SYSTEMATIC STUDIES OF PELAGIC HYPERIIDEAN AMPHIPODS OF THE INFRAORDER PHYSOCEPHALATA (CRUSTACEA: AMPHIPODA: HYPERIIDEA)

by

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within the University of Adelaide

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August 2000

Volume I: Text, Appendices and Bibliography

Contents

Abstract

The systematics of the hyperiidean amphipod infraorder Physocephalata is investigated, with particular emphasis on the higher classification of the superfamily Platysceloidea, that has proved to be the most problematical superfamily for zooplankton workers.

The study is based on collections held by major natural history museums in Australia, Europe and North America. All of these museums were visited personally, and in addition, specimens were borrowed from a number of other overseas institutions.

Current studies of the systematics of the Physocephalata support the hypothesis that this group is probably polyphyletic, and genera have sometimes been grouped together in families with no phylogenetic justification. Consequently a number of families are split, resulting in an increase in the number of monogeneric families, giving a classification that reflects the apparently ancient phylogenetic origins of the group. A new key to all families of the sub-order Hyperiidea is provided, as are keys to the genera, and most species, of the infraorder Physocephalata. New diagnoses, reflecting the results of this study, are given for all superfamilies and families, and most genera and species. Twenty-three families, 54 genera and 168 species of Physocephalata are recognised in this review.

The superfamily Vibilioidea now consists of the families Vibiliidae, Cyllopodidae and Paraphronimidae. The family Vibiliidae is reviewed. *Cyllopus* is placed in the family Cyllopodidae, while *Vibilioides* is recognised as a valid genus.

The family Cystisomatidae is reviewed, and placed in a new superfamily, Cystisomatoidea, because it has a number of characters that preclude it from the superfamily Vibilioidea.

The superfamily Phronimoidea is reviewed at the family and genus level. The families Phronimidae, Phrosinidae and Dairellidae remain unchanged but the family Hyperiidae is split into four. The genera *Hyperia, Themisto, Hyperiella, Hyperoche, Pegohyperia* and *Laxohyperia* are retained in the family Hyperiidae. The genera *Lestrigonus, Phronimopsis, Themistella, Hyperioides, Hyperietta* and *Hyperionyx* are transferred to the new family, Lestrigonidae. *Iulopis* and *Bougisia* do not fit into either of these families, nor do they resemble each other, and they are therefore placed in two new families, Iulopididae and Bougisidae.

The superfamily Lycaeopsoidea is maintained on the basis of the morphology of the antennae, the mouthparts and the extreme sexual dimorphism.

Genera of the superfamily Platysceloidea are diagnosed using the taxonomic database program DELTA (Dalwitz *et al*. 1999). This database is also used for a phylogenetic analysis of the genera using PAUP (Swofford 2000). Taxonomic changes as a result of this study are summarised as follows. The family Pronoidae is restricted to the monotypic genus *Pronoe*. *Amphithyrus* has characters in common with *Paralycaea* and the new genus *Amphithyropsis*, and together they form the new family Amphithyridae. The family Brachyscelidae is recognised for the genus *Brachyscelus*. *Thamneus* has a number of characters that differ considerably from any other genus and is therefore placed in the new family Thamneidae. *Eupronoe* is like *Parapronoe* in the morphology of the mouthparts, antennae and gnathopods, and together they form the new family Parapronoidae. The family Lycaeidae is limited to *Lycaea* and *Simorhynchotus*. The status of the family Anapronoidae is confirmed. The family Oxycephalidae seems to be polyphyletic but more work is required to resolve the systematic status of the eight genera recognised. *Metalycaea globosa*, previously included in the Oxycephalidae, is regarded a species of *Lycaea*. The family Platyscelidae is restricted to four genera, *Platyscelus, Paratyphis, Tetrathyrus* and *Hemityphis*. *Amphithyrus* is removed to the new family Amphithyridae. The family Parascelidae is also restricted to four genera, *Parascelus, Thyropus, Schizoscelus* and *Euscelus*. *Hemiscelus* is regarded a synonym of *Hemityphis*.

All records of associations with gelatinous zooplankton are documented. It is suggested that a more detailed study of this unusual relationship might help to resolve the evolutionary origins and phylogeny of the Hyperiidea.

Statement

This work contains no material that has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being made available for loan and photocopying.

Wolfgang Zeidler
August, 2000

Acknowledgments

I am indebted to my supervisor, Em. Prof. Bill Williams, and my co-supervisor for the latter half of my studies, Dr Derek Duckhouse, for providing invaluable guidance and encouragement.

I am very grateful to the South Australian Museum and the Department of Zoology at the University of Adelaide (now the Department of Environmental Biology) for providing the facilities and administrative support to enable me to undertake my research.

This study would not have been possible without the cooperation and assistance of numerous people in charge of collections, or facilities, at the major institutions of the world. All were exceptionally generous with their time, searching for specimens, arranging loans, or making me feel welcome and providing access to collections during personal visits, or helped in other ways. I am most grateful to all of them. There are so many that they are listed by continent and institution as follows.

In Europe: at the BMNH, Ms J. Ellis for the loan of specimens, Ms M. Lowe, Mr P. Clark and Prof. G.A. Boxshall for providing access to the collections and for the loan of specimens, the BMNH also gave permission to reproduce the drawings by Sydney Parkinson for one of my papers (Zeidler 1995a) and Mr A. Wheeler gave valuable advice, and Mr R. Banks and Mr P. Cooper organised copies of Parkinson's drawings for publication; at the MNHN, Dr D. Defaye for the loan of specimens and information on the collections; at the MOM, Dr C. Carpine for the loan of specimens; at the NMW, Dr V. Stagl for the loan of specimens; at the SMNH, Mr L. Sandberg for the loan of specimens, Ms K. Sindemark, Dr A. Waren and Prof. C. Erseus for their kind hospitality and for providing access to the collections; at the ZMB, Dr H. E. Gruner for the loan of specimens, Dr C.O. Coleman for this hospitality and for providing access to the collections; at the ZMH, Dr D. Keyser for information on the collections, Prof. A. Brandt and Ms G. Wegener for their hospitality and for providing access to the collections; at the ZMUC, Dr N.L. Bruce and Dr A. Klitgaard for the loan of specimens,

Ass. Prof. D. Eibye-Jacobsen for his hospitality and for providing access to the collections. The following are also thanked for searching collections in their care for specimens of hyperiideans, especially of probable type material; Dr F. Bentivegna, Stazione Zoologica Anton Dohrn, Napoli; Dr C. De Broyer, Institut Royale des Sciences Naturelles de Belgique, Bruxelles; Dr G. Doria, Museo Civico, di Storia Naturale, Genova; Dr C.H.J.M. Fransen, Rijksmuseum van Natuurlijke Historie, Leiden; Dr D. Platvoet, Zoölogisch Museum, Instituut voor Taxonomische Zoölogie, Amsterdam; Dr M.A.L. Zuffi, Museo di Storia Naturale, E del Territorio, Calci, Pisa. I am also very grateful to Dr M.H. Thurston, formerly of the Southampton Oceanography Centre, for his help and valuable discussions (via e-mail) regarding the taxonomy of hyperiideans.

In North America: at the American Museum of Natural History, New York, Dr W.K. Emerson, Mr W. Sage and Mr C. Boyko for access to the collections; at the ANSP, Dr G. Rosenberg and Mr N. Gilmore for the loan of specimens, Dr E.E. Spamer and Dr D. Robinson for providing access to the collections; at the Bernice P. Bishop Museum, Honolulu, Mr L.G. Eldredge and Ms B. Burch for providing access to the collections; at the CAS, Mr B. Van Syoc for providing access to the collections; at the CMN, Dr C.T. Shih and Dr D.R. Laubitz for their hospitality and for providing access to the collections; at the LACM, Dr J. Martin and Mr G.E. Davis for providing access to the collections; at the Monterey Bay Aquarium Research Institute, Dr G. Matsumoto for his hospitality and for providing access to the collections and for arranging a trip with the remote submersible to look at plankton; at the Scripps Institution of Oceanography, Dr A. Townsend for providing access to the collections; at the USNM, Dr T.E. Bowman, Dr C.W. Hart, Ms J. Clark-Walker and Ms K. Reed for their hospitality and for providing access to the collections, in particular, Ms J. Clark-Walker is acknowledged for providing lots of collection data and for the loan of specimens. During my tour of Californian institutions, Ms L. Gershwin, University of California, Berkeley provided logistical support and collected specimens; also the following provided a place for me on vessels so that I could collect fresh material; Dr J. Nybakken, Moss Landing Marine Laboratories, Dr M. Schaadt, Cabrillo Marine Aquarium and Dr R. Wells, L. A. Pierce College.

In Australia: at the AM, Dr P.B. Berents and Dr J.K. Lowry for the loan of specimens, for providing access to the collections and for many useful discussions regarding crustacean systematics; at the SAMA, Ms J. Thurmer prepared the bromides of my illustrations for most of my publications, Ms M. Anthony was expert at locating and obtaining copies of old and rare references, Ms S. Ducray volunteered her time sorting plankton samples, Dr S.C. Donnellan assisted with the phylogenetic analysis and the interpretation of results, Mr T. Peters provided photographic expertise, Mr R. Hamilton-Bruce scanned the figures and cleaned them up on the computer and Ms D. Churches provided invaluable word processing skills.

In addition to the above, Ms M.G. van der Merwe, at the SAM, facilitated the loan of a large amount of material from that institution, which proved invaluable to my study.

Finally I would like to thank my wife, Lyn, who put up with my many absences, late nights and weekends spent drawing or writing.

Chapter 1

Introduction

This thesis addresses some of the systematic problems of the hyperiidean amphipod infraorder Physocephalata, and in particular the higher classification of the superfamily Platysceloidea, which has proved to be the most problematical superfamily for zooplankton workers.

Hyperiidean amphipods are important marine crustacean zooplankters, ranking third in abundance behind the Copepoda and Euphausiacea (Shih 1982). They can be particularly abundant in cold waters, where they constitute an important food source for marine mammals, sea birds and fish (see Lavaniegos & Ohman 1999). Thus, a sound knowledge of the systematics and biology of major planktonic groups, such as Hyperiideans, is essential for responsible management of marine resources.

Hyperiideans are entirely pelagic, and mostly oceanic. The suborder Hyperiidea is currently divided into two infraorders, the smaller-eyed, mainly bathypelagic, Physosomata, and the generally larger-eyed, mainly epipelagic, Physocephalata. The Physocephalata, being epipelagic, are the most common hyperiideans in plankton collections. Most species appear to be associated with gelatinous zooplankton for at least part of their life cycle (Harbison *et al.* 1977, Madin & Harbison 1977, Laval 1980). Their association with gelatinous zooplankton makes members of the Physocephalata difficult to study in the laboratory and in the field.

Their association with gelatinous hosts also complicates the study of the biogeography of hyperiidean amphipods. Because of the lack of understanding that hyperiideans are parasitoids, most previous distributional and ecological studies are of limited value, except for those species that are known to be less host dependent, such as *Themisto* and the Phrosinidae. Generally, distributional studies of hyperiideans that take account of the host-parasite relationship remain to be done.

Laval (1980) provides a summary of our limited knowledge of their biology. Mostly this is limited to the more readily obtainable, and observable, Physocephalata. It is clear from the available evidence that hyperiideans are not well suited to a free-living pelagic existence and are usually closely associated with gelatinous plankton. There may be some host specificity, in that families and genera of hyperiideans appear to be restricted to certain host groups (e.g. Harbison *et al.* 1977).

The gelatinous host can provide shelter, provide food by involuntarily sharing prey, or become a source of food for adults and developing young. Female hyperiideans brood their young in a marsupium, and the larvae, or juveniles are transferred from the marsupium onto or into, the host by the female following special behavioural sequences (see Laval 1980). The host provides shelter for the developing juveniles, which may feed on its tissues. The parasitoid-host relationship varies from species to species. It may be symbiotic, or parasitic, depending on the supply of food and on the stages of development. Some species, such as *Phronima*, shape salps into protective gelatinous barrels that they use for their developing young (Laval 1978).

The mouthparts of hyperiideans are generally not as well developed as those of gammarideans, and suggest a dependence on a diet of soft-bodied animals. In the infraorder Physocephalata, and the superfamily Platysceloidea in particular, the mouthparts can be so reduced that they are difficult to dissect and their structure difficult to determine. In some species some mouthparts, such as the maxilla, are completely absent, suggesting a high dependence on the gelatinous host, or a relatively higher degree of parasitism.

The sexual dimorphism, exhibited by most species of the Physocephalata, suggests that the sexes occupy different ecological niches in the zooplankton community. Females appear to be more closely associated with their hosts, and observations and data of Harbison *et al.* (1977) and Laval (1980) suggest that males spend a greater proportion of their lives freely swimming. This is supported by the fact that males are morphologically more suited for swimming, and amongst the Physocephalata, males of most families have longer or more highly developed antennae, which probably assist them in locating females in order to reproduce. In the superfamily Platysceloidea, males have the first antennae with an enlarged callynophore with a dense brush of aesthestascs, while the second antennae are extremely long and folded beneath the head and body. Females, on the other hand, have reduced first antennae and their second antennae are often absent.

It is assumed that, as in the Gammaridea, the mandibular palps are used to clean the antennae. Thus, mandibular palps are usually present in males but are often absent in females. The presence or absence of mandibular palps points to different adaptations in life-style and may be an important phylogenetic character.

The morphology of the pleopoda has hitherto been ignored for taxonomic purposes. This is because they seem to vary little morphologically but may warrant closer examination.

Hyperiideans can be difficult to identify because of the lack of major revisionary works, and the unsatisfactory state of our knowledge of many genera and families. Although taxonomic revisions of some genera have appeared this century (Bowman 1973, 1978; Shih 1969), there have been no major systematic revisions since the pioneer works of the late 19th century. The standard text (Vinogradov *et al.* 1982 - English translation, 1996, Smithsonian Institution Libraries, Douglas Siegel-Causey, Scientific Editor) is a catalogue of species based almost exclusively on previously published works, and relies almost entirely on classifications little changed this century. Thus, a systematic revision of this group is long overdue.

The infraorder Physocephalata is currently divided into four superfamilies, Vibilioidea, Phronimoidea, Lycaeopsoidea and Platysceloidea (Bowman & Gruner 1973). In this thesis the systematics of each superfamily is reviewed; the degree of review according to the current knowledge, and the need for taxonomic revision.

The superfamily Vibilioidea currently consists of the families Vibiliidae, Cystisomatidae and Paraphronimidae, all of which are in need of revision, particularly the genera *Vibilia* and *Cystisoma*. Thus, these families are reviewed in detail to the specific level.

The superfamily Phronimoidea currently consists of the families Phronimidae, Phrosinidae, Hyperiidae and Dairellidae. The systematics of these families is mostly relatively well known. Thus, only minimal additional information is provided for species of the families Phronimidae and Phrosinidae. Similarly, most of the genera of the family Hyperiidae have either been reviewed by previous authors (except *Hyperoche*), or are monotypic. Thus, only limited information is provided for species, but the family is reviewed at the generic level because some genera differ in a number of significant characters. The genera *Iulopis* and *Bougisia* are reviewed in detail, as is the family Dairellidae.

The superfamily Lycaeopsoidea currently consists of the single family Lycaeopsidae. The systematics of this family has not received much attention in the past. Thus, it is reviewed in detail here.

The superfamily Platysceloidea currently consists of the families Pronoidae, Brachyscelidae, Anapronoidae, Lycaeidae, Oxycephalidae, Platyscelidae and Parascelidae (Vinogradov *et al.* 1982). However, not all authors agree on the familial placement of some genera, or the systematic status of some families (e.g. Shih & Chen 1995). Clearly the systematics of all families of this superfamily is in need of revision, and there is a need to examine the phylogenetic relationship of genera. Detailed revisions at the specific level are beyond the scope of this thesis, because of the large number of taxa involved, but the systematics and phylogenetic relationships of genera is examined, thus providing a firm basis for more detailed taxonomic revisions in the future. The taxonomic database program DELTA (Dalwitz *et al.* 1999) is used to generate the generic descriptions, based on the type species. This is the first time that this program has been used to describe hyperiideans. The advantage of using the DELTA program is that it enforces uniformity in taxonomic descriptions, and the database can be used for other purposes, such as the generation of keys and phylogenetic analyses. Hence, the phylogeny of the genera of the superfamily is analysed using PAUP (Swofford 2000), using characters extracted from the DELTA database.

The present study, of the systematics of the Physocephalata, suggests that this group is polyphyletic and that genera have sometimes been grouped together in families with no phylogenetic justification. This has added to the taxonomic difficulty of some families. As a result of these studies a number of families have been split, resulting in an increase in the number of monogeneric families, giving a classification which more readily reflects the apparently ancient phylogenetic origins of the group. A new key to all families of the sub-order Hyperiidea is provided, as are keys to the genera, and most species of the infraorder Physocephalata. Twenty-three families, 54 genera and 168 species of Physocephalata are recognised in this review. A revised classification is given in Appendix 1.

Chapter 2

Evolution/Phylogeny of Hyperiidean Amphipods

Hyperiidean amphipods appear to be an ancient group whose origins are unresolved. It is generally assumed that they evolved from a gammaridean ancestral type but to date no one has been able to establish any clear links to any particular family or group of Gammaridea.

Pirlot (1932) suggested that the Hyperiidea is an artificial group descended from several lines having characters in common due to their adaptations to pelagic life in association with gelatinous zooplankton. Such a hypothesis seems to be supported by the many monotypic genera and families, in addition to those proposed here. If one considers hyperiidean amphipods as leading a benthic-like existence on a pelagic substratum then it seems a reasonable hypothesis that this life-style has been exploited on numerous occasions, and that hyperiideans have evolved from more than one gammaridean ancestor. Gammarideans leading parasitic (or commensal) existences, or which are at least temporarily pelagic, would seem to be the most likely candidates (e.g. some members of the superfamilies Dexaminoidea, Leucothoidea, Liljeborgioidea, Lysianassoidea, Pardaliscoidea or Stegocephaloidea – as defined by Bousfield (1978)).

Kim and Kim (1993), using cladistic methods, tried to resolve the phylogenetic relationships among gammaridean families and amphipod suborders and concluded, "the Hyperiidea showed a close affinity with leucothoid members such as Amphilochidae and Stenothoidae". On the other hand, Bousfield and Shih (1994) suggest that "hyperiids may have evolved from a gammaridean ancestral type that was nearest to the present stegocephaloidean body form", based on the observation that the more primitive sciniform hyperiideans (Physosomata) have more characters in common with the Stegocephaloidea than with other gammaridean superfamilies. Furthermore, they suggest that "the fact that hyperiids exhibit several major differences from closest gammaridean relatives would also suggest that hyperiids have diverged from a common ancestor over a considerable period of geological time". Stegocephaloideans are symbiotic with sponges, tunicates, sessile coelenterates, and other cnidarians (Moore 1992), and while it may be true that "such associations indicate lengthy evolutionary development and classificatory stability, further underscoring the suitability of stegocephaloidean as a phyletic outgroup taxon for the Hyperiidea", it is equally likely that parasitism of gelatinous plankton evolved independently on more than one occasion.

