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# Decapod Crustacean Phylogenetics

edited by

**Joel W. Martin, Keith A. Crandall, and Darryl L. Felder**



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# Contents

Preface	ix
JOEL W. MARTIN, KEITH A. CRANDALL & DARRYL L. FELDER	
<b>I</b> <i>Overviews of Decapod Phylogeny</i>	
On the Origin of Decapoda	3
FREDERICK R. SCHRAM	
Decapod Phylogenetics and Molecular Evolution	15
ALICIA TOON, MAEGAN FINLEY, JEFFREY STAPLES & KEITH A. CRANDALL	
Development, Genes, and Decapod Evolution	31
GERHARD SCHOLTZ, ARKHAT ABZHANOV, FREDERIKE ALWES, CATERINA BIFFIS & JULIA PINT	
Mitochondrial DNA and Decapod Phylogenies: The Importance of Pseudogenes and Primer Optimization	47
CHRISTOPH D. SCHUBART	
Phylogenetic Inference Using Molecular Data	67
FERRAN PALERO & KEITH A. CRANDALL	
Decapod Phylogeny: What Can Protein-Coding Genes Tell Us?	89
K.H. CHU, L.M. TSANG, K.Y. MA, T.Y. CHAN & P.K.L. NG	
Spermatozoal Morphology and Its Bearing on Decapod Phylogeny	101
CHRISTOPHER TUDGE	
The Evolution of Mating Systems in Decapod Crustaceans	121
AKIRA ASAKURA	
A Shrimp's Eye View of Evolution: How Useful Are Visual Characters in Decapod Phylogenetics?	183
MEGAN L. PORTER & THOMAS W. CRONIN	
Crustacean Parasites as Phylogenetic Indicators in Decapod Evolution	197
CHRISTOPHER B. BOYKO & JASON D. WILLIAMS	
The Bearing of Larval Morphology on Brachyuran Phylogeny	221
PAUL F. CLARK	

## II *Advances in Our Knowledge of Shrimp-Like Decapods*

- Evolution and Radiation of Shrimp-Like Decapods: An Overview 245  
CHARLES H.J.M. FRANSEN & SAMMY DE GRAVE

- A Preliminary Phylogenetic Analysis of the Dendrobranchiata Based on Morphological Characters 261  
CAROLINA TAVARES, CRISTIANA SEREJO & JOEL W. MARTIN

- Phylogeny of the Infraorder Caridea Based on Mitochondrial and Nuclear Genes (Crustacea: Decapoda) 281  
HEATHER D. BRACKEN, SAMMY DE GRAVE & DARRYL L. FELDER

## III *Advances in Our Knowledge of the Thalassinidean and Lobster-Like Groups*

- Molecular Phylogeny of the Thalassinidea Based on Nuclear and Mitochondrial Genes 309  
RAFAEL ROBLES, CHRISTOPHER C. TUDGE, PETER C. DWORSCHAK, GARY C.B. POORE & DARRYL L. FELDER

- Molecular Phylogeny of the Family Callinassidae Based on Preliminary Analyses of Two Mitochondrial Genes 327  
DARRYL L. FELDER & RAFAEL ROBLES

- The Timing of the Diversification of the Freshwater Crayfishes 343  
JESSE BREINHOLT, MARCOS PÉREZ-LOSADA & KEITH A. CRANDALL

- Phylogeny of Marine Clawed Lobster Families Nephropidae Dana, 1852, and Thaumastocheilidae Bate, 1888, Based on Mitochondrial Genes 357  
DALE TSHUDY, RAFAEL ROBLES, TIN-YAM CHAN, KA CHAI HO, KA HOU CHU, SHANE T. AHYONG & DARRYL L. FELDER

- The Polychelidan Lobsters: Phylogeny and Systematics (Polychelida: Polychelidae) 369  
SHANE T. AHYONG

## IV *Advances in Our Knowledge of the Anomura*

- Anomuran Phylogeny: New Insights from Molecular Data 399  
SHANE T. AHYONG, KAREEN E. SCHNABEL & ELIZABETH W. MAAS

## V *Advances in Our Knowledge of the Brachyura*

- Is the Brachyura Podotremata a Monophyletic Group? 417  
GERHARD SCHOLTZ & COLIN L. MCLAY

Assessing the Contribution of Molecular and Larval Morphological Characters in a Combined Phylogenetic Analysis of the Superfamily Majoidea	437
KRISTIN M. HULTGREN, GUILLERMO GUERAO, FERNANDO P.L. MARQUES & FERRAN P. PALERO	
Molecular Genetic Re-Examination of Subfamilies and Polyphyly in the Family Pinnotheridae (Crustacea: Decapoda)	457
EMMA PALACIOS-THEIL, JOSÉ A. CUESTA, ERNESTO CAMPOS & DARRYL L. FELDER	
Evolutionary Origin of the Gall Crabs (Family Cryptochiridae) Based on 16S rDNA Sequence Data	475
REGINA WETZER, JOEL W. MARTIN & SARAH L. BOYCE	
Systematics, Evolution, and Biogeography of Freshwater Crabs	491
NEIL CUMBERLIDGE & PETER K.L. NG	
Phylogeny and Biogeography of Asian Freshwater Crabs of the Family Gecarcinucidae (Brachyura: Potamoidea)	509
SEBASTIAN KLAUS, DIRK BRANDIS, PETER K.L. NG, DARREN C.J. YEO & CHRISTOPH D. SCHUBART	
A Proposal for a New Classification of Portunoidea and Cancroidea (Brachyura: Heterotremata) Based on Two Independent Molecular Phylogenies	533
CHRISTOPH D. SCHUBART & SILKE REUSCHEL	
Molecular Phylogeny of Western Atlantic Representatives of the Genus <i>Hexapanopeus</i> (Decapoda: Brachyura: Panopeidae)	551
BRENT P. THOMA, CHRISTOPH D. SCHUBART & DARRYL L. FELDER	
Molecular Phylogeny of the Genus <i>Cronius</i> Stimpson, 1860, with Reassignment of <i>C. tumidulus</i> and Several American Species of <i>Portunus</i> to the Genus <i>Achelous</i> De Haan, 1833 (Brachyura: Portunidae)	567
FERNANDO L. MANTELATTO, RAFAEL ROBLES, CHRISTOPH D. SCHUBART & DARRYL L. FELDER	
Index	581
Color Insert	

# The Polychelidan Lobsters: Phylogeny and Systematics (Polychelida: Polychelidae)

SHANE T. AHYONG

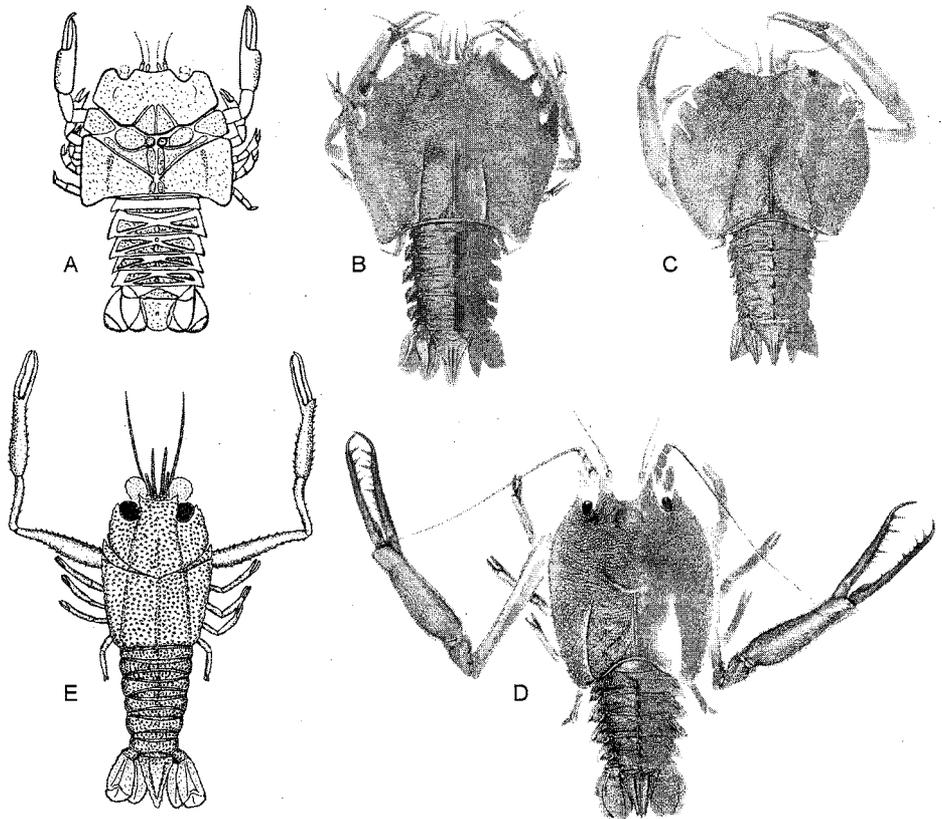
*National Institute of Water and Atmospheric Research, Kilbirnie, Wellington, New Zealand*

## ABSTRACT

Decapods of the infraorder Polychelida are unusual in having chelate pereopods 1–4 and reduced eyes in extant species. Polychelidans traditionally have been included with the achelate lobsters in the infraorder Palinura. Polychelida, however, is depicted as basal in the Reptantia by most recent studies. The polychelidan fossil record extends back to the Upper Triassic, with four families recognized to date, of which only Polychelidae is extant. Interrelationships of the fossil and living polychelidan lobsters were studied by cladistic analysis of morphology, with emphasis on Polychelidae. Coleiidae was found to be sister to Polychelidae, to the exclusion of *Palaeopentacheles*, previously placed in the latter. A new family, Palaeopentachelidae, is recognized for *Palaeopentacheles*. All other recognized polychelidan families are also diagnosed. An incomplete fossil taxon from the Upper Triassic attributed to Polychelidae, *Antarcticheles antarcticus*, is confirmed as a polychelid and is most closely related to the extant genus *Willemoesia*. The strong similarities between *Willemoesia* and *Antarcticheles* indicate that differentiation of the 'polychelid form' was well established by the late Jurassic. Among extant Polychelidae, *Willemoesia* is least derived, though the shallow dorsal orbits, regarded by some as plesiomorphic, are a derived condition. *Stereomastis* is removed from the synonymy of *Polycheles*. Six extant polychelid genera are recognized: *Cardus*, *Homeryon*, *Pentacheles*, *Polycheles*, *Stereomastis*, and *Willemoesia*. All extant polychelid genera are diagnosed, and keys to genera and species are provided. Phylogenetic trends within Polychelida include a general narrowing of the carapace and abdomen; shortening of the carapace front with respect to the anterolateral margins, leading to a shift in eye orientation from anterior to transverse; dorsal exposure of the base of the antennules and development of a stylocerite; and a shift in the form of the major chelipeds from relatively robust with short, triangular carpi to elongated and slender, with slender carpi. These trends within Polychelida appear to correspond to a shift from a shallow-water, epibenthic habit to the deep-water, fossorial lifestyle currently evident in Polychelidae. Phylogenetic trends within Polychelidae include a consistent reduction in length of the maxilliped 3 and pereopodal epipods. Epipod length is not known for any of the fossil taxa, but character polarization among extant taxa predicts that extinct taxa bore well-developed epipods.

