JOURNAL OF CRUSTACEAN BIOLOGY, 21(1): 205–230, 2001

ISOPODA VALVIFERA: DIAGNOSES AND RELATIONSHIPS OF THE FAMILIES

Gary C. B. Poore

Museum Victoria, GPO Box 666E, Melbourne, Victoria 3001, Australia
(e-mail: gpoore@museum.vic.gov.au)

A B S T R A C T

Eleven families of the isopod suborder Valvifera are diagnosed, and a key to differentiate them is presented. Three families, Antarcturidae, Rectarcturidae, and Arcturididae, are erected as new on the basis of a cladistic analysis of 14 families, genera, and genus-groups. Phylogenetic relationships between the families are suggested. The genera of each family, 81 in all, are listed. The generic name *Austridotea,* previously a *nomen nudum,* is made available within the Idoteidae. Differentiation of the families is based on fusion of the head and pereionite 1, length of the peduncle of pleopod 1, the male first pleopods, and fusion of the penes. Three families (Chaetiliidae, Holognathidae, Idoteidae) have pereionite 1 free from the head; pereiopod 1 subchelate, similar to others or larger; all pleopods simple and similar; and penes free or a basally fused penial plate. Those families with pereionite 1 fused to the head, pereiopod 1 smaller than other pereiopods and with different structure, an elongate pleopod 1 peduncle, and a fused penial plate have either the exopod of the male pleopod 1 laminar and excavate laterally (Arcturidae) or the exopod thickened and diagonally grooved (Arcturididae, Antarcturidae, Austrarcturellidae, Holidoteidae, Pseudidotheidae, Rectarcturidae, Xenarcturidae).

The Valvifera is a suborder of marine, and rarely estuarine, isopods inhabiting algal and benthic environments from the intertidal to the deep sea. They reach their greatest diversity in cold waters, being abundant on temperate shores, Antarctica, and the ocean basins. There are few tropical species. Forms include the herbivorous sea-centipedes (Idoteidae) and bizarre filter-feeding arcturids. The Valvifera (about 520 described species) comprise 81 genera presently included in seven families. There has never been any doubt about the monophyly of the Valvifera, the suborder erected by Sars (1882) for isopods in which the uropods hinge laterally along the length of the pleon and pleotelson so enclosing the pleopods in a branchial chamber.

In the course of taxonomic studies on the many undescribed valviferan isopods of Australia and adjacent seas it became apparent that (1) the family-level arrangement had changed over the past two decades, (2) no modern key to the families existed, (3) some species commonly referred to the largest families, Idoteidae and Arcturidae, could be placed in other groups worthy of family status, and (4) the relationships between them had been rarely investigated. This contribution presents a phylogeny of the suborder, diagnoses its eleven families of which three are new, provides a key for their differentiation, lists the genera in each family, and briefly reviews the recent literature.

I offer the work to establish a broad taxonomic framework now rather than await descriptions and publication of many new taxa which will take some time. First, the taxa chosen for analysis are discussed and justified in terms of their perceived synapomorphies. Next, characters and their states are discussed and figured. Finally, a new classification is derived from the cladistic analysis and all the families diagnosed. A key to separate them is presented. All valid genera are listed and the name of one idoteid genus is formalised.

Cladistic Analysis

Analytical Methods

The information presented here is based on examination of representatives of numerous species representing most genera in the collections of Museum Victoria. These have been supplemented by type specimens on loan from the U.S. National Museum of Natural History. The conclusions are based on examination of type species of most genera, numerous species from Australasian seas, the Southern Ocean, and elsewhere, and analysis of the literature. Phylogenetic (cladistic) methods were used to generate cladograms of monophyletic groups as hypotheses of the relationships between family-level taxa. An interim cladistic analysis of all the genera (unpublished) has failed to result in a fully resolved cladogram of relationships because of the high level of homoplasy shown by many trivial characters. Nevertheless, the cladograms have suggested some persistent high-level groupings which are or might be assigned family ranking. The approach described here is a phylogenetic analysis of these groupings (families, genera, or groups of genera) each of which is unambiguously monophyletic and holophyletic. The characters that define these groups are those associated with reproduction (especially male pleopods), feeding (pereiopods), fusion of body segments, and general habitus. In particular these characters are those that could define (*a priori*) large groups of genera and so contribute to a family-level classification. They contrasted with characters which varied in similar ways in different groups and were undoubtedly homoplasous, e.g., number of articles in maxillipeds or antennal flagella, or number of uropodal rami.

The phylogenetic analysis program Paup* 4.0 (beta version for Windows) (Swofford, 1998) was used to establish relationships of 14 taxa in order to derive a practical classification of monophyletic family-level taxa. A heuristic search was made using default options, and a strict consensus tree was generated. Characters were treated as unweighted and unordered (Table 1). The matrix was then treated to a bootstrap analysis using a heuristic search. A 50% majority-rule consensus tree was constructed of all bootstrap trees.

The cladogram was rooted against a hypothetical ancestor. The valviferans are a highly specialised derived group with relationships to flabelliferan isopod families (Wägele, 1989; Brusca and Wilson, 1991). The hypothetical ancestor is based, therefore, on more generalised families such as Cirolanidae and Sphaeromatidae.

In the following discussions of taxa and characters the word 'idoteoid' is used as a shorthand for the families Idoteidae, Chaetiliidae, and Holognathidae. The phylogenetic analysis does not support the monophyly of this group, but the term is used to contrast these families with the 'arcturoid' families which undoubtedly belong to a monophyletic clade. The words 'arcturid' and 'antarcturid' are used in the narrow senses which anticipate the classification resulting from the analysis.

Taxa Used In Analysis

Any phylogenetic analysis depends on having taxa of unambiguous monophyly. This is not the case for all the families of Valvifera as presently understood although for others, especially small ones, clear synapomorphies have been defined (although not always in phylogenetic language). Fourteen families, genera, and genus-groups (listed in Table 2 and printed in boldface type below) were selected. The genera represented by the two genus-groups (*Arcturus*-group and *Antarcturus*-group) are those listed in Arcturidae and Antarcturidae in the Systematics section. All taxa are scored for the most plesiomorphic states found, but examples of differences from these states are considered in the discussion of characters. The larger groups are represented by basal taxa with many plesiomorphic character states in common. Considerable divergence from the basal taxa within families has resulted in convergence in several characters. For example, in all the taxa treated here the maxillipedal palp is of five articles, but fusion to as few as one article has occurred in three families. The maxilliped and other characters that converge in this way and are therefore phylogenetically uninformative are discussed with the rest below. Justification of the taxa chosen necessitates some discussion of the characters pursued in more detail in the next section.

The major division of the suborder is based on two key characters, but others are more or less correlated with them: fusion of pereionite 1 to the head and the structure of pleopod 1. In three families (**Idoteidae, Chaetiliidae, Holognathidae**) pereionite 1 is free from the head and the pleopod peduncles are short and similar (Fig. 1a–d). Pereiopod 1 in these families is a subchelate limb not much different in size from other pereiopods (Fig. 2a, b). The body tends to be flattened because of lateral extension of dorsal coxal plates. The systematics of these three families is relatively well established, and each is treated as a monophyletic taxon in the analysis.

The Idoteidae are probably the archetypal

Table 1. Characters and character states used in cladistic analysis of valviferan families. Each character is terminated by a colon and states, 0, 1, etc. separated by semicolon. All characters are treated as unordered. Four characters marked * are not used in family diagnoses.

1. Body: 0, straight, more or less flattened or semicylindrical, all pereiopods ambulatory; 1, straight, cylindrical or vaulted, pereiopods 2–4 differentiated from 5–7; 2, flexed between pereionites 4 and 5, pereiopods 2–4 differentiated from 5–7.
2. Body: 0, tapering posteriorly; 1, parallel-sided over most of length.
3. Head and pereionite 1: 0, free; 1, fused.
4. Head: 0, more or less cylindrical or semicylindrical; 1, with prominent flat lateral lobes, sometimes with ocular notch.
5. Pereionite 4: 0, similar in length to pereionite 3; 1, at least 1.5 times as long as pereionite 3 (in males often much longer).
6. Pleonites: 0, pleonites 1–4 articulating with each other and fused pleotelson (others sometimes indicated but not articulating); 1, pleonites 1–3 articulating with each other and fused pleotelson (others sometimes indicated but not articulating); 2, pleonites 1 and 2 articulating with each other and fused pleotelson (others sometimes indicated but not articulating); 3, pleonite 1 articulating with fused pleotelson; 4, all pleonites fused into pleotelson.
7. *Pleonite 1: 0, of similar length to pleonite 2; 1, longer than pleonite 2.
8. Dorsal sculpture: 0, smooth or variously spinose; 1, strongly spinose with at least dorsal and dorsolateral pairs of spines, often dominated by pair near end of pleotelson.
9. Pleotelson: 0, without dorsolateral ridges ending in mediodorsal posterior spine; 1, with dorsolateral ridges usually ending in mediodorsal posterior spine.
10. Dorsal coxal plates 2–7 (rarely only 5–7): 0, more or less ventrally expanded over bases of pereiopods (body flattened); 1, obsolete, bases of pereiopods exposed (body usually cylindrical).
11. *Dorsal coxal plates 2–4: 0, visible dorsally (same as dorsal coxal plates 5–7); 1, obsolete (pereionites 2–4 with terga reaching lateral margin).
12. Mouthparts and pereiopod 1: 0, visible in lateral view; 1, enclosed in lateral view by lateral plates of head and pereionite 1.
13. Eyes: 0, well developed; 1, reduced or lost.
14. Antenna 2 flagellum: 0, multiarticulate; 1, of 2 or 3 articles plus distal claw.
15. Maxillipedal epipod: 0, as long as or longer than wide; 1, shorter than wide.
16. *Maxillipedal palp article 3: 0, at most 1.5 times as wide as article 4; 1, medially lobed, at least twice as wide as article 4.
17. Pereiopods: 0, pereiopod 1 slightly differentiated from pereiopod 2, its propodus broader than in pereiopod 2; 1, pereiopods differentiated, 1, 1–3, 1–5, or 1–6 subchelate; 2, pereiopod 1 a gnathopod, pereiopods 2–4 elongated, differentiated from ambulatory pereiopods 5–7.
18. Pereiopods 2–4: 0, with irregular fine setae and marginal robust setae; 1, with paired long setae along posterior margins evenly and well developed; 2, with scattered and uneven long setae along posterior margins; 3, raptorial, articles broad and with posterior robust setae.
19. Pereiopods 2–4: 0, with prominent dactylus, unguis short; 1, with short dactylus, unguis longer and setiform; 2, with minute dactylus, unguis setiform.
20. Pereiopod 4: 0, similar to pereiopod 3; 1, shorter and more spinose than pereiopods 3 and 5; 2, shorter and less setose than pereiopods 2 and 3; 3, different from pereiopod 3, similar to pereiopod 5.
21. Pereiopod 1 dactylus: 0, evenly curved; 1, with anterior lobe.
22. Pereiopods of males: 0, with dense fur of fine setae; 1, without dense fur of fine setae.
23. Uropodal exopod (smaller ramus): 0, ovate, fringed with setae (if present); 1, tapering (with terminal setae only).
24. Uropod: 0, exopod more than half as long as endopod, with at least three distal setae, exopod with few marginal setae; 1, exopod very short, both rami each bearing a single, prominent robust seta.
25. Oostegites 5: 0, functional; 1, vestigial lobes; 2, absent.
26. Oostegites 1–4: 0, not supported by coxal lobes; 1, supported by coxal lobes.
27. Penes: 0, paired, widely separate; 1, fused basally as a penial plate but divided over most of length; 2, fused as a single penial plate, rarely divided only apically.
28. Penial plate: 0, apically simple or barely slit; 1, apically bifid and splayed.
29. Pleopod 1 peduncle: 0, short (similar to other pleopods); 1, more elongate than on other pleopods.
30. Pleopod 1 with marginal setae on rami: 0, longer than or equal to length of rami; 1, much shorter than length of rami.
31. Pleopod 1 exopod of male: 0, laminar; 1, thickened and with groove on posterior face.
32. Pleopod 1 exopod of male: 0, with few simple setae along straight lateral margin; 1, with overlapping rows of simple and plumose setae along lateral margin, terminating at subdistal excavation.
33. Pleopod 1 of male with groove on posterior face of exopod: 0, ending distolaterally or laterally on simple margin; 1, ending in deep subdistal excavation; 2, ending on distolateral lobed tip, separated from most of lateral margin by notch; 3, ending on basally derived branch of exopod; 4, ending on tapering distolateral apical extension.
34. Pleopod 1 exopod of male: 0, without lateral excavation; 1, with lateral excavation.
35. Pleopod 2 of male with appendix masculina: 0, about as long as endopod; 1, twice length of endopod.
36. Pleopod 2 of male with appendix masculina: 0, basally less than half width of endopod; 1, basally as wide or wider than endopod.
37. *Pleopod 2 of male with appendix masculina: 0, apically tapering (not club-shaped); 1, apically club-shaped.

Table 2. Character matrix used in cladistic analyses of families and genus-groups of Valvifera.

Character numbers	1	2	3	4	5	6	7	8	9	1	1	2	3	4	5	6	7	8	9	2	1	2	3	4	5	6	7	8	9	3	1	2	3	4	5	6	7
hypanc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holognathidae	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Idoteidae	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Chaetiliidae	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Arcturus-group	2	0	1	0	1	4	0	0	0	1	0	1	0	1	0	0	2	1	0	0	0	1	1	0	0	0	2	0	1	0	0	0	0	1	0	1	0
Austroarcturus	1	0	1	0	0	3	0	0	0	1	1	0	0	1	0	1	2	2	1	0	0	1	1	1	2	1	2	1	1	0	1	1	1	0	0	0	0
Holidotea	1	0	1	0	0	4	0	0	0	1	1	0	0	1	0	1	2	2	1	0	0	1	1	1	2	1	2	1	1	0	1	1	2	0	0	0	0
Neoarcturus	2	0	1	0	0	4	0	0	0	1	0	0	0	1	0	0	2	1	1	0	0	1	1	1	2	1	2	1	1	0	1	1	1	0	0	0	1
Antarcturus-group	2	0	1	0	0	4	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	1	1	0	2	1	2	0	1	0	1	0	0	0	0	0	0
Rectarcturus	1	0	1	0	0	4	0	0	0	1	0	0	0	1	0	0	2	1	1	0	0	1	1	0	2	0	2	0	1	0	1	0	0	0	0	0	0
Dolichiscus	2	0	1	0	0	3	1	0	1	1	0	0	0	0	0	0	2	1	1	0	1	1	1	0	2	1	2	0	1	0	1	0	0	0	0	0	0
Austrarcturellidae	2	0	1	0	0	4	0	0	1	1	0	0	0	1	0	0	2	1	2	2	1	1	1	0	1	1	2	0	1	0	1	0	3	0	1	0	0
Xenarcturus	1	0	1	0	0	4	0	0	0	1	0	0	0	1	0	0	2	1	0	3	0	1	1	0	2	0	2	0	1	0	1	0	4	0	0	0	0
Pseudidothea	1	0	1	0	0	4	0	0	0	1	0	0	0	1	0	0	2	3	0	0	0	1	1	0	2	0	2	0	1	0	1	0	4	0	0	0	0
Arcturides	1	0	1	0	0	4	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0	1	1	0	2	1	2	0	1	0	1	0	4	0	0	0	0

valviferans, plesiomorphic for most characters (Poore and Lew Ton, 1993). The most plesiomorphic genera are *Austridotea,* a *nomen nudum* diagnosed here as a new genus, and *Idotea* which were used as sources for most characters. The Chaetiliidae are morphologically diverse but *Saduria* provided most plesiomorphic states. The Holognathidae are generally uniform for the characters of family significance (Poore and Lew Ton, 1990).