Another clue to the origin of hyperiideans is the presence of a callynophore on the first antennae. They are always present in males and in most females. In males the callynophore is often enlarged with numerous aesthestascs. Its main function appears to be the detection of pheromones produced by sexually receptive females. "This function probably occurs in all callynophoriferous amphipods, but it is most conspicuous in benthic species, where the mature reproductive male has a free-swimming stage" (Lowry 1986). It is likely that the hyperiideans evolved from such an ancestor, as the males appear to be largely free-swimming, while the females occupy a benthic-like habitat on gelatinous plankton. According to Lowry (1986) "it is hypothesised that the callynophore appeared early in the evolution of the peracaridans as part of the swimming male reproductive strategy".

Coleman (1994a) studied the anatomy of the alimentary canal of several species of hyperiideans, comparing them to the Gammaridea "in order to throw light on this phylogenic problem". The species studied were *Lanceola sayana, Scina crassicornis, Cyllopus lucasi, Phronima sedentaria, Phrosina semilunata, Brachyscelus globiceps* and *Platyscelus armatus*. Coleman found that "numerous structures of the gammaridean alimentary canal are so reduced or modified in hyperiids that it is difficult or impossible to decide if these structures are homologous". However, "despite the anatomical diversity of the hyperiid alimentary canal, there seems to be a common pattern, indicating that at least the species examined have a monophyletic origin. The only exception is *Cyllopus lucasi*. This species bears some plesiomorphic (and many apomorphic) characters in its alimentary canal that suggest a gammaridean condition."

At present our knowledge of the Hyperiidea and also the Gammaridea is insufficient to determine ancestral relationships. Future DNA studies may provide the answer where morphological and chromosome studies (Coleman 1994b) have failed. However, one of the main problems regarding genetic studies is that most plankton samples are preserved in formalin (at least initially) and so it will be necessary to collect hyperiideans specifically for such studies in order to resolve their phylogeny. Most recently, Ulrike English (University Bochum, Germany, pers. comm.), using 18S sequences, found that the two hyperiideans she sequenced (*Hyperia galba* and *Themisto compressa*) were completely different from all gammarideans studied to date. This result supports the hypothesis that hyperiideans separated quite early from other amphipods and evolved separately. I have since collected fresh material representing eight families (eight genera) of hyperiideans that we hope to analyse in the near future.

Chapter 3

Materials and Methods

This study is based on several major collections. A large collection borrowed from the South African Museum, consisting mainly of material collected by the *Meiring Naude* cruises (Louw 1977, 1980); collections from Eastern Australia in the Australian Museum, Sydney (Zeidler 1992a) and in the South Australian Museum, Adelaide (Zeidler 1998), and collections examined during my tenure of a Smithsonian Research Fellowship in 1993 (National Museum of Natural History, Smithsonian Institute, Washington D.C.; American Museum of Natural History, New York; Academy of Natural Sciences of Philadelphia; Canadian Museum of Nature, Ottawa and Bernice P. Bishop Museum, Honolulu, Hawaii).

In 1999 I also visited the following institutions to search for type material and to examine collections: British Museum (Natural History), London; Museum für Naturkunde, Humboldt-Universität, Berlin; Swedish Museum of Natural History, Stockholm; Zoologisches Institut und Zoologisches Museum, Hamburg; Zoologisk Museum, Copenhagen and in California, USA; California Academy of Sciences; Los Angeles County Museum; Monterey Bay Aquarium Research Institute and Scripps Institution of Oceanography. In addition, many specimens, including types, were borrowed from a number of overseas institutions (see acknowledgments).

Details of the material examined are not given, but are summarised to conserve space. More detailed information will be given in forthcoming publications.

A concerted effort was made to locate type material in the world's major museums, especially of taxa described pre-1900 (see acknowledgments). Unfortunately much of this material appears to be lost (see "Note on major pre-20th Century collections").

All, except a few, original references were checked to correct citation errors and errors in synonymy repeated by previous authors.

The synonymies of genera include only those references that give a diagnosis, or some discussion of the taxon.

The basic terminology used to describe hyperiideans is illustrated in Figure 1. The terminology used to describe setae and spines follows that of Lowry and Stoddart (1997) who recognise three main types: slender setae, robust setae ("spines") and spines (non-articulated of the cuticle). In addition, the first antennae of hyperiideans usually have some articles with aesthestascs, which are delicate inflated setae having a chemosensory function (see Oshel & Steele 1988). Aesthestascs are most numerous on a sensory organ called the callynophore (Lowry 1986) (usually the first flagellar article), terminology which is accepted here. Aesthestascs on the callynophore may be arranged in one or two-field brushes, and need to be removed in order to determine their arrangement clearly. Thus, in most figures only their insertions are shown.

For the review of the families and genera of the superfamily Platysceloidea, each genus was characterised using examples of the type species. This was not possible for *Lycaea* and *Thyropus,* as the type material is lost, and the true identity of the type species is uncertain. Thus, the next oldest available species were substituted, *L. pulex* Marion, 1874 (for *L. ochracea* Dana, 1853) and *T. sphaeroma* (Claus, 1879) (for *T. diaphanus* Dana, 1853). Most other species were also examined to determine how well they conformed to the generic diagnosis. This data was used to build a database using the taxonomic database program DELTA (Dalwitz *et al.* 1999). The characters (Appendix 2) were analysed as unordered and multistate. The DELTA program was used to generate the generic descriptions using the 'item descriptions' file (Appendix 3), generated from the 'characters file'. The phylogenetic analysis used characters extracted from the database into a NEXUS file format (Appendix 4), which can be read by PAUP (ver. 4.0, Swofford 2000). In the above analysis, *Vibilia* was used as an outgroup for comparison as it posses ancestral states such as well developed antennae and mouthparts in both sexes, and a non-reduction, or fusion of body parts.

Specimen length was measured along a lateral parabolic line drawn from the anterior extremity of the rostrum, through the middle of the body, to the posterior limit of the telson, using a scale and pair of dividers. Appendages were usually drawn from the left-hand side of the animal. Dissected appendages have been kept with the specimen, or cleared in lactic acid and mounted on a microscope slide in polyvinyl lactophenol mountant. The seven pairs of pereopods are called gnathopods 1 and 2 and pereopods 3-7.

The original line drawings were photographed and the images scanned onto a computer disc. Lettering, scale bars, arrows, and figure captions were then added using the program Corel Draw (version 9). This method was used to ensure that the figures were all reduced to the correct size, and that lettering was uniform. Unfortunately the quality of the scanned images is not as good as the original, or photographed copy, although images were improved considerably by manipulation, using Corel Draw.

Abbreviations used in text

AM	Australian Museum, Sydney Australia
ANSP	Academy of Natural Sciences of Philadelphia, USA
BMNH	The Natural History Museum, London, England (formerly the British Museum (Natural History))
CAS	California Academy of Sciences, San Francisco, USA
CMN	Canadian Museum of Nature, Ottawa, Canada
ICZN	International Commission on Zoological Nomenclature
LACM	Los Angeles County Museum of Natural History, Los Angeles, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MOM	Musée Oceanographique, Monaco
NMW	Naturhistorisches Museum Wien, Austria
SAM	South African Museum, Cape Town, South Africa
SAMA	South Australian Museum, Adelaide, South Australia
SMNH	Swedish Museum of Natural History, Stockholm, Sweden

USNM	United States National Museum, Smithsonian Institution, Washington DC, USA
ZMB	Muséum fur Naturkunde, Humboldt-Universität, Berlin, Germany
ZMH	Zoologisches Insitut und Museum, Universität Hamburg, Germany
ZMUC	Zoologisk Museum, University of Copenhagen, Denmark

Abbreviations used in illustrations

A1, A2	First and second antenna
G1, G2	First and second gnathopod (or pereopod)
LL	Lower lip
Md	Mandible
Mx1, Mx2	First and second maxillae
Mxp	Maxilliped
P3-7	Third to seventh pereopod
Pl	Pleon (pleonites 1-3)
U1-3	First to third uropod
UL	Upper lip
Us	Urosome (urosomites 1-3, uropoda and telson)
f	female
l	left
m	male
r	right

Chapter 4

Note on Major Pre-20TH Century Collections

Studies of the systematics of the Hyperiidea are complicated by the apparent loss of type material of many species described in the 18th and 19th century. Inadequate descriptions, and the lack of good figures (in most instances), have made it impossible to determine some species, and their status will never be known (e.g. Zeidler 1998).

Thus, it is useful to note the fate of some of the more important collections. They are listed here in chronological order, by author.

Fabricius

Fabricius (1775) described the hyperiidean amphipods illustrated by Sydney Parkinson, on the *Endeavour* voyage of 1768-1774 (Zeidler 1995a). Documentary and circumstantial evidence indicates that the specimens on which the drawings are based were not preserved at the time, or did not survive the voyage, so the descriptions are based solely on the drawings. The drawings are held in the BMNH, and the species of Hyperiidea described by Fabricius are the earliest in the scientific literature.

Guérin-Méneville

The crustacean collection of Guérin-Méneville was acquired by the ANSP in about 1850 (Spamer & Bogan 1992), and includes all but one of the hyperiidean amphipods described by him (1825, 1836a, 1836c, 1844). All of the specimens are long dry, having been alcohol preserved, but most are still distinguishable at the specific level (Zeidler 1997a).

Milne-Edwards

Most of the material described by Milne-Edwards (1830, 1840) appears to be lost. The MNHN has type material of only one species (Zeidler 1996b), and the ANSP has the type of one other, together with some probable syntypes of a further three species, amongst the Guérin-Méneville collection (Zeidler 1997a). No other type material or material that may have been seen by Milne-Edwards, could be found in any major Museum.

Dana

All of the hyperiidean material described by Dana (1852, 1853) appears to be lost. None could be found in the USNM or in any other North American Museum. It was most probably amongst the material borrowed from the Smithsonian institution by W. Stimpson, which was totally destroyed in the Great Fire of Chicago in 1871 (Evans 1967). Unfortunately Dana's descriptions are often inadequate, and his figures so small that it is difficult to determine the status of his species. As a result, most of his names have not been in use since the original description of his species.

Bate

Bate (1862) described a number of new species, mainly from material borrowed from the "Musée Jardin des Plantes" (=MNHN). None of this material could be found at the MNHN or BMNH and appears to be lost. Fortunately his descriptions and figures are sufficient to establish the status of most of his species.

Claus

Claus (1871, 1879b, 1887) described numerous species of Hyperiidea and laid the foundation for the systematics of the group. It is therefore most frustrating for taxonomists that most of his material seems to be lost. No type material could be found in the NMW, ZMH or ZMB, although some material from Claus's collection is in the BMNH and NMW. There are no collections in Leipzig (C. O. Coleman, ZMB, pers. comm.). Fortunately, most of Claus's descriptions are adequate and this, combined with his excellent figures, makes it relatively easy to establish the status of most of his species.

Bovallius

Bovallius was a prolific student of hyperiideans, but most of the material described by him in his monographic works (1887a, 1887c, 1889, 1890) appears to be lost. The BMNH, SMNH and ZMUC has some of his specimens, but Bovallius did not curate his material very well (Bowman 1973) and it is difficult to determine the type status of what remains extant. The species descriptions of Bovallius (1887a) are totally inadequate, and, except for those redescribed and figured later (1887c, 1889, 1890), their status cannot be determined with any confidence.

Stebbing

The material described by Stebbing (1888, 1895) is in the BMNH. The material in spirit is in relatively good condition but the material mounted on microscope slides has mostly dried, out making it difficult to determine the structure of appendages. It is possible that this material could be remounted.

Chapter 5

Systematics

Suborder **HYPERIIDEA** Milne-Edwards, 1830

The classification system used here follows that of Bowman and Gruner (1973), modified according to the current study. New keys to taxa have been constructed, reflecting the changes in systematics made here.

The suborder Hyperiidea is readily divided into two infraorders distinguished by the following key.

Key to the Infraorders of Hyperiidea

1. Head small, usually not longer than pereonite 1, never longer than pereonites 1& 2. Eyes very small, or absent. Gnathopods 1 & 2 usually simple; G1 rarely chelate; G2 always simple .... PHYSOSOMATA Pirlot, 1929
2. Head usually longer than pereonites 1 & 2. Eyes usually occupying most of head surface, sometimes reduced, or absent. Gnathopods 1 & 2 usually chelate or subchelate. If gnathopods simple, then eyes large. If eyes reduced or absent, then G2 always chelate.............PHYSOCEPHALATA Bowman & Gruner, 1973

Infraorder **PHYSOSOMATA** Pirlot, 1929

These are mainly deep-water species, and except for the family Scinidae, they are rarely encountered. They are not considered further in this thesis except that a key to families is provided, correcting some errors in the literature regarding diagnostic features.

Key to families of the infraorder PHYSOSOMATA

1. At least pereopods 6 & 7 with hooded dactylus 2
   Pereopods without hooded dactylus 4

2. Pereopods 3-7 with hooded dactylus. Antennae 1 inserted laterally on head, usually shorter than head, in males sometimes produced slightly beyond anterior margin of head ....CHUNEOLIDAE
   Pereopods 3 & 4 without hooded dactylus. Antennae 1 inserted anteriorly on head, usually longer than head 3

3. Mandible with 3-articulate palp .... LANCEOLIDAE
   Mandible without palp ....PROSCINIDAE (*Mimoscina*)

4. Uropods 1-3; endopod fused with peduncle ....SCINIDAE
   Uropods 1-3; endopod not fused with peduncle 5

5. Mandible with 3-articulate palp 6
   Mandible without palp (or rarely with 1 article)... 7

6. Antennae 2 about half as long as A1. Gnathopods 1 & 2; carpus not broadened distally. Pereopods 3-7 simple .... ARCHAEOSCINIDAE
   Antennae 2 much shorter, or slightly longer, than A1. Gnathopods 1 & 2; carpus distinctly broadened distally. Pereopod 5 (sometimes also P3 & 4) subchelate, or if all pereopods simple, then A2 is slightly longer than A1 ....MICROPHASMIDAE

7. Females with pereon much inflated anteriorly. Males without pereon inflated. Antennae 2 of males about one third as long as A1 .... MIMONECTIDAE

Females and males with similar body form, pereon not inflated. Antennae 2 of males as long as A1..PROSCINIDAE (*Proscina*)

Infraorder **PHYSOCEPHALATA** Bowman & Gruner, 1973

These are the most common hyperiideans in plankton collections because of their preference for shallow waters, where most collections are made. They also provide some of the more challenging taxonomic problems.

Diagnosis

Head large, longer than pereonite 1. Eyes usually large (small or moderately large in *Vibilia* and *Bougisia*), occupying most of head surface (excluding rostrum). Sexual dimorphism usually emphasised in structure of antennae, especially the second. Maxillae 1 usually without inner lobe. Maxilliped with inner lobes completely fused. Gnathopods usually chelate, or subchelate, rarely simple.

Five superfamilies: Vibilioidea, Cystisomatoidea **new superfamily**, Phronimoidea, Lycaeopsoidea and Platysceloidea.

Remarks

Prior to the present study the Physocephalata comprised four superfamilies encompassing 16 families, 52 genera and 167 species. The superfamilies are distinguished by the morphology of the antennae, and their positioning on the head.

The grouping of families into superfamilies in any taxon is usually contentious. Within the Physocephalata only the superfamilies Phronimoidea and Lycaeopsoidea seem to be stable groupings.

The following key to families is designed to be used by the novice using readily observable characters, even if only one of the sexes is available; hence some families may appear more than once.

Key to families of the infraorder PHYSOCEPHALATA

1. Body rolled into ball. Pereopods 5 & 6 with basis enlarged, covering remaining articles, and completely (or almost) covering other pereopods. Pereopod 6; basis with or without fissure, if with fissure than basis of P5 longer than, or subequal in length to, remaining articles combined. Telson fitting into telsonic groove of basis of P6 2

   Body slender or curved, usually not rolled into ball. Pereopods 5 & 6 with basis sometimes enlarged, usually not covering remaining articles, and never covering other pereopods. Pereopod 6; basis usually without fissure, if fissure present then basis of P5 is shorter than remaining articles combined. Pereopod 6, basis without telsonic groove. 3

2. Mouthparts in form of broad cylinder. Pereopod 7 usually reduced to basis, and one or two additional articles in adults, but sometimes complete, especially in juveniles. If G2 chelate, or subchelate, then P6 basis with small fissure, or fissure absent. If G2 simple, or weakly chelate, then P6 basis with small fissure, and articles of P3-6 with, or without few, short, slender setae .... PLATYSCELIDAE

   Mouthparts in form of pointed cone. Pereopod 7 complete. If G2 chelate then P6 basis with large fissure. If G2 simple then P6 basis without fissure or if fissure present then P3-6 with most articles with several long, slender setae .... PARASCELIDAE

3. Pereopod 5 distinctly subchelate 4

   Pereopod 5 simple, or at most prehensile 5

4. Uropods 1-3 composed of single foliaceous article. Head globular .... PHROSINIDAE

Uropods 1-3 with lanceolate exopods and endopods (U3 sometimes reduced). Head subconical .... PHRONIMIDAE

5. Body very large (up to 150 mm), transparent. Uropod 2 absent. Head very large with eyes on dorsal surface, ventral surface with dentate border .... CYSTISOMATIDAE

Body rarely longer than 50 mm, usually pigmented. Uropod 2 present. Head globular, or with rostrum, ventral surface without denticles. 6

6. Gnathopod 2 simple 7

Gnathopod 2 distinctly chelate, or subchelate 13

7. Gnathopod 1 weakly subchelate. Gnathopod 2; propodus produced into thin hollowed process on either side of dactylus. Eyes with facets arranged in dorsoventral rows. Body usually transparent .................PARAPHRONIMIDAE

Gnathopod 1 simple. Gnathopod 2; propodus not produced distally. Eyes with facets radiating from about centre of head. Body usually pigmented 8

8. Pereonites 1-2 fused dorsally. Coxae fused with pereonites ....DAIRELLIDAE

Pereonites all separate. Coxae not fused with pereonites 9

9. Antennae 2 of both sexes very short, curved. Pereopod 6 with relatively broad articles, especially basis and merus; in female distinctly longest pereopod. In male P5 is longest, but articles (except for basis) are very thin......................... ... . LYCAEOPSIDAE

Antennae 2 of female short, rudimentary, or absent; of male composed of several long articles, folded in zigzag fashion. Pereopod 5 longer than, or subequal in length, to P6 10

10. Pereopod 5 subequal in length to P6. Telson fused with double urosomite (G1 & 2 very weakly subchelate) .... LYCAEIDAE (*L. pachypoda*)

Pereopod 5 distinctly longer than P6. Telson not fused with double urosomite ... 11