## 1 INTRODUCTION

Among reptant decapods, polychelidans (Figs. 1, 2) are conspicuous in the possession of chelae on pereopods 1–4 and sometimes pereopod 5. Glaessner (1969) recognized four polychelidan families: Eryonidae, Coleiidae, Tetrachelidae, and Polychelidae. Polychelida was most morphologically diverse during the Mesozoic, with all known families then present. Only a single family, Polychelidae, survives to the present. Polychelids are often referred to as deep-sea blind lobsters because all extant forms live in deep water and have strongly reduced eyes. The well-developed eyes

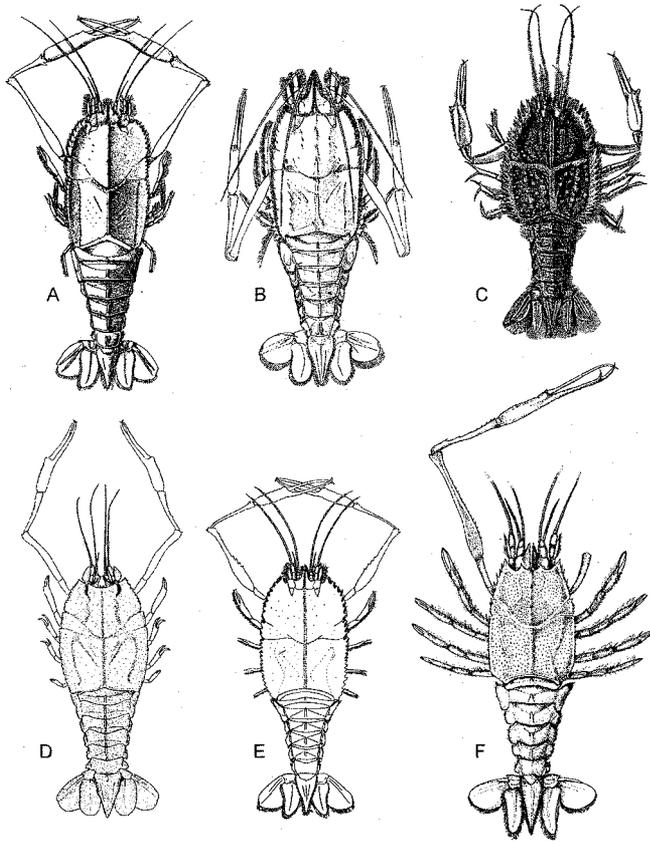


**Figure 1.** Fossil Polychelida. (A) *Tetrachela raiblana* (Tetrachelidae). (B) *Eryon arctiformis* (Eryonidae). (C) *Cycleron propinquus* (Eryonidae). (D) *Pentacheles roettenbacheri* (Palaeopentachelidae). (E) *Coleia longipes* (Coleiidae). A, from Glaessner (1969: fig. 272). B–D, from Garassino & Schweigert (2006: pl. 6, 7, 9). E, from Schweigert & Dietl (1999).

and palaeoecology of most extinct polychelidans, however, implies a shallow water origin for the group.

Polychelidae is thus the sole extant family of the infraorder Polychelida. The polychelids and achelate lobsters (Palinuroidea) have traditionally constituted Palinura (see Holthuis 1991), but recent morphological (Scholtz & Richter 1995; Schram 2001; Dixon et al. 2003) and molecular phylogenies (Ahyong & O'Meally 2004; Tsang et al. 2008) recognize independent status of both groups as separate infraorders: Achelata and Polychelida. Significantly, most of these analyses place the Polychelida as the sister group to all other reptants, apart from Tsang et al. (2008), which places Polychelida as sister to Achelata, though with low nodal support. Either way, all results recognize reciprocal monophyly of Polychelida and Achelata.

Internal relationships of Polychelidae have received scant attention aside from that implied by generic arrangements or from use of species exemplars in broader studies of decapod phylogeny (e.g., Dixon et al. 2003; Schram & Dixon 2004; Ahyong & O'Meally 2004). Unfortunately, the generic system of the Polychelidae has been in a constant state of confusion for more than a century. Over much of this period, four generic names have been applied to adult polychelids: *Polycheles* Heller, 1862 [type species *P. typhlops* Heller, 1862], *Pentacheles* Bate, 1878 [type species: *Pe. laevis* Bate, 1878], *Stereomastis* Bate, 1888 [type species: *S. suhmi* (Bate, 1878)], and



**Figure 2.** Extant Polychelidae. (A) *Polycheles typhlops*. (B) *Stereomastis sculpta*. (C) *Cardus crucifer*. (D) *Homeryon armarium*. (E) *Pentacheles laevis*. (F) *Willemoesia pacifica*. A, E, from Selbie (1914). B, from Smith (1882: pl. 3). C, from Bate (1888: fig. 31). F, from Kensley (1968: fig 4).

*Willemoesia* Grote, 1873 [type species: *W. leptodactyla* (Thomson, 1873)]. The status of *Willemoesia* has not been controversial owing to its distinctive shallow dorsal orbital concavities and the accessory spine on the pollex of the first cheliped. In contrast, the status of *Pentacheles*, *Polycheles*, and *Stereomastis* has been in constant flux. Much of the confusion has stemmed from inadequate original descriptions regarding the length of the epipod of the third maxilliped and the use of unreliable characters as diagnostic. This is particularly so in the case of *Pentacheles*, in which the original primary diagnostic character was the chelate or non-chelate condition of pereopod 5 (Bate 1878). The chelation of pereopod 5 was soon recognized to be subject to allometry and sexual dimorphism in species of *Pentacheles*, *Polycheles*, and *Stereomastis* (see Faxon 1895). Consequently, *Pentacheles* was treated as a synonym of *Polycheles* by most workers (Kemp & Sewell 1912; Selbie 1914; de Man 1916; Firth & Pequegnat 1971; Griffin & Stoddart 1995). Several workers have emphasized the reduced maxillipedal and pereopodal epipods as a defining character of *Stereomastis*, but characterization of *Polycheles* remained difficult because of variability in the length of the epipod of the third maxilliped in species then assigned to the genus (see Firth & Pequegnat 1971). Separation of *Stereomastis* from *Polycheles* has never been satisfactorily resolved, such that most workers could only distinguish the two genera based on a unitary difference in the number of lateral carapace spines — whether more or fewer than 20 — hardly a satisfactory situation. Further

progress in separating polychelid genera was stalled until Galil (2000) comprehensively revised the world species of the Polychelidae, emphasizing the lengths of the epipod of the third maxilliped and excluding the pereopodal epipods. Galil (2000) recognized two new genera, *Cardus* and *Homeryon*, for several unusual species previously assigned to *Polycheles*. One of the most significant advances made by Galil (2000), however, was resurrection of *Pentacheles*, but under a significantly different generic concept from that originally proposed by Bate (1878). In removing *Pentacheles*, *Cardus*, and *Homeryon* from *Polycheles*, Galil (2000) also regarded *Stereomastis* as a synonym of *Polycheles*. *Polycheles sensu* Galil (2000) became a speciose, morphologically diverse genus united by a vestigial epipod on the third maxilliped.

The obvious relationship between the polychelids and the extinct eryonids was recognized early on (see Glaessner 1969). The phylogenetic position of several taxa has been speculated on, such as a basal or derived position of *Willemoesia* on the basis of its shallow dorsal orbits (Bouvier 1917), but relationships have never been comprehensively studied. Therefore, the present study examines the interrelationships of the Polychelida by cladistic analysis with a focus on the extant Polychelidae.

## 2 MATERIALS AND METHODS

### 2.1 Terminal taxa

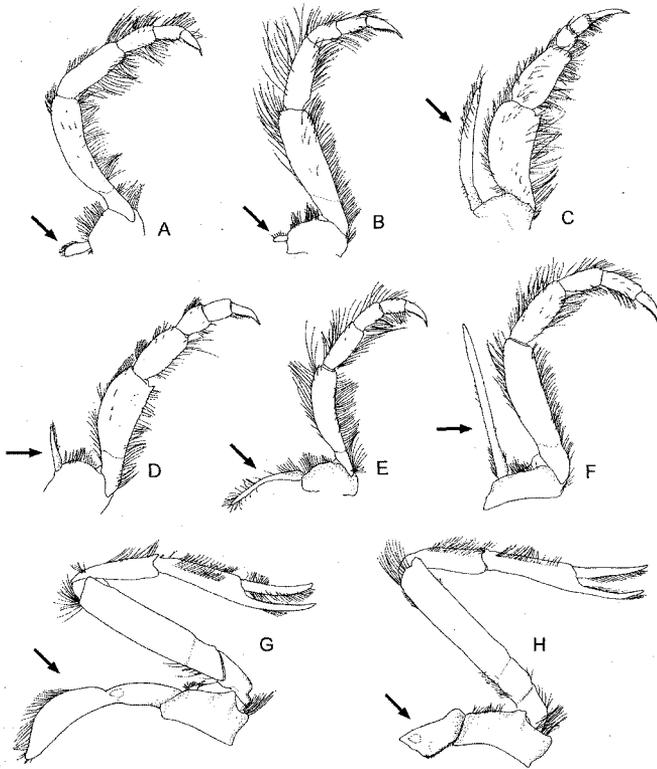
All 37 recognized extant species of Polychelidae (Galil 2000; Ahyong & Brown 2002; Ahyong & Chan 2004; Ahyong & Galil 2006) are included as terminals. Character state scoring for each species is derived from examination of specimens and/or published accounts (see Appendix 1). Characters were polarized using *Tetrachela raiblana* (Tetrachelidae) as the outgroup. In addition, *Cycleryon propinquus*, *Eryon arctiformis* and *Knebelia bilobata* (all Eryonidae), *Palaeopentacheles roettenbacheri* (originally placed in Polychelidae), and *Coleia longipes* (Coleiidae) were included in the ingroup as exemplars of the extinct polychelidan families, in order to assess their phylogenetic positions and act as potential tests of polychelid monophyly. Each of the aforementioned fossil taxa was selected because of the availability of excellent reconstructions including details of cheliped morphology (Schweigert & Dietl 1999; Garassino & Schweigert 2006). The extinct *Antarcticheles antarcticus* is known only from the carapace and partial abdomen but is regarded as a polychelid (Aguirre-Urreta et al. 1990); it was included in a separate analysis (Analysis 2) to assess its phylogenetic position. Specimens are deposited in the following institutions: Australian Museum (AM); Muséum National d'Histoire Naturelle, Paris (MNHN); National Fisheries University, Shimonoseki, Japan (NFU); National Institute of Water and Atmospheric Research, Wellington, New Zealand (NIWA); National Taiwan Ocean University (NTOU); Raffles Museum of Biodiversity Research, National University of Singapore (NUS); South Australian Museum (SAM); Texas A & M University, Texas (TAMU); National Museum of Natural History, Smithsonian Institution (USNM); Western Australian Museum, Perth (WAM); and Zoological Museum, Berlin (ZMB).

### 2.2 Morphological characters

The 71 morphological characters used in the analysis are listed in Appendix 3, along with character states, brief descriptions (and references to Fig. 3), and selected definitions.