In all other families pereionite 1 is fused to the head (Fig. 1e–h) and pereiopod 1 is at least reduced in size and often very different in structure from those following (Fig. 2c, d). The general body shape tends to be cylindrical and often sculptured and/or spinose. Body form is highly variable, but there is a strong division among the families of this second group based on the structure of the male pleopod 1. In the ***Arcturus*-group,** both rami of the male pleopod 1 are laminar and the exopod has a lateral excavation (Fig. 3f). The monotypic Amesopodidae, which includes only *Amesopous richardsonae* Stebbing, 1905, is similar. The only character that differentiates this species from highly derived arcturid genera like *Neastacilla* is the loss of pereiopods 3 and 4 (seen in another arcturid genus), and the family is treated as a junior synonym of Arcturidae, *sensu stricto*. In most remaining arcturoids, the ***Antarcturus*-group,** and **Austrarcturellidae, Pseudidotheidae,** and **Xenarcturidae,** the exopod of the male pleopod 1 is thickened, especially basally, variously sculptured and setose and always has an oblique groove opening distally (Fig. 3b, c, e; Poore, 1998: Fig. 3 g, h). These four taxa are accordingly included in the analysis.

While several genera resemble *Antarcturus* closely and can be represented by it when scoring the characters selected, others do not. Most arcturoids have a more or less elevated anterior body, flexing between pereionites 4 and 5 to lift pereiopods 2–4, which bear filtering setae, off the substrate. This is seen in extreme in *Antarcturus* where the ventral surface of the anterior pereionites is held horizontally and uppermost while the animal is feeding (Wägele, 1987). In other genera this flexion does not exist, although pereiopods 2–4 may be similarly differentiated from pereiopods 5–7. These (***Holidotea, Austroarcturus,*** and ***Rectarcturus***) are included as separate taxa in the analysis. A fourth genus, ***Arcturides,*** which is also straight rather than flexed but has six pairs of similar pereiopods, is also included as a monophyletic taxon. Another, ***Neoarcturus,*** has been shown in a work submitted elsewhere to be similar to *Holidotea* and *Austroarcturus* and is also included. Finally, the genus ***Dolichiscus,*** which shares features of both the *Antarcturus*-group and Austrarcturellidae, is treated independently.

Characters

Thirty-seven characters were included in the data matrix, but 13 of these are autapomorphies. Twenty-four (with 2–5 unordered states) are therefore parsimony-informative.

As in most isopods the body of idoteoids is straight and more or less flattened. The pereiopods, except perhaps the first, are am-

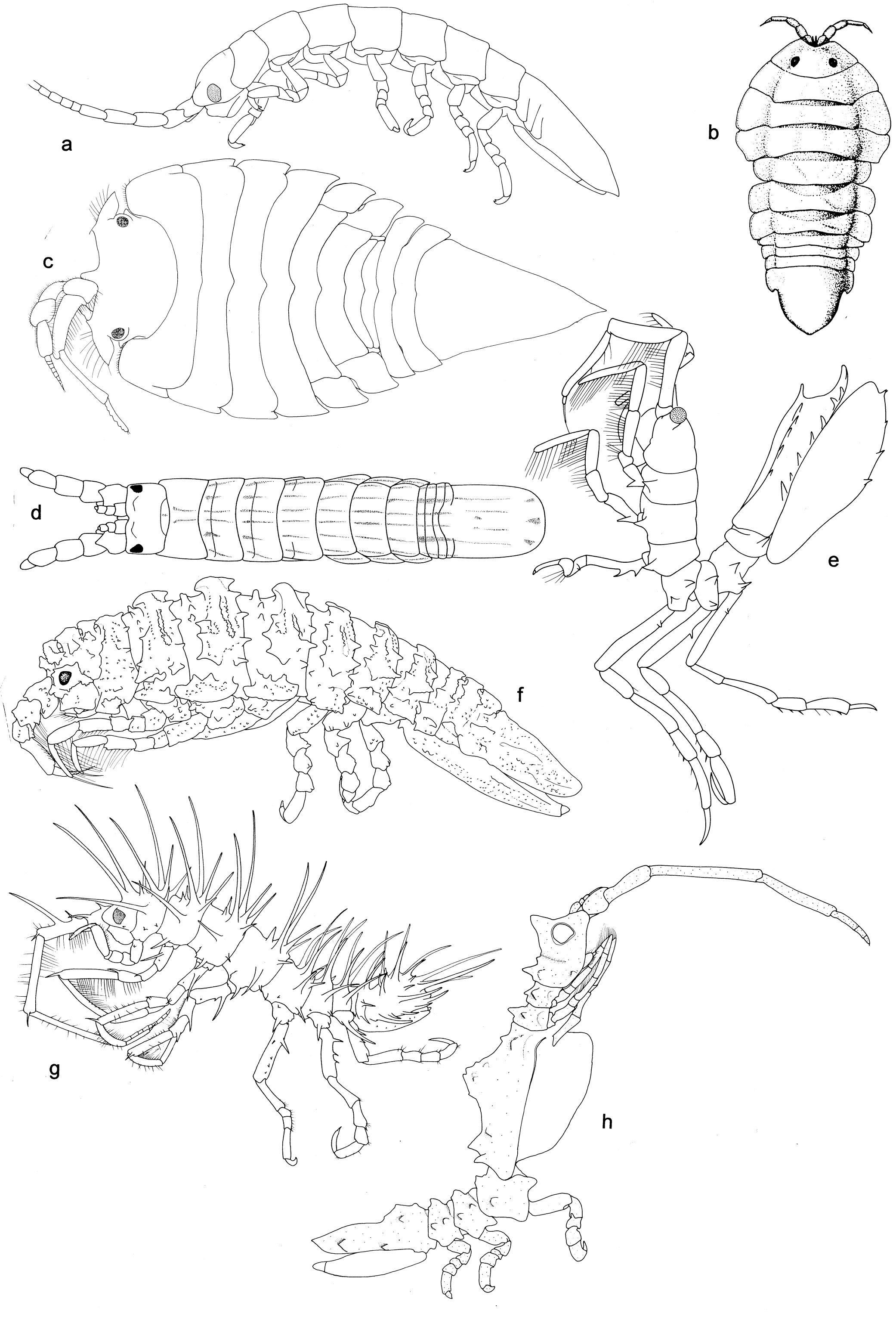

Fig. 1. Habitus of some families of Valvifera. a, *Euidotea durvillei* (Idoteidae); b, *Austroarcturus africanus* (Holidoteidae); c, *Chaetilia tasmanica* (Chaetiliidae); d, *Cleantioides striata* (Holognathidae); e, *Austrarcturella oculata* (Austrarcturellidae); f, *Rectarcturus* sp. (Rectarcturidae); g, *Antarcturus* sp. (Antarcturidae); h, *Neastacilla* sp. (Arcturidae).

Fig. 2. Pereiopods 1. a, *Idotea* (Idoteidae); b, *Chaetilia* (Chaetiliidae); c, new genus (Antarcturidae); d, *Neastacilla* (Arcturidae); e, dactylus only, *Austrarcturella* (Austrarcturellidae). Pereiopods 2. f, *Austroarcturus* (Holidoteidae); g, *Pseudidothea* (Pseudidotheidae); h, new genus (Antarcturidae); i, *Austrarcturella* (Austrarcturellidae) with detail of dactylus. Pereiopods 4. j, *Idotea* (Idoteidae); k, *Zenobianopsis* (Holognathidae); l, *Austrarcturella* (Austrarcturellidae) with detail of dactylus. Uropods. m, *Chaetilia* (Chaetiliidae); n, *Neastacilla* (Arcturidae); o, *Austroarcturus* (Holidoteidae); p, *Pentidotea* (Idoteidae).

bulatory (character 1, state 0; Fig. 1a, c, d). Most Idoteidae are herbivorous, and pereiopods play little part in feeding. Most arcturoids on the other hand are flexed dorsally between pereionites 4 and 5, and pereiopods 2–4 are differentiated from 5–7 (state 2; Fig. 1e, g, h). This flexion enables the filtering pereiopods 2–4 to be held above the substrate for feeding. An intermediate condition occurs in some genera where the body is straight, cylindrical, or vaulted, but the anterior pereiopods are partially differentiated (state 1; Fig. 1b, f). It is possible that this state is a stage on the way from benthic feeding, using the setose limbs to scrape minute epiflora from the substrate, to plankton feeding. The alternate hypothesis is that the straight body has been secondarily derived and another use found for reduced filtering setae. The condition is seen, for example, in two very different genera like *Austroarcturus* and *Xenarcturus,* which feed on the benthos. The body in *Arcturus* and *Antarcturus* is sigmoid, there being only a slight change in angle between the longitudinal axes of pereionites 4 and 5 while the animal is at rest. While it is probable that this condition evolved only once in the arcturoids, there are differences in degree between the state in *Antarcturus* (Fig. 1g) and *Arcturus* and that in more derived arcturids. In *Neastacilla* (Fig. 1h) and *Parastacilla,* for example, these two segments are strongly geniculate, virtually at right angles to each other with no possibility of the animal resting horizontally. This highly derived condition occurs only within the *Arcturus*-group and is not scored.

The typical isopod is oval in dorsal view, widest at pereionites 3 and 4, with the body tapering posteriorly to the end of the pleotelson (character 2, state 0; Fig. 1c). In the Holognathidae the body including the pleotelson is parallel-sided over most of its length (state 2; Fig. 1d). This is an autapomorphy of this family (Poore and Lew Ton, 1990). In members of some other families the pereion may be more or less parallel-sided or the body cylindrical but the pleotelson rarely tapers to a rounded apex.

Fusion of pereionite 1 with the head (character 3, state 1; Fig. 1e–h) is a synapomorphy of the arcturoids, without exception. The same condition is seen convergently in two unrelated genera of Idoteidae, *Crabyzos* (Poore and Lew Ton, 1993) and *Lyidotea* (Hale, 1929) but in these cases is not associated with the smaller pereiopod 1.

Prominent flat lateral lobes on the head, sometimes with an ocular notch (character 4, state 1; Fig. 1c) are a synapomorphy of Chaetiliidae (Poore, 1985), all other families having the head more or less cylindrical or semi-cylindrical (state 0).

Pereionite 4 is of a similar length to other pereionites in all valviferans (character 5, state 0) except in the *Arcturus*-group (Fig. 1h). In this group, pereionite 4 is usually at least 1.5 times as long as pereionite 3 and in males often much longer (state 1; Fig. 1h). The degree of elongation varies, but in species of the flattened genus *Arcturinoides* no elongation is evident (Kensley, 1977). This one case must be treated as a reversal.

Fusion of the pleonites (character 6) varies considerably between genera. Early workers did not differentiate between pleonal sutures that allowed articulation between segments and those that were simply cuticular indications of divisions between fused pleonites. Poore and Lew Ton (1990, 1993) resolved this differentiation for the Holognathidae and Idoteidae, where it is important in defining genera. On the assumption that fusion is more derived than articulation, families were scored for the most plesiomorphic state known. In no valviferan family are five pleonites free and articulating. Fusion of pleonite 6 with the telson is a synapomorphy of the Isopoda. The most plesiomorphic condition, where pleonites 1–4 articulate with each other and with fused remaining segments of the pleotelson, is seen in some Chaetiliidae (state 0; Fig. 1c). Other pleonites are sometimes indicated by complete or lateral suture lines but do not articulate. As many as three free pleonites is the case in Holognathidae (state 1; Fig. 1d). The most plesiomorphic state in Idoteidae is where two pleonites articulate with each other and the pleotelson. In this family as many as three other pleonites may be indicated by full or partial sutures (state 2) or all pleonites may be fused. In most arcturoids all pleonites are fused into the pleotelson, others being sometimes indicated by lateral incisions (state 4; Fig. 1f–h). A rare intermediate condition in arcturoids, where only the first pleonite articulates with the pleotelson, is found in *Austroarcturus* (Poore, in preparation) and most species of *Dolichiscus* (state 3; Poore, 1998). These two genera are not otherwise similar, and it seems probable that the state is a reversal.

Pleonite 1 is generally of a similar length to pleonite 2 (character 7, state 0), but it is longer than pleonite 2 (state 1) in *Dolichiscus* (Poore, 1998).

Specific features of body sculpture are generally too variable to be useful in a family-level analysis. Idoteids and holognathids tend to be smooth although dorsal crests are seen in some idoteid genera. Some genera of Chaetiliidae are quite smooth while others are dorsally ornamented (Poore, 1984, 1985). Arcturoids may be tuberculate or spinose, and sculpture may indicate generic relationships (Brandt, 1990). Only two characters were found to be informative. The sculpture of members of the *Antarcturus*-group is strongly spinose, with at least dorsal and dorsolateral pairs of spines, often dominated by a larger pair near the end of the pleotelson (character 8, state 1; Fig. 1g). This pattern is found in various forms among the genera included here in the antarcturids (Brandt, 1990). If it is assumed that this is a synapomorphy of this group of genera, some reduction in spination must be accepted in genera such as *Cylindrarcturus*. However, none of the potential sister taxa have this type of ornamentation. The following character contrasts.