11. Pereopods 5 & 6 with broad articles, distally prehensile with dactylus closing against produced anterodistal corner of propodus .... TRYPHANIDAE
    Pereopods 5 & 6, only basis substantially broadened, not prehensile, dactylus attached in normal manner 12

12. Gnathopods 1 & 2; basis relatively broad, especially of G1. Uropod 3; exopods and endopods articulated with peduncle .... PRONOIDAE
    Gnathopods 1 & 2; basis not especially broader than following articles. Uropod 3; endopod fused with peduncle..................... AMPHITHYRIDAE (part) **fam. nov.**

13. Pereopod 6; basis with distinct fissure .... AMPHITHYRIDAE (part) **fam. nov.**
    Pereopod 6; basis without fissure 14

14. Antennae 1 inserted on anterior surface of head, not in groove; first flagellar article inflated, lanceolate, as long, or longer than head; distal articles very small, or absent. Antenna 2 of several articles, as long (or almost) as A1 15
    Antennae 1 inserted in groove on anterior or ventral surface of head; first flagellar article never as long as head. Antenna 2 of female often reduced, or absent, rarely as long as A1; male A2 with long flagellum of several articles, or folded under head and pereon. 16

15. Antennae 2 inserted on anterior surface of head.................................... VIBILIIDAE
    Antennae 2 inserted on ventral surface of head .............................CYLLOPODIDAE

16. Antennae inserted on anterior surface of head.. 17
    Antennae inserted on ventral surface of head 20

17. Coxae fused with pereonites ....LESTRIGONIDAE **fam. nov.**
    Coxae free from pereonites 18

18. Mandible without palp in both sexes .... IULOPIDIDAE **fam. nov.**
    Mandible with palp in both sexes 19

19. Pereonites all separate.. HYPERIIDAE
    Pereonites 1-2 fused... BOUGISIDAE **fam. nov.**

20. Gnathopod 1 simple, or if weakly subchelate then U2 & 3 with foliaceous exopods and endopods... 21
    Gnathopod 1 distinctly chelate or subchelate 22

21. Uropods; exopods and endopods articulated with peduncle.................................. ... . PARAPRONOIDAE **fam. nov.**
    Uropods 2 & 3; endopod fused with peduncle .... LYCAEIDAE (*Simorhynchotus*)

22. Head produced into broad, chisel-shaped rostrum, slightly upturned in males. Body plump, very broad .... THAMNEIDAE **fam. nov.**
    Head produced into sharp or rounded rostrum, or rostrum absent and head rounded, sometimes produced in males. Body elongate, or not especially broad............ 23

23. Head produced into rostrum in both sexes; if rostrum short then telson fused with double urosomite.. OXYCEPHALIDAE
    Head rounded, sometimes produced in male; if produced in female, telson not fused with double urosomite.. 24

24. Uropod 3; endopod fused with peduncle. Telson fused with double urosomite .... LYCAEIDAE (*Lycaea*)
    Uropod 3; endopod not fused with peduncle. Telson not fused with double urosomite.. 25

25. Gnathopods with very broad basis, width at least 0.6 x length. Antennae 2 of males, partly folded, in diagonal groove on ventral surface of head .... ANAPRONOIDAE
    Gnathopods with narrow basis, width less than 0.5 x length. Antennae 2 of males folded, posterior folds accommodated in pocket of basis of G1 .... BRACHYSCELIDAE

5.1 Superfamily VIBILIOIDEA Bowman & Gruner, 1973

Diagnosis

Antennae straight and relatively short. Antennae 1 inserted on anterior surface of head; peduncle of three short articles; flagellum composed of enlarged first article (callynophore), with dense brush of aesthestascs medially, and one or two tiny terminal articles. Antennae 2 inserted on anterior or ventral surface of head, composed of a few slender articles, sometimes reduced in females. Pereopods 3-7 always simple. Developing eggs and young held in brood pouch underneath pereon, made up of oostegites on pereonites 2-5.

Three families: Vibiliidae, Paraphronimidae and Cyllopodidae.

Remarks

Prior to this review this superfamily consisted of the families Vibiliidae, Cystisomatidae and Paraphronimidae; a grouping that is not entirely satisfactory since it relies entirely on the morphology and positioning of the first antennae.

The family Cystisomatidae is unusual in that the second antennae are reduced to small spines, just anterior to the buccal mass, in both sexes. In all other members of the infraorder, except for some species of *Phronima,* the second antennae of males are always well developed. The brooding of young in a brood sac, between the second gnathopods, is also a character unique to this family. In all other species of Hyperiidea the brooding young are held together by brood plates (oostegites) underneath the pereon, between the pereopods. The eye type is also unusual and, according to Land (1989), is characteristic of deep-water forms, but this is not supported by the evidence of collections. The genus is most abundant at 200-1000m and is found regularly in the epipelagic zone (0-200m) (M. Thurston pers. comm.). It also seems to be relatively common in near-surface waters off California (CAS and LACM collections).

The Cystisomatidae and Paraphronimidae also have mandibles that lack a palp in both sexes, a character shared only with the Phronimidae, Dairellidae and Iulopidae **fam. nov.** (superfamily Phronimoidea). In addition, the Paraphronimidae have maxillipeds with fused inner and outer lobes, a character only found in one other family, the Dairellidae, and the mandibles are without a molar, a character shared with the Lycaeopsoidea and Platysceloidea. Thus, the Paraphronimidae share some unusual characters with the other three superfamilies, and the Cystisomatidae do not readily fit into any currently recognised superfamilies. Therefore, the new superfamily Cystisomatoidea is proposed for the family Cystisomatidae, based on the unique method of brooding young, the remnant second antennae both sexes, and other minor characters not consistent with the Vibilioidea. However, the family Paraphronimidae should remain in the Vibilioidea for the time being, because *Paraphronima* is similar to *Cyllopus* in the morphology and positioning of the antennae.

Family **VIBILIIDAE** Dana, 1852

Diagnosis

Body length 5-20 mm, slightly flattened laterally, cuticle relatively thick, and smooth (except for minute cuticular markings). Head rather small, rarely longer than first two pereonites, subquadrangular, with weakly developed rostrum. Eyes small to moderate (absent in *V. caeca*) but never occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antenna 1 longer than head; peduncle short, 3-segmented; first flagellar article (callynophore) enlarged, spatuliform with slightly concave medial surface, with dense brush (two fields) of aesthestascs; remaining flagellar articles rudimentary, reduced to one or two minute articles. Antenna 2 inserted on anterior surface of head in small, almost lateral pocket; composed of 5-9 (rarely 2-4) slender articles; slightly longer than A1 in males, slightly shorter than A1 in females. Mandibles with palp in both sexes, third article of palp longer (*Vibilia*), or shorter than second (*Vibilioides*), molar process well developed (*Vibilia*), or reduced to simple conical projection (*Vibilioides*). Maxillae 1 with palp and well developed outer lobe, inner lobe present as small round process. Maxillae 2 consisting of two small lobes in *Vibilia*, reduced to single lobe in *Vibilioides*. Maxilliped with short rounded inner lobe, about half as long as outer lobes. Gnathopod 1 simple. Gnathopod 2 chelate. Pereopods 5 & 6 the longest. Pereopod 7 reduced in size, with enlarged basis, with full compliment of articles, with dactylus modified, clavate or knife-shaped (*Vibilia*), or with only three small articles in addition to basis (*Vibilioides*). Uropods with articulated exopods and endopods. Telson shorter than peduncle of U3, triangular, or semicircular. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

Two genera: *Vibilia* and *Vibilioides*.

Remarks

Prior to this review the family Vibiliidae consisted of three genera, *Vibilia, Vibilioides* and *Cyllopus*. In *Cyllopus* the second antennae are attached to the ventral surface of the head, just anterior to the buccal mass, as in *Paraphronima,* while in *Vibilia* the second antennae are inserted on the anterior surface of the head, in a small, almost lateral pocket. Also, in *Cyllopus* the eyes are very large, occupying most of the head surface. These and other minor differences warrant the removal of *Cyllopus* from the family Vibiliidae. Thus it is proposed to resurrect the family Cyllopodidae Bovallius, 1887 for *Cyllopus*. The diagnosis of Vibiliidae is amended accordingly.

Bowman and Gruner (1973) synonymised *Vibilioides* with *Vibilia,* believing that the difference in the morphology of pereopod 7 was insufficient to maintain generic status. However, as Vinogradov *et al.* (1982) point out, the morphology of the mouthparts of *Vibilioides* differs considerably from *Vibilia*. Generally they are reduced; the mandibular molar consists of a simple conical projection; the first maxillae have a much-reduced inner lobe and the second maxillae are rudimentary. Thus, *Vibilioides* should be maintained.

Key to the genera of the family VIBILIIDAE

Pereopod 7 with full complement of articles, basis considerably shorter, or only slightly, longer than remaining articles combined .... *Vibilia* Milne-Edwards, 1830

Pereopod 7 reduced, with only three small articles attached to basis, basis more than twice as long as remaining articles combined .... *Vibilioides* Chevreux, 1905

Genus ***Vibilia*** Milne-Edwards, 1830

Vibilia Milne-Edwards, 1830: 386. – Milne-Edwards 1838: 308. Milne-Edwards 1840: 72-73. Lucas 1840: 233. Dana 1852: 315. Dana 1853: 980. Bate 1862: 299-300. Bate & Westwood 1868: 524. Carus 1885: 421. Gerstaecker 1886: 492. Bovallius 1887b: 554. Bovallius 1887c: 43. Stebbing 1888: 1278-1279. Vosseler 1901: 118-119. Behning 1913b: 212. Stephensen 1918: 33-34. Behning 1925: 379. Chevreux & Fage 1925: 382. Schellenberg 1927: 615. Pirlot 1929: 91. Hurley 1955: 124-125. Bowman & Gruner 1973: 24. Zeidler 1978: 5. Vinogradov *et al.* 1982: 199. Shih & Chen 1995: 37. Vinogradov 1999a: 1178.

Thaumalea Templeton, 1836: 186.

Orattrina Natale, 1850b: 11.

Elasmocerus Costa in Hope, 1851.

Type species

Vibilia peronii Milne-Edwards, 1830, by monotypy. Type material could not be found at the MNHN, BMNH or ANSP and is considered lost. This is not an ideal situation since the true identity of *V. peronii* is uncertain. However, although Milne-Edwards (1830) provided only a brief description of this species, his figures of *V. peronii,* published a decade later (Milne-Edwards 1840) are clearly of a species of *Vibilia.*

Type species of synonyms

The type species of *Thaumalea* is *T. depilis* Templeton, 1836. Type material could not be found at the BMNH and is considered lost. The figures and description of Templeton (1836) are insufficient to determine this species. However, the illustration is clearly of a species of *Vibilia*, possibly of a juvenile specimen. *Thaumalea* Templeton, 1836 is a primary homonym of the dipteran genus *Thaumalea* Ruthe, 1831.

The type species of *Orattrina* is *O. pulchella* Natale, 1850. Type material could not be found in any major Italian museum (see acknowledgments) and is considered lost. The figures and description of Natale (1850b) are insufficient to determine this species. However, the figures represent a rather bizarre-looking *Vibilia.*

The type species of *Elasmocerus* is *E. speciosus* Costa, 1851. Type material could not be found in any major Italian museum (see acknowledgments) and is considered lost. This species is merely listed without description or figures, and is a nomen nudum. Previous authors have regarded it a species of *Vibilia,* probably because it may have been an earlier name for *V. speciosa* Costa, 1853.

Diagnosis

Body shape robust or globular. Head quadrate; lacking latero-ventral teeth. Rostrum absent in both sexes. Eyes occupying part of lateral head surface; grouped in one field on each side of head. Antenna 1 inserted on anterior surface of head, but lacking groove. Antenna 1 male peduncle 3-articulate; flagellum with spatulate callynophore and 1–2 tiny articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with spatulate callynophore and 1–2 tiny articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on anterior surface of head, lacking groove. Antenna 2 males multi-articulate, more than 6-articulate; moderately long and straight; on anterior surface of head. Antenna 2 females multi-articulate with more than 5 articles. Mandibular palp present in both sexes; females 3-articulate; males 3-articulate.

Mandibular molar well developed. Mandibular incisor relatively broad, straight with several teeth, without medial lobe; in male orientated more or less parallel to palp. Maxilla 1 well developed; bilobed; palp present. Maxilla 2 well developed; bilobed, with numerous strong setae. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes without fringe of setae or membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 chelate; carpal process knife-shaped, or spoon-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus modified, rounded with microscopic scale-like structures. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Fifteen species.

Sexual dimorphism

The sexes are very similar morphologically and very difficult to distinguish (Stephensen 1918, Brusca 1973). The oostegites of females are more difficult to discern than in other hyperiideans, being small and without setae, and ovigerous females are rarely captured, probably because the young are transferred to the salp host at a very early stage (Laval 1963).

Some sexual differences have been observed, but they are not always consistent. Generally the head of males is slightly larger and more quadrate anteriorly, and the eyes are also larger. In some species the endopod of uropod 3 is broadened and longer than the exopod in males, but in females they are similar in size and shape. Sometimes the ornamentation of the rami of the uropods is also coarser in males. The most reliable character to differentiate the sexes seems to be the relative length of the second antennae. Generally, in males, antenna 2 is longer than antenna 1, consisting of 7-9 articles, while in females antenna 2 is shorter than antenna 1, consisting of 5-7 articles. Exceptions are *V. australis,* which has antenna 2 much shorter than antenna 1, consisting of 2-4 articles and *V. caeca,* in which antenna 2 extends only to the middle of antenna 1 and consists of four articles.

As females use the modified seventh pereopods to transfer young to the salp host (Laval 1963) it seemed reasonable that there might be some sexual dimorphism of that appendage, particularly in the ultra-structure of the dactylus. This possibility was investigated but no distinct sexual differences could be determined, even when ovigerous females were available for examination.

Remarks

Vibilia is a very distinctive genus and, apart from *Vibilioides*, does not resemble any other hyperiidean. Species are very similar in gross morphology and, apart from a few distinctive species, most require expert knowledge for a correct identification. In addition, researchers should be aware of ontogenetic changes, such as documented for *V. robusta* (Zeidler 1998) and *V. armata* (Laval 1963, 1965). These are most likely paralleled in other species and add to the difficulty of determining juvenile specimens. A thorough taxonomic revision of the genus is long overdue.

There are forty nominal species referable to *Vibilia*. However, the types of many are lost, and original descriptions are so poor, that it is impossible to determine their status with certainty. The genus has been reviewed by Bovallius (1887c) who recognised 15 species, and by Behning (1913b), who recognised 24 species. Since then, more information has been provided by Behning (1925, 1927), but only two new species have been described, one by Behning (1939) and another by Bulycheva (1955). More recently, Vinogradov *et al.* (1982) reviewed the genus and reduced the number of recognisable species to seventeen. The current review, based on an examination of most of the world's collections, is in general agreement with Vinogradov *et al.* (1982), except for *V. affinis* and *V. bovallii*, which are regarded indeterminable species (see notes on species of indeterminable status). However, it is limited by the loss of the types of many nominal species.

Species of *Vibilia* live in surface waters, usually in association with salps, which they use for shelter and as a source of food (Madin & Harbison 1977, Laval 1980). Developing larvae also reside on salps, and Laval (1963) describes the larval development of *V. armata* and its association with salps. The genus is relatively common in the tropical and subtropical regions of the world's oceans, but some species venture beyond the Subtropical Convergence.

Morphologically, *Vibilia* is readily divided into two species groups, one in which the posterior lateral corners of the last urosomite project slightly next to the peduncle of uropod 3, and the other in which there is no such projection. This appears to be a good character, which is readily discernible in all species of *Vibilia* except perhaps for *V. chuni*. In this species the lateral projection can sometimes be minor and it is thus included in both parts of the following key. Fortunately *V. chuni* is one of the more easily recognisable species of *Vibilia*.

Key to the species of the genus *Vibilia*

1. Posterior lateral corners of last urosomite more or less in line with distal margin.... 2
   Posterior lateral corners of last urosomite project slightly next to peduncle of U3. 13

2. Eyes absent ....*V. caeca* Bulycheva, 1955
   Eyes present 3

3. Eyes with ocelli in three rows.. *V. australis* Stebbing, 1888
   Eyes with ocelli in oval, or round, cluster 4

4. Pereopod 7; basis as long as, or longer than, remaining articles combined................ .... *V. chuni* Behning & Woltereck, 1912
   Pereopod 7; basis considerably shorter than remaining articles combined 5

5. Uropod 2 reaching limit of U3, or marginally longer. Gnathopod 2; basis inflated (mature specimens), merus with fringe of robust setae on lateral and anterior margins. Antennae 1 bulbous.................................... *V. robusta* Bovallius, 1887
   Uropod 2 distinctly shorter than U3. Gnathopod 2; basis with more or less parallel margins, merus with few setae. Antennae 1 often truncate................................ 6

6. Antennae 1 with rounded distal margin... 7
   Antennae 1 with truncate or pointed distal margin... 11

7. Gnathopod 2; carpal process usually extends to dactylus. Pereopods 3 & 4 with thick articles, dactylus almost as long as propodus .... *V. viatrix* Bovallius, 1887
   Gnathopod 2; carpal process extends to 0.5-0.7x length of propodus. Pereopods 3 & 4 with relatively thin articles, dactylus less than half-length of propodus........ 8

8. Antennae 1; flagellum slightly narrower or equal in width to peduncle. Pereopod 7; basis with relatively narrow, posterodistal lobe overlapping ischium and half of merus. Telson pointed.. *V. propinqua* Stebbing, 1888
   Antennae 1; flagellum slightly wider than peduncle. Pereopod 7; basis with relatively broad posterodistal lobe barely overlapping ischium. Telson rounded 9

9. Pereopods 5 & 6; dactylus longer than 0.3x length of propodus............................. .... *V. gibbosa* Bovallius, 1887
   Pereopods 5 & 6; dactylus short, about 0.2x length or less of propodus................ 10

10. Pereopods 3 & 4; dactylus relatively short and stubby, length less than 0.2x propodus. Head with anterior margin rounded, or oblique, not projected above A1 .... *V. jeangerardi* Lucas, 1846

    Pereopods 3 & 4; dactylus more slender, length more than 0.2x propodus. Head with anterior margin forming vertical, or rounded projection above base of A1 (more prominent in males) .... *V. borealis* Bate & Westwood, 1868

11. Gnathopod 2; carpal process extends to about middle of propodus. Pereopod 7; basis with small, sharp anterodistal lobe overlapping most of ischium. Maximum size usually less than 6 mm .... *V. stebbingi* Behning & Woltereck, 1912

    Gnathopod 2; carpal process usually extends to dactylus. Pereopod 7; basis with anterodistal corner not produced distally to overlap ischium. Maximum size 12-17 mm 12

12. Pereopods 3 & 4 with thick articles, dactylus distinctly longer than half of propodus .... *V. viatrix* Bovallius, 1887

    Pereopods 3 & 4 with relatively thin articles, dactylus distinctly shorter than half of propodus .... *V. antarctica* Stebbing, 1888

13. Antennae 1 lanceolate, almost diamond-shaped, gradually tapering to point anteriorly .... *V. armata* Bovallius, 1887

    Antennae 1 bulbous, rounded sometimes slightly truncate anteriorly 14

14. Pereopod 7; basis as long as, or longer than, remaining articles combined. Uropod 3, peduncle distinctly longer than endopod . *V. chuni* Behning & Woltereck, 1912

    Pereopod 7; basis considerably shorter than remaining articles combined. Uropod 3, peduncle subequal in length to endopod 15

15. Pereopod 7; carpus & propodus with distinct anterodistal, bulbous process; dactylus lanceolate, knife-like. Uropod 3; peduncle only slightly narrowed at base .... *V. cultripes* Vosseler, 1901

    Pereopod 7; carpus & propodus with minor or no anterodistal process; dactylus rounded. Uropod 3; peduncle constricted at base 16

16. Gnathopod 2; carpal process reaches to about middle of propodus. Pereopod 7, carpus & propodus without anterodistal process .... *V. pyripes* Bovallius, 1887
Gnathopod 2; carpal process reaches dactylus. Pereopod 7; carpus & propodus with small anterodistal process .... *V. longicarpus* Behning, 1913.