### 2.3 Analytical methods

The data matrix was constructed in MacClade 4.0 (Maddison & Maddison 2000) and includes 44 taxa and 71 characters (Appendix 2). Some characters are applicable only to some species and



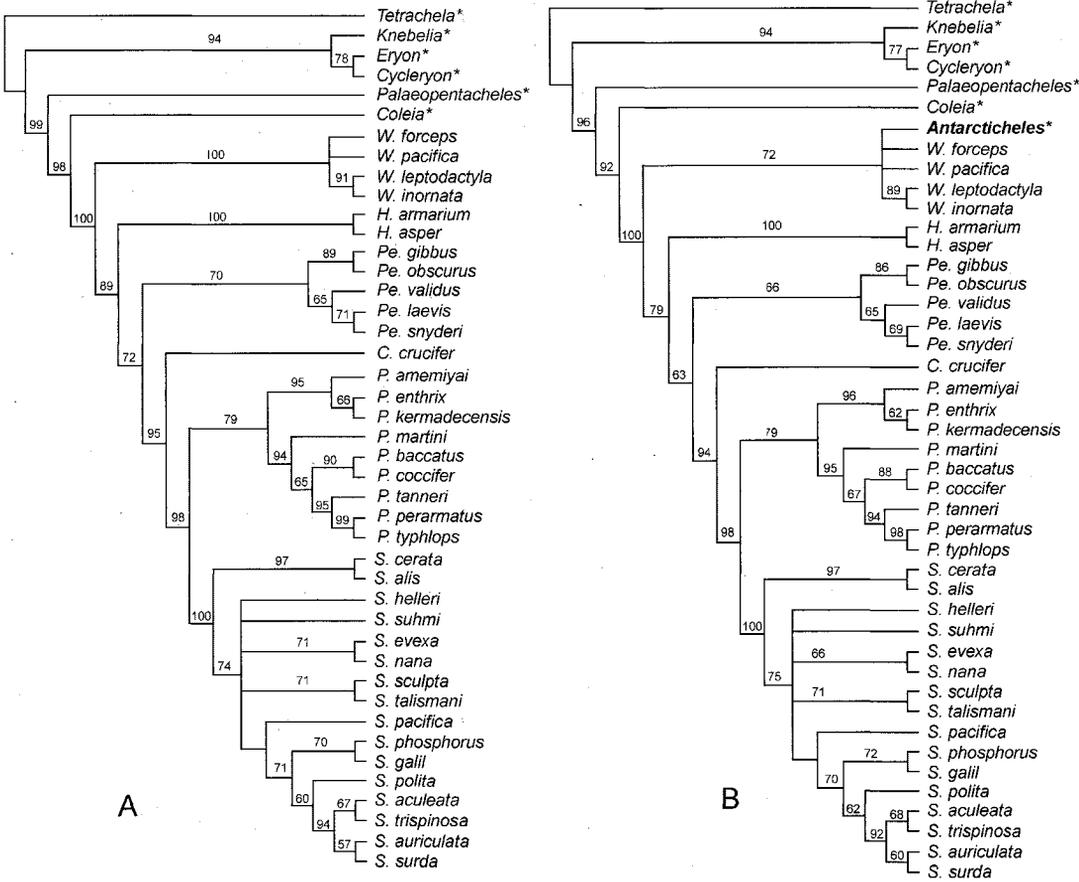
**Figure 3.** Extant Polychelidae. A–F, maxilliped 3. G–H, pereopod 3 (branchiae omitted). (A, G) *Polycheles enthrix*. (B, H) *Stereomastis suhmi*. (C) *Cardus crucifer*. (D) *Homeryon armarium*. (E) *Pentacheles laevis*. (F) *Willemoesia forceps*. Arrows indicate epipod.

cannot be meaningfully scored for the remaining taxa. Coding of inapplicable characters, either as a '?' or as a state called 'inapplicable,' has been shown to be problematic based on currently available computer algorithms (Maddison 1993). Although Platnick et al. (1991) suggested that the '?' coding can lead to implications of unlikely ancestral states, the alternative coding as a character may lead to branches being supported by the non-existent character state 'inapplicable.' Inapplicables were therefore scored '?' but are indicated as '-' in Appendix 2 to distinguish them from unknowns.

All characters were unordered (non-additive) and equally weighted, missing data were scored unknown, and polymorphisms were scored as such rather than assuming a plesiomorphic state. Characters were unordered, so the score given for each state (i.e., 0, 1, 2) implies nothing about order in a transformation series. Trees were generated in PAUP\*4.0b10 (Swofford 2002) under the heuristic search (MULTREES, tree-bisection-reconnection, 500 replications with random input order). Relative stability of clades was assessed by parsimony jackknifing (Farris et al. 1996) with 500 pseudoreplicates and 30% character deletion as implemented in PAUP\*.

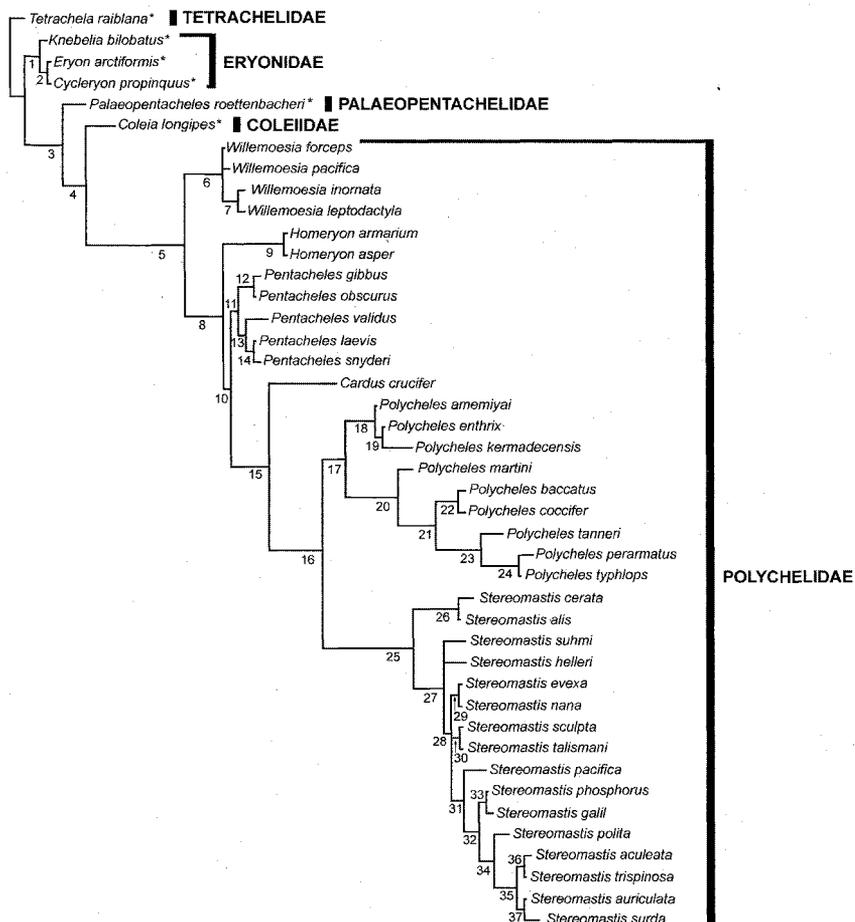
### 3 RESULTS

Analysis 1 retrieved 10 minimal length trees of length 191, consistency index (CI) 0.4974, and retention index (RI) 0.8580 (Fig. 4A). Unambiguous character state changes for 1 of 10 most parsimonious topologies are listed in Appendix 3 and correspond to nodes numbered in Fig. 5. All



**Figure 4.** Phylogeny of the Polychelida. (A) Analysis 1, strict consensus of 10 most parsimonious topologies (TL = 191, CI = 0.4974, RI = 0.8580). (B) Analysis 2, strict consensus of 20 most parsimonious topologies (TL = 192, CI = 0.4948, RI = 0.8578). Jackknife proportions indicated at nodes. Generic names abbreviated as: *Cardus* (C.), *Homeryon* (H.), *Pentacheles* (Pe.), *Polycheles* (P.), *Stereomastis* (S.), *Willemoesia* (W.). Extinct taxa (\*).

polychelid genera as recognized by Galil (2000) were recovered by the analysis. The most basal polychelid clade is *Willemoesia*, followed by *Homeryon* and *Pentacheles*. *Cardus* is sister to *Polycheles sensu Galil* (2000). *Polycheles sensu Galil* (2000) comprises two major clades corresponding to *Stereomastis* and *Polycheles sensu stricto*. Monophyly of crown-group Polychelidae received 100% jackknife support, suggesting a monophyletic origin for all extant forms. *Coleia* (Coleiidae), rather than *Palaeopentacheles*, was sister to crown-group polychelids, suggesting that the latter should be excluded from Polychelidae. The eryonid clade is sister to *Palaeopentacheles* + (*Coleia* + Polychelidae). Jackknife values for the genera are as follows: *Homeryon* (100%), *Stereomastis* (100%), *Pentacheles* (70%), *Polycheles* (79%), and *Willemoesia* (100%). The *Polycheles* + *Stereomastis* clade is robust to jackknifing (98%), but relationships between other genera received lower jackknife support (72–95%). Analysis 2 (including *Antarcticheles*) recovered 20 minimal-length trees of length 192, CI = 0.4948, RI = 0.8578 (Fig. 4B). The strict consensus reflected the strict consensus of Analysis 2, with *Antarcticheles* in a clade with *Willemoesia*. Jackknife proportions for most nodes in Analysis 2 were similar to those of Analysis 1.



**Figure 5.** Phylogeny of the Polychelida. 1 of 10 most parsimonious topologies derived from Analysis 1 (TL = 191, CI = 0.4974, RI = 0.8580). Clade number indicated at nodes. Unambiguous character state changes for nodes are given in Appendix 4.

## 4 DISCUSSION

### 4.1 The polychelid sister group and the position of Palaeopentacheles

Coleiidae is sister to the Polychelidae (to the exclusion of *Palaeopentacheles*). Both share distinct cervical and postcervical incisions in the carapace margins, with a well-marked postcervical groove, distinct postorbital carinae, and the slender, elongate carpus of pereopod 1. Note, however, that the pereopod 1 carpus condition is not strictly uniform in coleids and polychelids: the carpus is short and stout in one polychelid (*Cardus crucifer*) and several coleids: *Proeryon hartmanni* (von Meyer, 1836) and several species of *Coleia* (see Teruzzi 1990; Schweigert 2000; Karasawa et al. 2003). Coleiidae otherwise differs from Polychelidae chiefly in the 2-segmented uropodal exopod, in having postorbital carinae (when present) that are aligned with the branchial carinae and a second abdominal pleuron that is similar to that of the third pleuron, rather than being distinctly larger. The unisegmental uropodal exopod of Polychelidae is not unique, being present in all polychelidans except Coleiidae and Tetrachelidae. The distinctly enlarged second pleuron that overlaps both the first and third pleura, however, is a synapomorphy of Polychelidae. As with other known fossil polychelidans, the eyes of coleids are well developed rather than reduced as in extant polychelidans. Further synapomorphies of extant Polychelidae (unknown in the fossil *Antarcticheles*) are the reduced eyes and laterally expanded basal antennular segment with stylocerite.

The position of *Palaeopentacheles* as sister to Coleiidae + Polychelidae is significant. Though *Palaeopentacheles* has always been assigned to Polychelidae on account of its unisegmental uropodal exopod, well-marked cervical groove (only medially), and deep orbits, each of these features is plesiomorphic. *Palaeopentacheles* is excluded from the Coleiidae + crown-group polychelid clade by lacking postorbital carinae; in lacking an anterior median carina on the carapace; in the possession of sharp, angular, pleural terminations; and in lacking any trace of cervical and postcervical incisions on the lateral carapace margin. *Palaeopentacheles* is herein placed in a new family, Palaeopentachelidae, diagnosed below (section 5.1).