The pleotelson of arcturoids usually ends in a distal acute apex, and if otherwise ornamented, bears pairs of tubercles or spines. Austrarcturellidae (Poore and Bardsley, 1992) and *Dolichiscus* (Poore, 1998) share a unique condition in which the pleotelson bears dorsolateral ridges ending in middorsal posterior spine above the apex (character 9, state 1; Fig. 1e). The pattern, especially the degree of spination, is variable, and the pleotelson was referred to as "boat-shaped" by Poore and Bardsley (1992).

Lateral extensions of the terga or of the coxae over the bases of the pereiopods and of epimera over the pleopods are typical of most isopods. This is the situation in most idoteoids (character 10, state 0; Fig. 1a) although there is variation in these families between whether the terga or the coxae are implicated (and on what pereionites). There is also reduction of the size of dorsal coxal plates in genera such as *Paridotea* (Poore and Lew Ton, 1993). In arcturoids, on the other hand, dorsal coxal plates are obsolete and bases of pereiopods are exposed (state 1; Fig. 1e–h). Here, too, there are exceptions as in *Holidotea* and *Austroarcturus* in which tergal expansions on pereionites 2–4 reflect some idoteids (character 11, state 1; Fig. 1b). A similar convergence is seen in the undoubted arcturid *Arcturinoides* (Kensley, 1977).

Mouthparts and pereiopod 1 are primitively visible in lateral view in arcturoids (character 12, state 0; Fig. 1g). Correlated with the reduction of pereiopod 1 is a secondary expansion of lateral plates of head and pereionite 1 so that the mouthparts and pereiopod 1 are not visible laterally (state 1; Fig. 1h).

Loss of eyes occurs frequently in Isopoda, especially in deep-sea species and is rarely of family value. Idoteoid valviferans are shallow-water species, but reduced or lost eyes is general for Chaetiliidae (character 13, state 1; Fig. 1c). Blind valviferans occur also in arcturid, antarcturid, and austrarcturellid genera.

The flagellum of antenna 2 is plesiomorphically multiarticulate, terminating in a simple setose article (character 14, state 0; Fig. 1g). This is the state seen in most idoteoids, but three of the four genera of Holognathidae and some of those of Idoteidae possess a clavate flagellum of a major and minor article (Poore and Lew Ton, 1990, 1993). This state is not informative at the family level. The more specialised condition where the flagellum is of two or three articles plus a distal curved non-setose claw (state 1; Fig. 1 e, h) is true of most arcturoids. However, the plesiomorphic condition is seen in *Antarcturus* and all similar genera, and in *Dolichiscus*.

The structure of mandibles and maxillae is uninformative at the family level and rarely so at the genus level. Valvifera are characterised by absence of the mandibular palp and this is true with only one exception. The species *Holognathus stewarti* (Filhol) is unique in the suborder in possessing a palp; its sister species *H. karamea* does not (Poore and Lew Ton, 1990). The only family in which the mandibular molar and incisor structure varies is Chaetiliidae (Poore, 1985), but the most plesiomorphic condition resembles that in all other families. The maxillipedal palp is informative at the generic level but rarely for families. The most plesiomorphic condition, palp of five articles, is found in all families and is universal in arcturoids. Reduction in this number is usual in idoteoids, but Poore and Lew Ton (1990, 1993) showed that Holognathidae and Idoteidae differed in how this fusion occurred. There are differences too between genera of Chaetiliidae. The maxillipedal epipod is usually as long as or longer than wide (character 15, state 0), but in Chaetiliidae is shorter than wide. In arcturoids the palp is usually evenly tapering (character 16, state 0) but in two genera, *Holidotea* and *Austroarcturus,* article 3 is much wider than article 4 (state 1; Kensley, 1975).

Typical isopods, as the name implies, have all pereiopods much alike. In the plesiomorphic valviferan condition, pereiopod 1 is slightly differentiated from pereiopod 2, its propodus broader and with a setose mesial face (character 17, state 0; Fig. 2a). In the Chaetiliidae the pereiopods are variously differentiated, the first, first three, five or six subchelate (state 1; Fig. 2b). It is probable that differentiation of the chaetiliid pereiopods is independently derived in the various genera, but they do at least share a highly modified pereiopod 1. In most arcturoids pereiopod 1 is a small gnathopod (Fig. 2d), pereiopods 2–4 are elongated and all differentiated from ambulatory pereiopods 5–7 (state 3; Fig. 2f, h). Absence of pereiopods 3 and 4 was used to differentiate the species *Amesopous richardsonae* at the family level from Arcturidae (Stebbing, 1905). It and other species lacking one or more pereiopods are treated as derived within the *Arcturus*-group.

Setation of pereiopods of idoteoids is similar to that in most other isopods, short robust setae along the posterior margin of distal articles with occasional longer fine setae (character 18, state 0; Fig. 2j). The long, paired, evenly spaced filtering setae along the narrow carpus and propodus and sometimes dactylus of pereiopods 2–4 is a feature of many arcturoids (state 1; Fig. 2h) and is usually associated with the flexed body and feeding from the plankton. In *Rectarcturus* the body is straight and filter-setae numerous, while in *Holidotea* and *Austroarcturus* the setae are not as regular or as numerous (state 2; Fig. 2f). In these three genera with straight bodies, feeding is benthic, but it is uncertain whether few filter-setae is an evolutionary step that the filter-feeders went through or a secondary reduction—probably both. In *Pseudidothea* pereiopods 2–4 are raptorial (state 3; Fig. 2g).

A prominent dactylus and a short unguis is the plesiomorphic condition of pereiopods 2–4 (character 19, state 0; Fig. 2f, j). Within some arcturoids a short dactylus bearing a longer and setiform unguis is seen (state 1; Fig. 2h). The condition is carried to extreme in Austrarcturellidae where the dactylus is minute and the unguis setiform (state 2; Fig. 2i).

Pereiopod 4 is plesiomorphically similar to pereiopod 3 whether ambulatory or of the elongate form (character 20, state 0; Fig. 2j). Various autapomorphic states occur. In Holognathidae pereiopod 4 is shorter and more spinose than pereiopods 3 and 5 (state 1; Fig. 2k). In Austrarcturellidae it is shorter and less setose than pereiopods 2 and 3 (state 2; Fig. 2l), and in *Xenarcturus* it is different from pereiopod 3 but similar to pereiopod 5 (state 3; Sheppard, 1957).

The dactylus of pereiopod 1 is plesiomorphically evenly curved (character 21, state 0), but in *Dolichiscus* and Austrarcturellidae it bears an anterior lobe distinct from a tapering end bearing the unguis (state 1; Fig. 2e).

The pereiopods of male isopods are rarely different from those of females (except that the mesial face of the propodus of pereiopod 1 is often more setose). In many sphaeromatids and serolids, some pereiopods of males carry a dense fur of fine setae along the posterior margin of distal articles, the extent of this depending on species. As these families are probable members of the sister taxon of Valvifera, the presence of this fur in Idoteidae and Holognathidae is considered plesiomorphic (character 22, state 0; see, e.g., Poore and Lew Ton, 1993: Fig. 48). Absence of this kind of male differentiation in arcturoids is apomorphic (state 1).

The number of uropodal rami is not useful to differentiate families, two rami being the plesiomorphic condition in all families. Loss of the exopod occurs in two of four genera of Holognathidae, all genera except *Austridotea* in Idoteidae (Fig. 2p), never in Chaetiliidae, and less frequently in arcturoids. When present, the exopod is oval with all margins setose in idoteoids (character 23, state 0; Fig. 2m) but is always tapering and with distal setae only in arcturoids (state 1; Fig. 2n). Extreme reduction of the exopod to a very short article bearing a single prominent robust seta (the endopod also with a robust seta) is a characteristic of three genera (character 24, state 1; Fig. 2o).

The plesiomorphic marsupium comprises broad overlapping oostegites on pereiopods

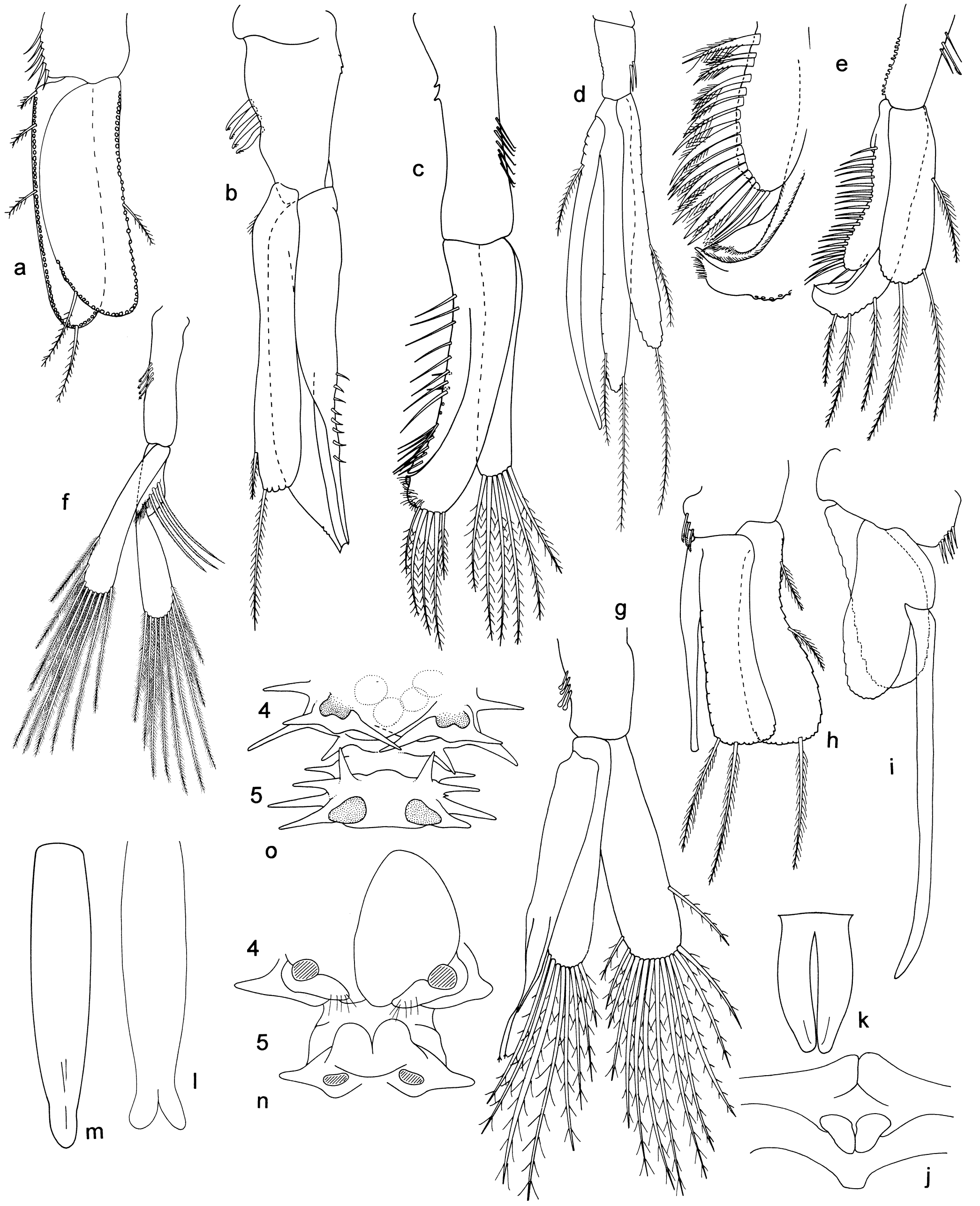

Fig. 3. Male pleopods 1. a, *Idotea* (Idoteidae); b, *Pseudidothea* (Pseudidotheidae); c, *Mixarcturus* (Antarcturidae); d, *Austrarcturella* (Austrarcturellidae); e, *Austroarcturus* (Holidoteidae) with detail; f, *Astacilla* (Arcturidae). Male pleopod 2. g, *Arcturopsis* (Arcturidae); h, *Austroarcturus* (Holidoteidae); i, *Chaetilia* (Chaetiliidae). Penes and penial plates. j, *Chaetilia* (Chaetiliidae) on pereionite 7; k, *Paridotea* (Idoteidae); l, *Austroarcturus* (Holidoteidae); m, *Dolichiscus* (Austrarcturellidae). Ventral views of pereionites 4 and 5 with oostegites. n, *Austrarcturella* (Austrarcturellidae) with left oostegite 4 and paired oostegites 5; o, *Dolichiscus* (Austrarcturellidae) with edges of oostegites 4, coxal supports and no oostegite 5.

1–5 (character 25, state 0). In highly geniculate species oostegites 5 cannot play a part in holding the eggs and young so is absent completely (state 2; Fig. 3o). Intermediate states are found where oostegites 5 are fleshy lobes which appear to act only as egg guides between the oopores on pereionite 5 and the marsupium (state 1; Fig. 3n). There is some variability within families. *Arcturus,* for example, is the only member of the *Arcturus*-group with functional fifth oostegites; its absence is typical of other members of the family where oostegite 4 dominates in formation of the marsupium (Fig. 1h). Five pairs of oostegites are typical of Idoteidae, but *Synidotea* is unique within this family in possessing only four pairs (Poore and Lew Ton, 1993). In many arcturoids the marsupium is supported by mesially directed extensions of the coxal plates (character 26, state 1; Fig. 3o).

Penes are primitively paired digitiform appendages on the sternite of pereionite 7 (character 27, state 0; Fig. 3j). This condition is seen in Chaetiliidae, but in some genera the paired pores may open almost directly on the sternite. In Idoteidae and Holognathidae the penes are fused basally as a penial plate, divided over most of their length and attached on the posterior margin of pereionite 7 (state 1; Fig. 3k). In arcturoids there is a single elongate penial plate, rarely divided apically (state 2). This penial plate is usually simple (Fig. 3m) or split for a short distance apically, but in three genera it is apically bifid and splayed (character 28, state 1; Fig. 3l).

The major dichotomy between valviferan families is between the idoteoids, where the pleopod 1 peduncle is short and similar to those of pleopods 2–5 (character 29, state 0; Fig. 3a), and arcturoids, where it is more elongate than on other pleopods (state 1; Fig. 3b–f). Within the idoteoids, the Idoteidae differ from the others in having marginal setae on rami of pleopod 1 much shorter than the length of the rami (character 30, state 1; Fig. 3a), whereas setae are longer in the other families (state 0). The male pleopod 1 exopod is laminar like the endopod in the *Arcturus*-group (character 31, state 0; Fig. 3f) but strongly thickened and with a groove on its posterior face in other arcturoid families (state 1; Fig. 3b, c, e).