Vibilia jeangerardi Lucas
(Figs 2 & 3)

Vibilia jeangerardi Lucas, 1846: 56, pl. 5, fig. 4. – Bate 1862: 303, pl. 49, fig. 9. Marion 1874: 5-11, pl. 1, 2, figs 1i. Carus 1885: 421-422. Bovallius 1887c: 47-49, pl. 7, figs 1-11. Chevreux 1900: 125-126, pl. 15, fig. 3. Vosseler 1901: 119. Behning 1913a: 533. Behning 1913b: 212, 214. Stewart 1913: 247-248. Stephensen 1918: 34-36, chart 4. Pesta 1920: 33, fig. 6a-c. Spandl 1924b: 263. Behning 1925. 480, figs 1-2. Chevreux & Fage 1925: 383-384, fig. 388. Chevreux 1927: 138. Pirlot 1929: 98-99. Chevreux 1935: 173-174. Evans 1961: 203. Madin & Harbison 1977: 453 (table), 455. Vinogradov *et al.* 1982: 202-203, fig. 101. Vinogradov 1999a: 1179-1180, fig. 4.85.

?*Vibilia speciosa* Costa, 1853: 178. – Bate 1862: 304. Carus 1885: 422 (as synonym of *V. jeangerardi*).

?*Vibilia mediterranea* Claus, 1872: 467. – Claus 1880: 586.

Type material

The type of *V. jeangerardi* could not be found at the MNHN (de Fage pers. comm., Laperousaz searched 1997) and is considered lost. Although the description and figures by Lucas (1846) are inadequate, the status of this, relatively common, Mediterranean species has been established by Marion (1874), Bovallius (1887c) and Chevreux (1900). The type locality is the Mediterranean Sea, harbour at Bône, Algeria.

Type material of synonyms

The type of *V. speciosa* could not be found in any major Italian Museum (see acknowledgments) and is considered lost. This species is most likely a synonym of *V. jeangerardi* based on Costa's description, and the fact that it is a common Mediterranean species.

The type of *V. mediterranea* could not be found in any major European museum (see acknowledgments) and is considered lost. Claus merely lists this species as occurring in salps; there is no description or figures. Thus, it is a nomen nudum. It seems a synonym of *V. jeangerardi,* based solely on geographical grounds, and has been regarded as such, by subsequent authors. It has not been recognised as a valid species since Claus (1880).

Material examined

Several lots from the **Mediterranean** and **North Atlantic** in the ZMUC (especially CRU 2855-2860; over 350 specimens) and ZMB (2 lots).

Diagnosis

Body length up to 14 mm. Antennae 1 as long as head and first pereonite; flagellum oval, distal margin rounded. Gnathopod 2; carpal process about half-length of propodus. Pereopods 3 & 4; dactylus relatively short about 0.2x length of propodus. Pereopods 5 & 6; dactylus length slightly more than 0.1x length of propodus. Pereopod 7; basis rectangular, width about 0.8x length, slightly longer than ischium to carpus combined, with slight rounded posterodistal lobe barely overlapping ischium. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami; sexual dimorphism of endopod not evident. Telson semi-circular, almost half as long as peduncle of U3.

Remarks

This species most closely resembles *V. propinqua,* and perhaps also *V. gibbosa,* but is readily distinguished by the relatively short dactylus of the pereopods, particularly pereopods 5 and 6, and by the rounded telson.

Vibilia jeangerardi is a well-known associate of *Salpa maxima* (Marion 1874, Madin & Harbison 1977, Laval 1980).

The publication date for this species is not clear from the literature with some authors referring it to 1849, which is the date of the title page of the work, while others quote 1845 (e.g. Bovallius 1887c, Vinogradov *et al.* 1982). According to Sherborn and Woodward (1901) and Woodward (1904), that part of the work by Lucas describing *V. jeangerardi* was actually published in 1846.

Distribution

This species is most common in the Mediterranean Sea and the North Atlantic Ocean but, has also been recorded from the Indian Ocean, northeast of Madagascar (Stephensen 1918).

Vibilia borealis Bate & Westwood

(Figs 4 & 5)

Vibilia borealis Bate and Westwood, 1868: 524-526, text fig. – Bovallius 1887c: 57-58, text fig.. Norman 1900: 137. Behning 1913b: 215-216. Stephensen 1923: 11-12. Schellenberg 1927: 615-616, fig. 24. Pirlot 1929: 94-95. Stephensen 1929: 42, fig. 13.2. Pirlot 1930: 10. Stephensen 1932a: 375. Grice & Hart 1962: 300. Vinogradov *et al.* 1982: 219-221, fig. 108. Vinogradov 1990a: 56.

Vibilia kroeyeri Bovallius, 1887a: 8. – Bovallius 1887b: 555. Bovallius 1887c: 58-60, pl. 8, figs 18-25. Behning 1913b: 216.

Vibilia kroyeri – Stephensen 1918: 38-40, fig. 10 (part), 11, chart 5. Chevreux 1935: 174. Madin & Harbison 1977: 453 (table), 455.

Type material

The only likely type material of *V. borealis* in the BMNH is a specimen from the Norman collection (11,719-20) labelled "cotypes". The designation of "type" by Norman is suspect as there are many instances in the Norman Collection of material labelled as "types' which was collected after the species name was published (see also Thurston & Allen 1969). The type locality is the North Sea, off Banff, Scotland.

Type material of synonyms

The types of *V. kroeyeri* could not be located at the SMNH, ZMUC or in Uppsala and are considered lost. However, Stephensen (1923) mentions two specimens in the ZMUC which he believes might be types, marked "*V. borealis* B&B?", but these could not be located. The synonymy of *V. kroeyeri* has been confirmed by the examination of specimens in museum collections labelled either *V. borealis* or *V. kroeyeri.*

Material examined

North Atlantic: 25 lots (ZMUC), several lots (USNM), 40 specimens. **Mediterranean:** 1 lot (ZMH), 1 lot (ZMUC), 11 specimens. **Philippines:** 1 lot (USNM), 11 specimens.

Diagnosis

Body length up to 13 mm but usually 6-7 mm. Antennae 1 as long as head and first two pereonites in males, slightly less in females; flagellum oval shaped, distal margin rounded. Head with anterior margin forming a vertical or rounded projection above the base of A1; more prominent in males. Gnathopod 2; carpal process slightly longer than half of propodus. Pereopods 3 & 4; dactylus length about 0.3-0.4x length of propodus. Pereopods 5 & 6; dactylus length about 0.2x length of propodus. Pereopod 7; basis rectangular, width about 0.8x length, slightly shorter than ischium to carpus combined, with slight rounded posterodistal lobe barely overlapping ischium. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami; sexual dimorphism of endopod not evident. Telson roundish-triangular, about half as long as peduncle of U3.

Remarks

This species is very similar to *V. jeangerardi,* but differs in the head shape, the relatively longer first antennae, the relatively longer dactylus of pereopods 3-6, the relatively narrower articles of pereopods 5 and 6, and the slightly more triangular telson.

The figures and description of Bate and Westwood (1868) are insufficient to characterise the species, but Norman (1900), who apparently had some specimens from Bate and Westwood, concluded that it was the same as *V. kroeyeri,* which had been adequately described and figured by Bovallius (1887c).

Vibilia borealis, like the preceding species, has been recorded in association with *Salpa maxima* (Madin & Harbison 1977).

Distribution

This species has a similar distribution pattern to *V. jeangerardi,* but is more common in the North Atlantic Ocean (up to 60°N), whereas *V. jeangerardi* is more common in the Mediterranean Sea. It has also been recorded from the southeastern Pacific Ocean, off the northwest coast of South America (Vinogradov 1990a), and near New Zealand (Vinogradov *et al.* 1982). The record of Pirlot (1930) from the Sulu and Molucca Sea, near the Philippines, and the specimens examined from the USNM may represent a misidentification, as *V. borealis* seems to prefer colder waters.

Vibilia gibbosa Bovallius

(Figs 6 & 7)

Vibilia gibbosa Bovallius 1887a: 7. – Bovallius 1887c: 53-54, pl. 8, figs 9-17. Vosseler 1901: 119-120, pl. 10, figs 16-19, pl. 11, figs 1-5. Behning 1913a: 529, 533, fig. 1. Behning 1913b: 215. Stephensen 1918: 36-37, fig. 8. Chevreux & Fage 1925: 384-385, fig. 389. Behning 1927: 115-116, 121 (table), fig. 1. Pirlot 1929: 93-94. Chevreux 1935: 173. Reid 1955: 14. Hurley 1956: 12. Irie 1959: table 4. Evans 1961: 203. Grice & Hart 1962: 300. Yoo 1971b: 50-51, fig. 7: Semenova 1973: 171, fig. 2. Brusca 1981a: 18 (key), 39, fig. 4h. Vinogradov *et al.* 1982: 216-218, fig. 107. Vinogradov 1990a: 56, 93 (table). Shih & Chen 1995: 39-40, fig. 18. Zeidler 1998: 34, figs 23-24. Vinogradov 1999a: 1179, fig. 4.84.

Type material

No type material was found at the ZMUC, SMNH or in Uppsala and it thus appears to be lost. However, the description and figures of Bovallius (1887c) are sufficient to distinguish this species. Bovallius (1887a) gives the type locality as "tropical parts of Atlantic", but later (1887c) is more specific, "17°30'S 2°20'W" (near St. Helena).

Material examined

North Atlantic: 1 lot (CMN), 7 lots (USNM), 2 lots (ZMB), 1 lot (ZMH), 3 lots (ZMUC), 27 specimens. **North Pacific:** 2 lots (CAS), 2 specimens. **Tasman Sea:** 2 lots (SAMA), 4 specimens.

Diagnosis

Body length up to 8 mm. Antennae 1 as long as head and first pereonite; flagellum oval, slightly more inflated medially, distal margin rounded. Gnathopod 2; carpal process about 0.7x length of propodus. Pereopods 3 & 4; dactylus length about half of propodus. Pereopods 5 & 6; dactylus length about 0.3x, or slightly more, than length of propodus. Pereopod 7; basis rectangular, slightly longer than wide, as long as ischium to carpus combined, with slight rounded posterodistal lobe barely overlapping ischium. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami; sexual dimorphism of endopod not evident. Telson; rounded, almost semi-circular, about half as long as peduncle of U3.

Remarks

This species is readily distinguished from its congeners by the bulbous nature of the flagellum of the first antennae, in combination with other minor characters. It is most similar to *V. propinqua* Stebbing, 1888, but in that species the flagellum of antennae 1 is no wider than the peduncular articles, and the structure of pereopod 7 is slightly different. It is also similar to *V. jeangerardi* Lucas, 1846, but in that species the dactylus of pereopods 3-6 is relatively shorter, especially those of pereopods 5 and 6 (only about 0.7x length propodus). In the shape of antennae 1, *V. gibbosa* also resembles *V. longicarpus* Behning, 1913, but that species differs in many respects particularly in the shape of the urosome and gnathopod 2, in which the carpal process is slightly longer than the propodus.

The salp associate has not been determined for this species.

Distribution

This is an uncommon, widely distributed species in the Atlantic Ocean and the Mediterranean Sea. It is also found in tropical and warm-temperate waters of other oceans, but has not been recorded from the Indian Ocean.

Vibilia robusta Bovallius

(Figs 8-10)

Vibilia robusta Bovallius, 1887a: 7-8. – Bovallius 1887c: 54-57, pl. 7, figs 12-34. Vosseler 1901: 123. Walker 1909: 50, 53. Behning 1913a: 529. Behning 1913b:

215. Stephensen 1918: 37-38, fig. 9. Behning 1927: 116-117, 121 (table), fig. 2. Chevreux 1935: 175. Hurley 1960a: 110. Semenova 1973: 170: Semenova 1976: 136-138. Brusca 1981a: 18 (key), 39, fig. 4i. Vinogradov *et al.* 1982: 214-216, fig. 106. De Broyer & Jazdzewski 1993: 112. Zeidler 1998: 37, figs 25-27. Vinogradov 1999a: 1180, fig. 4.88.

Vibilia hirsuta Behning & Woltereck, 1912: 6-8, figs 4-6. – Behning 1913b: 220. Behning 1925: 489-491, figs 42-51.

Type material

Type material of *V. robusta* could not be found at the SMNH, ZMUC or in Uppsala and is considered lost. However, in the SMNH are several lots from the Atlantic that may have been part of Bovallius's original material. Fortunately the descriptions and figures of Bovallius (1887c) readily characterise this species. No precise type locality is given by Bovallius (1887a, c). He merely lists the distribution as "Atlantic, Indian Ocean" (1887a), and "North Atlantic, tropical Atlantic" (1887c).

Type material of synonyms

Type material of *V. hirsuta* could not be found in the ZMB, or ZMH and is considered lost. However, this species is clearly the same as *V. robusta*, judging by the figures and description of Behning and Woltereck (1912).

Material examined

Tasman Sea: 9 lots (SAMA), 14 specimens. **Great Australian Bight:** 4 lots (SAMA), 13 specimens. **North Atlantic:** 1 lot (ZMB), 2 lots (ZMH), 3 lots (ZMUC), numerous specimens. **North Pacific:** 1 lot (CAS), 2 lots (LACM), 1 lot (USNM), 11 specimens. **South Pacific:** 2 lots (BMNH), 20 specimens. **Philippines:** 1 lot (USNM), 4 specimens.

Diagnosis

Body length up to 20 mm. Antennae 1; as long as head and first pereonite; flagellum oval, evenly rounded terminally, slightly truncate ventrally in mature specimens. Gnathopod 2; basis inflated in mature specimens, width about 0.7x length; carpal process about 0.7x length of propodus. Pereopods 3 & 4; dactylus length about 0.3x of propodus. Pereopods 5 & 6; dactylus length about 0.2x of propodus. Pereopod 7; basis rectangular, a little longer than wide, slightly longer than ischium to carpus combined, without prominent posterodistal lobe in juvenile specimens. Lateral corners of last urosomite not produced. Uropod 2 reaching to tip of U3, or slightly beyond. Uropod 3; peduncle distinctly longer than rami, subequal in juvenile specimens; sexual dimorphism of endopod not evident. Telson triangular, with rounded point, about half as long as peduncle of U3.

Remarks

This is one of the largest species of *Vibilia*. The relatively long uropod 2 and the relatively wide basis of the gnathopods, especially gnathopod 2, are distinctive features not found in any other species of *Vibilia*. Juvenile specimens differ slightly from mature ones and may present taxonomic difficulties. Thus, an immature female is illustrated (Figs 8-10) for comparison. In particular mature specimens have slightly larger eyes; the main flagellar article of antennae 1 is slightly truncate ventrally; the basis of the gnathopods is considerably wider ; the merus of gnathopod 2 has more spines; the basis of pereopod 7 has a distinct posterodistal lobe overlapping the ischium; the ridges on coxae 5-7 and the pleon are more prominent, and the peduncle of uropod 3 is distinctly longer than the rami. Specimens less than about 5 mm in length also have a much shorter telson, and pereopod 7 is often considerably reduced in size. However, despite these differences, juvenile specimens of *V. robusta* can be readily distinguished by the relatively long uropod 2.

This species is often recorded in association with salps but the host species is rarely recorded. Behning (1927) records it with *Salpa tilesii* (= *Thetys vagina*). In Californian waters it is found with *Thetys vagina* (specimens in LACM).

Distribution

This species is widely distributed in all the world's oceans, ranging from tropical to temperate regions.

Vibilia viatrix Bovallius

(Figs 11 & 12)

Vibilia viatrix Bovallius, 1887a: 9. – Bovallius 1887c: 63-64, pl. 9, figs 1-13. Vosseler 1901: 124. Walker 1909: 50 (list), 53. Behning & Woltereck 1912: 5. Behning 1913a: 529, 533. Behning 1913b: 217. Stewart 1913: 247. Stephensen 1918: 41-43, fig. 13. Spandl 1924a: 22. Behning 1925: 482, fig. 12. Chevreux & Fage 1925: 385-386, fig. 390. Shoemaker 1925: 41. Behning 1927: 117-118. Chevreux 1927: 138. Pirlot 1929: 95. Barnard 1930: 403. Pirlot 1930: 10-11. Barnard 1931: 126. Barnard 1932: 262-263. Chevreux 1935: 175-176. Shoemaker 1945: 234, fig. 34. Reid 1955: 13-14. Hurley 1956: 11. Irie 1959: table 4. Hurley 1960b: 279. Evans 1961: 204, Siegfried 1963: 8. Pillai 1966b: 207, fig. 2. Brusca 1967a: 389, 390 (table). Brusca 1967b: 453-454. Hurley 1969: 33, pl. 18 (maps). Dick 1970: 34 (key), 53, fig. 4 (part). Yoo 1971b: 49 (key), 49-50. Yoo 1972b: 167-169, fig. 2. Brusca 1973: 9 (table), 13. Semenova 1973: 173. Semenova 1976: 139. Thurston 1976: 405. Madin & Harbison 1977: 453 (table). Shulenberger 1977: 378 (table). Tranter 1977: 647, 648 (table). Brusca 1981a. 18 (key), 39, fig. 4n. Watson & Chaloupka 1982: 29, fig. 6-4, 54 (key). Vinogradov *et al.* 1982: 203-206, fig. 102. Young & Anderson 1987: 716 (table). Vinogradov 1990a: 55, 93 (table). De Broyer & Jazdzewski 1993: 112. Vinogradov 1993b: 43 (table). Shih & Chen 1995: 40-42, fig. 19. Zeidler 1998: 41. Vinogradov 1999a: 1180-1181, fig. 4.90.