#### 4.2 *The genera of the Polychelidae*

Galil (2000) synonymised *Stereomastis* with *Polycheles*, but present results indicate that both genera are monophyletic and readily distinguished. Both are recognized herein. *Stereomastis* and *Polycheles* differ from all other polychelids by the vestigial instead of well-developed epipod on maxilliped 3. *Stereomastis* is readily distinguished from *Polycheles* by the following synapomorphies: the reduced instead of long epipod on pereopods 1–5, deep; U-shaped instead of V-shaped dorsal orbital sinuses in the frontal margin of the carapace; the bilobed instead of unilobate eye; and the presence of a pleural spine on abdominal tergite 1 (except in *S. cerata* and *S. alis*; present in *Polycheles tanneri*). The aforementioned diagnostic characters of *Stereomastis* are far more 'satisfactory' than former distinctions that relied on lateral spine counts of the carapace, whether more than or fewer than 20 (Firth & Pequegnat 1971). Within *Stereomastis*, species allied to *S. phosphorus*, namely *S. aculeata*, *S. auriculata*, *S. galil*, *S. polita*, *S. surda*, and *S. trispinosa*, are united by the presence of spines on the coxae of pereopods 2–3. *Stereomastis alis* and *S. cerata* form a clade that is sister to the remaining species of the genus. Though *Polycheles* is monophyletic in the present analysis, its support is low, suggesting possible heterogeneity. Few unambiguous characters support monophyly of *Polycheles* (Clade 17), and, at present, the genus is most easily recognized by a combination of character states, most of which are plesiomorphies: the V-shaped dorsal orbital sinus (plesiomorphic), vestigial epipod of maxilliped 3 (plesiomorphic), rounded anterolateral margin of the basal antennular segment (plesiomorphic), and absence of an arthrobranch on maxilliped 3 (apomorphic). Although overall monophyly of *Polycheles* is not well supported, it consists of two well-supported clades (jackknife > 90%). One clade contains six species including the type species, and the other contains *P. enthrix*, *P. kermadecensis*, and *P. amemiyai*. The most important characters separating the second clade from the first are the chelate instead of simple pereopod 5 in males and the articulating instead of fused ischium and basis on pereopods 3–5. The pereopod 3–5 ischium and basis is fused in all other extant polychelids except *Homeryon*. Further study may justify removal of *P. enthrix* and allies to a separate genus.

Support for monophyly of *Pentacheles* is low, suggesting that it could be paraphyletic. Species of *Pentacheles* share similar general morphology, but most previously employed diagnostic characters, such as the well-developed epipod of the third maxilliped and angular anterolateral margin of the basal antennular segment, are plesiomorphies present also in *Homeryon* and *Willemoesia*. The single synapomorphy of *Pentacheles* identified here is the indistinct to absent branchial carina. In other polychelids, the branchial carina is well defined.

*Homeryon* is readily recognized by its strongly curved pereopod 2–4 dactyli, prominently angled carina laterally bordering the buccal cavity, and elongate pereopodal epipods. An unusual feature of *Homeryon* shared with *Polycheles amemiyai*, *P. enthrix*, and *P. kermadecensis* is the articulated rather than fused basis and ischiomerus, with a diagonal rather than transverse junction (Char. 69, 70). In other polychelids the basis and ischiomerus are fused, with a transverse junction (except in *Willemoesia*, with a diagonal junction).

*Cardus* is unique among extant polychelids for its ovate carapace, short pereopod 1 carpus, and small maximum size (reaching about 30 mm carapace length). The median spines on the abdominal

terga are also unusual for their slenderness, being usually stout and triangular in other genera. In these respects, *Cardus* resembles the eryoneic larva and as such may be neotenus.

#### 4.3 The position of *Willemoesia*

Bouvier (1917) identified *Willemoesia* as the most 'primitive' of extant polychelids based on the eryonid-like shallow dorsal orbits and well-developed pereopodal epipods. Although *Willemoesia* (or *Willemoesia* + *Antarcticheles*) was found to be sister to remaining extant genera, present results suggest that the resemblance to eryonids is superficial. The eyes of eryonids are well developed and directed forwards. Conversely, the eyes of *Willemoesia* are poorly developed and the stalk is oriented transversely along the anterior wall of the carapace as in all other extant polychelids. In extant polychelids (other than *Willemoesia*), the base of the eyestalk is swollen and protrudes dorsally, occupying the dorsal orbital sinus, and the cornea protrudes laterally through the lateral orbital sinus. In *Willemoesia*, however, the eye is shorter than in other polychelids, not reaching the lateral carapace margins. The cornea is fused with the anterior wall of the carapace. Although the base of the eyestalk is reduced and does not protrude through the carapace, the homologous position and apparent outline of the dorsal orbital sinuses present in other polychelids are visible in most species of *Willemoesia* as a depressed, aspinulate area above the eyestalk bases. Thus, in *Willemoesia*, degeneration of the eyes possibly has been accompanied by closure of the dorsal orbits. Species of *Willemoesia* are the deepest living polychelids (exceeding 5000 m; Galil 2000), and it appears that vision is correspondingly degenerate. The shallow dorsal orbits of *Willemoesia* thus appear to be a derived feature, not homologous with those of eryonids. Moreover, the presence of deep dorsal orbital sinuses in the extinct palaeopentachelids and most coleiids, which are more closely related to the polychelids than are the eryonids, indicates that the orbital condition in *Willemoesia* is probably derived. Further study of the diverse coleiids, however, is required to assess the degree of the orbital variation and thus the likely stem condition in Polychelidae. Bouvier (1917) was incorrect to homologize the orbital condition of *Willemoesia* with that of eryonids, but the polarization of character 59 suggests that well-developed pereopodal epipods are plesiomorphic as supposed. Other plesiomorphies of *Willemoesia* placing it outside the remaining extant polychelids are the absence of a lateral orbital sinus, a bulbous rather than slender cornea, and an unarmed anterolateral margin of the basal antennular segment (Clade 8).

The sister relationship between *Willemoesia* and *Antarcticheles* recovered by Analysis 2 is noteworthy. Appendages, pereopods, and the tailfan are unknown in *Antarcticheles*, but discernable carapace characters are virtually identical to those of *Willemoesia*, with the full complement of carapace grooves and carinae that are present in extant polychelids. Aguirre-Urreta et al. (1990) interpreted the dorsal orbits of *Antarcticheles* as 'very deep,' but their fig. 2b appears to show broad, shallow dorsal orbits as in *Willemoesia*. The presence in *Antarcticheles* of carapace morphology resembling contemporary taxa suggests that differentiation of the 'polychelid form' was well established by the late Jurassic.

#### 4.4 Morphological trends

Extant polychelids differ most obviously from extinct polychelidans in the degenerate instead of well-developed eyes and distinctly concave anterior carapace margin. The polarization of character 6 indicates that a general shortening of the frontal carapace margin has occurred in Polychelidae. In other polychelidans, especially *Palaeopentacheles* and coleiids, the frontal margin is level with or advanced beyond the anterolateral carapace margins, concealing the bases of the antennae and antennules. This suggests that the projecting carapace front was probably a feature of at least some stem-lineage Polychelidae. In crown-group polychelids, the frontal margin does not extend anteriorly as far as the anterolateral carapace margins, exposing the bases of the antennae and antennules. In coleiids and *Palaeopentacheles*, the eyes project laterally into wide dorsal orbital sinuses.

In Polychelidae, the shortening of the front is accompanied by a corresponding shortening and narrowing of the dorsal orbits. The eyes become positioned at the far anterior of the frontal region, lying parallel to the frontal margin. In extant Polychelidae (except *Willemoesia*), the bases of the eyes fill the dorsal orbits, and the cornea (or its remnants) is narrow and elongated, projecting laterally into the lateral orbits. In *Willemoesia*, the dorsal orbits are reduced to a shallow concavity and the remnants of the eyes are fused to the anterior wall of the carapace; the cornea is globular but does not project laterally as far as the lateral carapace margin as in other polychelids.

An additional characteristic feature of polychelids (but unknown in *Antarcticheles*) is the well-developed basal antennular segment with stylocerite. The degenerate eyes of polychelids are plausibly accounted for by their deep-water habitat. The structure of the stylocerite, however, bears little relationship to bathymetry, instead probably reflecting a fossorial habit. The stylocerites, when placed together, form what appears to be a respiratory canal enabling individuals to breathe whilst buried in the substrate (Gore 1984) in a similar fashion to penaeoid prawns.

The major chelipeds exhibit a general trend towards elongation within Polychelida. In tetrachelids, eryonids, and palaeopentachelids, the chelipeds are robust and the carpus is short, being, at most, little longer than high (Fig. 1A–D). In polychelids (except *Cardus*; unknown in *Antarcticheles*), the major chelipeds are long, slender, and considerably less robust than those of tetrachelids, eryonids, and palaeopentachelids, with the carpus slender and distinctly longer than high (Fig. 2). Interestingly, the coleids, which are phylogenetically intermediate between palaeopentachelids and polychelids, exhibit both robust and slender cheliped forms, though the latter condition is apparently more common (Teruzzi 1990; Schweigert & Dietl 1999). Coleiidae has a late Triassic to late Jurassic geologic range (Teruzzi & Garassino 2007), and it is not inconceivable that coleids may be paraphyletic with respect to Polychelidae. If so, the shift from shallow to deep-water habitats may have commenced within the coleids, in which case the stem polychelids evolved in deep water. In this context, it is significant that the late Jurassic *Coleia longipes* has been attributed superposition eyes, suggesting adaptation to reduced light conditions (Schweigert & Dietl 1999).

Modern polychelids appear to be ambush predators, striking from a buried position with the chelipeds folded against the lateral margins of the carapace. In underwater footage, polychelids are typically buried in the substrate, as reported by Gore (1984) for species of *Willemoesia*. In contrast to extant polychelids, the unspecialized basal antennular segment and more robust major cheliped of extinct forms suggest that they may have actively foraged or were at least epibenthic. Another derivation in polychelids, including the Jurassic *Antarcticheles*, is the antrorse median spine or tooth on one of more of the abdominal tergites of most species, and the prominently enlarged second abdominal pleuron that overlaps the first and third pleura. Dorsal median spines, when present in other fossil families, are directed posteriorly instead of anteriorly as in modern forms.

Thus, general morphological trends within Polychelida include a shortening of the carapace front with respect to the anterolateral margins, leading to dorsal exposure of the base of the antennules and a shift in eye orientation from anterior to transverse; development of the basal antennular segment stylocerite to form a respiratory canal; and a shift in the form of the major chelipeds from relatively robust with short, triangular carpi to elongated and slender, with slender carpi. A further trend is toward narrowing of the body, marked by a reduction in carapace width, and stronger taper of the abdomen including enlargement of the second pleuron (compare Figs. 1, 2). The carapace in tetrachelids and eryonids distinctly overhangs the pereopods, covering much of the merus of pereopod 1. The posterior width of the carapace in tetrachelids and eryonids significantly exceeds the width of the anterior abdomen, which is itself relatively broad with little taper. In palaeopentachelids, the carapace is proportionally narrower than eryonids and tetrachelids, though distinctly wider than the anterior abdomen. In coleids and polychelids, the carapace is generally narrowed and 'box-like' with little lateral overhang of pereopod 1. The posterior width of the carapace is similar to the anterior abdominal width so the dorsal outline of the carapace is confluent with that of the abdomen. The abdomen is tapered in coleids, but is even more so in polychelids, enabling more efficient

burying. The lateral surfaces of the carapace of extant polychelids are near vertical, allowing individuals to fold the chelipeds against the carapace sides and strike prey from a buried position. These general morphological trends within Polychelida appear to correspond to a shift from a shallow-water, epibenthic habit to the deep-water, fossorial lifestyle, currently evident in Polychelidae.