The pleopod 1 exopod of males of most arcturoids has few simple setae along a straight lateral margin (character 32, state 0; Fig. 3c); in the three genera that comprise the Holidoteidae, there are complex overlapping rows of simple and plumose setae along the lateral margin, terminating at a subdistal excavation (state 1; Fig. 3e). The position of the end of the groove on the posterior face of exopod of pleopod 1 of males is variable and will prove valuable in differentiating genera in the higher arcturoids. Plesiomorphically it ends distolaterally or laterally on a simple margin (character 33, state 1; Fig. 3c), and this is the condition in the *Antarcturus*-group. *Austroarcturus* and *Neoarcturus* are similar in that the groove ends in a deep subdistal excavation (state 1; Fig. 3e). In *Holidotea* it ends on a distolateral rounded tip, separated from most of lateral margin by a notch (state 2). In austrarcturellids but not *Dolichiscus,* the groove is carried on a basally derived branch of the exopod (state 3; Fig. 3d), and in three genera the exopod tapers to a distolateral apical extension (state 4; Fig. 3b). Homologies between the various structures involved in the apex of the exopod are difficult to determine. A unique apomorphy of the *Arcturus*-group is a lateral excavation on the male pleopod 1 exopod (character 34, state 1; Fig. 3f). In many genera, but not in *Arcturus*, two or three long oblique setae attach near this excavation.

The appendix masculina on pleopod 2 of males is usually about as long as the endopod (character 35, state 0; Fig. 3h) but can be twice its length (state 1; Fig. 3i). The appendix masculina is typically basally less than half the width of the endopod (character 36, state 0) but in the *Arcturus*-group is basally as wide or wider than the endopod (state 1; Fig. 3g). The nature of appendages and grooves on the appendix masculina is useful for diagnosing genera. For example, it is apically club-shaped in *Neoarcturus* (character 37, state 1).

Results of Phylogenetic Analysis

The cladogram (Fig. 4a) provides a well-resolved hypothesis about relationships between the families and genera of Valvifera. Using unweighted and unordered characters, six equal-length trees of 60 steps were discovered. The strict consensus tree (60 steps, CI = 0.82 excluding uninformative characters, RI = 0.88) supported three basal clades whose relationships were not further resolved: Chaetiliidae; Idoteidae + Holognathidae as sister taxa; and an arcturoid clade. The *Arc-*

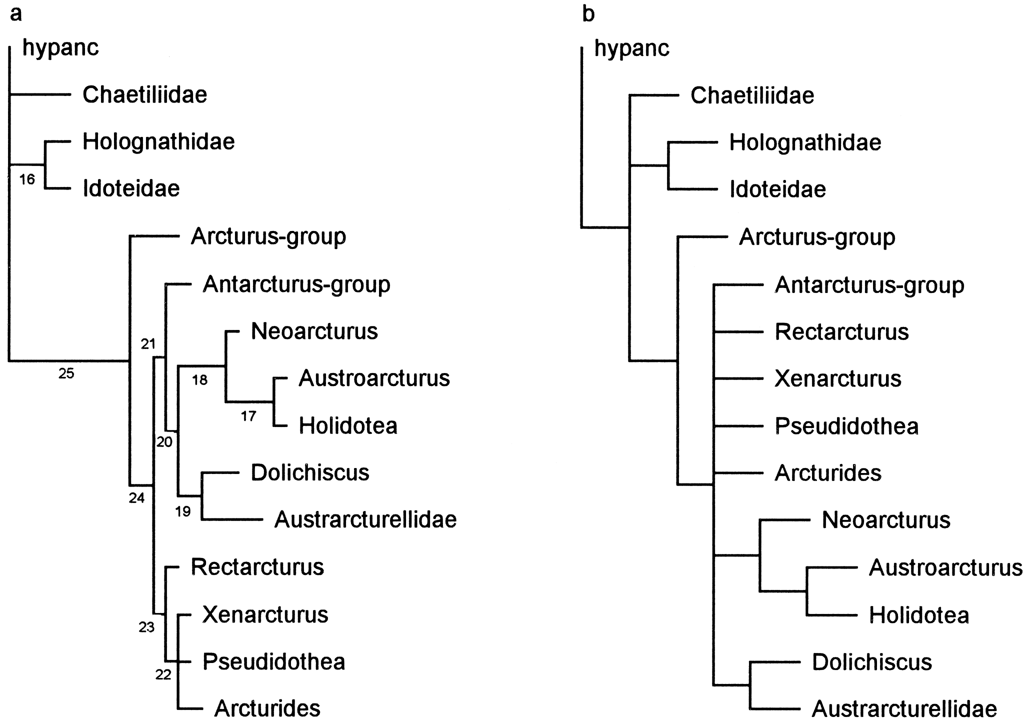

Fig. 4. Cladograms depicting relationships between families, genus-groups, and genera of Valvifera derived by Paup*. a, strict consensus tree, clade lengths (numbered as in Table 3) are proportional to the numbers of steps supporting them; b, 50% majority rule consensus tree from bootstrap analysis, clade lengths are proportional to bootstrap values. Both trees are rooted against a hypothetical ancestor.

turus-group is sister taxon to all other arcturoids. Within the remaining arcturoids are two clades: *Rectarcturus,* sister taxon to *Xenarcturus* + *Pseudidothea* + *Arcturides;* and a fully resolved clade comprising the remaining genera. Of these, *Antarcturus* is sister taxon to the rest, one clade comprising *Dolichiscus* + Austrarcturellidae and another *Neoarcturus* + *Austroarcturus* + *Holidotea*. The clades of the bootstrap analysis are not as well resolved (Fig. 4b). Bootstrap values varied ±2% over four Paup* runs.

The 60 synapomorphies of the clades in Fig. 4a are listed in Table 3 and discussed below. Family autapomorphies are considered in the Systematics section.

Idoteidae + Holognathidae (clade-16), with 78% bootstrap support, share: at least pleonites 1–3 articulating with each other and fused pleotelson; and a fused penial plate divided over most of its length.

The arcturoids (clade-25), with 100% bootstrap support, are well defined by 11 synapomorphies, as follows: dorsal coxal plates 2–7 obsolete, bases of pereiopods exposed laterally (body usually cylindrical); pereiopods differentiated, pereiopod 1 a gnathopod, pereiopods 2–4 usually with paired long setae along posterior margins, and pereiopods 5–7 ambulatory; pereiopods of males with a dense fur of fine setae on some articles; head and pereionite 1 fused; all pleonites fused into pleotelson (rarely reversed); antenna 2 flagellum of 2 or 3 articles plus distal claw (sometimes multiarticulate); uropodal exopod tapering (with terminal setae only); a fully fused penial plate; and pleopod 1 peduncle more elongate than on other pleopods.

Clade-24, containing all the arcturoids except the *Arcturus*-group, has 70% bootstrap support and two synapomorphies: oostegites 5 absent, and the exopod of the male pleopod 1 thickened and with a groove on its posterior face. A reversal to oostegites 5 being present as vestigial lobes seems probable for some genus-groups.

Clades-21 and 20 (not supported by the bootstrap analysis) have one synapomorphy

Table 3. Synapomorphies of each clade and taxon in the strict consensus cladogram generated by PAUP* (Fig. 4a). Unannotated characters change from state 0 to state 1, a minus sign indicates a reversal from 1 to 0, and superscripts other changes from 0 or another state to a second.

Clade number or taxon	Characters changing
clade-16	6, 27
Holognathidae	2, 20
Idoteidae	$6^{1>2}$, 30
Chaetiliidae	4, 13, 15, 17, 35
clade-25	12^2, 3, 6^4, 10, 14, 17^2, 18, 22, 23, 27^2, 29
Arcturus-group	5, 12, 34, 36
clade-24	25^2, 31
clade-21	26
clade-20	19
clade-18	24, 28, 32, 33
clade-17	$1^{2>1}$, 11, 16, $18^{1>2}$
Austroarcturus	$6^{4>3}$
Holidotea	$33^{1>2}$
Neoarcturus	37
clade-19	9, 21
Dolichiscus	$6^{4>3}$, 7, –14
Austrarcturellidae	$19^{1>2}$, 20^2, $25^{2>1}$, 33^3, 35
Antarcturus-group	8, –14
clade-23	$1^{2>1}$
Rectarcturus	19
clade-22	33^4
Xenarcturus	20^3
Pseudidothea	$18^{1>3}$
Arcturides	–18, 26

each: oostegites supported by coxal lobes, and pereiopods 2–4 with short dactylus respectively.

Clade-18 (*Neoarcturus* + *Austroarcturus* + *Holidotea*), with 91% bootstrap support, is well defined by four synapomorphies, all with CI = 1: uropod exopod very short, both rami each bearing a single, prominent robust seta; penial plate apically bifid and splayed; pleopod 1 exopod of male with overlapping rows of simple and plumose setae along lateral margin, terminating at subdistal excavation, and with its groove ending in deep subdistal excavation.

The original Austrarcturellidae plus *Dolichiscus* (clade-19), with 76% bootstrap support, is defined by two synapomorphies, each with CI = 1: pleotelson with dorsolateral ridges usually ending in middorsal posterior spine; and pereiopod 1 dactylus usually with an anterior lobe.

Clade-23, without bootstrap support, depends on a reversal from a flexed to a straight body retaining differentiated setose pereiopods 2–4 while pereiopods 5–7 are ambulatory.

Finally, clade-22 (*Xenarcturus* + *Pseudidothea* + *Arcturides*), also without bootstrap support, shares one unique synapomorphy: pleopod 1 of male with the groove on the posterior face of exopod ending on tapering distolateral apical extension.

Comparison with Other Views

Sheppard (1957) discussed the similarities between some families and genera of Valvifera but did not propose a phylogeny. She interpreted the structure of coxae, oostegites, and penial processes. Recent views of the phylogeny of the Valvifera suffer from a narrow view of the Holognathidae (one species with a mandibular palp) now shown to be restrictive (Poore and Lew Ton, 1990). Brusca (1984) (reported as the traditional system by Wägele (1989)) treated the Holognathidae as sister taxon to all other families that lack a mandibular palp. This observation is no longer true if the expanded Holognathidae is accepted (Poore and Lew Ton, 1990).

Brusca's cladogram is a very different view of valviferan relationships from that presented here. He treated Idoteinae and the "glyptonotine-group" (= Chaetiliidae) as sister taxa of Idoteidae sharing reduced maxillipedal palp. It is true that some genera of the three families Idoteidae, Chaetiliidae, and Holognathidae have fewer than five articles in the maxillipedal palp and that this never happens in the arcturoids. However, the most plesiomorphic condition (five articles) occurs in all three families, and this is not a character in my analysis. The propensity to fuse articles is a synapomorphy of the idoteoid families, but fusion itself is not. Brusca recognised the monophyly of the arcturoids sharing a copulatory function for the male pleopod 1, fusion of the head with pereionite 1, and elongation of the peduncle of pleopod 1. However, there is no similarity between his cladogram relating the four arcturoid families he recognised and the one presented here.

Wägele's (1989: Fig. 63) treatment of the idoteoids maintained the ancestry of *Holognathus* and placed the Chaetiliidae as sister taxon to Idoteidae (including most Holognathidae) plus arcturoids, very different from my analysis. His treatment of Arcturidae (= arcturoids) (1989: Fig. 67, 68) recognised four subfamilies. Three of these are smaller groups more or less similar to the families recognised here: Holidoteinae (to which I add another genus), Pseudidotheinae (from which I separate *Arcturides*), and monotypic Xenarcturinae. His cladogram of Arcturinae was weakly resolved but recognised the similarity between *Pseudarcturella* and *Dolichiscus* (now Austrarcturellidae) and the monophyly of the *Acturina-Parastacilla-Astacilla*-group, which share an elongated pereionite 4. This last group I call the Arcturidae, *sensu stricto,* and place as sister taxon to all other arcturoids, a different scheme from that of Wägele. My new phylogeny places *Arcturus* and *Antarcturus* in very different families (see, too, Nordenstam (1933)); Wägele (1989) suggested that they possibly shared a secondarily elongated antenna 2 with multiarticulate flagellum.

Systematics

Nomenclatural implications that flow from this analysis are influenced by the retention of existing family-level names. Thus, Idoteidae, Holognathidae, and Chaetiliidae remain as recently treated by most authors. Arcturidae, which until now included most of the remaining valviferan genera, is here confined to the smaller *Arcturus*-group. Wägele's (1989) Holidoteinae, erected for *Austroarcturus* and *Holidotea* must be expanded to include *Neoarcturus* and elevated to full family rank. The Austrarcturellidae is expanded to include *Dolichiscus* which is clearly more similar to this group of genera than to any other. *Xenarcturus* is the only genus in Xenarcturidae, and *Pseudidothea* is the only one in Pseudidotheidae. The two are similar to *Arcturides,* but none of the phylogenetic hypotheses provides good support for including this genus in either family. I propose a third family, Arcturididae, for it.

The *Antarcturus*-group and *Rectarcturus* clades remain independent of all others, and new families are proposed for each, Antarcturidae and Rectarcturidae.

The characters and states used for the phylogenetic analysis were used for preparing a character file for DELTA treatment (Dallwitz *et al.,* 1997). The number of taxa was reduced from 14 to 11, the number of families recognised, and some characters appropriately edited to accommodate this change. Diagnoses were prepared directly; there are no implicit characters. The order of the families in the following text follows that in the key.

Suborder Valvifera Sars, 1882

Diagnosis.—Isopoda with uropods attached laterally to pleotelson, folding under and enclosing pleopods. Pleonite 5 (and often others) fused with pleotelson. Mandibular palp absent (1 exception).

Remarks.—One unique synapomorphy defines all Valvifera, the way in which the uropod is rotated and folded under the pleotelson to enclose the pleopods in a branchial chamber. The uropods are posterior, lateral, and styliform or flattened in other suborders. Branchial chambers are found in other suborders but are variously formed by operculiform pleopods. A second character involves pleonites. Some pleonites are often fused with the pleotelson, sometimes all pleonites, but the most plesiomorphic condition is fusion of pleonite 5 with the pleotelson. Pleonite fusion is seen to various degrees in other suborders. A third character state, absence of the mandibular palp, is a synapomorphy seen in many other isopods. There is only one valviferan species (*Holognathus stewarti*) out of more than 500 described carrying a palp, and this is certainly a reversal of the subordinal synapomorphic state (Poore and Lew Ton, 1990).