Vibilia viator Stebbing, 1888: 1286-1287, pl. 148B, fig. E – Stebbing 1910: 654.

Vibilia hirondellei Chevreux, 1900: 126-129, pl. 15, fig. 4.

Vibilia dentata Chevreux, 1900: 129-131, pl. 16, fig. 1. – Behning 1913b: 218.

Vibilia californica Holmes, 1908: 490-492, figs 1-2. – Shoemaker 1925: 41 (part).

Vibilia stebbingi [misidentification – in part]. – Zeidler 1998: 37 (SAMA C4434-38).

Type material

Type material of *V. viatrix* could not be located at the SMNH, ZMUC or in Uppsala and is considered lost. However in the SMNH are several lots which may represent type material, in particular one lot (No. 123) labelled "23°-27°N 36° W Det. C. Bov." The description and figures of Bovallius (1887c) readily distinguish this species. No precise type locality is given by Bovallius (1887a, c). He merely lists the distribution as "Atlantic" (1887a) and "the North and South Atlantic, the Pacific, the Indian Ocean" (1887c).

Type material of synonyms

The unique type of *V. viator* is in the BMNH (89.5.15.180). It is readily identified as a synonym of *V. viatrix*. Stebbing (1888) acknowledges that his species is in close agreement with *V. viatrix*, but for the fusion of urosomites 2 & 3. Bovallius believed, incorrectly, that the urosomites were separate.

Two syntypes of *V. hirondellei* are in the MNHN (AM 1882), but the remainder (100+ specimens) could not be found in the MNHN or MOM and are considered lost. The description and figures of Chevreux (1900) are consistent with that of *V. viatrix*. Also five specimens from the Norman Collection (11,726-4), in the BMNH, labelled "Types, Azores", are clearly *V. viatrix*.

One Syntype (the type?) of *V. dentata* is in the MNHN (AM 1857), the other 12 syntypes are in the MOM. The description and figures of Chevreux (1900) are consistent with that of *V. viatrix*. The scalloped distal margin of the inner lobe of the maxilliped, illustrated by Chevreux, is probably an artefact of collection, or preservation, as similar 'damage' has been observed in specimens of other species.

The two syntypes (one labelled "type") of *V. californica* are in the USNM (Cat. No. 38533). Both of these specimens are clearly *V. viatrix*. Holmes (1908} illustrated the first antennae with an even convex margin, but in the larger specimen, the one illustrated by Holmes, the antennae are actually truncate ventrally, as is characteristic of *V. viatrix*.

Material examined

Types. The unique type of *V. viator* from Cape York, *Challenger,* September, 1874: 2 microscope slides of head, G1 & 2, P3-7 and urosome; remainder in spirit. Two syntypes of *V. californica* from the North Pacific off point Loa, USA (*Albatross* Stn. 4305), 67-116 fathoms: in spirit.

Other material examined. **Coral Sea:** 2 lots (BMNH), 3 specimens. **Tasman Sea:** 9 lots (SAMA), 28 specimens. **Great Australian Bight:** 3 lots (SAMA), 19 specimens. **North Atlantic:** 4 lots (BMNH), 19 lots (CMN), 18 lots (USNM), 9 lots (ZMB), 4 lots (ZMH), 15 lots (ZMUC), numerous specimens. **South Atlantic:** 6 lots (BMNH), 7 specimens. **North Pacific:** 8 lots (LACM), 7 lots (USNM), 48 specimens. **South Pacific:** 8 lots (BMNH), numerous specimens. **Mediterranean:** 8 lots (ZMUC), 9 specimens. **Philippines:** 5 lots (USNM), 7 specimens.

Diagnosis

Body length up to 12 mm. Antennae 1 as long as head and first pereonite; flagellum more or less oval, distal margin rounded, slightly truncate ventrally. Gnathopod 2; carpal process about as long as propodus. Pereopods 3 & 4; dactylus almost as long as propodus. Pereopods 5 & 6; dactylus length about 0.4x length of propodus. Pereopod 7; basis rectangular, width about 0.7x length, about as long as ischium to carpus combined, with rounded posterodistal lobe overlapping ischium. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami; sexual dimorphism of endopod not evident. Telson triangular with rounded point, about half, or slightly more, as long as peduncle of U3.

Remarks

Distinctive features of this species are the long carpal process of gnathopod 2, the relatively long dactylus of pereopods 3-6, and the relatively thick articles of pereopods 3 and 4.

It most closely resembles *V. antarctica*, but the anterodistal corner of the basis of pereopod 7 is not extended anteriorly, and there is no sexual dimorphism of uropod 3. Other minor characters which help to distinguish this species are as follows: the posterodistal corner of the propodus of gnathopod 1 is slightly produced instead of tapering gradually towards the dactylus, a feature not found in any other congener except perhaps *V. caeca*; pereopod 6 has a row of robust setae on the anterior margin of the carpus and the distal half of the merus, whereas related species such as *V. antarctica* and *V. propinqua* tend to have them restricted to the carpus; the anterodistal corner of the carpus of pereopod 7 is sharp and slightly projected anteriorly, whereas in allied species such as *V. antarctica* and *V. stebbingi* this anterodistal corner is rounded and not projected.

This species has been recorded as an associate of the salps *Pegea socia, P. confoederata, Salpa maxima, S. cylindrica* (Madin & Harbison 1977) and *P. confoederata* var. *bicaudata* (Laval 1980).

Distribution

This is a relatively common species, widely distributed in tropical and temperate regions of the world's oceans.

Vibilia armata Bovallius

(Fig 13)

Vibilia armata Bovallius, 1887a: 10. – Bovallius 1887c: 69-70, pl. 10, figs 15-22. Vosseler 1901: 125. Lo Bianco 1901: 446. Walker 1903: 232. Lo Bianco 1904:

42, pl. 21, fig. 62. Stebbing 1904: 31. Tattersall 1906: 15. Sexton 1911: 222. Behning & Woltereck 1912: 5. Behning 1913a: 529, 533. Behning 1913b: 220. Stewart 1913: 250. Stephensen 1918: 46-52, figs 15-16, chart 6. Behning 1925: 491-494, figs 52-61. Barnard 1925: 376. Chevreux & Fage 1925: 387-388, fig. 391. Behning 1927: 119, 121 (table). Schellenberg 1927: 618, fig. 27. Pirlot 1929: 100-101. Barnard 1930: 404. Pirlot 1930: 11. Barnard 1931: 126. Barnard 1932: 264-265. Chevreux 1935: 169-170. Barnard 1937: 182. Reid 1955: 13. Guiler 1952: 31. Hurley 1956: 10-11. Irie 1959: table 4. Hurley 1960b: 279. Evans 1961: 203. Kane 1962: 299. Vinogradov 1962: 16. Laval 1963: 1389-1392, figs 1B, 2. Siegfried 1963: 8. Pillai 1966b: 203-207, fig. 1. Brusca 1967a: 388-389. Brusca 1967b: 453. Hurley 1969: 33, pl. 18 (map 3).' Dick 1970: 51-52. Yoo 1971b: 50, fig. 6 (distn. map). Brusca 1973: 12-13. Semenova 1973: 173-174. Laval 1974: 57-87. Lorz & Pearcy 1975: 1444. Semenova 1976: 139. Thurston 1976: 402-404, fig. 5 (graphs). Shulenberger 1977: 378 (table). Tranter 1977: 646, 648 (table), 659. Zeidler 1978: 5-6, fig. 2. Brusca 1981a: 17 (key), 39, fig. 4c, 4e. Watson & Chaloupka 1982: 29, fig. 6-3. Vinogradov *et al.* 1982: 226-228, fig. 112. Young & Anderson 1987: 716 (table). Vinogradov 1990a: 56. Zeidler 1992a: 92. De Broyer & Jazdzewski 1993: 111. Vinogradov 1993b: 43 (table). Shih & Chen 1995: 42-44, figs 20, 21. Zeidler 1998: 33-34. Vinogradov 1999a: 1179, fig. 4.80.

Vibilia gracilis Bovallius 1887a: 9. – Bovallius 1887c: 65-66, pl. 9, figs 14-28.

Vibilia gracilenta Bovallius 1887a: 9-10. – Bovallius 1887c: 67-68, pl. 10, figs 1-14. Vosseler 1901: 125. Walker 1909: 50, 53. Stewart 1913: 250-251. Barnard 1925: 376-377. Chevreux 1935: 173.

Vibilia erratica Chevreux 1892: 32-35, figs 1-3. – Chevreux 1935: 170-172, pl. 16, figs 14, 25, 31.

Type material

Type material of *V. armata* could not be located at the SMNH, ZMUC or in Uppsala and is considered lost. However the description and figures of *V. armata* by Bovallius (1887c) readily distinguish this species. No precise type locality is given by Bovallius

(1887a, c). He merely lists the distribution as "South Atlantic" (1887a), and "tropical parts of the Atlantic, and the South Atlantic" (1887c).

Type material of synonyms

Type material of *V. gracilis* and *V. gracilenta* could not be located at the SMNH, ZMUC or in Uppsala and is considered lost. The specific differences attributed to these two species by Bovallius (1887a, c) are considered minor, and within the range of the specific limits of *V. armata*.

Type material of *V. erratica* could not be located in the MNHN or MOM and is considered lost. However, the descriptions and figures of Chevreux (1892, 1935) readily confirm the synonymy. Also, eight specimens from the Norman Collection (11,726-9), in the BMNH, labelled "Types, Antibes S. France", are clearly *V. armata*.

Material examined

Coral Sea: 2 lots (BMNH), 2 specimens. **Tasman Sea:** 1 lot (AM), 34 lots (SAMA), numerous specimens. **North Atlantic:** 3 lots (BMNH), 5 lots (USNM), 2 lots (ZMH), 19 lots (ZMB), 28 lots (ZMUC), numerous specimens. **South Atlantic:** 8 lots (BMNH), 14 lots (USNM), 28 lots (ZMB), numerous specimens. **Mediterranean:** numerous lots (ZMUC). **North Pacific:** several lots (LACM), 10 lots (USNM), numerous specimens. **South Pacific:** 1 lot (USNM), numerous specimens. **Philippines:** 3 lots (BMNH), 1 lot (CAS), 2 lots (USNM), numerous specimens. **Indian:** 1 lot (BMNH), 4 specimens. **Arabian Sea:** 5 lots (BMNH), 57 specimens.

Diagnosis

Body length up to 13 mm but usually 5-8 mm. Antennae 1 slightly shorter than head and first two pereonites; flagellum elongated, lanceolate, almost diamond-shaped, ending in sharp point terminally. Gnathopod 2; carpal process about as long as propodus; anterodistal corner of propodus slightly produced over dactylus. Pereopods 3 & 4; dactylus length slightly more than half-length of propodus. Pereopods 5 & 6;

dactylus length about half-length of propodus. Pereopod 7; basis rectangular, slightly dilated posteriorly, width about 0.7x length, about as long as ischium to carpus combined, with almost negligible posterodistal lobe. Lateral corners of last urosomite produced, partly overlapping peduncle of U3. Uropod 3; peduncle distinctly longer than rami; endopod slightly longer than, or subequal in length to, exopod in females, in males the endopod is slightly broader, and up to one-third longer than the exopod. Telson triangular, pointed terminally, about half, or slightly more, as long as peduncle of U3.

Remarks

The combination of characters given in the diagnosis, particularly the shape of antennae 1 and the urosome, readily distinguish *V. armata* from all its congeners.

Two synonyms of this species, *V. gracilis* and *V. gracilenta*, have page priority but neither name has been in use for over 50 years whereas *V. armata* is a well established species in the literature. Thus, consistent with nomenclatural stability, *V. armata* should continue to be used for this species (ICZN, article 79c amended).

Laval (1963, 1965, 1980) has described the larval biology of V. armata, and its association with salps. It has been recorded as a associate of the salps *Salpa fusiformis, Thalia democratica, Ihlea punctata* (Laval 1963) and *Pegea confoederata* var. *bicaudata* (Laval 1980).

Distribution

This is a relatively abundant species in the tropical and temperate regions of the world's oceans.

Vibilia pyripes Bovallius

(Figs 14 & 15)

Vibilia pyripes Bovallius 1887a: 10. – Bovallius 1887c: 71-72, pl. 10, figs 23-30. Vosseler 1901: 125. Behning & Woltereck 1912: 5. Behning 1913a: 533. Behning 1913b: 221. Stephensen 1918: 52-53, fig. 17, chart 5 (part). Behning 1925: 494-495, fig. 62. Schellenberg 1927: 617-618, fig. 26. Barnard 1930: 405. Barnard 1932: 267. Chevreux 1935: 175. Barnard 1937: 182. Reid 1955: 14. Irie 1959: table 4. Vinogradov 1962: 16. Hurley 1969: 33, pl. 18 (map 3). Semenova 1973: 175. Semenova 1976: 139-140. Madin & Harbison 1977: 453 (table). Tranter 1977: 647, 648 (table). Brusca 1981a: 18 (key), 39, fig. 4g, 41. Vinogradov *et al.* 1982: 232-234, fig. 115. Young & Anderson 1987: 712, 716 (table). De Broyer & Jazdzewski 1993: 111. Shih & Chen 1995: 45-47, figs 22, 23. Zeidler 1998 (part): 34, 37. Vinogradov 1999a: 1180, fig. 4.87.

Vibilia grandicornis Chevreux, 1900: 131-134, pl. 16, fig. 2. – Behning 1913b: 221. Stephensen 1918: 53. Pirlot 1929: 102. Chevreux 1935: 173.

Type material

Type material of *V. pyripes* could not be located at the SMNH, ZMUC or in Uppsala and is considered lost. However, the description and figures of Bovallius (1887c) readily distinguish this species. No precise type locality is given by Bovallius (1887a, c). He merely lists the distribution as "Tropical parts of Atlantic".

Type material of synonyms

The syntypes of *V. grandicornis* (one male and one female) are in the MOM. The descriptions and figures of Chevreux (1990, 1935) readily confirm the synonymy.

Material examined

Tasman Sea: 3 lots (SAMA), 4 specimens. **North Atlantic:** 1 lot (BMNH), 3 lots (USNM), 5 lots (ZMB), 4 lots (ZMUC), 26 specimens. **South Atlantic:** 1 lot (BMNH), 3 lots (ZMB), 10 specimens. **North Pacific:** 6 lots (LACM), 8 specimens. **South Pacific:** 1 lot (BMNH), 2 specimens. **Red Sea** (Gulf of Elat): 1 lot (USNM), 3 specimens.

Diagnosis

Body length up to 11 mm but usually less than 5-7 mm. Antennae 1 as long as head and first two pereonites; flagellum with dorsal margin relatively straight, ventral margin convex, rounded terminally. Gnathopod 2; carpal process less than half-length of propodus. Pereopods 3 & 4; dactylus length about 0.7x length of propodus. Pereopods 5 & 6; dactylus length about 0.2x length of propodus. Pereopod 7; basis rectangular, width about 0.7x length, about as long as ischium to carpus combined, with rounded posterodistal lobe extending to about mid-merus. Lateral corners of last urosomite produced, partly overlapping peduncle of U3. Uropod 3; peduncle slightly shorter than rami; sexual dimorphism of endopod not evident. Telson relatively large, circular, reaching a little beyond the middle of peduncle of U3.

Remarks

A characteristic feature of this species is the very short carpal process of gnathopod 2 and the shape of the urosome. In the shape of the urosome, *V. pyripes* resembles *V. longicarpus*, but differs in most other respects. The shape of antennae 1 is similar to *V. bovalli* Bonnier, 1896, but that species is insufficiently known for a comparison.

Vibilia pyripes has been recorded as an associate of the salp *Iasis zonaria* (Madin & Harbison 1977).

Distribution

This is a relatively rare species, found in both tropical and temperate waters of the Atlantic and Pacific Oceans but only in tropical waters of the Indian Ocean.

Vibilia propinqua Stebbing

(Figs 16 & 17)

Vibilia propinqua Stebbing, 1888: 1279-1283, pl. 157. – Vosseler 1901: 124-125. Stebbing 1904: 31-32. Tattersall 1906: 14-15. Walker 1907: 6. Behning & Woltereck 1912: 5. Behning 1913a: 533, 549. Behning 1913b: 218. Stewart 1913: 246-247. Stephensen 1918: 43-46, fig. 14. Behning 1925: 484-486, figs 23-25. Behning 1927: 118, 121 (table). Schellenberg 1927: 616-617, fig. 25. Pirlot 1929: 97-98. Barnard 1930: 404. Barnard 1932: 263. Chevreux 1935: 174-175. Barnard 1937: 182. Waterman *et al.* 1939: 268, fig. 5B (graph). Bulycheva 1955: 1048 (table). Hurley 1960b: 279. Evans 1961: 203. Laval 1963: 1389-1392, fig. 1A. Siegfried 1963: 8. Hurley 1969: 33, pl. 18 (map 3). Lewis & Fish 1969: 8-9. Dick 1970: 34 (key), 52-53: Semenova 1973: 173. Lorz & Pearcy 1975: 1444 (table). Semenova 1976: 138, fig. 2 (map). Shulenberger 1977: 378 (table). Thurston 1976: 404. Madin & Harbison 1977: 453 (table), 454. Tranter 1977: 647, 648 (table). Brusca 1981a: 17 (key), 39, fig. 4d, 4q. Vinogradov *et al.* 1982: 211-213, fig. 105. Vinogradov 1990a: 55-56, 93 (table). Zeidler 1991: 128-130, figs 2, 3. De Broyer & Jazdzewski 1993: 111. Vinogradov 1993b: 43 (table). Shih & Chen 1995: 47-49, figs 24, 25. Vinogradov 1999a: 1180, fig. 4.86.

Vibilia milnei Stebbing, 1888: 1284-1285, pl. 148A.

Vibilia sp. Stebbing, 1888: 1285-1286, pl. 148B, figs C, D.

Vibilia stebbingi [misidentification]. – Young & Anderson 1987: 712, 716 (table), fig. 2. Zeidler 1992a: 96 (part). Zeidler 1998: 37 (part).

Type material

The four syntypes of *V. propinqua* are in the BMNH (89.5.15:177). The type locality is the Pacific Ocean, off Volcano Island, 25°30'N 138°0'E, surface.

Type material of synonyms

The unique type of *V. milnei* is in the BMNH (89.5.15.178). Although the remains of the specimen, on three microscope slides, are in poor condition, it appears to be the same as *V. propinqua*. Stebbing (1888) himself says that "this species does not differ greatly in general appearance and structure from *Vibilia propinqua*".

Material examined

Types. Four syntypes of *V. propinqua*, *Challenger*, 4th April, 1875: 3 specimens in spirit and 3 microscope slides of head, G1 & 2, P3-7 and pleon. The unique type of *V. milnei* from the South Atlantic, surface, *Challenger*, 5th October, 1873: 3 microscope slides of head, G1 & 2, P3-7 and pleon.