Within Polychelidae, several topological trends are noteworthy. First, the length of the maxilliped 3 epipod shows a consistent reduction in living taxa. In *Cardus*, *Willemoesia*, and *Pentacheles*, the maxilliped 3 epipod is as long as or longer than the ischium, and in *Homeryon*, it is about one-third the ischium length. In *Polycheles* and *Stereomastis*, the maxilliped 3 epipod is vestigial. Though the maxilliped 3 epipod length is not known for any of the fossil taxa, the polarization of character 57 predicts that they bore well-developed epipods. Similarly, the reduced epipods of pereopods 1–5 in *Stereomastis* is a derived state, so the well-developed condition of other extant genera could be expected in the fossil taxa.

### 5 SYSTEMATICS

The focus of this study is extant Polychelidae, but appraisal of polychelid phylogeny has required assessment of the overall polychelidan system. Notably, *Palaeopentacheles*, formerly placed in Polychelidae, is demonstrated above to lie outside a Polychelidae + Coleiidae clade. Therefore, *Palaeopentacheles* is referred to a new family, Palaeopentachelidae, diagnosed below. Many fossil taxa are poorly known and require revision, but as basis for further research, the families of Polychelida are all diagnosed below. The stratigraphic ranges of the polychelidan families are illustrated in Fig. 6.

#### 5.1 Diagnoses of higher taxa

Infraorder Polychelida de Haan, 1841

*Diagnosis.* Reptantia. Carapace dorsoventrally flattened; lateral margins cristate, well-defined. Antennal segments free. Pereopods 1–4 chelate. Pereopod 5 chelate in one or both sexes.

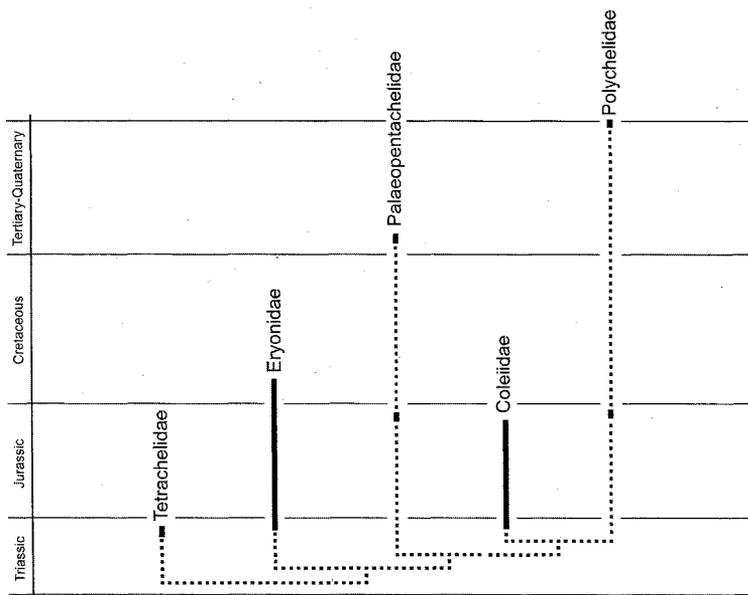


Figure 6. Stratigraphic range of Polychelidan families. Broken lines are inferred ranges.

*Remarks.* Polychelida presently includes five families of which Palaeopentachelidae is diagnosed as new. The chief synapomorphy uniting polychelidans is the chelate pereopods 1–4. Other features also unite the extant polychelidans, such as the unique abdominal–thoracic ‘fastening’ device (Scholtz & Richter 1995) and the dorsally directed aperture of the renal gland. These features remain to be confirmed in fossil forms.

#### Family Coleiidae Van Straelen, 1924

*Diagnosis.* Carapace with deeply incised, U-shaped dorsal orbits; eyes well-developed, directed laterally; with or without distinct median carina anterior to cervical groove; postorbital carinae (when present) aligned with branchial carinae; cervical and postcervical grooves distinct across carapace, indicated at lateral margins by shallow notches. Abdominal pleuron 2 similar to pleuron 3, not overlapping pleuron 1. Uropodal exopod with curved diaeresis. Telson triangular.

*Composition.* *Coleia* Broderip, 1835; *Hellerocaris* Van Straelen, 1925; *Proeryon* Beurlen, 1928; *Pseudocoleia* Garassino & Teruzzi, 1993; *Tropifer* Gould, 1857; *Willemoesiocaris* Van Straelen, 1925. *Stratigraphic range.* Late Triassic to late Jurassic (Teruzzi & Garassino 2007).

*Remarks.* *Willemoesiocaris* Van Straelen, 1925, from the mid-Jurassic of France, regarded as a polychelid by Glaessner (1969), is transferred to Coleiidae. *Willemoesiocaris* is known only from the carapace of its type species, *W. ovalis* (Van Straelen, 1923). According to Van Straelen (1923), *W. ovalis* lacks a median carina anterior to the cervical groove, the postorbital carinae is aligned with the branchial carina, and the carapace front extends anteriorly slightly beyond the anterolateral margins, features of Coleiidae.

#### Family Eryonidae de Haan, 1841

*Diagnosis.* Carapace with shallow orbits, located on anterior margin, eyes well-developed, directed anteriorly; usually without median carina anterior to cervical groove; cervical groove absent or indicated medially and at carapace margins, not extending across carapace; postcervical groove indicated only at carapace margins. Branchiocardiac grooves absent. Abdominal pleuron 2 similar to pleuron 3, not overlapping pleuron 1. Uropodal exopod entire, without diaeresis. Telson triangular or subrectangular. Pereopod 1 dactylus with triangular subdistal lobe, longer than pollex.

*Composition.* *Eryon* Desmarest, 1822; *Cycleryon* Glaessner, 1965; *Knebelia* Van Straelen, 1922; *Rosenfeldia* Garassino, Teruzzi, & Dalla Vecchia, 1996.

*Stratigraphic range.* Late Triassic to Lower Cretaceous (Glaessner 1969; Garassino et al. 1996).

#### Family Palaeopentachelidae, new family

*Diagnosis.* Carapace with dorsal orbits deeply incised, narrow, U-shaped; eyes well-developed, directed laterally; without median carina anterior to cervical groove; cervical groove indicated medially only, not extending to lateral carapace margins; branchiocardiac grooves absent. Posterior margin of carapace distinctly wider than anterior margin of abdomen. Abdominal pleuron 2 similar to pleuron 3, not overlapping pleuron 1. Uropodal exopod entire, without diaeresis. Telson triangular. Pereopod 1 dactylus tapering distally, as long as pollex; occlusal margins of dactylus and pollex lined with spines.

*Composition.* *Palaeopentacheles* von Knebel, 1907 (type genus).

*Stratigraphic range.* Upper Jurassic, possibly to the Oligocene (Schweitzer & Feldmann 2001).

*Remarks.* *Palaeopentacheles* was previously placed in Polychelidae, but results of the present study exclude it from Polychelidae *sensu stricto* by the incursion of Coleiidae. As sister to Coleiidae + Polychelidae, *Palaeopentacheles* cannot be accommodated within either Coleiidae or Polychelidae.

without subsuming all three taxa into an enlarged Polychelidae, significantly diluting the concept of the family. Thus, the new family Palaeopentachelidae is herein proposed for *Palaeopentacheles*. Moreover, Palaeopentachelidae differs from Coleiidae and Polychelidae by lacking postorbital carinae, in lacking an anterior median carina on the carapace, in the possession of sharp pleural terminations, in having entire lateral carapace margins without any trace of cervical or postcervical incisions, and in the multispinose occlusal margins of the pereopod 1 dactylus and pollex. *Palaeopentacheles* is presently known only from its type species, *P. roettenbacheri* (Upper Jurassic of Germany), and from *P. starri* Schweitzer & Feldmann, 2001 (Oligocene of North America). The holotype of *P. starri* is in poor condition, though, so its assignment to *Palaeopentacheles* was tentative, based on the spinose fingers of the major cheliped (Schweitzer & Feldmann 2001).

Family Polychelidae Wood-Mason, 1874

*Diagnosis.* Carapace with dorsal orbits shallow or deeply incised, U- or V-shaped; eyes reduced, fused to anterior margin of carapace, directed laterally; with distinct median carina anterior to cervical groove; postorbital carinae not aligned with branchial carinae but terminating distinctly mesial to branchial carinae; cervical and branchiocardiac grooves distinct across carapace, indicated at lateral margins by notches. Abdominal pleuron 2 distinctly larger than, and overlapping, pleura 1 and 3. Uropodal exopod entire, without diaeresis. Telson triangular. Pereopod 1 dactylus tapering distally, as long as pollex.

*Stratigraphic range.* Upper Jurassic to Recent (Aguirre-Urreta et al. 1990).

*Composition.* *Antarcticheles* Aguirre-Urreta, et al. 1990 (upper Jurassic); *Cardus* Galil, 2000; *Homeyron* Galil, 2000; *Pentacheles* Bate, 1878; *Polycheles* Heller, 1862; *Stereomastis* Bate, 1888; *Willemoesia* Grote, 1873.

*Remarks.* The Jurassic *Antarcticheles* is retained in Polychelidae on the basis of carapace characters: a median carina anterior to the cervical groove is present, and the cervical and postcervical grooves are distinct dorsally and marked laterally by notches in the carapace margins. Unfortunately, the pereopods and tailfan are not known in *Antarcticheles*. *Willemoesiocaris*, placed in Polychelidae by Glaessner (1969), is transferred above to Coleiidae.

Family Tetrachelidae Beurlen, 1930

*Diagnosis.* Carapace with shallow orbits located on anterior margin; eyes well-developed, apparently directed anteriorly; without median carina anterior to cervical groove; cervical and branchiocardiac grooves distinct across carapace, not meeting, indicated at lateral margins by notches. Abdominal pleuron 2 similar to pleuron 3, not overlapping pleuron 1. Uropodal exopod with straight diaeresis. Telson rounded distally. Pereopod 1 dactylus tapering distally, longer than pollex. (Based on Glaessner 1969.)

*Composition.* *Tetrachela* Reuss, 1858.

*Stratigraphic range.* Upper Triassic (Glaessner 1969).

5.2 Diagnoses of Recent genera and keys to species of Polychelidae

Key to Recent genera of Polychelidae

- 1. Carapace ovate, slightly long than wide ..... *Cardus*  
    - Carapace distinctly longer than wide ..... 2
- 2. Dorsal orbital sinuses forming a shallow concavity. Pollex of major chela with perpendicular spine on inner margin. Anterolateral margin of basal antennular segment unarmed ..... *Willemoesia*

- Dorsal orbital sinuses deep, slit-like, U- or V-shaped. Pollex of major chela without perpendicular spine on inner margin. Anterolateral margin of basal antennular segment with 1 or more spines ..... 3
- 3. Dorsal orbital notch U-shaped. Epipod of pereopods 1–5 reduced, shorter than coxal width ..... *Stereomastis*  
 - Dorsal orbital notch V-shaped or slit-like. Epipod of pereopods 1–5 well-developed, markedly longer than coxal width ..... 4
- 4. Basal antennular segment with rounded anterolateral margin (though bearing 1 or 2 small spines). Maxilliped 3 epipod vestigial ..... *Polycheles*  
 - Basal antennular segment with quadrate anterolateral margin. Maxilliped 3 epipod well-developed ..... 5
- 5.. Dactylus and pollex of pereopods 2–4 strongly curved. Basal antennular segment with 2 anterolateral spines. Maxilliped 3 epipod one-third to half length of ischium ..... *Homeryon*  
 - Dactylus and pollex of pereopods 3–4 relatively straight, weakly curved. Basal antennular segment with 1 outer spine. Maxilliped 3 epipod as long as or longer than ischium. .... *Pentacheles*

#### Genus *Cardus* Galil, 2000

*Diagnosis.* Carapace ovate, slightly longer than wide. Dorsal orbital sinus slit-like. Pollex of major chela without perpendicular spine on inner margin. Anterolateral margin of basal antennular segment with rounded outer margin and 1 or 2 anterolateral spines. Dactylus and pollex of pereopods 2–4 relatively straight. Maxilliped 3 epipod as long as ischium. Pereopods 1–5 epipod well-developed.