A review of the systematics and phylogeny of the group (Brusca, 1984) recognised six families (one, the Idoteidae with five subfamilies) but recent revisions (Wägele, 1989; Poore and Lew Ton, 1990, 1993; Poore and Bardsley, 1992) suggested that his was not a satisfactory taxonomic arrangement.

Key to Families of Valvifera

1. Head free from pereionite 1 (rarely fused) (Fig. 1a, b, d); pereiopod 1 subchelate and similar to (Fig. 2a) or larger than pereiopod 2 (Fig. 2b); pleopod 1 peduncle not elongate (Fig. 3a); with separate penes or penial plate fused only basally 2
– Head fused with pereionite 1 (Fig. 1e–h); pereiopod 1 smaller than pereiopod 2, sometimes gnathopod-like, very different in structure from pereiopod 2 (Fig. 2c, d); pleopod 1 peduncle elongate (Fig. 3b–f); with penial plate bifid apically if at all . . . 4
2. Pereiopods 1, 1–3, 1–5 or 1–6 subchelate or prehensile (Fig. 1b) and different from remaining limbs; head with flat lateral lobes, sometimes notched (Fig. 1c); uropod with 2 rami (Fig. 2m) . . . Chaetiliidae
– Only pereiopod 1 subchelate (Fig. 2a), others ambulatory; head without flat lateral lobes, never deeply notched (Fig. 1d); uropod with 1 (Fig. 2m) or 2 rami 3
3. Pereiopod 4 similar to other pereiopods (Fig. 2j); body oval or elongate; pleotelson posteriorly acute, rarely rounded . . . . Idoteidae

– Pereiopod 4 shorter than others and with spinose distal articles (Fig. 2k); body more or less parallel-sided; pleotelson posteriorly rounded (Fig. 1d) . . . . Holognathidae

4. Pereiopod 1 coxal plate and head expanded ventrally (Fig. 1h) and enclosing gnathopod-like pereiopod 1 (Fig. 2d); male pleopod 1 exopod laminar, with lateral notch, a tuft of fine setae, 2 or 3 long plumose setae, or a combination of these (Fig. 3f) . . . . Arcturidae

– Pereiopod 1 coxal plate not expanded to enclose pereiopod 1 (Fig. 1g); pereiopod 1 a grasping limb (Fig. 2c); male pleopod 1 exopod thickened, with groove (Fig. 3b, c, e) or with lateral secondary ramus (Fig. 3d) 5

5. Uropodal rami each with apical strong robust seta, exopod minute, shorter than wide (Fig. 2o); penial plate apically bifid and splayed (Fig. 3l); exopod of male pleopod 1 with overlapping rows of simple and plumose setae along lateral margin, terminating at subdistal excavation into which groove opens (Fig. 3e); body cylindrical or often flattened (Fig. 1b) . . . . Holidoteidae

– Uropodal rami, if present, without apical strong robust seta, exopod longer than wide, usually with 2 or 3 long apical setae (Fig. 2n); penial plate apically simple or weakly bifid (Fig. 3m); exopod of male pleopod 1 with simple row of setae along lateral margin; groove opens distolaterally or laterally (Fig. 3c); body cylindrical or rarely flattened (Fig. 1e–h) . . . 6

6. Body strongly geniculate between pereionites 4 and 5 (Fig. 1e, g, h) 7

– Body straight, not flexed between pereionites 4 and 5 (Fig. 1f) 8

7. Pleotelson variously sculptured, often with paired posterior pleotelsonic spines (Fig. 1g), but without single medial posterior spine dorsal to apex; pereiopods 2–4 with dactylus strong, unguis short (rarely setiform) (Fig. 2h); pereiopods 2–4 similar; pleonite 1 not articulating with pleotelson; groove on exopod of male pleopod 1 opening distolaterally or laterally . . . . Antarcturidae

– Pleotelson with dorsolateral ridges usually ending in middorsal posterior spine dorsal to apex (or transverse ridge of spines) (Fig. 1e); pereiopods 2–4 with dactylus shortened, unguis setiform, longer than dactylus (Fig. 2i); pereiopod 4 usually smaller and less setose than pereiopods 2 and 3 (Fig. 2l); pleonite 1 weakly or not articulating with pleotelson; groove on exopod of male pleopod 1 opening distolaterally or exopod with prominent basally derived lateral lobe . . . . Austrarcturellidae

8. Body dorsoventrally flattened, dorsally setose, without spines; pereiopods 2 and 3 with even rows of long setae, pereiopods 4–7 ambulatory . . . Xenarcturidae

– Body cylindrical, ornamented; pereiopods 2–4 differentiated from ambulatory pereiopods 5–7 or pereiopods 2–7 ambulatory 9

9. Pereionites cylindrical, longer than wide, each with paired simple dorsal spines; pereiopods 2–7 similar, ambulatory . . . . Arcturididae

– Pereionites wider than long, with complex dorsal plate-like spination (Fig. 1f); pereiopods 2–4 differentiated from ambulatory pereiopods 5–7 . . . 10

10. Pereiopods 1–4 with strong robust setae on broad articles, dactyli with short unguis (Fig. 2g); exopod of male pleopod 1 with groove ending on curved distolateral apical extension (Fig. 3b) . . Pseudidotheidae

– Pereiopods 2–4 with weak rows of long setae, dactyli with long, setiform unguis; exopod of male pleopod 1 with groove ending distolaterally (Fig. 3c) . . . . Rectarcturidae

Chaetiliidae Dana, 1853

Chaetiliidae Dana, 1853: 711.—Poore, 1985: 154 (synonymy).

Diagnosis.—Body straight, more or less flattened or semicylindrical, or strongly vaulted; tapering posteriorly. Head and pereionite 1 free. Head with prominent flat lateral lobes, sometimes with ocular notch. Pereionite 4 of similar length to pereionite 3. Pleonites 1–4 articulating with each other and fused pleotelson, or pleonites 1–3 articulating with each other and fused pleotelson, or pleonites 1 and 2 articulating with each other and fused pleotelson (other pleonites sometimes indicated laterally or dorsally). Body smooth or slightly sculptured, or variously spinose or rugose. Dorsal coxal plates 2–7 more or less ventrally expanded over bases of pereiopods, or 5–7 expanded over bases of pereiopods and tergites marginal on pereionites 2–4. Eyes reduced or lost.

Antenna 2 flagellum multiarticulate (sometimes of few articles). Maxillipedal epipod shorter than wide. Pereiopods differentiated, 1, 1–3, 1–5, or 1–6 subchelate. Pereiopods 2–4 with irregular fine setae and marginal robust setae. Pereiopods of males without dense fur of fine setae. Uropodal exopod (smaller ramus) ovate, fringed with setae (if present), more than half as long as endopod, or rami styliform.

Oostegites 1–5 functional (as far as known). Penes paired, widely separate (sometimes obsolete). Pleopod 1 peduncle short (similar to other pleopods); with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male laminar. Pleopod 2 of male with appendix masculina twice length of endopod, basally less than half width of endopod.

Included Genera (with numbers of described species).—*Austrochaetilia* Poore, 1978 (1); *Chaetilia* Dana, 1849 (4); *Chiridotea* Harger, 1878 (6); *Glyptonotus* Eights, 1852 (1); *Macrochiridothea* Ohlin, 1901 (11); *Maoridotea* Jones and Fenwick, 1978 (1); *Parachiridotea* Daguerre de Hureaux and Elkaïm, 1972 (1); *Proidotea* Racovitza and Sevastos, 1910 (1); *Saduria* Adams, 1852 (4); *Saduriella* Holthuis, 1964 (1); *Stegidotea*

Poore, 1985 (6); *Symmius* Richardson, 1904 (3) (40 species in all).

Remarks.—Several synapomorphies define the Chaetiliidae. The flattened shape relative to idoteids is reliable for some genera, whereas others are quite deep. All have lateral lobes on the head. The eyes are often lost and never as well developed as in Idoteidae or Holognathidae. The presence of subchelate limbs is regarded as synapomorphic, but the number and shape of the prehensile propodus and dactylus do vary between genera. As far as is known the appendix masculina is much longer than the endopod of pleopod 2.

Poore (1984) listed the genera then known as "non-idoteine Idoteidae" but mistakenly included *Austridotea* and *Notidotea,* treated as synonymous and idoteids here. Later, I reviewed the status of the family, synonymising the five subfamilies of Idoteidae, which it comprises (Poore, 1985). Wägele (1989: Fig. 62) presented a dendrogram and discussion of the genera.

Members of the Chaetiliidae are marine benthic species of sandy beaches, shelf or deep-sea environments. The family includes the only known valviferan fossil species, *Proidotea haugi*.

Holognathidae Thomson, 1904

Holognathidae Thomson, 1904: 67.—Poore and Lew Ton, 1990: 58.

Diagnosis.—Body straight, more or less flattened or semicylindrical; parallel-sided over most of length. Head and pereionite 1 free. Head more or less semi-cylindrical. Pereionite 4 of similar length to pereionite 3. Pleonites 1–3 articulating with each other and fused pleotelson, or pleonites 1 and 2 articulating with each other and fused pleotelson, or pleonite 1 articulating with fused pleotelson (other pleonites sometimes indicated laterally or dorsally). Body smooth or slightly sculptured. Dorsal coxal plates 2–7 more or less ventrally expanded over bases of pereiopods. Eyes well developed, or reduced or lost (*Zenobianopsis* only).

Antenna 2 flagellum multiarticulate, or clavate (usually with minute terminal article(s)). Maxillipedal epipod as long as or longer than wide. Pereiopod 1 slightly differentiated from pereiopod 2, its propodus broader than in pereiopod 2. Pereiopods 2–4 with irregular fine setae and marginal robust setae; with prominent dactylus, unguis short; pereiopod 4 shorter and more spinose than pereiopods 3 and 5. Pereiopods of males with dense fur of fine setae. Uropodal exopod (smaller ramus) ovate, fringed with setae (if present), more than half as long as endopod.

Oostegites 1–5 functional. Penes fused basally as a penial plate but divided over most of length. Pleopod 1 peduncle short (similar to other pleopods); with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male laminar. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Included Genera (with numbers of described species).—Cleantioides Kensley and Kaufman, 1978 (13); *Cleantis* Dana, 1849 (8); *Holognathus* Thomson, 1904 (2); *Zenobianopsis* Hale, 1946 (2) (25 species total).

Remarks.—Poore and Lew Ton (1990) removed genera from the Idoteidae and grouped them on the basis of body-plan and specialised pereiopod 4, synapomorphies of the family. They provided a key to genera and listed all species. This is the only family in which a species with a mandibular palp is found.

Shallow-water species of *Cleantis* and *Cleantioides* are often associated with seagrasses and live in short segments of the dead hollow stems of these plants. *Holognathus* from the shelf of New Zealand is thought to be associated with wood. *Zenobianopsis* is a deep-water Antarctic genus.

Idoteidae Samouelle, 1819

Idoteadae Samouelle, 1819: 106.
Idoteidae.—Kussakin, 1982: 71, 72.—Brusca, 1984: 106 (for synonymy).—Poore and Lew Ton, 1993: 199.

Diagnosis.—Body straight, more or less flattened or semicylindrical, or strongly vaulted; tapering posteriorly. Head and pereionite 1 free, or fused (*Crabyzos, Lyidotea* only). Head more or less semicylindrical. Pereionite 4 of similar length to pereionite 3. Pleonites 1 and 2 articulating with each other and fused pleotelson, or pleonite 1 articulating with fused pleotelson, or all pleonites fused into pleotelson (other pleonites sometimes indicated laterally or dorsally). Body smooth or slightly sculptured, or variously spinose or rugose. Dorsal coxal plates 2–7 more or less ventrally expanded over bases of pereiopods (coxal plates often very reduced), or 5–7 expanded over bases of pereiopods and tergites marginal on pereionites 2–4 (*Synidotea* only), or 2–7 obsolete and with expanded marginal tergites (*Synischia* only). Eyes well developed, or reduced or lost.

Antenna 2 flagellum multiarticulate, or clavate (usually with minute terminal article(s)). Maxillipedal epipod as long as or longer than wide. Pereiopod 1 slightly differentiated from pereiopod 2, its propodus broader than in pereiopod 2. Pereiopods 2–4 with irregular fine setae and marginal robust setae; with prominent dactylus, unguis short; pereiopod 4 similar to pereiopod 3. Pereiopods of males with dense fur of fine setae. Uropodal exopod (smaller ramus) ovate, fringed with setae (if present) (usually absent), more than half as long as endopod.

Oostegites 1–5 functional, or 1–4 functional, 5 absent (*Synidotea* only). Penes fused basally as a penial plate but divided over most of length, or fused as a single penial plate (*Synidotea* only), or paired, elongate (*Lyidotea* only). Pleopod 1 peduncle short (similar to other pleopods); with marginal setae on rami much shorter than length of rami. Pleopod 1 exopod of male laminar. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Included Genera (with numbers of described species).—Austridotea, new genus (4); *Batedotea* Poore and Lew Ton, 1993 (1); *Cleantiella* Richardson, 1912 (2); *Colidotea* Richardson, 1899 (4); *Crabyzos* Bate, 1863 (1); *Edotia* Guérin-Méneville, 1843 (18); *Engidotea* Barnard, 1914a (2); *Erichsonella* Benedict, 1901 (7); *Euidotea* Collinge, 1917a (8); ***Eusymmerus*** Richardson, 1899, new combination (2); *Glyptidotea* Stebbing, 1902 (1); *Idotea* Fabricius, 1798 (27); *Lyidotea* Hale, 1929 (1); *Moplisa* Moreira, 1974 (1); *Parasymmerus* Brusca and Wallerstein, 1979 (1); *Paridotea* Stebbing, 1900 (13); *Pentias* Richardson, 1904 (3); *Pentidotea* Richardson, 1905 (11); *Platidotea* Park and Wägele, 1995 (1); *Synidotea* Harger, 1878 (56); *Synischia* Hale, 1924 (2); *Synisoma* Collinge, 1917b (10) (176 species in all).

Remarks.—One genus name, *Austridotea, nomen nudum,* is formalised here with a short diagnosis. Its four species have been enigmatic, but a close comparison of abundant material of *A. lacustris* with *Idotea* discovered few generic differences. The most critical is the presence of two uropodal rami, making it the only idoteid genus to possess a uropodal exopod. In this and the presence of two free pleonites, it is the most plesiomorphic of idoteid genera.

The genus *Ronalea* Menzies and Bowman, 1956, is proposed as a junior synonym of *Eusymmerus*. Both share a tubercle on the head, similar maxilliped, and pleotelson. The only difference between the two species involved, in the shape of the coxae, is trivial.