Other material examined. **Tasman Sea:** 3 lots (SAMA), 22 specimens. **North Atlantic:** 8 lots (BMNH), 2 lots (CMN), 15 lots (USNM), 10 lots (ZMB), 1 lot (ZMH), 30 lots (ZMUC), numerous specimens. **South Atlantic:** 3 lots (BMNH), 17 lots (USNM), 28 specimens. **Mediterranean:** 24 lots (ZMUC), numerous specimens. **North Pacific:** 16 lots (LACM), 7 lots (USNM), 1 lot (MNHN), numerous specimens. **South Pacific:** 6 lots (BMNH), 1 lot (USNM), 32 specimens. **Philippines:** 3 lots (USNM), 1 lot (MNHN), 5 specimens. **Indian:** 1 lot (BMNH), 3 specimens. **Arabian Sea:** 1 lot (BMNH), 5 specimens.

Diagnosis

Body length up to 12 mm. Antennae 1 as long as head and first pereonite; flagellum oval with slightly straighter dorsal margin, slightly pointed distally (especially in males). Gnathopod 2; carpal process slightly longer than half-length of propodus. Pereopods 3-6; dactylus length about 0.3x length of propodus. Pereopod 7; basis rectangular, width about 0.8x length, marginally longer than ischium to carpus combined, with rounded posterodistal lobe extending to first third of merus. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami (relatively longer in males); endopod slightly longer, or subequal in length to exopod in females, in males the endopod is slightly broader, and up to one-third longer than the exopod. Telson triangular, length about 0.7x length of peduncle of U3.

Remarks

This species most closely resembles *V. antarctica* but is distinguished by the shorter carpal process of gnathopod 2, the less truncate first antennae, and in preferring warmer waters. It has been confused with *V. stebbingi* because of the short carpal process of gnathopod 2 but *V. stebbingi* is a much smaller species and is distinguished by the narrow anterodistal lobe of the basis of pereopod 7. Also, sexual dimorphism of uropod 3 is not evident in *V. stebbingi.*

Vibilia propinqua also resembles *V. jeangerardi*, and *V. gibbosa*, but is distinguished by the relatively narrower and more pointed flagellum of antennae 1, the relatively longer and more pointed telson, and by the relatively larger posterodistal lobe of the basis of pereopod 7.

Laval (1963, 1965) has described the larval biology of *V. propinqua*, and its association with salps. It has been recorded as an associate of the salps *Salpa fusiformis, Thalia democratica, Ihlea punctata* (Laval 1963); *Salpa maxima, S. cylindrica* (Madin & Harbison 1977) and *Pegea confoederata* var. *bicaudata* (Laval 1980).

Distribution

This is a relatively common species, widely distributed in the tropical and temperate regions of the world's oceans. It is recorded here from Australian waters for the first time.

Vibilia australis Stebbing

(Figs 18 & 19)

Vibilia australis Stebbing, 1888: 1287-1290, pl. 149. – Vosseler 1901: 124. Stebbing 1910: 654. Behning & Woltereck 1912: 5. Behning 1913a: 529, 533. Behning 1913b: 219. Spandl 1924a: 21. Behning 1925: 488, figs 32-34. Behning 1927: 119, 121 (table). Barnard 1932: 264. Guiler 1952: 31. Bulycheva 1955: 1048 (table). Reid 1955: 14. Hurley 1956: 11-12. Sheard 1965: 244 (list). Pillai 1966b: 208-209, fig. 3. Sheard 1967: 979 (table), 982 (table), 983 (table). Stuck *et al.* 1980: 361. Thurston 1976: 404. Tranter 1977: 646, 648 (table). Brusca 1981a: 17 (key), 39, fig. 4b. Vinogradov *et al.* 1982: 223-224, fig. 110. De Broyer & Jazdzewski 1993: 111. Shih & Chen 1995: 49-51, fig. 26. Vinogradov 1999a: 1179, fig. 4.81.

Vibilia australis var. *pelagica* Behning & Woltereck 1912: 9, figs 9-10. – Behning 1913b: 219. Behning 1925: 488-489, figs 35-41.

Vibilia seriocellatus Stephensen, 1932b: 498-501, fig. 5.

Vibilia woltereckі Behning, 1939: 358-361, pl. 6. – Bulycheva 1955: 1048 (table). Lorz & Pearcy 1975: 1444 (table). Shulenberger 1977: 378 (table). Brusca 1981: 18 (key), 39, figs 4j, 4m. **New synonymy**.

Type material

The three syntypes of *V. australis* are in the BMNH (89.5.15.181). The type locality is south of Australia, 48°18'S 130°04'E, surface.

Type material of synonyms

Type material of *V. australis* var. *pelagica* and *V. woltereckі* could not be found at the ZMB or ZMH and is considered lost. Judging by the description and figures of Behning and Woltereck (1912) and Behning (1925) there is no good reason to maintain the variety. Similarly, Behning's (1939) description and figures of *V. woltereckі* readily characterise *V. australis*. Vinogradov *et al.* (1982) do not mention *V. woltereckі*!

The syntypes of *V. seriocellatus* are in the ZMUC (CRU 2830). All of the specimens are clearly identifiable with *V. australis*. Stephensen (1932b) seems to be unaware of Stebbing's species for he makes no mention of it.

Material examined

Types. Three syntypes of *V. australis*, *Challenger*, 9th & 10th March, 1874: 2 specimens in spirit; 3 microscope slides of head, G1 & 2, P3-7 and pleon. Seven syntypes of *V. seriocellatus* from Matsu Bay, northern Honshu, Japan, December, 1931, in "body cavity of a *Salpa*": in spirit.

Other material examined. **East China Sea:** 3 lots (SAMA), 3 specimens. **North Atlantic:** 1 lot (USNM), 10 lots (ZMB), 1 lot (ZMUC), 19 specimens. **South Atlantic:** 1 lot (off Rio de Janeiro), 1 lot (BMNH), 1 lots (ZMB), 11 specimens. **North Pacific:** 3 lots (CAS), 9 lots (USNM), 60 specimens.

Diagnosis

Body length up to 6 mm. Eyes with ocelli in three, almost vertical, rows. Antennae 1 as long as head and first two pereonites; flagellum with parallel margins, tapering gradually toward apex, with relatively straight ventral margin. Antennae 2 very short, consisting of 2-4 articles. Gnathopod 2; carpal process about as long as propodus. Pereopods 3 & 4; dactylus length about half-length of propodus. Pereopods 5 & 6; dactylus length about 0.3x length of propodus. Pereopod 7; basis rectangular, width about 0.7x length, as long as ischium to middle of propodus combined, with rounded posterodistal lobe overlapping ischium. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami; sexual dimorphism of endopod not evident. Telson triangular, length 0.5-0.7x length of peduncle of U3.

Remarks

In general appearance this species is similar to *V. caeca* but is readily distinguished by the eyes. *Vibilia australis* is also unusual in having very short second antennae of only 2-4 articles, a character, which it shares only with *V. caeca*.

This is the smallest species of *Vibilia*.

The salp associate has not been recorded for this species but specimens found off British Columbia, Canada have been found associated with *Cyclosalpa bakeri* (Moira Galbraith pers. comm.). Stephensen (1932b) records his specimens from the body cavity of *Salpa*.

Distribution

This is an uncommon species, widely distributed in the tropical and temperate regions of the world's oceans.

Vibilia antarctica Stebbing
(Figs 20 & 21)

Vibilia antarctica Stebbing, 1888: 1290-1293, pl. 150. – Behning & Woltereck 1912: 9-11, fig. 11. Chilton 1912: 514. Behning 1913a: 529-530, 533. Behning 1913b: 219. Behning 1925: 486-488, figs 26-31. Behning 1927: 118-119, 121 (table). Barnard 1930: 404. Barnard 1932: 263-264. Hurley 1960a: 110. Hurley 1960b: 278. Vinogradov 1962: 16. Hurley 1969: 33, pl. 18 (map 3). Dick 1970: 51. Semenova 1973: 171. Semenova 1976: 138. Vinogradov *et al.* 1982: 208-211, fig. 104. Jazdzewski & Presler 1988: 63, 66-70, figs 3, 4. Andres 1990: 141, fig. 281. Vinogradov 1990: 55. Weigmann-Haass 1990: 419-426, figs 1-23. De Broyer & Jazdzewski 1993: 111. Vinogradov 1999a: 1178-1179, fig. 4.79.

?*Vibilia* sp. Stebbing, 1888: 1293.

Vibilia stebbingi [misidentification]. – Hurley 1955: 125-129, fig. 1. Hurley 1960a: 111. Vinogradov 1962: 15-16. Nagata 1986: 268-270, figs 8-9.

Type material

The unique type of *V. antarctica* is in the BMNH (89.5.15.182), recorded from the Antarctic, 52°4'S 71°22'E, surface.

Material examined

Types. The unique holotype of *V. antarctica*, *Challenger*, 2nd February, 1874: juvenile specimen on two microscope slides, head, G1 & 2, P3-7 and pleon.

Other material examined. **Antarctic:** 1 lot (BMNH), 12 lots (SAMA), 2 lots (USNM), 1 lot (ZMB), 1 lot (ZMH), 69 specimens. **South Atlantic:** 23 lots (BMNH), 1 lot (USNM), 1 lot (ZMB), 1 lot (ZMH), 1 lot (ZMUC), numerous specimens. **South Pacific:** 1 lot (BMNH), 6 specimens.

Diagnosis

Body length up to 17 mm. Antennae 1 as long as head and first two pereonites; flagellum with more or less parallel margins, obliquely truncate ventrally for distal third (slightly more acute in males). Gnathopod 2; carpal process reaches to dactylus, or slightly beyond. Pereopods 3 & 4; dactylus length about 0.3-0.5x length of propodus. Pereopods 5 & 6; dactylus length about 0.3x length of propodus. Pereopod 7; basis with almost straight anterior margin, with slight anterodistal projection with spinule, posterior margin convex with rounded posterodistal lobe extending to middle of merus, width about 0.8x length, a little longer than ischium to carpus combined. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami; endopod slightly longer, or subequal in length to exopod in females, in males the endopod is up to one-third longer than the exopod. Telson triangular, length slightly longer than half of peduncle of U3.

Remarks

The similarity of this species to *V. propinqua* has already been discussed under that species. It also resembles *V. stebbingi*, but is much larger, and the body more plump, the carpal process of gnathopod 2 is almost as long as the propodus, the dactylus of pereopods 3-6 is relatively shorter, and the endopod of uropod 3 exhibits sexual dimorphism. The basis of pereopod 7 is also similar, but in *V. stebbingi* the anterodistal corner forms a narrow, pointed lobe partly overlapping the ischium.

The salp associate has not been recorded for this species. Information on the biology and distribution of *V. antarctica* in Antarctic waters is given by Weigmann-Haass (1990).

Distribution

This is a cold-water species, relatively common in south of the Subtropical Convergence. Incursions further north are most likely as the result of the influx of cold water currents.

Vibilia cultripes Vosseler

(Fig 22)

Vibilia cultripes Vosseler, 1901: 121-123, pl. 11, figs 6-18. – Behning & Woltereck 1912: 5. Behning 1913a: 529, 533. Behning 1913b: 222. Chevreux 1913: 16. Stephensen 1918: 53-55, fig. 18, chart 7. Behning 1925: 495-496, figs 63-67. Chevreux & Fage 1925: 388-389, fig. 392. Behning 1927: 119-120, 121 (table). Pirlot 1929: 99-100. Barnard 1932: 265. Chevreux 1935: 172-173. Shoemaker 1945: 234, fig. 33. Siegfried 1963: 8. Dick 1970: 52. Yoo 1971a: 50. Semenova 1973: 174. Brusca 1981a: 17 (key), 39, fig. 4f, 4k. Vinogradov *et al.* 1982: 228-230, fig. 113. Young & Anderson 1987: 716 (table). Vinogradov 1990a: 56, 93 (table). Zeidler 1992a: 95-96, fig. 8. Vinogradov 1993b: 43 (table). Shih & Chen 1995: 51-52, fig. 27. Vinogradov 1999a: 1179, fig. 4.83.

Type material

The type of *V. cultripes* could not be found at the ZMB or ZMH and is considered lost. Fortunately this is a very distinctive species adequately characterised by Vosseler's (1901) figures and description. The type locality is the Atlantic Ocean, southern equatorial current, 0-400 m (J. N. 213), 5.3°S 37.6°W.

Material examined

Tasman Sea: 1 lot (AM), 1 specimen. **North Atlantic:** 4 lots (BMNH), 6 lots (USNM), 7 lots (ZMB), 13 lots (ZMUC), numerous specimens. **South Atlantic:** 2 lots (BMNH), 3 specimens. **North Pacific:** 12 lots (LACM), 5 lots (USNM), 44 specimens. **Indian:** 10 lots (ZMB), several specimens. **Mediterranean:** 38 lots (ZMUC), numerous specimens. **Philippines:** 2 lots (USNM), 2 specimens.

Diagnosis

Body length up to 19 mm, but usually 12-15 mm. Antennae 1 as long as head and first pereonite; flagellum oval, distal margin rounded. Gnathopod 2; carpal process about 0.7x length of propodus. Pereopods 3-6; dactylus length about 0.2x length of propodus. Pereopod 7; basis rectangular, width about 0.7x length, slightly longer than ischium to carpus combined, with slight posterodistal lobe barely overlapping ischium; carpus and propodus with distinct, rounded anterodistal process; dactylus pointed with knife-like anterior margin. Lateral corners of last urosomite produced, partly overlapping peduncle of U3. Uropod 3; peduncle about as long as endopod; endopod slightly longer than exopod in females, in males the endopod is up to one-third longer than the exopod, having almost parallel margins and two widely spaced teeth on the terminal margin. Telson rounded, almost circular, about 0.7x as long as, but only extending to middle, of peduncle of U3.

Remarks

This is one of the larger species of *Vibilia* only exceeded in size by *V. robusta*. It most closely resembles *V. longicarpus*, but is distinguished from it by the relatively shorter carpal process of gnathopod 2, the distinctive anterodistal process of the carpus and propodus of pereopod 7, and by presence of two terminal teeth on the endopod of uropod 3 (absent in *V. longicarpus*); particularly evident in males.

The salp associate has not been recorded for this species.

Distribution

This is a relatively uncommon species widely distributed in tropical and temperate regions, particularly in the Atlantic Ocean and Mediterranean Sea.

Vibilia stebbingi Behning & Woltereck

(Figs 23 & 24)

Vibilia stebbingi Behning & Woltereck, 1912: 5-6, figs 1-3. – Behning 1913a: 529, 533. Behning 1913b: 217-218. Stephensen 1918: 40-41, fig. 12. Behning 1925: 482-484, figs 13-22. Behning 1927: 118, 121 (table). Pirlot 1929: 96-97. Barnard 1930: 403-404. Chevreux 1935: 175. Hurley 1960b: 279. Grice & Hart 1962: 300. Kane 1962: 298-299. Hurley 1969: 33, pl. 18 (map-part). Dick 1970: 34 (key), 53. Semenova 1973: 172. Semenova 1976: 138, 139 (table). Thurston 1976: 404-405. Madin & Harbison 1977. 453 (table 2), 454. Shulenberger 1977: 378 (table). Tranter 1977: 647, 648 (table). Brusca 1981a: 18 (key), 39. Vinogradov 1982: 206-208, fig. 103. Vinogradov 1990a: 55, 93 (table). Zeidler 1992a: 96. De Broyer & Jazdzewski 1993: 112. Shih & Chen 1995: 52-53, figs 28-29. Zeidler 1998: 37, 41. Vinogradov 1999a: 1180, fig. 4.89.

Type material

Four syntypes of *V. stebbingi* are in the ZMB (unregistered). Behning and Woltereck (1912) do not specify a holotype. They record six specimens from the mid-Atlantic, from *Valdivia* Stns 48b (0°9'S 8°30'W), 49 (0°20'N 6°45'W), 54 (1°51'N 0°31'E) and 55 (2°37'N 3°38'E). The figured female is from Stn. 54.

Material examined

Types. Four syntypes of *V. stebbingi* from *Valdivia* Stns 48b, 54 and 55: all in spirit, the one from Stn. 54 with head missing.

Other material examined. **Tasman Sea:** 7 lots (SAMA), 11 specimens. **North Atlantic:** 5 lots (BMNH), 13 lots (CMN), 3 lots (USNM), 7 lots (ZMB), 3 lots (ZMUC), 48 specimens. **South Atlantic:** 1 lot (BMNH), 1 specimen. **North Pacific:** 1 lot (LACM), 3 lots (USNM), 10 specimens. **South Pacific:** 2 lots (BMNH), 23 specimens. **Indian:** 1 lot (BMNH), 2 specimens. **Philippines:** 1 lot (USNM), 1 specimen. **Gulf of Eilat:** 1 lot (ZMB), 1 specimen.

Diagnosis

Body length up to 5-6 mm. Antennae 1 length slightly shorter than head and first three pereonites; flagellum with more or less parallel margins, obliquely truncate ventrally for distal third (broader and longer in males). Gnathopod 2; carpal process about half-length of propodus (or marginally more). Pereopods 3 & 4; dactylus about half-length of propodus. Pereopods 5 & 6; dactylus about 0.3x length of propodus. Pereopod 7; basis rectangular, width about half length, slightly longer than ischium to carpus combined, with small, sharp anterodistal lobe and narrow, rounded posterodistal lobe overlapping ischium and about half of merus. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami; sexual dimorphism of endopod not evident. Telson triangular, pointed, length about half of peduncle of U3.

Remarks

This is a very small species of *Vibilia*. Its similarity to *V. antarctica* and *V. propinqua* has already been discussed under those species. It is also similar to *V. viatrix*, but in that species the carpal process of gnathopod is as long as the propodus, pereopods 3 and 4 have relatively thicker articles and a longer dactylus, and the basis of pereopod 7 is without an anterodistal lobe.

Apart from its small size and short carpal process of gnathopod 2, the most readily distinguishing character for *V. stebbingi* seems to be the shape of the basis of pereopod 7. In no other congener, except perhaps for *V. australis*, is the anterodistal corner as well developed, overlapping the ischium.

Vibilia stebbingi has been recorded as an associate of the salps *Salpa fusiformis, S. maxima* and *Cyclosalpa polae* (Madin & Harbison 1977).

Distribution

This is a relatively uncommon, but widely distributed species in tropical and subtropical waters including the Mediterranean Sea.

Vibilia chuni Behning & Woltereck

(Fig 25)

Vibilia chuni Behning & Woltereck, 1912: 8-9, figs 7-8. – Behning 1913a: 529, 533. Behning 1913b: 222-223. Behning 1925: 496-498, figs 68-78. Behning 1927: 120, 121 (table). Pirlot 1929: 99. Barnard 1930: 405, fig. 53. Barnard 1940: 483-484. Hurley 1960b: 279. Siegfried 1963: 8. Dick 1970: 52. Semenova 1973: 176. Madin & Harbison 1977: 453 (table), 454. Shulenberger 1977: 378 (table). Tranter 1977: 646-647, 648 (table). Brusca 1981a: 17 (key), 39, fig. 4r. Vinogradov *et al.* 1982: 221-222, fig. 109. Vinogradov 1990a: 56, 93(table).