*Type species.* *Deidamia crucifer* Thomson, 1873, by original designation and monotypy.

*Composition.* *Cardus crucifer* (Thomson, 1873).

#### Genus *Homeryon* Galil, 2000

*Diagnosis.* Carapace distinctly longer than wide. Dorsal orbital sinus V-shaped or slit-like. Pollex of major chela without perpendicular spine on inner margin. Anterolateral margin of basal antennular segment with quadrate outer margin and 1 anterolateral spine. Dactylus and pollex of pereopods 2–4 strongly curved. Maxilliped 3 epipod one-third to half length of ischium. Pereopods 1–5 epipod well-developed.

*Type species.* *Homeryon armarium* Galil, 2000, by original designation.

*Composition.* *H. armarium* Galil, 2000, *H. asper* (Rathbun, 1906).

#### Key to species of *Homeryon*

1. Lateral margins of carapace posterior to postcervical incision cristate, serrulate. Median abdominal carinae blunt. Abdominal pleuron 2 cordiform. Uropods smooth ..... *H. asper*  
 - Lateral margins of carapace posterior to postcervical incision rounded, bearing rows of antrorse spinules. Median abdominal carinae with distinct notch. Abdominal pleuron 2 reniform. Uropods granulate ..... *H. armarium*

#### Genus *Pentacheles* Bate, 1878

*Diagnosis.* Carapace distinctly longer than wide. Dorsal orbital sinuses deep, V-shaped. Pollex of major chela without perpendicular spine on inner margin. Anterolateral margin of basal antennular segment with quadrate outer margin and 1 anterolateral spine. Dactylus and pollex of pereopods 3–4

relatively straight, weakly curved. Maxilliped 3 epipod as long as or longer than ischium. Pereopods 1–5 epipod well-developed.

*Type species.* *Pentacheles laevis* Bate, 1878, designated by Fowler (1912).

*Composition.* *Pe. Gibbus* Alcock, 1894; *Pe. Laevis* Bate, 1878; *Pe. Obscurus* Bate; 1878, *Pe. Snyderi* (Rathbun, 1906); *Pe. Validus* A. Milne-Edwards, 1880.

Key to species of *Pentacheles*

1. Inner angle of dorsal orbital sinus unarmed ..... 2  
 - Inner angle of dorsal orbital sinus spinose ..... 3
2. Carapace depressed, flattened. Abdominal tergites and pleura nearly smooth ... *Pe. obscurus*  
 - Carapace strongly convex in lateral profile. Abdominal tergites and pleura set with conical tubercles ..... *Pe. gibbus*
3. Abdominal tergites 1–3 with distinct antrorse tooth ..... *Pe. laevis*  
 - Abdominal tergites 1–3 without antrorse tooth, at most with blunt rounded prominence . . 4
4. Outer angle of dorsal orbit unarmed or with at most 2 spines ..... *Pe. validus*  
 - Anterior margin of carapace between outer orbital angle and anterolateral spine lined with 3 or 4 spines ..... *Pe. snyderi*

Genus *Polycheles* Heller, 1862

*Diagnosis.* Carapace distinctly longer than wide. Dorsal orbital sinuses V-shaped. Pollex of major chela without perpendicular spine on inner margin. Anterolateral margin of basal antennular segment rounded, with anterolateral spines. Maxilliped 3 epipod vestigial. Pereopod 15 epipod well-developed. Dactylus and pollex of pereopods 34 relatively straight, weakly curved.

*Type species.* *Polycheles typhlops* Heller, 1862, by monotypy.

*Composition.* *P. amemiyai* Yokoya, 1933; *P. baccatus* Bate, 1878; *P. coccifer* Galil, 2000; *P. enthrinx* Bate, 1878; *P. kermadecensis* Sund, 1920; *P. martini* Ahyong & Brown, 2002; *P. perarmatus* Holthuis, 1952; *P. tanneri* Faxon, 1893; *P. typhlops* Heller, 1862.

Key to species of *Polycheles*

1. One (rarely two) rostral spine. Inner basal margin of dorsal orbit spinose ..... 2  
 - Two rostral spines. Inner basal margin of dorsal orbit unarmed ..... 3
2. Abdominal pleuron 2 trianguloid anteriorly with rounded apex. Uropodal exopod ventrally bicarinate ..... *P. typhlops*  
 - Abdominal pleuron 2 semicircular anteriorly, evenly rounded. Uropodal exopod ventrally tricarinate ..... *P. perarmatus*
3. Frontal submarginal tooth prominent, longer than separate rostral spines ..... 4  
 - Frontal submarginal tooth shorter than rostrum, or rostrum bifid ..... 5
4. Gastro-orbital region bispinose; median postrostral and postcervical carinae irregularly granulate. Abdominal pleuron 2 with broadly convex anteroventral margin. Dorsal margin of first chela prominently spinulose ..... *P. baccatus*  
 - Gastro-orbital region quadrispinose; median postrostral and postcervical carinae set with antrorse tubercles. Abdominal pleuron 2 with concave anteroventral margin. Dorsal margin of first chela granulose ..... *P. coccifer*

5. Frontal margin of carapace with several spinules on either side of rostral spines ..... 6  
 - Frontal margin of carapace on either side of rostral spines unarmed except for spine on inner angle of dorsal orbital sinus ..... *P. tanneri*
6. Median carina on abdominal tergites 2–5 notched or crenulate. Abdominal tergites 2–5 with distinct, oblique grooves. Dorsal surface of carapace strongly granulate ..... *P. martini*  
 - Median carina on abdominal tergites 2–5 entire, without median notch. Abdominal tergites 2–5 relatively smooth, without distinct oblique grooves. Dorsal surface of carapace smooth or sparsely spinose but not strongly granulate ..... 7
7. Branchial carina indicated at most by low granules; branchial groove not flanked by row of spines; gastric region of carapace with 1 or 2 spines of similar size to spines of median carina; postcervical groove without antrorse spine on posterior margin between median carina and branchial carina ..... 8  
 - Branchial carina indicated by row of 4–6 spines; branchial groove flanked by row of 4 or 5 small spines; gastric region of carapace covered by numerous spines of similar size to spines of median carina; postcervical groove with antrorse spine on posterior margin between median carina and branchial carina ..... *P. kermadecensis*
8. Frontal margin with 1 spine between rostral spines and spine of inner angle of dorsal orbit ..... *P. amemiyai*  
 - Frontal margin with 2 or more spines between rostral spines and spine of inner angle of dorsal orbit ..... *P. enthrix*

#### Genus *Stereomastis* Bate, 1888

*Diagnosis.* Carapace distinctly longer than wide. Dorsal orbital sinuses U-shaped. Pollex of major chela without perpendicular spine on inner margin. Anterolateral margin of basal antennular segment rounded, with 1 or 2 anterolateral spines. Maxilliped 3 epipod vestigial. Pereopods 1–5 epipod vestigial. Dactylus and pollex of pereopods 3–4 relatively straight, weakly curved.

*Type species.* *Pentacheles suhmi* Bate, 1878, designated by Holthuis (1962).

*Composition.* *S. alis* (Ahyong & Galil, 2006) comb. nov.; *S. aculeata* (Galil, 2000) comb. nov.; *S. auriculata* (Bate, 1878) comb. nov.; *S. cerata* (Alcock, 1894) comb. nov.; *S. evexa* (Galil, 2000) comb. nov.; *S. galil* (Ahyong & Brown, 2002) comb. nov.; *S. helleri* (Bate, 1878) comb. nov.; *S. nana* (Smith, 1884) comb. nov.; *S. pacifica* (Faxon, 1893); *S. phosphorus* (Alcock, 1894) comb. nov.; *S. polita* (Galil, 2000) comb. nov.; *S. sculpta* (Smith, 1880) comb. nov.; *S. suhmi* (Bate, 1878), *S. surda* (Galil, 2000) comb. nov.; *S. talismani* (Bouvier, 1917) comb. nov.; *S. trispinosa* (de Man, 1905) comb. nov.

#### Key to species of *Stereomastis*

1. Outer proximal margin of basal antennular segment with 1 spine ..... 2  
 - Outer proximal margin of basal antennular segment with 2 spines ..... 4
2. Median carina of abdominal tergites 1–5 with antrorse spine ..... *S. galil*  
 - Median carina of abdominal tergites 1–4 with antrorse spine ..... 3
3. Dorsum of carapace between branchial and median postcervical carinae unarmed; branchial carina obsolescent; branchial groove unarmed ..... *S. polita*  
 - Dorsum of carapace between branchial and median postcervical carinae with antrorse spine; branchial carina indicated by row of spines; branchial groove with row of spines ..... *S. phosphorus*
4. Inner angle of dorsal orbital sinus unarmed ..... 5  
 - Inner angle of dorsal orbital sinus spinose ..... 7

5. Branchial carina unarmed ..... 6  
 - Branchial carina spinose ..... *S. helleri*
6. Antrorse spine on abdominal tergite 5 large, overhanging anterior margin of tergite 4. Postorbital carina ill-defined, without spines ..... *S. cerata*  
 - Antrorse spine on abdominal tergite 5 not overhanging anterior margin of tergite 4. Postorbital carina defined by arcuate row of spines ..... *S. alis*
7. Median carina on abdominal tergite 5 (usually also tergites 2–4) with short, upright posterior tooth in addition to strong antrorse spine. Ischium and merus of pereopod 2 articulated ..... *S. suhmi*  
 - Median carina on abdominal tergites 2–5 without short, upright posterior tooth. Ischium and merus of pereopod 2 fused ..... 8
8. Branchial groove with 1 or more anterior spines ..... 9  
 - Branchial groove unarmed ..... 12
9. Median carina on abdominal tergite 5 without antrorse spine ..... 10  
 - Median carina on abdominal tergite 5 with antrorse spine ..... 11
10. Median carina on abdominal tergite 4 with strong antrorse spine. Region of carapace between branchial and median postcervical carinae unarmed posteriorly. .... *S. pacifica*  
 - Median carina on abdominal tergite 3 bearing long antrorse spine; median carina on abdominal tergite 4 unarmed anteriorly. Region of carapace between branchial and median postcervical carinae posteriorly spinose. .... *S. trispinosa*
11. Antrorse spine on abdominal tergite 3 largest; lyre-shaped carina on abdominal tergite 6 prominently denticulate; basal tubercle on telson pointed ..... *S. nana*  
 - Antrorse spine on abdominal tergite 5 largest; lyre-shaped carina on abdominal tergite 6 smooth; basal tubercle on telson blunt ..... *S. evexa*
12. Median carina of abdominal tergite 5 with antrorse spine ..... 13  
 - Median carina of abdominal tergite 5 without antrorse spine ..... 14
13. Abdominal tergite 6 bearing denticulate, lyre-shaped, mesial carinae. Lateral margins of carapace posterior to postcervical incision, usually with 7–10 spines ..... *S. talismani*  
 - Abdominal tergite 6 bearing parallel smooth carinae, confluent anteriorly and posteriorly. Lateral margins of carapace posterior to postcervical incision, usually with 6–8 spines ..... *S. sculpta*
14. Posterior margin of cervical groove with single antrorse spine midway between median postcervical and branchial carinae. Frontal submarginal tooth prominent, visible in dorsal view ..... *S. aculeata*  
 - Posterior margin of cervical groove with 2–4 (usually 3 or 4) antrorse spines midway between median postcervical and branchial carinae. Frontal submarginal tooth small ..... 15
15. Lateral margins of carapace posterior to postcervical incision with 7 or 8 spines. Oblique grooves on abdominal tergites deeply marked; lyre-shaped carina on sixth tergite prominent ..... *S. auriculata*  
 - Lateral margins of carapace posterior to postcervical incision with 10–14 spines. Oblique grooves on abdominal tergites obsolescent; lyre-shaped carina on sixth tergite obsolescent ..... *S. surda*

Genus *Willemoesia* Grote, 1873

*Diagnosis.* Carapace distinctly longer than wide. Dorsal orbital sinuses obsolete, indicated by shallow concavities. Pollex of major chela with perpendicular spine on inner margin. Anterolateral margin of basal antennular segment quadrate, without anterolateral spine. Maxilliped 3 epipod as

long as ischium. Pereopods 1–5 epipod well-developed. Dactylus and pollex of pereopod 3 crossing; relatively straight, weakly curved on pereopod 4.