The only identifiable synapomorphy of the family is the presence of short setae on the margins of the pleopods. All genera except *Austridotea* lack a uropodal exopod. The largest genus, *Synidotea,* differs from all the others in possession of a completely fused short penial plate, only four pairs of oostegites, and sexually dimorphic mouthparts.

Brusca (1984) discussed the phylogeny of the Idoteidae and Holognathidae together (as Idoteinae), and his work is a key source for identification of some genera and for biogeography. Wägele's (1989: Fig. 63) dendrogram and discussion did not resolve relationships between the genera. Poore and Lew Ton (1993) reinterpreted the structure of the pleon, a traditional character, and provided keys to the Australian and New Zealand species. It is probable that many species of *Idotea,* especially those with fused pleonites, do not belong to this genus.

Idoteids are shallow water species, and in Australia few species are found below 20 m depth. Most are associated with seagrass and algae and are probably herbivores. Diversity is highest in temperate waters of the Southern Hemisphere, and the most plesiomorphic genus, *Austridotea,* is confined to freshwater streams of southern New Zealand. Only the largest genus, *Synidotea,* is rich in species in the Northern Hemisphere.

Austridotea, new genus

Austridotea Nicholls, 1937: 115–118.—Hurley, 1961: 265 (*nomen nudum*).

Austridotea (*Austridotea*) Nicholls, 1937: 118 (*nomen nudum*).

Austridotea (*Notidotea*) Nicholls, 1937: 126–128 (*nomen nudum*).

Notidothea.—Nierstrasz, 1941: 280.

Notidotea.—Hurley, 1961: 266.

Type Species.—*Idotea lacustris* Thomson, 1879.

Diagnosis.—Pleon with 2 freely articulating, full-width pleonites and pleotelson, with 1 or 2 pleonites indicated laterally by partial suture. Antenna 1 flagellum of 1 clavate article. Antenna 2 flagellum multiarticulate. Maxillipedal palp with 5 articles, or articles 4 + 5 fused. Uropod with free exopod and endopod.

Remarks.—Nicholls (1937) proposed the generic name *Austridotea,* with subgenera *Austridotea* and *Notidotea,* for three species from New Zealand and one from southern South America without designating a type species. The genus-level names are therefore *nomina nuda* (ICZN Article 13(b)). This contribution makes *Austridotea* available. The genus has sometimes been treated as a member of the Chaetiliidae (Poore, 1991a) on the basis of the slightly flattened habitus, free pleonites, and possession of two uropodal rami. However, the pereiopods, mouthparts, and general body proportions of two species examined (*A. lacustris* (Thomson, 1879) and *A. benhami* Nicholls, 1937) are so similar to species of *Idotea* that it is impossible to place them in another family. *Austridotea* and *Idotea* are the only two idoteid genera with truly articulating pleonites (Poore and Lew Ton, 1993). The only substantial difference between them is the uropodal rami, two in the former rather than one as is the case in all other members of Idoteidae.

Arcturidae Bate and Westwood, 1868, new combination

Arcturidae Bate and Westwood, 1868: 359, 360.—Kensley, 1978a: 16, 17 (part).—Kensley and Schotte, 1989: 252 (part).—Kussakin, 1982: 270–272 (part).
Arcturinae.—Wägele, 1989: 138.—Wägele, 1991: 88 (part).
Amesopodidae Stebbing, 1905: 44.

Diagnosis.—Body flexed between pereionites 4 and 5, or strongly geniculate between pereionites 4 and 5 (especially in male), or straight, more or less flattened or semicylindrical (*Arcturinoides* only). Head and pereionite 1 fused. Pereionite 4 at least 1.5 times as long as pereionite 3 (in males often much longer). All pleonites fused into pleotelson. Body smooth or slightly sculptured, or variously spinose or rugose; pleotelson without dorsolateral ridges ending in mediodorsal posterior spine. Dorsal coxal plates 2–7 obsolete, bases of pereiopods exposed, or 2–7 obsolete and with expanded marginal tergites (*Arcturinoides* only). Mouthparts and pereiopod 1 enclosed in lateral view by lateral plates of head and pereionite 1. Eyes well developed, or reduced or lost (rare).

Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereiopod 1 a gnathopod, pereiopods 2–4 elongated, differentiated from ambulatory pereiopods 5–7 (some of pereiopods 2–4 rarely absent). Pereiopod 1 dactylus evenly curved along anterior margin, evenly tapering if present. Pereiopods 2–4 with paired long setae along posterior margins evenly and well developed; with prominent dactylus, unguis short (or dactylus lost in some pereiopods); pereiopod 4 similar to pereiopod 3. Pereiopods of males without dense fur of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod (usually).

Oostegites 1–4 functional, 5 absent, or 1–5 functional (*Arcturus* only); oostegites 1–4 not supported by coxal lobes. Penes fused as a single penial plate; penial plate apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male laminar; with lateral excavation. Pleopod 2 of male with appendix masculina about as long as endopod (or longer), basally as wide or wider than endopod.

Included Genera (with numbers of described species).—*Agularcturus* Kensley, 1984 (1); *Amesopous* Stebbing, 1905 (1); *Arctopsis* Barnard, 1920 (1); *Arcturella* Sars, 1897 (15); *Arcturina* Koehler, 1911 (5); *Arcturinella* Poisson and Maury, 1931 (1); *Arcturinoides* Kensley, 1977 (2); *Arcturopsis* Koehler, 1911 (3); *Arcturus* Latreille, 1829 (24); *Astacilla* Cordiner, 1793 (27); *Edwinjoycea* Menzies and Kruczynski, 1983 (1); *Idarcturus* Barnard, 1914b (3); *Neastacilla* Tattersall, 1921 (35); *Parastacilla* Hale, 1946 (2); *Parapleuroprion* Kussakin, 1972 (1); *Spectarcturus* Schultz, 1981 (1) (123 described species in all).

Remarks.—As now confined, the Arcturidae possess an exopod on male pleopod 1 with a lateral notch, and either a tuft of fine setae, 2 or 3 long plumose setae, or a combination of these. The appendix masculina is undivided, bifid, or trifid. Amesopodidae are the same and very different from the situation in the antarcturid-like families. Pereiopod 1 is very small, one of the mouthparts, and enclosed by lateral plates of the first coxae. Pereiopods 2–4 have long setae and interlock closely against the ventral body. Pereionite 4 may be exceptionally elongate in one or both sexes but this is not universal. A similar condition never occurs in the Antarcturidae, the new family erected here to receive non-conforming genera. The two species of *Arcturinoides* are exceptional in adopting a limpet-like habitus while retaining all important features of the family. *Arcturus* is the least apomorphic genus, with five pairs of oostegites and a barely flexed body.

The Amesopodidae (only species, *Amesopous richardsonae*) differ from most arcturids in the absence of pereiopods 2 and 3. Another similar species, *Edwinjoycea horologium* Menzies and Kruczynski, 1983, has a single-articled pereiopod 2 and lacks pereiopods 3 and 4 (Müller, 1993). Müller erected the subfamily Edwinjoycinae [*sic*] to accommodate this species. The two species of *Arturinoides* lack pereiopod 4. Loss of distal articles of pereiopods 1–4 is common in the family. All three genera are otherwise similar to *Neastacilla*. The Amesopodidae and Edwinjoyceinae, both representing single species, cannot be recognised as valid taxa within the Arcturidae. All other species comprise a paraphyletic or polyphyletic group.

This use of Arcturidae is not equivalent to Wägele's (1989) Arcturinae which included these genera and others here assigned to Antarcturidae and Austrarcturellidae.

The family is globally widespread in shallow and shelf depths, especially in cooler waters.

Holidoteidae Wägele, 1989

Holidoteinae Wägele, 1989: 137.

Diagnosis.—Body straight, more or less flattened or semicylindrical, or flexed between pereionites 4 and 5. Head and pereionite 1 fused. Pereionite 4 of similar length to pereionite 3. All pleonites fused into pleotelson, or pleonite 1 articulating with fused pleotelson (weakly). Body smooth or slightly sculptured, or variously spinose or rugose; pleotelson without dorsolateral ridges ending in mediodorsal posterior spine. Dorsal coxal plates 2–7 obsolete, bases of pereiopods exposed, or 2–7 obsolete and with expanded marginal tergites (females only). Mouthparts and pereiopod 1 visible in lateral view (may be hidden by expanded tergites). Eyes well developed, or reduced or lost (rare).

Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereiopod 1 a gnathopod, pereiopods 2–4 elongated, differentiated from ambulatory pereiopods 5–7. Pereiopod 1 dactylus evenly curved along anterior margin, evenly tapering. Pereiopods 2–4 with scattered and uneven long setae along posterior margins; with short dactylus, unguis longer and setiform; pereiopod 4 similar to pereiopod 3. Pereiopods of males without dense fur of fine setae. Uropodal exopod very short, bearing a single prominent robust seta, endopod also with robust apical seta.

Oostegites 1–4 functional, 5 absent; oostegites 1–4 supported by coxal lobes. Penes fused as a single penial plate; penial plate apically bifid and splayed. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with overlapping rows of simple and plumose setae along lateral margin, terminating at subdistal excavation; with groove on posterior face of exopod ending on distolateral lobed tip, separated from most of lateral margin by notch. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Included Genera (with numbers of described species).—Austroarcturus Kensley, 1975 (6); *Holidotea* Barnard, 1920 (1); *Neoarcturus* Barnard, 1914a (9) (16 species in all).

Remarks.—Austroarcturus, Holidotea and *Neoarcturus* (all southern African) share three important characteristics, synapomorphies uniting them as a family. The penial plate is apically bifid and splayed; both uropodal rami are present and possess a robust terminal seta, microscopically serrate (the exopod is shorter than wide); and the exopod of the male pleopod 1 has overlapping rows of simple and plumose setae along its lateral margin, terminating at subdistal excavation. Other synapomorphies that are homoplasous in other arcturids are pereiopods 2–4 with weak filter setation and a short dactylus and setiform unguis.

Wägele (1989) erected the subfamily Holidoteinae to include *Holidotea* and *Austroarcturus*. Three synapomorphies define the subfamily in his cladogram: head and pereionites 1–4 shortened, pereion flattened and eyes dorsal; head with a keel; and uropodal rami short and with a stout seta. Only the last of these character states is true for the three genera united by the new cladistic analysis that includes *Neoarcturus*. Full family rank is warranted. A revision of the family and resolution of complex nomenclatural issues resulting from use of the *nomen nudum Microarcturus* (Poore, 1991b) is in preparation for the *Annals of the South African Museum.*

Species of *Neoarcturus* have a form similar to antarcturids, but the other two genera are quite flattened and limpet-like. *Neoarcturus* is a shelf and slope genus while the others are only from more shelf depths. The family is confined to southern Africa.

Antarcturidae, new family

Arcturidae auctorum (part).
Arcturinae.—Wägele, 1989: 138.—Wägele, 1991: 88 (part).

Type Genus.—*Antarcturus* zur Strassen, 1902.

Diagnosis.—Body flexed between pereionites 4 and 5. Head and pereionite 1 fused. Pereionite 4 of similar length to pereionite 3. All pleonites fused into pleotelson. Body strongly spinose, with at least dorsal and dorsolateral pairs of spines, often dominated by pair near end of pleotelson; pleotelson without dorsolateral ridges ending in mediodorsal posterior spine. Dorsal coxal plates 2–7 obsolete, bases of pereiopods exposed. Mouthparts and pereiopod 1 visible in lateral view. Eyes well developed, or reduced or lost.

Antenna 2 flagellum multiarticulate, or of 2 or 3 articles plus distal claw. Pereiopod 1 a gnathopod, pereiopods 2–4 elongated, differentiated from ambulatory pereiopods 5–7. Pereiopod 1 dactylus evenly curved along anterior margin, evenly tapering. Pereiopods 2–4 with paired long setae along posterior margins evenly and well developed; with prominent dactylus, unguis short; pereiopod 4 similar to pereiopod 3. Pereiopods of males without dense fur of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod (when present).

Oostegites 1–4 functional, 5 absent; oostegites 1–4 supported by coxal lobes. Penes fused as a single penial plate; penial plate apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with few simple setae along straight lateral margin; with groove on posterior face of exopod ending distolaterally or laterally on simple margin. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Included Genera (with numbers of described species).—Abyssarcturus Kussakin and Vasina, 1995 (1); *Acantharcturus* Schultz, 1981 (1); *Antarcturus* zur Strassen, 1902 (26); *Caecarcturus* Schultz, 1981 (1); *Chaetarcturus* Brandt, 1990 (20); *Cylindrarcturus* Schultz, 1981 (2); *Fissarcturus* Brandt, 1990 (9); *Globarcturus* Kussakin and Vasina, 1994 (1); *Litarcturus* Brandt, 1990 (7); *Mixarcturus* Brandt, 1990 (3); *Oxyarcturus* Brandt, 1990 (3); *Pleuroprion* zur Strassen, 1903 (11); *Spinarcturus* Kensley, 1978b (1); *Thermoarcturus* Paul and Menzies, 1971 (1); *Tuberarcturus* Brandt, 1990 (3) (90 species in all).

Remarks.—The new family is erected to differentiate a large group of genera traditionally placed in the Arcturidae. Nordenstam (1933) diagnosed what he called the "*Antarcturus* group" to include what I am calling Antarcturidae, but he included *Dolichiscus* (now an austrarcturellid) and his *nomen nudum Microarcturus* (most species now holidoteids). His diagnostic characters are complete fusion of the head and pereionite 1, complete fusion of pleonites, lateral margins of the head and pereionite 1 not expanded downwards, pereiopod 1 subchelate, and the exopod of the male pleopod 1 with a diagonal groove.

Antarcturid genera vary considerably in form. All have cylindrical, slightly geniculate bodies. None is as strongly bent as austrarcturellids. The body is typically spinose or tuberculose, and sculpture has been used to distinguish genera (Brandt, 1990). While sculpture is diverse, it does provide the only probable synapomorphy of the family. Most species are spinose, with the spines in longitudinal rows on most body segments. The pair of stronger spines near or at the apex of the pleotelson is characteristic, and a homologue is not seen in any other family.

Wägele (1989: Fig. 68) analysed the former Arcturidae (as a subfamily) but discovered few hierarchical groups of genera. He did not use the form of pereiopod 1 and male pleopod 1 as characters and so discovered no grouping equivalent to Antarcturidae.