Zeidler 1992a: 95, fig. 7. Shih & Chen 1995: 55-57, figs 30, 31. Vinogradov 1999a: 1179, fig. 4.82.

Vibilia hodgsoni Stewart, 1913: 251-253, pl. 6, figs 1-6. – Barnard 1925: 376.

Type material

The five syntypes of *V. chuni* are in the ZMB (209190). Behning and Woltereck (1912) do not specify a holotype. They record four specimens from the mid-Atlantic, from *Valdivia* Stns 46 (1°27.8'N 10°16.5'W) and 49 (0°20'N 6°45'W). The figured female is from Stn. 46.

Type material of synonyms

The type of *V. hodgsoni* is in the BMNH (1914.2.25.117). It is clearly the same as *V. chuni*. Stewart (1913) had most likely written her paper before the publication of Behning and Woltereck (1912) became available and thus was unaware that her species had already been described.

Material examined

Types. Five syntypes of *V. chuni* from *Valdivia* Stns. 46 and 49: all in spirit; one intact female and three other specimens, one with A1 missing and one with the Us missing, from Stn. 49 and one female, dissected on the left with Us missing, from Stn. 46. Holotype of *V. hodgsoni*, male(?), approximately 6 mm, from near Cape of Good Hope, 36°03'S 12°50'E, *Discovery*, 1st October, 1901: microscope slide of G1 & 2 and P7, remainder in spirit.

Other material examined. **Tasman Sea:** 1 lot (AM), 1 specimen. **North Atlantic:** 1 lot (USNM), 7 lots (ZMB), 8 specimen. **North Pacific:** 2 lots (LACM), 3 lots (USNM), 6 specimens. **South Pacific:** 2 lots (BMNH), 3 specimens.

Diagnosis

Body length up to 7.5 mm. Antennae 1 slightly longer than head and first two pereonites; flagellum oval ventral margin somewhat oblique for distal third. Gnathopod 2; carpal process about half-length of propodus. Pereopods 3 & 4; dactylus about 0.3x length of propodus. Pereopods 5 & 6; dactylus about 0.2x length of propodus. Pereopod 7; basis rectangular, almost twice as long as wide, half as long again as ischium to dactylus combined, with rounded margins and rounded posterodistal lobe overlapping ischium. Lateral corner of last urosomite produced, partly overlapping peduncle of U3. Uropod 3; peduncle distinctly longer than rami; endopod subequal in length to exopod in females, in males the endopod is slightly broader and longer and apically rounded. Telson triangular, rounded terminally, length about half of peduncle of U3.

Remarks

This is one of the most readily recognisable species of *Vibilia*. The combination of characters given in the diagnosis, particularly the shape of antennae 1, the urosome, and pereopod 7, readily distinguish *V. chuni* from all its congeners.

Vibilia chuni has been recorded as an associate of the salps *Cyclosalpa polae* and *Salpa maxima* (Madin & Harbison 1977).

Distribution

This is a relatively rare species known mainly from the tropical waters of the world's oceans.

Vibilia longicarpus Behning

(Figs 26 & 27)

Vibilia longicarpus Behning, 1913a: 530-533, figs 2-6. – Behning 1913b: 222. Semenova 1973. 174-175, fig. 3. Vinogradov *et al.* 1982: 230-232, fig. 114. Shih & Chen 1995: 57-58, fig. 32.

Vibilia pyripes [misidentification – in part]. – Zeidler 1998: 34 (SAMA C4420, 4422, 4423).

Type material

Six syntypes of *V. longicarpus* are in the ZMB (20922). The type locality is the eastern mid-Pacific Ocean. Behning (1913a) does not specify a holotype, or the number of specimens examined. He illustrates a female from *Albatross* Stn. 4709 (10°15'12"S 95°40'48"W), and a male from "Alb. 4.ix.1899", which is presumably near the preceding locality but is not Stn. 4710 judging by the data.

Material examined

Types. Six syntypes of *V. longicarpus* from *Albatross* Stn. 4709 30th December 1904 and Stn. 4710: all in spirit; the female from Stn. 4709 is dissected on the left and has the Us missing. The specimens from Stn. 4710 are juveniles that could not be determined as this species with confidence.

Other material examined. **North Atlantic:** 1 lot (ZMH), 1 specimen. **North Pacific:** 2 lots (USNM), 2 specimens. **Philippines:** 1 lot (USNM), 1 specimen. **Tasman Sea:** 3 lots (SAMA), 3 juv. specimens. **Arabian Sea:** 2 lots (BMNH), 28 specimens.

Diagnosis

Body length up to 12 mm. Antennae 1 as long as head and first pereonite; flagellum elongate, oval, ventral margin the more convex. Gnathopod 2; carpal process as long as, or slightly longer than, propodus. Pereopods 3 & 4; dactylus about 0.3x length of propodus. Pereopods 5 & 6; dactylus about 0.3x length of propodus. Pereopod 7; basis narrowed proximally, maximum width almost equal to length, about as long as ischium to carpus combined, with relatively large rounded posterodistal lobe extending well past the ischium; carpus and propodus with small anterodistal process. Lateral corners of last urosomite produced, partly overlapping peduncle of U3. Uropod 3; peduncle subequal in length to rami; endopod subequal in length to exopod in females, in males the endopod is slightly broader and longer. Telson almost circular, length about 0.7x peduncle of U3.

Remarks

This species most closely resembles *V. cultripes*, but is distinguished by the longer carpal process of gnathopod 2, and the much smaller anterodistal processes on pereopod 7. Also the dactylus of pereopod 7 is rounded and not knife-shaped. In the shape of the urosome it is similar to *V. pyripes*.

There are three specimens from the Tasman Sea (SAMA C4420, 4422, 4423), which had been identified as *V. pyripes* (Zeidler 1998), which are now considered to be this species. They all appear to be juveniles measuring 4 mm or less. In the shape of the first antennae, pereopods 3 and 4, and the telson they resemble *V. longicarpus*, but in the shape of pereopod 7 and the peduncle of uropod 3 they resemble *V. armata* (Fig. 13). The dactylus of pereopods 3-6 is also slightly longer than is usual for *V. longicarpus*, but this is probably a juvenile character.

The salp associate has not been recorded for this species.

Distribution

This is a rare species, found only in the tropical parts of the eastern Pacific Ocean, South China Sea and the northwestern part of the Indian Ocean.

Vibilia caeca Bulycheva

(Fig 28)

Vibilia caeca Bulycheva, 1955: 1050. – Vinogradov 1956: 208-209, fig. 7. Vinogradov *et al.* 1982: 224-226, fig. 111. Vinogradov 1990b: 106, fig. 1. Zeidler 1992a: 93-94, fig. 6.

Type material

The syntypes of *V. caeca* are in the Zoological Institute, St. Petersburg, Russia. The type locality is the northwestern Pacific Ocean, near the Kuril Islands.

Material examined

Tasman Sea: 1 lot (AM), 1 specimen. **North Pacific:** 2 lots **(**SAMA**),** 4 lots (USNM), 12 specimens.

Diagnosis

Body length up to 6 mm. Eyes absent. Pleon distinctly broader than pereon. Antennae 1 inserted mid-laterally on head, as long as head and first three pereonites combined; flagellum elongate, lanceolate, excised on ventral margin for distal half. Antennae 2 very short, consisting of four articles. Gnathopod 2; carpal process almost as long as propodus. Pereopods 3 & 4; dactylus about 0.5x length of propodus. Pereopods 5 & 6; dactylus about 0.4x length of propodus. Pereopod 7; basis rectangular, almost twice as long as wide, as long as ischium to carpus combined, with small, sharp, anterodistal projection and rounded posterodistal lobe overlapping ischium. Lateral corners of last urosomite not produced. Uropod 3; peduncle distinctly longer than rami; sexual dimorphism of endopod not evident. Telson triangular, pointed terminally, about half as long as peduncle of U3.

Remarks

This species most closely resembles *V. australis*, but the absence of eyes is a unique feature amongst species of *Vibilia*.

The salp associate has not been recorded for this species.

Distribution

This species is only known from a few records from the northern Pacific Ocean, the northern Indian Ocean, the southwestern part of the Bering Sea and Kuril Islands (Bussol Strait), and the Tasman Sea. I have also collected it recently from the San Pedro Basin, off Los Angeles, California.

Notes on species of indeterminable status

Vibilia peronii Milne-Edwards

Vibilia peronii Milne-Edwards, 1830: 386-387. – Lamarck 1838: 308. Milne-Edwards 1840: 73, pl. 30, fig. 1. Bate 1862: 303. Bovallius 1887c: 45-47, text fig.. Behning 1913b: 212.

Type material

Type material could not be located at the MNHN or ANSP and is presumed lost. No type locality is given by Milne-Edwards (1830) but Milne-Edwards (1840) gives "Seas of Asia" as the locality for his species.

Remarks

The descriptions of Milne-Edwards (1830, 1840) and figures (1840) are insufficient to characterise this species. The specimen figured by Milne-Edwards (1840) appears to be a male, judging by the length of the second antennae. The posterior lateral corners of the last urosomite are not projected thus, it is not *V. armata, V. pyripes, V. cultripes, V. chuni* or *V. longicarpus*. Of the remainder, it is obviously not *V. australis* or *V. caeca*, and probably not *V. antarctica*, which does not occur in the Asian region. If one can trust the figures of Milne-Edwards (1840) then, apart from other minor characters, it does not seem to be *V. stebbingi* as it is too large (4 lignes = 9.2 mm), or *V. robusta* as uropod 2 is too short, or *V. viatrix* because pereopods 3 and 4 are too long and have a short dactylus, or *V. propinqua* or *V. gibbosa* which have a much shorter carpal process on gnathopod 2. That leaves only *V. jeangerardi* and *V. borealis* neither of which have gnathopod 2 with a carpal process as long as that illustrated by Milne-Edwards and, perhaps apart from *V. borealis*, have not been recorded from 'Asian Seas'. It is therefore impossible to assign Milne-Edwards's species to any known species of *Vibilia*.

Thaumalea depilis Templeton

Thaumalea depilis Templeton, 1836: 186-187, pl. 20. fig. 2. – Lamarck 1838: 308. Bate 1862: 304-305, pl. 49, fig. 10.

Type material

Type material could not be located at the BMNH and is presumed lost. The type locality is given as "off Port Natal, in the summer of 1835, in lat. 37°S and 21° East".

Remarks

The figures and description given by Templeton are insufficient to determine this species. However, the illustration is clearly of a species of *Vibilia*, possibly of a juvenile specimen.

Orattrina pulchella Natale

Orattrina pulchella Natale, 1850b: 11, figs 1, 2.

Type material

Type material could not be located in any major Italian museum (see acknowledgments) and is presumed lost. The type locality is the Mediterranean Sea, Port of Messina, Gulf of Naples.

Remarks

Stebbing (1888: 1624) suspects that this may be *V. jeangerardi*, but the description of Natale is insufficient to verify this, and the figures represent a rather bizarre-looking *Vibilia*.

Elasmocerus speciosus Costa

Elasmocerus speciosus Costa in Hope, 1851: 21.

Type material

Type material could not be located in any major Italian museum (see acknowledgments) and is presumed lost. The type locality is given as the Mediterranean Sea, presumably the Gulf of Naples.

Remarks

This species is merely listed without description or figures and is a nomen nudum. It may have been an earlier name for *Vibilia speciosa* Costa, 1853.

Vibilia speciosa Costa

Vibilia speciosa Costa, 1853: 178. – Bate 1862: 304; Carus 1885: 422.

Type material

Type material could not be located in any major Italian museum (see acknowledgments) and is presumed lost. The type locality is the Mediterranean Sea, coast of Naples.

Remarks

Costa's description is too brief and insufficient to characterise the species. Carus (1885) lists it as a synonym of *V. jeangerardi* as do Vinogradov *et al.* (1982)

Vibilia edwardsi Bate

Vibilia edwardsi Bate, 1861: 2-4, pl. 1, figs 1, 2. – Bate 1862: 300-302, pl. 49, figs 6, 7. Streets 1877: 128. Bovallius 1887c: 62-63, text fig. Behning 1913b: 216-217.

Types material

Type material could not be located at the BMNH or MNHN and is presumed lost. The type locality is given as the South Atlantic Ocean, "Near Iles de Powel" (South Orkney Islands).

Remarks

This is most likely *V. antarctica* as suggested by Barnard (1932) and Vinogradov *et al.* (1982). However, Bate figures and describes pereopods 5 and 6 as being twice as long as pereopods 3 and 4, which is unlike any species of *Vibilia*. Also, the carpal process of gnathopod 2 is too short for typical *V. antarctica*. Thus, *Vibilia edwardsi* is at best, a doubtful synonym of *V. antarctica*.

Vibilia affinis Bate

Vibilia affinis Bate 1862: 302-303, pl. 49, fig. 8. – Bovallius 1887c: 50, text fig. Behning 1913b: 214. Irie 1959: table 4. Vinogradov *et al.* 1982: 235-236, fig. 117.

Type material

Type material could not be located at the BMNH or MNHN and is presumed lost. The type locality is given as "Java".

Remarks

The figures and description given by Bate are insufficient to determine this species. No known species of *Vibilia* have the first antennae as long as those illustrated for this species. Dried specimens sometimes have the edges of the antennae curled inward thus, giving them a more elongate appearance, and perhaps the specimen Bate saw had become dry at some stage thus, giving the appearance of having elongate antennae.

Vinogradov *et al.* (1982) include this species with those in which the lateral corners of the last urosomite are produced, as short third uropods are characteristic of this group. This is based on the statement by Bate, "ultimate pair of pleopoda not reaching beyond the two preceding pairs", presumably an error actually referring to the uropoda. However, all species of *Vibilia* have uropod 3 extending beyond uropod 1 or 2. Bate's observation is most likely erroneous because he probably observed the specimen in a curled state, possibly because it was dry, and could not be straightened. Never the less it would seem that the third uropoda are relatively short.

***Vibilia mediteranne*a** Claus

Vibilia mediterranea Claus, 1872: 467. – Claus 1880: 586.

Type material

Type material could not be located in any major German museum or at the NMW and is presumed lost. The type locality is the Mediterranean Sea.

Remarks

Claus (1872) merely lists this species without any description or figures. Thus, it is a nomen nudum. It is regarded a questionable synonym of V. jeangerardi based solely on geographical grounds.

Vibilia longipes Bovallius

Vibilia longipes Bovallius, 1887a: 8. – Bovallius 1887c: 60-61, pl. 8, figs 26-32. Vosseler 1901: 123. Walker 1909: 50 (list). Behning 1913b: 216. Stewart 1913: 250.

Type material

Type material could not be located at the SMNH or ZMUC and is presumed lost. No precise type locality is given by Bovallius (1887a, c). He merely lists the distribution as "Pacific, South Atlantic".

Remarks

This species is very similar to *V. antarctica* and, but for the shape of antennae 1, would have been included in the synonymy of that species. Bovallius's (1887c) illustration may be inaccurate in this regard, but without being able to examine the type one cannot be certain.

Vibilia bovallii Bonnier

Vibilia bovallii Bonnier, 1896: 612-614, pl. 35, fig. 3. – Behning 1913b: 221. Vinogradov *et al.* 1982: 234-235, fig. 116.

Type material

Type material could not be located at the MNHN and is presumed lost. The type locality is the Bay of Biscay, 44°17'N 4°38'E.

Remarks

According to Bonnier this species differs from all it congeners by gnathopod 2 which has an elongated merus and no carpal process. However, he illustrates gnathopod 2 with eight articles,so that it seems he mistook the carpal process for the merus and then added on another propodus. If this assumption is correct, then the carpal process would be almost as long as the propodus. Vinogradov *et al.* (1982) infer that the lateral corners of the last urosomite are slightly produced, but Bonnier makes no mention of this, nor does he illustrate this character. The shape of antennae 1, the urosome, and the telson, makes this species most similar to *V. viatrix*, if the assumption regarding the carpal process of gnathopod 2 is correct.

Genus ***Vibilioides*** Chevreux, 1905

Vibilioides Chevreux, 1905: 1. – Behning 1913b: 223; Pirlot 1929: 102. Vinogradov *et al.* 1982: 236. Vinogradov 1999a: 1181.

Type species

Vibilioides alberti Chevreux, 1905, by monotypy.

Diagnosis

Pereonites, pleonites and urosomite 1 with lateral transverse folds. Antennae 2 of six articles. Mandibles with molar reduced to conical projection; third article of palp shorter than second. Maxillae 1 with much reduced inner lobe. Maxillae 2 reduced to small, single lobe. Pereopod 7 reduced to basis and three small additional articles; basis more than twice as long as remaining articles combined. Telson extends just beyond middle of peduncle of U3.

Monotypic.

Sexual dimorphism

Insufficient material of this genus is available to determine any sexual dimorphism and none is mentioned in the literature. If any sexual dimorphism exists it is most likely similar to that found in *Vibilia*.

Remarks

The similarity of *Vibilioides* to *Vibilia* has already been discussed under that genus.

Vibilioides alberti Chevreux

(Figs 29 & 30)

Vibilioides alberti Chevreux, 1905: 1-5, figs 1, 2. – Behning 1913a: 533-534. Behning 1913b: 223. Stephensen 1918: 56. Pirlot 1929: 103. Chevreux 1935: 176-178, pl. 15, figs 1, 2. Vinogradov *et al.* 1982: 237-239, fig. 118. Vinogradov 1990a: 57, 93 (table), fig. 10. Vinogradov 1990b: 107, fig. 3 (map).Vinogradov 1993b: 43 (table). Vinogradov 1999a: 1181, fig. 4.91.

Type material

There are five syntypes. Two from *Princesse-Alice* Stn 1851 (36°17'N 28°53'W) are in the MNHN (unregistered) and the remainder, including the figured female, are in the MOM. No precise type locality is designated by Chevreux (1905), but he had specimens from near the Canary Islands (26°16'N 16°11'W) and from near the Azores (37°08'N 28°28'30"W; 36°17'N 28°53'W; 36°46'N 26°41'W).

Material examined

Only two female specimens of this species are available for study. One from *Thor* Stn 74, southern side of the Bay of Biscay (ZMUC CRU 2831) and one from off Rio de Janeiro (ZMUC CRU 2832) (see Stephensen 1918).