*Type species. Deidamia leptodactyla* Willemoes-Suhm, 1873, by monotypy.

*Composition. W. forceps* A. Milne-Edwards, 1880; *W. inornata* Faxon, 1893; *W. leptodactyla* (Willemoes-Suhm, 1873); *W. pacifica* Sund, 1920.

#### Key to species of *Willemoesia*

1. Abdominal tergite 6 sculptured ..... 2  
   - Abdominal tergite 6 nearly smooth ..... 3
2. Lateral margins of carapace posterior to postcervical incision with 10 or fewer spines. Dorsal margin of chela of pereopod 1 with 2 rows of spines ..... *W. inornata*  
   - Lateral margins of carapace posterior to postcervical incision with 15 or more spines. Dorsal margin of chela of pereopod 1 with several rows of spines ..... *W. leptodactyla*
3. Lateral margins of carapace anterior to cervical incision with 15–19 spines. Abdominal tergites 2–5 with deep, oblique grooves. Telson with rounded apex ..... *W. forceps*  
   - Lateral margins of carapace anterior to cervical incision with 6–10 spines. Abdominal tergites smooth, without deep, oblique grooves. Telson with sharp apex ..... *W. pacifica*

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#### NOTE

After this chapter went to press, the description of a new species, *Stereomastis panglao* (Ahyong & Chan 2008), was published. *Stereomastis panglao* is closest to *S. polita* and *S. galil*; it differs from *S. galil* by having unarmed branchial grooves, and from *S. polita* in having an antrorse spine on abdominal tergite 5.

APPENDIX 1

Terminal taxa and sources of character scoring. Extinct (\*).

**TETRACHELIDAE\***

***Tetrachela* Reuss, 1858**

*T. raiblana* (Bronn, 1858): Glaessner (1969).

**ERYONIDAE\***

***Eryon* Desmarest, 1822**

*E. arctiformis* (Schlotheim, 1820): AM; Garassino & Schweigert (2006).

***Cycleryon* Glaessner, 1965**

*C. propinquus* (Schlotheim, 1822): Garassino & Schweigert (2006).

***Knebelia* Van Straelen, 1922**

*K. bilobatus* (Münster, 1839): Garassino & Schweigert (2006).

**PALAEOPENTACHELIDAE new family\***

***Palaeopentacheles* von Knebel, 1907**

*Pa. roettenbacheri* (von Münster, 1839): Garassino & Schweigert (2006).

**COLEIIDAE\***

***Coleia* Broderip, 1835**

*C. longipes* (O. Fraas, 1855): Schweigert & Diel (1999).

**POLYCHELIDAE**

***Antarcticheles* Aguirre-Urreta, Buatois, Chernoglasov & Medina, 1990\***

*A. antarcticus* Aguirre-Urreta et al., 1990: Aguirre-Urreta et al. (1990).

***Cardus* Galil, 2000**

*C. crucifer* (Thomson, 1873): TAMU, males and females.

***Homeryon* Galil, 2000**

*H. armarium* Galil, 2000: NFU, females; Galil (2000). *H. asper* (Rathbun, 1906): Rathbun (1906); Galil (2000).

***Pentacheles* Bate, 1878**

*Pe. gibbus* Alcock, 1894: Alcock (1894); Galil (2000). *Pe. laevis* Bate, 1878: AM, NIWA, males and females.

*Pe. validus* A. Milne-Edwards, 1880: AM, NIWA, males and females. *Pe. snyderi* Rathbun, 1906: MNHN, female; Galil (2000).

***Polycheles* Heller, 1862**

*P. amemiyai* Yokoya, 1933: NTOU, NUS, males and females. *P. baccatus* Bate, 1878: AM, males and females.

*P. coccifer* Galil, 2000: NTOU, NUS, males and females. *P. enthrix* (Bate, 1878): AM, NIWA, males and females.

*P. kermadecensis* (Sund, 1920): AM, males and females. *P. martini* Ah Yong & Brown, 2002: AM, males and females.

*P. perarmatus* Holthuis, 1952: USNM, MNHN, males and females. *P. tanneri* Faxon, 1893: ZMB, male; Galil (2000).

*P. typhlops* Heller, 1862: AM, SAM, NTOU, males and females.

***Stereomastis* Bate, 1888**

*S. aculeata* (Galil, 2000) comb. nov.: AM, MNHN, males and females. *S. alis* (Ah Yong & Galil, 2006) comb. nov.:

MNHN, female holotype. *S. auriculata* (Bate, 1878) comb. nov.: AM, MNHN, males and females. *S. cerata* (Alcock, 1894) comb. nov.:

Alcock (1894); Galil (2000); de Man (1916). *S. evexa* (Galil, 2000) comb. nov.: Galil (2000); Faxon (1895) (as *P. nana*).

*S. galil* (Ah Yong & Brown, 2002) comb. nov.: WAM, AM, NTOU, males and females. *S. helleri* (Bate, 1878) comb. nov.:

AM, NTOU, males and females. *S. nana* (Smith, 1884) comb. nov.:

AM, NIWA, males and females. *S. pacifica* (Faxon, 1893) comb. nov.: AM, male. *S. phosphorus* (Alcock, 1894) comb. nov.:

AM, SAM, males and females. *S. polita* (Galil, 2000) comb. nov.: MNHN, males and females. *S. suhmi* (Bate, 1878) comb. nov.:

AM, NIWA, males and females. *S. surda* (Galil, 2000) comb. nov.:

AM, NIWA, males and females. *S. sculpta* (Smith, 1880) comb. nov.: AM, NTOU, males and females.



APPENDIX 3

Morphological characters used in analysis.

1. Carapace, buccal carina: absent (0); present (1). The buccal carina, unique to *Homeryon*, is a prominent, angular projection along the lateral margins of the buccal cavity (Galil 2000).
2. Carapace, sublateral carina: indistinct, indicated by setae or granules (0); distinct, spinose (1). The sublateral carina is present on the lateral surface of the carapace starting behind the lateral orbit and is indicated by rows of setae or granules or by a row of spines. In most taxa, the sublateral carina reaches to almost the posterior margin, though in species of *Polycheles* related to *P. typhlops* and *P. baccatus*, the carina reaches posteriorly only to about the carapace midlength.
3. Carapace, sublateral carina, length: long, almost reaching posterior margin of carapace (0); short, reaching to about midlength of carapace (1).
4. Carapace, rostral spines: one (0); two (1); absent (2); two, basally fused (3).
5. Carapace, frontal submarginal tooth: absent or obsolete (0); small, rounded (1); prominent, conical (2).
6. Carapace, frontal margin, position: reaching or projecting anteriorly beyond anterolateral carapace margin (0); distinctly behind anterolateral carapace margin (1). A synapomorphy of the Polychelidae is the position of the frontal margin of the carapace, being distinctly behind the level of the anterolateral margins.
7. Carapace, anterior margin between outer orbital margin and anterolateral spine: unarmed (0); spinose (1).
8. Carapace, lateral orbital sinus: absent (0); present (1). In extant polychelids, the eyes are aligned transversely along the frontal margin of the carapace. The bases of the eyes are exposed dorsally via the dorsal orbital sinus, but the remnants of the cornea are directed laterally through the lateral margin of the carapace, forming the lateral orbital sinus. A lateral orbit is present only in those species whose eyes project laterally beyond the dorsal orbit.
9. Carapace, dorsal orbit, shape: broadly concave (0); V-shaped (1); U-shaped (2); slit (3). The dorsal orbits range in shape from broadly concave in *Willemoesia* and *Tetrachela* to U-shaped in eryonids, *Stereomastis*, *Coleia*, and *Palaeopentacheles*; V-shaped in *Pentacheles*; and a narrow slit in *Homeryon* and *Cardus*.
10. Carapace, dorsal orbit, length: distinctly shorter than wide (0); as long as or longer than wide (1). In tetrachelids, eryonids, *Willemoesia*, and *Antarcticheles*, the dorsal orbital length is very short, distinctly shorter than wide. In other taxa, the dorsal orbit is as long as or longer than wide.
11. Carapace, inner angle of dorsal orbit: rounded (0); spinous (1); triangular (2).
12. Carapace, inner margin of dorsal orbit: smooth (0); spinous (1).
13. Carapace, outer orbital spine: absent (0); present (1).
14. Carapace, outer orbital margins: smooth (0); spinose (1).
15. Carapace, lateral spine spacing: evenly spaced (0); spacing becoming wider posteriorly (1). In most polychelidans with lateral spines on the carapace, the spines are evenly spaced. In *Stereomastis*, however, the lateral spines become more widely spaced posteriorly.
16. Carapace, postorbital carina: indistinct or absent (0); distinct (1). The position of the postorbital carina is usually indicated by slight surface swelling and a row of spines or granules.
17. Carapace, postorbital carina, orientation: arcuate, divergent anteriorly (0); subparallel or slightly convergent anteriorly (1). The postorbital carina is present in the fossil *Antarcticheles*, but its orientation cannot be satisfactorily interpreted from Aguirre-Urreta et al.'s (1990) account, so it is scored as unknown.
18. Carapace, postorbital carina, ornamentation: unarmed (0); spined (1); tuberculate (2).