Most of the species previously treated as arcturids from Antarctica, where they are diverse and abundant (Brandt, 1990; Wägele, 1991), are, in my view, members of Antarcturidae. The family is most diverse in the Southern Ocean and is the dominant valviferan group in the deep sea of both hemispheres.

Austrarcturellidae Poore and Bardsley, 1992

Austrarcturellidae Poore and Bardsley, 1992: 845.

Diagnosis.—Body flexed between pereionites 4 and 5. Head and pereionite 1 fused. Pereionite 4 of similar length to pereionite 3. All pleonites fused into pleotelson, or pleonite 1 articulating with fused pleotelson (most species of *Dolichiscus*). Body variously tuberculate or spinose but never with posterior dorsolateral pair of strong spines on pleotelson; pleotelson with dorsolateral ridges usually ending in mediodorsal posterior spine. Dorsal coxal plates 2–7 obsolete, bases of pereiopods exposed. Mouthparts and pereiopod 1 visible in lateral view. Eyes well developed, or reduced or lost.

Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereiopod 1 a gnathopod, pereiopods 2–4 elongated, differentiated from ambulatory pereiopods 5–7. Pereiopod 1 dactylus usually with anterior lobe on anterior margin, constricted and tapering distally. Pereiopods 2–4 with paired long setae along posterior margins evenly and well developed; with minute dactylus, unguis setiform; pereiopod 4 shorter and less setose than pereiopods 2 and 3. Pereiopods of males without dense fur of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod (when present).

Oostegites 1–4 functional, 5 vestigial lobes, or 1–4 functional, 5 absent; oostegites 1–4 supported by coxal lobes. Penes fused as a single penial plate; penial plate apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with few simple setae along straight lateral margin; with groove on posterior face of exopod ending distolaterally or laterally on simple margin (*Dolichiscus*), or ending on basally derived branch of exopod. Pleopod 2 of male with appendix masculina twice length of endopod, basally less than half width of endopod.

Included Genera (with numbers of described species).—*Austrarcturella* Poore and Bardsley, 1992 (14); *Abyssarcturella* Poore and Bardsley, 1992 (2); *Dolichiscus* Richardson, 1913 (23); *Pseudarcturella* Tattersall, 1921 (2); *Scyllarcturella* Poore and Bardsley, 1992 (1) (42 species in all).

Remarks.—The original definition of the Austrarcturellidae included four genera. It is here expanded to include *Dolichiscus*.

The family, as originally defined, was strongly united on the “boat-shaped” pleotelson with middorsal posterior spine, vestigial dactyli with setiform unguis on pereiopods 2–4, smaller pereiopod 4, lateral lobe on the male pleopod 1 exopod, and presence of reduced oostegites 5. *Dolichiscus* shares a similar pleotelson and pereiopod 1 dactylus but does not possess the lateral lobe of the male pleopod 1 nor oostegites 5. All genera possess an elongate pleonite 1, weakly articulating with the pleotelson in most species of *Dolichiscus,* and more elongate pereiopods 5–7 than is typical in antarcturids. Wägele (1989: Fig. 68) recognised the similarity of the pereiopod 1 and pleotelson of *Pseudarcturella* and *Dolichiscus.* Christoph Held (Ruhr Universitat, Bochum) has found molecular evidence from a 500 basepair fragment of the mitochondrial large subunit ribosomal gene (16S rDNA) that supports the distinction of *Dolichiscus* from *Antarcturus* and similar antarcturid genera (personal communication). He was not able to compare it with other austrarcturellids.

The four original members of the Austrarcturellidae comprise a well-defined clade of species on the Australian shelf and slope and nearby Tasman Sea. *Dolichiscus* is more widespread, most species being in the deep Southern Ocean but others in deep environments just north of the equator.

Xenarcturidae Sheppard, 1957

Xenarcturidae Sheppard, 1957: 182–184.
Xenarcturinae.—Wägele, 1989: 138 (part).

Diagnosis.—Body strongly vaulted. Head and pereionite 1 fused. Pereionite 4 of similar length to pereionite 3. All pleonites fused into pleotelson. Body setose, not tuberculate; pleotelson without dorsolateral ridges ending in mediodorsal posterior spine. Dorsal coxal plates 2–7 more or less ventrally expanded over bases of pereiopods. Mouthparts and pereiopod 1 visible in lateral view. Eyes well developed.

Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereiopod 1 a gnathopod, pereiopods 2 and 3 elongated, differentiated from ambulatory pereiopods 4–7. Pereiopod 1 dactylus evenly curved along anterior margin, evenly tapering. Pereiopods 2 and 3 with scattered long setae along posterior margins; with prominent dactylus, unguis short; pereiopod 4 different from pereiopod 3, similar to pereiopod 5. Pereiopods of males without dense fur of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod.

Oostegites 1–4 functional, 5 absent; oostegites 1–4 not supported by coxal lobes. Penes fused as a single penial plate; penial plate apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with few simple setae along straight lateral margin; with groove on posterior face of exopod ending on tapering distolateral apical extension. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Included Genus (with number of described species).—Xenarcturus Sheppard, 1957 (1).

Remarks.—This monotypic family is recognised by the flat habitus and by pereiopod 4 being ambulatory rather than setose like pereiopods 3 and 4 (Park, 1995). In this the pereiopod symmetry differs from that in all other valviferans. Wägele (1989) treated the family as a subfamily of Arcturidae s. l.

Arcturididae, new family

Pseudidotheidae.—Hale, 1946: 168 (part).
Pseudidotheinae.—Wägele, 1989: 137.—Wägele, 1991: 80 (part).

Type Genus.—Arcturides Studer, 1882.

Diagnosis.—Body straight, more or less cylindrical. Head and pereionite 1 fused. Pereionite 4 of similar length to pereionite 3. All pleonites fused into pleotelson. Body variously tuberculate or spinose but never with posterior dorsolateral pair of strong spines on pleotelson; pleotelson without dorsolateral ridges ending in mediodorsal posterior spine. Dorsal coxal plates 2–7 obsolete, bases of pereiopods exposed. Mouthparts and pereiopod 1 visible in lateral view. Eyes well developed.

Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereiopod 1 a gnathopod, pereiopods 2–4 scarcely differentiated from ambulatory pereiopods 5–7. Pereiopod 1 dactylus evenly curved along anterior margin, evenly tapering. Pereiopods 2–4 with irregular fine setae and marginal robust setae; with prominent dactylus, unguis short; pereiopod 4 similar to pereiopod 3. Pereiopods of males without dense fur of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod.

Oostegites 1–4 functional, 5 absent; oostegites 1–4 supported by coxal lobes. Penes fused as a single penial plate; penial plate apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with few simple setae along straight lateral margin; with groove on posterior face of exopod ending on tapering distolateral apical extension. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Included Genus (with number of described species).—Arcturides Studer, 1882 (2).

Remarks.—The cylindrical body with essentially similar ambulatory pereiopods characterises the family which otherwise has antarcturid-type male pleopods (Hale, 1946). This combination of characters suggests that the ancestral arcturoid was a straight isopod and that an erect body with filtering setae on anterior pereiopods probably arose more than once. Only two species of *Arcturides* are known, both from hydroids near subantarctic islands of the Southern Indian Ocean.

Pseudidotheidae Ohlin, 1901

Pseudidotheidae Ohlin, 1901: 274–276.
Pseudidotheinae.—Wägele, 1989: 137.—Wägele, 1991: 80 (part).

Diagnosis.—Body strongly vaulted. Head and pereionite 1 fused. Pereionite 4 of similar length to pereionite 3. All pleonites fused into pleotelson. Body variously tuberculate or spinose but never with posterior dorsolateral pair of strong spines on pleotelson; pleotelson without dorsolateral ridges ending in mediodorsal posterior spine. Dorsal coxal plates 2–7 obsolete, bases of pereiopods exposed. Mouthparts and pereiopod 1 visible in lateral view. Eyes well developed.

Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereiopod 1 a gnathopod, pereiopods 2 and 3 differentiated from ambulatory pereiopods 4–7. Pereiopod 1 dactylus evenly curved along anterior margin, evenly tapering. Pereiopods 2–4 raptorial, articles broad and with posterior robust setae; with prominent dactylus, unguis short; pereiopod 4 similar to pereiopod 3. Pereiopods of males without dense fur of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod.

Oostegites 1–4 functional, 5 absent; oostegites 1–4 not supported by coxal lobes. Penes fused as a single penial plate; penial plate apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with few simple setae along straight lateral margin; with groove on posterior face of exopod ending on tapering distolateral apical extension. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Included Genus (with number of described species).—Pseudidothea Ohlin, 1901 (3).

Remarks.—The pereiopods are the major features separating this family from Antarcturidae. In the new phylogenetic analysis, the raptorial pereiopods are a unique apomorphy for the family and genus. Wägele (1989) treated the family as a subfamily of Arcturidae, *sensu lato,* and included *Arcturides* in it. The only synapomorphy defining the subfamily in his cladogram is fusion of pleonites, a character state of most arcturoids.

The three described species of *Pseudidothea* are from subantarctic islands and New Zealand. An undescribed species is common in southern Australia.

Rectarcturidae, new family

Type Genus.—Rectarcturus Schultz, 1981.

Diagnosis.—Body strongly vaulted. Head and pereionite 1 fused. Pereionite 4 of similar length to pereionite 3. All pleonites fused into pleotelson. Body variously tuberculate or spinose but never with posterior dorsolateral pair of strong spines on pleotelson; pleotelson without dorsolateral ridges ending in mediodorsal posterior spine. Dorsal coxal plates 2–7 obsolete, bases of pereiopods exposed. Mouthparts and pereiopod 1 visible in lateral view. Eyes well developed.

Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereiopod 1 a gnathopod, pereiopods 2–4 elongated, differentiated from ambulatory pereiopods 5–7. Pereiopod 1 dactylus evenly curved along anterior margin, evenly tapering. Pereiopods 2–4 with paired long setae along posterior margins evenly and well developed; with short dactylus, unguis longer and setiform; pereiopod 4 similar to pereiopod 3. Pereiopods of males without dense fur of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod.

Oostegites 1–4 functional, 5 absent; oostegites 1–4 not supported by coxal lobes. Penes fused as a single penial plate; penial plate apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with few simple setae along straight lateral margin; with groove on posterior face of exopod ending distolaterally or laterally on simple margin. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Included Genus (with number of described species).—Rectarcturus Schultz, 1981 (4).

Remarks.—The genus *Rectarcturus* is enigmatic, combining features of the Antarcturidae and Holidoteidae. Like both of these, pereiopods 2–4 bear filtering setae, and the male pleopod 1 is of the thickened, grooved type. The body is straight like Holidoteidae, but the uropodal rami are not of the peculiar holidoteid form. The straight body and absence of paired pleotelsonic spines distinguish it from most antarcturids. The cladistic analysis cannot align the genus with either group, nor with the other minor families, so a separate family is justified. It is unclear whether the combined presence of filtering setae with a straight body shown in *Rectarcturus* is ancestral to the flexed situation seen in antarcturids and austrarcturellids or vice versa. It is possible that the long setae on pereiopods 2–4 arose first for benthic scraping rather than filter feeding from the plankton. As well as the four described species from the far southwestern Atlantic (Park and Wägele, 1995) are six undescribed species from Australian and nearby shelf and deep habitats.

Acknowledgements

This paper results from discussions over many years with my collaborators, Helen Lew Ton and Tania Bardsley, whom I thank for their considerable contribution. The paper benefited from discussion with Angelika Brandt. The work was supported by grants from the Australian Biological Resources Study. I thank curators of numerous museums who lent material. This paper is offered to *Journal of Crustacean Biology* as a tribute to the substantial contribution of Arthur Humes, its editor from 1981 to 1999.

Literature Cited

Adams, A. 1852. Zoology. Pp. 201–216 *in* P. C. Sutherland, ed. Journal of a voyage in Baffin's Bay and Barrow Straits, in the years 1850–1851 performed by H.M. ships "Lady Franklin" and "Sophia", under the command of Mr. William Penny, in search of the missing crews of H.M. ships "Erebus" and "Terror": with . . . observations on the natural history and physical features of the countries and frozen seas visited. Vol. 2. Longman Group Ltd, London.

Barnard, K. H. 1914a. Contributions to the crustacean fauna of South Africa. 1. Additions to the marine Isopoda.—Annals of the South African Museum 10: 197–230.

———. 1914b. Contributions to the crustacean fauna of South Africa. 3. Additions to the marine Isopoda, with notes on some previously incompletely known species.—Annals of the South African Museum 10: 325a–358a, 359–442.

———. 1920. Contributions to the crustacean fauna of South Africa. No. 6. Further additions to the list of marine Isopoda.—Annals of the South African Museum 17: 319–438.

Bate, C. S. 1863. On some new Australian species of Crustacea.—Proceedings of the Zoological Society of London 1863: 498–505.

———, and J. O. Westwood. 1868. A history of the British sessile-eyed Crustacea. Vol. 2. edition. John Van Voorst, London. 536 pp.

Benedict, J. E. 1901. [*Erichsonella* Benedict, new name.] P. 542 *in* Richardson, 1901, cited below.

Brandt, A. 1990. Antarctic valviferans (Crustacea, Isopoda, Valvifera) new genera, new species and redescriptions. E. J. Brill, Leiden. 176 pp.

Brusca, R. C. 1984. Phylogeny, evolution and biogeography of the marine isopod subfamily Idoteinae (Crustacea: Isopoda: Idoteidae).—Transactions of the San Diego Society of Natural History 20: 99–134.

———, and B. R. Wallerstein. 1979. The marine isopod crustaceans of the Gulf of California II. Idoteidae: new genus and species, range extensions, and comments on evolution and taxonomy within the family.—Proceedings of the Biological Society of Washington 92: 253–271.

———, and G. D. F. Wilson. 1991. A phylogenetic analysis of the Isopoda with some classificatory recommendations.—Memoirs of the Queensland Museum 31: 143–204.

Collinge, W. E. 1917a. On the oral appendages of certain species of marine Isopoda.—Zoological Journal of the Linnean Society 34: 65–92.

———. 1917b. A revision of the British Idoteidae, a family of marine Isopoda.—Transactions of the Royal Society of Edinburgh 51: 721–760.

Cordiner, C. 1793. Remarkable ruins, and romantic prospects, of North Britain. With ancient monuments, and singular subjects of natural history. Peter Mazell, London. 96 pp., plates with letterpress.

Daguerre de Hureaux, N., and B. Elkaïm. 1972. Contribution à l'étude des isopodes marins du Maroc: *Parachiridotea* n. genre *panousei* nelle espèce (Valvifère, Idoteidae, Mesidoteinae).—Bulletin de la Société des Sciences Naturelles et Physiques du Maroc 52: 147–149.

