, 10, 295–304.
- Brooks, D. R. & McLennan, D. A. (1991). *Phylogeny, Ecology, and Behavior. A Research Program in Comparative Biology*. Chicago: University of Chicago Press.
- Bulycheva, A. I. (1957). The sea-fleas of the seas of the U.S.S.R and adjacent waters (Amphipoda, Talitroidea). *Akademiia Nauk SSSR, Opredeliteli po Faune SSSR*, 65, 1–185.
- Chilton, C. (1909). Note on the amphipodan genera *Bircenna*, *Kuria*, and *Wandelia*. *Transactions of the New Zealand Institute*, 41, 59–63.
- Chilton, C. (1919). *Ceina*, an aberrant genus of the amphipodan family Talitridae. *Transactions of the New Zealand Institute*, 51, 118–129.
- Conlan, K. E. (1991). Precopulatory mating behavior and sexual dimorphism in the amphipod Crustacea. *Hydrobiologia*, 223, 255–282.
- Dahl, E. (1977). The amphipod functional model and its bearing upon systematics and phylogeny. *Zoologica Scripta*, 6, 221–228.
- Dahl, E. & Hessler, R. R. (1982). The crustacean lacinia mobilis: a reconsideration of its origin, function and phylogenetic implications. *Zoological Journal of the Linnean Society*, 74, 133–146.
- Duncan, K. W. (1985). A critique of the concept of genetic assimilation as a mechanism in the evolution of terrestrial amphipods (Amphipoda). *Canadian Journal of Zoology*, 63, 2230–2232.
- Friend, J. A. & Richardson, A. M. M. (1986). Biology of terrestrial amphipods. *Annual Review of Entomology*, 31, 25–48.
- Giovannini, R. (1965). Révision des espèces benthiques méditerranéennes du genre *Hyale*. *Recueil des Travaux de la Station Marine d'Endoume, Bulletin*, 37, 277–340.
- Griffiths, C. L. (1975). The Amphipoda of southern Africa Part 5. The Gammaridea and Caprellidea of the Cape Province west of Cape Agulhas. *Annals of the South African Museum*, 67, 91–181.
- Gurjanova, E. F. (1953). Novye dopolnenija k dal'nevostochnoi faune morskich bokoplavov. *Akademiia Nauk SSSR, Trudy Zoologicheskogo Institut*, 13, 216–241.
- Gurjanova, E. F. (1958). K faune amfipod (Amphipoda) Ostrova Makkuori. *Biol. Sovetskoi Antart. Exped.*, 3, 55–56.
- Hennig, W. (1966). *Phylogenetic Systematics*. Urbana: University of Illinois Press.
- Hessler, R. R. & Watling, L. (1999). Les Pécarides: Un groupe controversé. *Traité de Zoologie. Anatomie, Systematique, Biologie. Tome VII, Fascicule IIIA — Crustacés Pécarides. Mémoires de l'Institut Océanographique*, 19, 1–450.
- Hurley, D. E. (1959). Notes on the ecology and environmental adaptations of the terrestrial Amphipoda. *Pacific Science*, 13 (2), 107–128.
- Hurley, D. E. (1968). Transition from water to land in amphipod crustaceans. *American Zoologist*, 8, 327–353.
- Kim, C. B. & Kim, W. (1993). Phylogenetic relationships among gammaridean families and amphipod suborders. *Journal of Natural History*, 27 (4), 933–946.
- Krapp-Schickel, G. (1972). Ratselhafte *Hyale carinata* (Amphipoda, Crustacea). *Memorie del Museo Civico di Storia Naturale, Verona*, 19, 177–189.
- Krapp-Schickel, G. (1974). Camill Hellers Sammlung adriatischer Amphipoden — 1866 und heute. *Annalen der Naturhistorisches Museum, Wien*, 78, 319–379.
- Krapp-Schickel, G. (1976). Marine Amphipods from Pantelleria and Catania (Sicily). *Bulletin Zoologisch Museum, Universiteit van Amsterdam*, 5, 31–45.