19. Carapace, anterior median carina: absent or indistinct (0); present, well-developed (1).
20. Carapace, anterior median carina, ornamentation: unarmed (0); irregularly spinous or tuberculate (1); with spine formula 1:1:2:1, 1:2:1 (2). In *Stereomastis*, the median carina of the carapace is armed with spines in the arrangement 1:1:2:1 anterior to the cervical groove, and 1:2:1 posterior to the cervical groove.
21. Carapace, posterior median carina, ornamentation: unarmed (0); irregularly spinous (1); unarmed at midlength (2); paired spines at midlength (3).
22. Carapace, cervical groove: absent or only faintly indicated (0); distinct across dorsum (1); indicated medially only (2). The cervical groove is distinct across the dorsum in polychelids, coleids, and tetrachelids. The cervical groove is indicated only medially in *Palaeopentacheles* and is faintly indicated or absent in eryonids.
23. Carapace, cervical and postcervical groove, lateral notches: shallow (0); deeply incised (1); absent (2). The cervical and postcervical grooves are indicated by shallow notches in the carapace margins in most polychelidans. *Palaeopentacheles* lacks any trace of cervical and postcervical notches in the carapace margins. In *Eryon*, *Cycleryon*, and *Cardus*, the cervical and postcervical notches are deeply incised.
24. Carapace, cervical groove, midpoint spines: absent (0); one spine (1); two or more spines (2).
25. Carapace, spine on cervical groove near junction with postcervical groove: absent (0); present (1).
26. Carapace, branchial groove, ornamentation: unarmed (0); spined (1); tuberculate (2); absent (3).
27. Carapace, branchial groove, orientation: absent or indistinct (0); divergent (1); parallel (2).
28. Carapace, branchial carina: indistinct (0); distinct (1); absent (2).
29. Carapace, branchial carina, ornamentation: unarmed (0); spined (1); tuberculate (2).
30. Carapace, posterior margin with median spines: absent (0); present (1).
31. Carapace, posterior margin, ornamentation on either side of midline: unarmed (0); with row of spines (1).
32. Abdominal tergite 1, sublateral spine: absent (0); present (1). The sublateral spine is present on the anterior margin of abdominal tergite 1, slightly dorsal to the pleuron. It is present in all species of *Stereomastis* and in *Polycheles martini*, *P. kermadecensis*, *P. enthrix* and *P. amemiyai*.
33. Abdominal tergite 1, anterior pleural spine: absent (0); present (1). The spine is present in *Polycheles tanneri* and most species of *Stereomastis*.
34. Abdominal tergites 2–5, submedian groove: absent (0); distinct (1); indistinct (2).
35. Abdominal tergites 4–5, antrorse spine: absent on AS4–5 (0); absent on AS5 (1); present on AS5 (2). A feature of most polychelids is the presence of an anterodorsally directed spine (termed 'antrorse') on one or more of the abdominal tergites.
36. Abdominal pleural terminations: sharp, angular (0); rounded (1). The pleural terminations in coleids and polychelids are rounded; they are sharp and angular in other taxa. The pleura of *Stereomastis suhmi* are ventrally rounded, but with a small spine present; it is scored as state 1.
37. Abdominal tergite 2, pleuron size: similar to that of pleuron 3 (0); distinctly larger than pleuron 3 (1). The second abdominal pleuron is distinctly enlarged in all extant polychelids, unknown in *Antarcticheles*, and similar to pleuron 3, in other taxa.
38. Abdominal tergite 2, pleuron shape: ovate (0); triangular (1).
39. Abdominal tergite 2, pleuron, anterior spine: absent (0); present (1).
40. Abdominal tergite 2, pleuron, surface carina: absent (0); crescent shaped (1).
41. Abdominal tergite 6, surface, double carina: absent (0); present (1); partial (2).
42. Abdominal tergite 6, surface: uniform or slightly irregular (0); sculptured (1). This character distinguishes species of *Willemoesia* in which two species have a distinctly sculptured surface of abdominal tergite 6. In other polychelidans, the surface of tergite 6 is uniform or slightly irregular.

43. Eye orientation: directed anteriorly (0); transverse, directed laterally (1). The eyes are directed laterally in polychelids, coleids, and palaeopentachelids, and anteriorly in eryonids. The eyes of tetrachelids are not known, but the anterior position of the orbits, as in eryonids, suggests an anterior orientation.
44. Eye articulation: free (0); fused to anterior margin of carapace (1). The eyes of extant polychelids are fused to the anterior margin of the carapace; the condition is unknown in *Antarcticheles*. The eyes of other polychelidans are articulated.
45. Cornea shape: globular (0); slender (1). The cornea is globular in extinct taxa and *Willemoesia* and is tapering in other extant polychelids.
46. Apex of eye: simple (0); bilobed (1). In *Stereomastis*, the apex of the eye is distally widened and somewhat T-shaped or bilobed.
47. Basal antennular segment, anterolateral margin: obsolete, not expanded (0); expanded, quadrate (1); expanded, round (2). The basal antennular segment in non-Polychelidae is unspecialized and similar to the following segment. In extant Polychelidae, the basal antennular segment is expanded anterolaterally, and the stylocerite is strongly produced anteromedially to form a spiniform or triangular projection. The antennules are not known in *Antarcticheles*.
48. Basal antennular segment, stylocerite: absent (0); present (1).
49. Basal antennular segment, stylocerite length: not extending beyond peduncle, upturned medially (0); as long as or longer than peduncle (1); obsolete (2).
50. Basal antennular segment, anterolateral spines: absent (0); one or two (2).
51. Basal antennular segment, stylocerite form: triangular (0); foliaceous (1); spinular (2); obsolete (3). The stylocerite is triangular in most Polychelidae, but is spinular in *Cardus*, and foliaceous in *Pentacheles gibbus* and *Pe. obscurus*.
52. Antennular peduncle, segment 1, inner spine: absent (0); present (1).
53. Antennal protopod, segment 1, inner spine: absent (0); large, prominent (1); small (2).
54. Antennal peduncle, segment 1, inner spine or tooth: absent (0); present (1).
55. Antennal peduncle, segment 2, inner spine or tooth: absent (0); present (1).
56. Antennal scale shape: lanceolate (0); convex outer margin (1); circular (2).
57. Maxilliped 3, epipod: vestigial (0); about one-third ischium length (1); as long as or longer than ischium (2). The maxilliped 3 epipod is as long as or longer than the ischium in *Cardus*, *Willemoesia*, and *Pentacheles* (Fig. 3C, E, F); about one-third the ischium length in *Homeryon* (Fig. 3D); and vestigial in *Polycheles* and *Stereomastis* (Fig. 3A, B).
58. Maxilliped 3, arthrobranch: absent (0); present (1).
59. Pereopods 1-5 epipod: reduced (0); well-developed (1). The epipods of pereopods 1-5 are very short and reduced in *Stereomastis* (Fig. 3H) and well-developed in other extant polychelids (Fig. 3G). Bate (1888) used the length of the pereopods 1-5 epipods to distinguish *Stereomastis* from *Pentacheles*, but his concept of *Pentacheles* included species now assigned to *Polycheles*, which have vestigial rather than well-developed maxilliped 3 epipods. The epipod length is not known in any extinct taxa.
60. Pereopod 1, pollex accessory spine: absent (0); present (1). The pereopod 1 pollex accessory spine is unique to *Willemoesia* (Fig. 2F).
61. Pereopod 1, dactylus: distally evenly tapering (0); with small, triangular subdistal lobe. Distally tapering pereopod dactyli are present in all taxa except eryonids, in which the dactylus terminates in a small, triangular subdistal lobe.
62. Pereopod 1, carpus length: very short, triangular (0); elongate, slender (1). The short, triangular carpus is a feature of tetrachelids, eryonids, palaeopentachelids, and the extant *Cardus*. In other taxa, where known, the carpus is elongate and slender.
63. Pereopod 1, carpus, upper distal spine: absent (0); present (1).
64. Pereopod 2, ischium-merus: articulating (0); fused (1). The pereopod 2 ischium and merus are fused in most species of *Stereomastis* and articulated in other polychelids. The condition in fossil taxa is not known except for *Cycleryon*, in which the ischium and merus are articulated.

65. Pereopod 2, coxal spines: absent (0); present (1).
66. Pereopod 3, coxal spines: absent (0); present (1).
67. Pereopods 2–4, dactyli curvature: weak (0); strong (1). Strongly curved pereopods 2–4 dactyli are a synapomorphy of *Homeryon*. In other taxa, the pereopods 2–4 dactyli are only weakly curved.
68. Pereopod 3, cheliped fingers: apices not crossing (0); apices crossing (1). State 1 is unique to *Willemoesia*.
69. Pereopods 3–5, basis-ischium-merus fusion: articulating (0); fused (1). Scholtz & Richter (1995) proposed that a fused basis-ischium-merus of pereopods 3–5 is a synapomorphy of Polychelidae. Although the basis-ischium-merus are fused in most extant polychelids, the basis and ischiomerus segments are articulated in *Homeryon* and *P. amemiyai*, *P. enthrix*, and *P. kermadecensis*. The condition in fossil taxa is not known except for *Cycleryon*, in which the basis and ischiomerus are articulated.
70. Pereopods 3–5, basis-ischium-merus junction: diagonal (0); perpendicular (1). The basis-ischium-merus junction of pereopods 3–5 is perpendicular to the segment axis in extant polychelids except for *Willemoesia*, *Homeryon*, *P. amemiyai*, *P. enthrix*, and *P. kermadecensis*, in which the junction is diagonal to the segment axis. The condition in fossil taxa is not known except for *Cycleryon* and *Eryon*, in which the basis-ischium-merus junction is also diagonal to the segment axis.
71. Pereopod 5, dactylus in adult males: simple (0); partially chelate, dactylus distinctly longer than pollex (1); fully chelate, dactylus as long as pollex (2).

## APPENDIX 4

Unambiguous character state changes for 1 of 10 most parsimonious topologies derived from Analysis 1 shown in Fig. 5. Clade numbers correspond to those indicated in Fig. 5.

**Clade 1.** 22: 1→0, 61: 0→1. **Clade 2.** 23: 0→1. **Clade 3.** 10: 0→1, 11: 0→2, 43: 0→1, 71: 0→1. **Clade 4.** 16: 0→1, 32: 0→1, 62: 0→1. **Clade 5.** 6: 0→1, 11: 2→1, 19: 0→1, 27: 0→1, 29: 2→0, 37: 0→1, 44: 0→1, 47: 0→1, 48: 0→1, 49: 2→0, 51: 3→0. **Clade 6.** 10: 1→0, 60: 0→1, 63: 0→1, 68: 0→1, 71: 1→2. **Clade 7.** 35: 0→2, 42: 0→1. **Clade 8.** 8: 0→1, 45: 0→1, 50: 0→1. **Clade 9.** 1: 0→1, 7: 0→1, 14: 0→1, 52: 0→1, 56: 0→1, 57: 2→1, 67: 0→1. **Clade 10.** 70: 0→1. **Clade 11.** 28: 1→0. **Clade 12.** 11: 1→0, 51: 0→1. **Clade 13.** 63: 0→1. **Clade 14.** 13: 0→1. **Clade 15.** 30: 0→1, 35: 0→2, 47: 1→2, 55: 0→1. **Clade 16.** 2: 0→1, 18: 0→1, 32: 0→1, 41: 0→1, 49: 0→1, 57: 2→0. **Clade 17.** 53: 2→1; 58: 1→0. **Clade 18.** 34: 1→0, 41: 1→2, 69: 1→0, 70: 1→0. **Clade 19.** 31: 0→1. **Clade 20.** 7: 0→1, 13: 0→1, 29: 0→2, 71: 1→0. **Clade 21.** 3: 0→1, 11: 1→2, 32: 1→0. **Clade 22.** 15: 0→1, 35: 2→1, 52: 0→1. **Clade 23.** 14: 0→1, 24: 0→2, 29: 2→1, 31: 0→1. **Clade 24.** 4: 0→1, 12: 0→1, 40: 0→1, 63: 0→1. **Clade 25.** 4: 1→3, 9: 1→2; 15: 0→1, 20: 1→2, 21: 1→3, 24: 0→1, 40: 0→1, 46: 0→1, 59: 1→0, 63: 0→1. **Clade 26.** 5: 0→1, 11: 1→0, 34: 1→0, 35: 2→1. **Clade 27.** 25: 0→1, 29: 0→1, 33: 0→1. **Clade 28.** 64: 0→1. **Clade 29.** 31: 0→1. **Clade 30.** 20: 2→3. **Clade 31.** 35: 2→1, 53: 2→0. **Clade 32.** 5: 0→1, 65: 0→1. **Clade 33.** 42: 0→1. **Clade 34.** 26: 1→0, 39: 0→1. **Clade 35.** 52: 0→1, 53: 0→2, 66: 0→1. **Clade 36.** 5: 1→2. **Clade 37.** 24: 1→2.

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