Dallwitz, M. J., T. A. Paine, and E. J. Zurcher. 1997. User's guide to the DELTA system. A general system for processing taxonomic descriptions. CSIRO Division of Entomology, Canberra. 160 pp.

Dana, J. D. 1849. Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae, Foederate Duce, lexit et descripsit (continued.).—American Journal of Sciences and Arts 8: 424–428.

———. 1853. Crustacea. Part II.—United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N. 13: 691–1618, with a folio atlas of 96 plates.

Eights, J. 1852. Of a new animal belonging to the Crustacea, discovered in the Antarctic seas, by the author.—Transactions of the Albany Institute 2: 331–334.

Fabricius, J. C. 1798. Supplementum Entomologiae Systematicae. Proft and Storch, Hafniae. 572 pp.

Guérin-Méneville, F. E. 1843. Crustacés. P. 48, 35 pls. *in* G. Cuvier, ed. Iconographie du Règne animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables et souvent non encore figurées de chaque genre d'animaux. Vol. 3. Baillière, Paris.

Hale, H. M. 1924. Notes on Australian Crustacea. No. 3.—Transactions of the Royal Society of South Australia 48: 209–225.

———. 1929. Crustacea from Princess Charlotte Bay, North Queensland. The Isopoda and Stomatopoda.—Transactions of the Royal Society of South Australia 53: 33–36.

———. 1946. Isopoda–Valvifera.—B.A.N.Z. Antarctic Research Expedition, 1929–1931. Reports-Series B (Zoology and Botany) 5: 161–212.

Harger, O. 1878. Descriptions of new genera and species of Isopoda, from New England and adjacent regions.—American Journal of Sciences and Arts 15: 373–379.

Holthuis, L. B. 1964. *Saduriella* a new genus of Isopoda Valvifera from northwestern Spain.—Zoologische Mededelingen, Leiden 40: 29–35.

Hurley, D. E. 1961. A checklist and key to the Crustacea Isopoda of New Zealand and Subantarctic Islands.—Transactions of the Royal Society of New Zealand (Zoology) 1: 259–292.

Jones, M. B., and G. D. Fenwick. 1978. *Maoridotea naylori,* a new genus and species of isopod (Valvifera, Idoteidae, Chaetilinae) from the Kaikoura Peninsula, New Zealand.—Journal of Natural History 12: 617–625.

Kensley, B. 1975. Marine Isopoda from the continental shelf of South Africa.—Annals of the South African Museum 67: 35–89.

———. 1977. New records of marine Crustacea Isopoda from South Africa.—Annals of the South African Museum 72: 239–265.

———. 1978a. Guide to the marine isopods of southern Africa. Trustees of the South African Museum, Cape Town. 173 pp.

———. 1978b. The South African Museum's *Meiring Naude* cruises. Part 7. Marine Isopoda.—Annals of the South African Museum 74: 125–157.

———. 1984. The South African Museum's *Meiring Naude* Cruises. Part 15. Marine Isopoda of the 1977, 1978, 1979 cruises.—Annals of the South African Museum 93: 213–301.

———, and H. W. Kaufman. 1978. *Cleantioides,* a new idoteid isopod genus from Baja California and Panama.—Proceedings of the Biological Society of Washington 91: 658–665.

———, and M. Schotte. 1989. Guide to the marine isopod crustaceans of the Caribbean. Smithsonian Institution Press, Washington, D.C., and London. 308 pp.

Koehler, R. 1911. Arcturidés nouveaux provenant des campagnes de la "Princesse-Alice" ou appartenant au Musée Océanographique de Monaco.—Bulletin de l'Institut Océanographique de Monaco 214: 1–65.

Kussakin, O. G. 1972. Isopoda from the coastal zone of the Kurile Islands. III. Three new arcturids from the Middle Kuriles with taxonomic remarks on the family Arcturidae.—Crustaceana Supplement 3: 178–189.

———. 1982. Marine and brackish-water Crustacea (Isopoda) of cold and temperate waters of the Northern Hemisphere. Suborders Anthuridea, Microcereberidea, Valvifera, Tyloidea.—Opredeliteli po Faune SSR, Akademiya Nauk, SSSR 131: 1–461. [In Russian.]

———, and G. S. Vasina. 1994. Description of *Globarcturus angelikae* gen. et sp. n., the first Antarctic hadal arcturid from the South Sandwich Trench (Crustacea, Isopoda: Arcturidae).—Zoosystematica Rossica 2: 241–245.

———, and ———. 1995. Antarctic hadal arcturids, with descriptions of a new genus and five new species (Isopoda: Valvifera: Arcturidae).—Zoosystematica Rossica 3: 207–228.

Latreille, P. A. 1829. Les Crustacés, les Arachnides et les Insectes, distribués en familles naturelles. Pp. i–xxvii, 1–584 *in* G. Cuvier, ed. Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Vol. 4. Déterville, Paris.

Menzies, R. J., and T. E. Bowman. 1956. Emended description and assignment to the new genus *Ronalea* of the idotheid isopod *Erichsonella pseudoculata* Boone.—Proceedings of the United States National Museum 106: 339–343.

———, and W. L. Kruczynski. 1983. Isopod Crustacea (exclusive of Epicaridea).—Memoirs of the Hourglass Cruises 6: 1–126.

Moreira, P. S. 1974. *Moplisa,* a new genus of idoteid isopod from southern South America.—Crustaceana 26: 149–154.

Müller, H. G. 1993. Arcturidae (Isopoda) from the Santa Marta area, northern Columbia, with a review of the shallow-water species from the Caribbean Sea and Gulf of Mexico.—Mitteilungen aus dem Zoologischen Museum in Berlin 69: 317–337.

Nicholls, G. E. 1937. On the freshwater Idoteidae of New Zealand (Crustacea, Isopoda).—Annals and Magazine of Natural History (10)19: 113–136.

Nierstrasz, H. F. 1941. Die Isopoden der Siboga-Expedition. IV. Isopoda Genuina. III. Gnathiidea, Anthuridea, Valvifera, Asellota, Phreatocoidea.—Siboga Expéditie 19: 235–308.

Nordenstam, A. 1933. Marine Isopoda of the families Serolidae, Idotheidae, Pseudidotheidae, Arcturidae, Parasellidae and Stenetriidae mainly from the South Atlantic.—Further Zoological Results of the Swedish Antarctic Expedition, 1901–1903 3: 1–284, 2 pls., errata.

Ohlin, A. 1901. Isopoda from Tierra del Fuego and Patagonia.—Wissenschaftliche Ergebnisse der Schwedischen Expedition nach den Magellansländern 1895–1897 2: 261–306.

Park, J.-Y. 1995. *Xenarcturus spinulosus* Sheppard, 1957 (Crustacea, Isopoda, Valvifera): redescription of a specimen from the Strait of Magellan.—Bulletin Zoölogisch Museum, Universiteit van Amsterdam 14: 145–152.

———, and J. W. Wägele. 1995. On a small collection of Valvifera (Crustacea Isopoda) from the Magellan Strait, with a description of *Platidotea magellanica* n. gen. n. sp.—Bulletin Zoölogisch Museum, Universiteit van Amsterdam 14: 57–99.

Paul, A. Z., and R. J. Menzies. 1971. Sub-tidal isopods of the Fosa de Cariaco, Venezuela, with descriptions of two new genera and twelve new species.—Boletín del Instituto Oceanografico, Universidad de Oriente 10: 29–48.

Poisson, R., and A. Maury. 1931. *Arcturinella banyulensis* nov. gen., nov. sp., Crustacé Isopode nouveau (tribu des Valvifera, famille des Arcturidae), capturé à Banyuls (Pyr. Orientales).—Bulletin de l'Institut Océanographique de Monaco 573: 1–14.

Poore, G. C. B. 1978. *Austrochaetilia capeli,* a new genus and species of chaetiline idoteid (Isopoda) from Port Phillip Bay, Australia.—Crustaceana 33: 113–118.

———. 1984. Clarification of the monotypic genera *Chiriscus* and *Symmius* (Crustacea: Isopoda: Idoteidae).—Proceedings of the Biological Society of Washington 97: 71–77.

———. 1985. Australian chaetiliids (Crustacea: Isopoda: Valvifera): a new genus, new species and remarks on the family.—Memoirs of the Museum of Victoria 46: 153–172.

———. 1991a. Crustacea Isopoda: Deep-sea Chaetiliidae (Valvifera) from New Caledonia and the Philippines.—Mémoires du Muséum National d'Histoire Naturelle, Paris (Zoologie) 152: 139–153.

———. 1991b. *Neoarcturus* Barnard, 1914: Diagnoses of the genus and its type species and substitution for the *nomen nudum* '*Microarcturus*' Nordenstam, 1933 (Isopoda, Arcturidae).—Annals of the South African Museum 101: 1–8.

———. 1998. Deep-water Arcturidae (Crustacea, Isopoda, Valvifera) from French collections in the south-western Pacific Ocean.—Zoosystema 20: 379–399.

———, and T. M. Bardsley. 1992. Austrarcturellidae (Crustacea: Isopoda: Valvifera), a new family from Australasia.—Invertebrate Taxonomy 6: 843–908.

———, and H. M. Lew Ton. 1990. The Holognathidae (Crustacea: Isopoda: Valvifera) expanded and redefined on the basis of body-plan.—Invertebrate Taxonomy 4: 55–80.

———, and ———. 1993. Idoteidae of Australia and New Zealand (Crustacea: Isopoda: Valvifera).—Invertebrate Taxonomy 7: 197–278.

Racovitza, É.-G., and R. Sevastos. 1910. *Proidotea haugi,* n. g. n. sp. isopode Oligocène de Roumanie et les Mesidoteini nouvelle sous-famille des Idotheidae.—Archives de Zoologie Expérimentale et Générale 6: 175–200, pl. 9.

Richardson, H. 1899. Key to the isopods of the Pacific Coast of North America, with descriptions of twenty-two new species.—Proceedings of the United States National Museum 21: 815–869.

———. 1901. Key to the isopods of the Atlantic coast of North America with descriptions of new and little known species.—Proceedings of the United States National Museum 23: 493–579.

———. 1904. Contributions to the natural history of the Isopoda. I. Isopoda collected in Japan in 1900 by the U.S. Fish Commission steamer "Albatross", and in the year 1881 by the U.S.S. "Palos".—Proceedings of the United States National Museum 27: 1–89.

———. 1905. A monograph on the isopods of North America.—United States National Museum Bulletin 54: VII–LIII, 1–727.

———. 1912. Description of a new species of isopod of the genus *Cleantis* from Japan.—Proceedings of the United States National Museum 42: 27–29.

———. 1913. Crustacés isopodes.—Deuxième Expédition Antarctique Française (1908–10) 3: 1–25.

Samouelle, G. 1819. The entomologists' useful compendium; or an introduction to the knowledge of British Insects, comprising the best means of obtaining and preserving them, and a description of the apparatus generally used; together with the genera of Linné, and modern methods of arranging the Classes Crustacea, Myriapoda, spiders, mites and insects, from their affinities and structure, according to the views of Dr. Leach. Also an explanation of the terms used in entomology; a calendar of the times of appearance and usual situations of near 3,000 species of British Insects; with instructions for collecting and fitting up objects for the microscope. Thomas Boys, London. 496 pp., 12 pls.

Sars, G. O. 1882. Oversigt af Norges Crustaceer med forlöbige Bemaerkninger over de nye eller mindre bekjendte Arter.—Forhandlinger i Videnskaps-Selskapet in Kristiania 1882: 1–124.

———. 1897. An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. 2. Isopoda. Parts 5, 6. Idotheidae, Arcturidae, Asellidae, Ianiridae, Munnidae. Pp. 81–116, pls. 33–48. Bergen Museum, Bergen. 270 pp.

Schultz, G. A. 1981. Arcturidae from the Antarctic and Southern Seas (Isopoda, Valvifera) Part I. Pp. 63–94 *in* Biology of the Antarctic Seas 10. Antarctic Research Series. Vol. 32. American Geophysical Union.

Sheppard, E. M. 1957. Isopod Crustacea Part II. The suborder Valvifera. Families: Idoteidae, Pseudidotheidae and Xenarcturidae fam. n. With a supplement to isopod Crustacea, Part 1. The family Serolidae.—Discovery Reports 29: 141–197.

Stebbing, T. R. R. 1900. On Crustacea brought by Dr. Willey from the South Seas. Pp. 609–690 *in* A. Willey, ed. Zoological Results based on material from New Guinea, New Britain, Loyalty Islands and elsewhere . . . 1895, 1896 and 1897. Vol. 5.

———. 1902. South African Crustacea. Part 2.—Marine Investigations in South Africa. Department of Agriculture, Cape Town: 1–92.

———. 1905. Report on the Isopoda collected by Professor Herdman at Ceylon, in 1902.—Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, Supplementary Report 4: 1–64.

zur Strassen, O. 1902. Über die Gattung *Arcturus* und die Arcturiden der Deutschen Tiefsee-Expedition.—Zoologischer Anzeiger 25: 682–689.

———. 1903. Zusatz su meinem Artikel über die Arcturiden.—Zoologischer Anzeiger 26: 31.

Studer, T. 1882. Über eine neue Art *Arcturus* und eine neue Gattung der Idotheiden.—Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1882: 56–58.

Swofford, D. L. 1998. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Mass. 128 pp.

Tattersall, W. M. 1921. Crustacea. Part VI.—Tanaidacea and Isopoda.—British Antarctic "Terra Nova" Expedition, Natural History Reports, Zoology 3: 191–258.

Thomson, G. M. 1879. Description of a new species of isopodous crustacean (*Idotea*).—Transactions of the New Zealand Institute, Zoology 1878: 250, 251.

———. 1904. A new family of Crustacea Isopoda.—Annals and Magazine of Natural History (7)14: 66–69.

Wägele, J. W. 1987. The feeding mechanism of *Antarcturus* and a redescription of *A. spinacoronatus* Schultz, 1978 (Crustacea: Isopoda: Valvifera).—Philosophical Transactions of the Royal Society of London B 316: 429–458.

———. 1989. Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse.—Zoologica (Stuttgart) 140: 1–262.

———. 1991. Antarctic Isopoda Valvifera. Koeltz Scientific Books, Königstein. 213 pp. [Theses Zoologicae Volume 14, Synopses of the Antarctic Benthos Volume 2.]

RECEIVED: 18 October 1999.
ACCEPTED: 10 July 2000.