- Kunkel, B. W. (1910). The Amphipoda of Bermuda. *Transactions of the Connecticut Academy of Arts and Sciences*, 16, 1–116.
- Lazo-Wasem, E. A. & Gable, M. F. (2001). A revision of *Parhyalella* Kunkel (Crustacea: Amphipoda: Gammaridea). *Bulletin of the Peabody Museum of Natural History, Yale University*, 46, 1–80.
- Leite, F. P. P., Wakabara, Y. & Tararam, A. S. (1986). On the morphological variations in oostegites of gammaridean species (Amphipoda). *Crustaceana*, 51 (1), 77–94.
- MacIntyre, R. J. (1963). The supra-littoral fringe of New Zealand sand beaches. *Transactions of the Royal Society, New Zealand*, 8, 89–103.
- Maddison, W. P. & Maddison, D. R. (1992). *MacClade — Analysis of Phylogeny and Character Evolution Ver 3*. Sunderland, MA: Sinauer.
- Matsuda, R. (1982). The evolutionary process in talitrid amphipods and salamanders in changing environments, with a discussion of 'genetic assimilation' and some other evolutionary concepts. *Canadian Journal of Zoology*, 60, 733–749.
- Morino, H. (1981). Studies on the Talitridae (Amphipoda, Crustacea) in Japan. IV. The development of gnathopod II in *Orchestia platensis* Kroyer. *Publications of the Seto Marine Biology Laboratory*, 26, 1–13.
- Myers, A. A. & Lowry, J. K. (2003). A phylogeny and a new classification of the Corophiidea Leach, 1814 (Amphipoda). *Journal of Crustacean Biology*, 23 (2).
- Nicholls, G. E. (1939). The Prophiantidae. A proposed new family of Amphipoda, with description of a new genus and four new species. *Records of the Southern Australian Museum*, 6 (3), 309–334.
- Nixon, K. C. & Carpenter, J. M. (1993). On outgroups. *Cladistics*, 9, 413–426.
- Sheard, K. (1936). Amphipods of the phliantid group in the south Australian museum, with a suggested division of the family. *Records of the Australian Museum*, 5 (4), 445–468.
- Shoemaker, C. R. (1941). A new genus and a new species of Amphipoda from the Pacific coast of North America. *Proceedings of the Biological Society of Washington*, 54, 183–186.
- Shoemaker, C. R. (1956). Observations on the genus *Parhyale*. *Proceedings of the United States National Museum*, 106, 345–358.
- Stebbing, T. R. R. (1899). Amphipoda from the Copenhagen Museum and other sources Part II. *Transactions of the Linnean Society of London*, 8, 395–432.
- Stebbing, T. R. R. (1906). Amphipoda I. Gammaridea. *Das Tierreich*, 21.
- Steele, D. H. (1991). Is the oostegite structure of amphipods determined by their phylogeny or it is an adaptation to their environment? *Hydrobiologia*, 223, 27–34.
- Stock, J. H. (1987). Stygofauna of the Canary Islands, 5. A hypogean population of *Parhyale* (Amphipoda) in the Jameos del Agua lava tunnel (Lanzarote), a supposed case of recent evolution. *Stygologia*, 3 (2), 167–184.
- Swofford, D. L. (1993). *PAUP. Phylogenetic Analysis Using Parsimony Ver 3.1* [Computer software and manual]. Champaign, IL: Illinois Natural History Survey.
- Walker, A. O. & Scott, A. (1903). Decapoda and sessile-eyed crustaceans from Abd-el-Kuri. In: *The Natural History of Sokotra and Abd-el-Kuri*, 216–232.
- Watling, L. & Thurston, M. (1989). Antarctica as an evolutionary incubator: evidence from the cladistic biogeography of the amphipod family Iphimediidae. *Geological Society of London Special Publication*, 47, 297–313.
- Wiens, J. J. (ed.) (2000). *Phylogenetic Analysis of Morphological Data*. Washington, DC: Smithsonian Institution Press.