Diagnosis

Body length up to 22 mm. Antennae 1 as long as head and first pereonite; flagellum elongate, oval, with anterior margin rounded, almost flat, with dorsal margin projected above peduncular articles. Gnathopod 1; posterior margin of merus, posterior and anterior margin of carpus, and anterior margin of propodus, with fringe of long setae. Gnathopod 2; posterior margin of ischium and merus, and anterior margin of carpus and propodus, with fringe of long setae; carpal process about 0.7x length of propodus. Pereopods 3-6; dactylus about 0.4x length of propodus. Pereopod 7; basis oval, width about 0.6x length. Lateral corners of last urosomite not produced. Uropod 3; peduncle slightly longer than rami; endopod slightly longer than exopod.

Remarks

This is a relatively rare species easily recognised by its general shape and the morphology of pereopod 7. Chevreux (1905) presumed that its rarity was due to its deep-water habitat, because most of the catches were at a depth of 1000 m or more. However, some subsequent records are from near the surface.

It has only been figured twice in the literature, the figures of Chevreux (1935) and Vinogradov *et al.* (1982) being copies of the original (Chevreux 1905). More detailed figures, especially of the mouthparts and pereopods 3-6, are thus provided here (Figs 29 & 30). Fortunately the specimen from off Rio de Janeiro (ZMUC CRU 2832) is very large (21.5 mm) enabling an easy examination of the mouthparts. The maxilliped and mandible are as illustrated by Chevreux (1905) and Vinogradov (1990a), but the first maxillae have a reduced inner lobe similar to that found in *Vibilia*, and the second maxillae, although reduced, are present as small rounded lobes; the inner and outer lobes being completely fused. Accordingly, the generic diagnosis has been amended to include these characters which were previously thought to be absent.

Distribution

This species is only known from a few localities in the Atlantic Ocean (Bay of Biscay, Canary Islands, Azores and near Rio de Janeiro), the Indian Ocean (33°S 45°E) and the Pacific Ocean (22°S 83°W).

Family **CYLLOPODIDAE** Bovallius, 1887

Diagnosis

Body length up to 26 mm, slightly compressed laterally, cuticle relatively thick and smooth. Head moderately large, as long as first 3-4 pereonites, almost globular. Eyes large, occupying most of head surface, adjoining dorsally. Pereonites all separate. Coxae separate from pereonites. Antennae 1 subequal in length to head, or slightly longer in males; peduncle short, 3-articulate; first flagellar article (callynophore) slender, conical, medial surface with two-field brush of aesthestascs, with, or without, two minute terminal articles. Antennae 2 inserted on ventral surface of head, just anterior to buccal mass; composed of 6-7 slender articles; longer than A1 in males, subequal in length to A1 in females. Mandibles with palp in both sexes, second article of palp broader and longer than third; molar process well developed. Maxillae 1 with palp and well developed outer lobe, inner lobe present as small oval process. Maxillae 2 with two small lobes, relatively small. Maxilliped with short, rounded inner lobe, about one-third as long as outer lobes. Gnathopod 1 simple, or weakly chelate. Gnathopod 2 chelate. Pereopods 5 & 6 the longest. Pereopod 7 reduced in size, with enlarged basis, longer than following articles combined; with only 3-5 articles in addition to basis. Uropods with articulated endopods and exopods. Telson very small, triangular. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Cyllopus*.

Remarks

Prior to this review, *Cyllopus* was included in the family Vibiliidae. It is here placed in its own family on the basis of the positioning of the antennae, the presence of an anterior groove on the head to accommodate the mandibular palps, the large eyes, and the laterally compressed body. In body proportions it is most similar to *Themisto* (Hyperiidae). Pereopods 3-6 are also somewhat prehensile, as in *Themisto*, but pereopod 7 bears some similarity to *Vibilia*.

Bovallius (1887a) proposed the family name Cyllopodidae for *Cyllopus* and *Cyllias* (= a genus of Platyscelidae), but this name has not been in use for the last century (except for Spandl 1927 and Pirlot 1929), thus it is resurrected here for *Cyllopus*.

Genus ***Cyllopus*** Dana, 1853

Cyllopus Dana, 1853: 989. – Bate 1862: 305. Gerstaecker 1886: 490. Bovallius 1887b: 555. Stebbing 1888: 1296. Bovallius 1889: 4. Spandl 1927: 174. Barnard 1930: 405-408. Hurley 1955: 129. Hurley 1960a: 111. Vinogradov 1962: 16-17.

Bowman & Gruner 1973: 25. Vinogradov *et al.* 1982: 239. Weigmann-Haass 1983: 2. Vinogradov 1999a: 1177.

Type species

Cyllopus magellanicus Dana, 1853, by monotypy. Type material could not be found at the USNM or in any other major North American museum and is considered lost (see note on major pre-20th century collections). However, *Cyllopus* is a readily recognisable genus.

Diagnosis

The characters of the family are also those of the genus.

Two species.

Sexual dimorphism

As in *Vibilia*, the sexes of *Cyllopus* are very similar morphologically. The most reliable character to differentiate them is the relative length of the second antennae. In males antennae 2 are longer than antennae 1 because of the elongation of articles, while in females the antennae are subequal in length. The shape of the callynophore of antennae 1 also differs slightly, tapering gradually in females but in males with a slight proximal bulge. Generally the head of males is slightly larger, and less rounded, with darker, almost black eyes, and the rami of uropod 2 are narrower and more distinctly denticulate in females, and in males the endopod is distinctly broader than the exopod.

Remarks

Cyllopus is a very distinctive genus somewhat resembling *Themisto*. Two species are currently recognised (Weigmann-Haass 1983), both of which are restricted to the colder waters of the southern Hemisphere.

Virtually nothing is known about the biology of either species. The large eyes indicate an active pelagic life-style, but the rounded dactyls of pereopod 7 are like those of *Vibilia* and, as in *Vibilia*, may be used to transfer larvae to a gelatinous host (Laval 1963, 1980). This view is supported by Weigmann-Haass (1983) who first described the larvae of *Cyllopus* and concluded "due to special morphological similarities ... the larvae of both species display a parasitic way of life like *Vibilia*". To what extent adults are parasitic or commensal is not known.

As the genus has been reviewed by Weigmann-Haass (1983) only essential information and synonymies are provided for each species.

Key to the species of the genus *Cyllopus*

Gnathopod 1 simple. Gnathopod 2; carpal process extends to middle of propodus. Pereopod 7 with oval basis..*C. magellanicus* Dana, 1853

Gnathopod 1 weakly chelate. Gnathopod 2; carpal process extends to limit of propodus. Pereopod 7; basis triangular with concave posterior margin...*C. lucasii* Bate, 1862

Cyllopus magellanicus Dana

(Fig 31)

Cyllopus magellanicus Dana, 1853: 990-991, pl. 68, fig. 1a-g.
Cyllopus danae Bate, 1862: 308, pl. 50, fig. 3.
Vibilia macropis Bovallius, 1887a: 11.
Cyllopus batei Bovallius, 1887a: 11-12.
Cyllopus armatus Bovallius, 1887a: 11-12.
Cyllopus levis Bovallius, 1887a: 12.
Cyllopus hookeri Stebbing, 1888: 1296-1300.
Vibilia serrata Stewart, 1913: 248-250, pl. 4; pl. 5, figs 1-6.

Type material

The type of *C. magellanicus* could not be found at the USNM or in any other major North American museum and is considered lost. Although the description and figures by Dana (1853) are poor, they are sufficient to determine this species. The type locality is Orange Bay, Tierra del Fuego, on *Fucus*.

Type material of synonyms

The type of *C. danae* could not be found at the BMNH or MNHN and is considered lost. However, the description and figures by Bate (1862) readily identify it with *C. magellanicus*.

Type material of *V. macropis, C. batei, C. armatus* and *C. levis* could not be located at the SMNH, ZMUC or in Uppsala and is considered lost. Although Bovallius (1887a) provided only brief descriptions of these species, he provided more information and figures in his monographs (Bovallius 1887c, 1889) enabling one to determine them as synonyms of *C. magellanicus*. Hurley (1955) gave a detailed rational for maintaining *C. macropus* as a separate species, but he only had juvenile specimens (about 5 mm), and the characters he used to distinguish *C. macropus* from *C. magellanicus* are mainly as a result of ontogenetic changes (Weimann-Haass 1983).

The unique type of *C. hookeri* is in the BMNH (89.5.15.184). Although the specimen, on two microscope slides, is in poor condition, it appears to be the same as *C. magellanicus*. Stebbing (1888) relied on the inadequate description, and inaccurate drawings of Dana (1853) to distinguish his species.

Type material of *V. serrata* could not be located at the BMNH and is considered lost. However, it is clearly a synonym of *C. magellanicus*, judging by the description and figures of Stewart (1913), particularly of the gnathopods and pereopod 7.

Material examined

Types. The unique type of *C. hookeri* from the South Atlantic (37°47'S 30°20'W), surface, *Challenger*, 9th March 1876: on 2 microscope slides.

Other material examined. **South Atlantic** (mainly near Sth. Georgia): 25 lots (BMNH), 2 lots (USNM), 5 lots (ZMB), several lots (ZMUC), numerous specimens. **South Pacific** (near Tasman Sea): 9 lots (BMNH), 8 lots (SAMA), 1 lot (USNM), numerous specimens.

Diagnosis

Body length up to 19 mm. Antennae 1 with slender, conical flagellum, with two, very small, terminal articles. Gnathopod 1 simple. Gnathopod 2; carpal process reaching to about middle of propodus. Pereopod 7 with oval basis. Uropod 1; endopod slightly longer than peduncle, sometimes reaching beyond U3.

Distribution

This is a relatively common species restricted to the cool-temperate and polar regions of the southern Hemisphere.

Cyllopus lucasii Bate

(Fig 31)

Cyllopus lucasii Bate, 1862: 306-307, pl. 50, fig. 2.
Cyllopus antarcticus Spandl, 1927: 175-176, fig. 12a-h.

Type material

Type material of *C. lucasii* could not be found at the BMNH or MNHN and is considered lost. Fortunately the description and figures of Bate (1862) are sufficient to define this species. The type locality is "the Powel Islands" (South Orkney Islands).

Type material of synonyms

Type material of *C. antarcticus* is in the ZMB (20773). These specimens are all clearly conspecific with *C. lucasii.*

Material examined

Types. Several syntypes of *C. antarcticus* from a penguin's stomach (*Pigoscelis papua*) caught off South America (65°18'S 80°27'E), Deutschen Südpolar-Expedition, 27th March 1903: in spirit.

Other material examined. **South Atlantic** (Sth. Georgia/Weddell Sea)**:** 13 lots (BMNH), 1 lot (ZMB), 2 lots (ZMH), several specimens. **Antarctic:** 1 lot (BMNH), 1 specimen; **Prydz Bay:** 32 lots (SAMA), numerous specimens.

Diagnosis

Body length up to 26 mm. Antennae 1 with very slender, conical flagellum, without additional terminal articles. Gnathopod 1 weakly chelate, with slightly inflated carpus. Gnathopod 2; carpal process reaching to about limit of propodus. Pereopod 7 with basis narrowed distally, with concave posterior margin. Uropod 1; endopod subequal in length to peduncle, barely reaching limit of U3.

Distribution

This is a circum-Antarctic species restricted to south of the Antarctic convergence.

Family **PARAPHRONIMIDAE** Bovallius, 1887

Diagnosis

Body length up to 30 mm, relatively transparent. Head large, cuboid in shape, as long as first 3-4 pereonites. Eyes large, occupying most of head surface, divided into dorsal and ventral (smaller) parts. Pereonites all separate. Coxae fused with pereonites in males, separate on pereonites 2-5 in females. Antennae 1 slightly shorter than head in males, less than half length of head in females; peduncle short, 3-articulate; flagellum of single, enlarged article (callynophore), medial surface with two-field brush of aesthestascs in males. Antennae 2 inserted on ventral surface of head, just anterior to buccal mass; composed of two small articles in females, four articles in males, with basal and terminal articles greatly elongated, together as long as, or slightly longer than, A1. Mandibles without palp, or molar process, in both sexes. Maxillae 1 with palp and well developed outer lobe; inner lobe absent. Maxillae 2 reduced to single broad lobe. Maxilliped with fused inner and outer lobes, forming single broad plate. Gnathopod 1 weakly double subchelate, with posterodistal process on merus and carpus. Gnathopod 2, simple with dactylus inserted in hollowed process. Pereopods 3-6 subequal in length, about twice as long as gnathopods. Pereopod 7 slightly shorter than P6. Uropods with articulated endopods and exopods. Telson very small, quadrate. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Paraphronima.*

Remarks

This is a very distinctive family that is most similar to the family Cyllopodidae in the morphology and positioning of the antennae. It has a number of unusual characters rarely found in other hyperiidean families. The structure of the eyes resembles the Phronimidae; mandibles lacking a palp in both sexes is a character only shared with the Cystisomatidae, Phronimidae, Dairellidae and Iulopidae **fam. nov.**; mandibles lacking a molar is a character shared with the Lycaeopsidae and the families of Platysceloidea, and a maxilliped with fused inner and outer lobes is a character only found in one other family, the Dairellidae.

The mouthparts are reduced relative to *Vibilia* and *Cyllopus*. Although the mandibles lack a molar, the spine row is well developed with a number of tubercles, and may substitute for the molar. The first maxillae are similar to those found in *Vibilia* and *Cyllopus*, but the second maxillae are reduced to a single, broad plate (Fig. 33). However, Bovallius (1889) illustrated the second maxillae of *Paraphronima crassipes* as consisting of two broad plates. This apparent error may have resulted from the maxillae lying on top of one another during dissection. This error does not seem to have been corrected in the literature.

Genus ***Paraphronima*** Claus, 1879

Paraphronima Claus, 1879a: 6-7. – Bovallius 1885: 9-10. Carus 1885: 424. Gerstaecker 1886: 489. Stebbing 1888: 1335-1337. Bovallius 1889: 23-25. Chevreux & Fage 1925: 389. Pirlot 1929: 104. Hurley 1955: 136. Vinogradov *et al.* 1982: 256. Vinogradov 1999a: 1177.

?*Daira* Milne-Edwards, 1830: 392-393. – Milne-Edwards 1840:83.

Dairinia – (part) Bate 1862: 309.

Type species

Paraphronima gracilis Claus, 1879. Type material could not be found at the ZMB or ZMH and is considered lost. However, *Paraphronima* is a readily recognisable genus.

Diagnosis

The characters of the family are also those of the genus.

Two species.

Sexual dimorphism

Paraphronima is unusual in that coxae 2-5 are separate in females, whereas in males all of the coxae are fused with the pereonites.

As with most hyperiideans, the morphology of the antennae is a useful means to differentiate the sexes. The first antennae are slightly shorter than the head in males and less than half the length of the head in females, and the callynophore of males is slightly inflated, with a two-field brush of aesthestascs on the medial surface. The second antennae of females are reduced to two articles, and are only about half as long as the first antennae, whereas in males they are about as long as the first antennae, with the basal and terminal article greatly elongated. The head of males also seems to be slightly smaller and more rounded than in females.

Remarks

Paraphronima is a very distinctive genus that does not resemble any other hyperiidean. There are six nominal species referable to *Paraphronima*, but only two are recognised in this review.

The large eyes indicate an active pelagic life-style, and in freshly caught plankton samples *Paraphronima* is usually the most active hyperiidean. Both species are often found in surface waters but rarely below 500 m (Vinogradov *et al.* 1982), and seem to undergo diurnal vertical migrations (Brusca 1967a, Thurston 1976). The main reproductive period seems to be at the end of Summer and in Autumn (Brusca 1967b, Vinogradov *et al.* 1982), although females with eggs are found throughout the year (Brusca 1967b). Only one species, *P. crassipes*, has been found in association with siphonophores (Lo Bianco 1909, Harbison *et al.* 1977, Laval 1980).

The two species are very similar morphologically, and many errors in identifications were found in the various collections examined. Often both species are present in the one sample! It is therefore pointless to provide a full reference list for each species, thus only synonymies are given in the following text.

Key to the species of the genus *Paraphronima*

Pleonite 1, ventral margin of epimeral plate forms acute angle with body axis anteriorly. Pereopod 7 much shorter than P6, only reaching limit of carpus of P6 ....*P. gracilis* Claus, 1879.

Pleonite 1, ventral margin of epimeral plate evenly rounded, almost perpendicular to body axis. Pereopod 7 only slightly shorter than P6 ....*P. crassipes* Claus, 1879.

Paraphronima gracilis Claus

(Figs 32 & 33)

Paraphronima gracilis Claus, 1879a: 7(65)-8(66), pl. 1, figs 4 & 5.

Paraphronima edwardsi Bovallius, 1885: 12.

Type material

Type material of *P. gracilis* could not be found at the ZMB or ZMH and is considered lost. However, the description and figures provided by Claus (1879a) are sufficient to characterise this species. The type locality is the "Atlantic Ocean". No specific locality is given by Claus (1879a).

Type material of synonyms

Type material of *P. edwardsi* could not be located at the SMNH, ZMUC or in Upsala and is considered lost. Bovallius (1889) regards it a synonym of *P. gracilis*, which is consistent with his original description.

Material examined

Tasman Sea: 8 lots (SAMA), 8 specimens. **North Atlantic:** 1 lot (BMNH), 2 lots (CMN), 13 lots (USNM), 8 lots (ZMB), several lots (ZMUC), numerous specimens. **South Atlantic:** 3 lots (BMNH), 3 specimens. **North Pacific:** 2 lots (CMN), several lots (LACM), 13 lots (USNM), numerous specimens. **Indian:** 1 lots (BMNH), 1 specimen. **Arabian Sea:** 1 lot (BMNH), 3 specimens. **Philippines:** 3 lots (USNM), 5 specimens.

Diagnosis

Body length up to 17 mm but usually 10 mm. Head slightly shorter than deep. Pereonites 1-2 much narrower than pereonite 3. Pereopods 5-7; anterior margin of ischium to propodus with several small robust setae. Pereopod 7 only as long as basis to carpus of P6. Pleonite 1; ventral margin of epimeral plate forms acute angle with body axis anteriorly.

Remarks

This species closely resembles its only congener, *P. crassipes*, and Hurley (1956) even suggested (but rejected) the idea that *P. crassipes* may be a later moult stage, because it tends to be larger and more robust than *P. gracilis*. However, the characters given in the key and the above diagnosis readily distinguish *P. gracilis*. According to Brusca (1981), the spination of pereopods 5-7 and the shape of pleonite 1 are particularly reliable characters.

This species has not been recorded with a gelatinous plankton associate but because of its similarity to *P. crassipes*, like that species, it is probably associated with siphonophores.

Distribution

This species is widely distributed in tropical and temperate regions, including the eastern part of the Mediterranean Sea. It does not occur beyond the limits of the Subtropical Convergences (Vinogradov *et al.* 1982).

Paraphronima crassipes Claus
(Figs 32 & 33)

Hyperia pedestris Guérin-Méneville, 1836a: pl. 25, fig. 5.
Paraphronima crassipes Claus, 1879a: 7(65)-8(66), pl. 1, figs 6-9; pl. 2, fig. 10.
Paraphronima clypeata Bovallius, 1885: 11, fig. 2.
Paraphronima pectinata Bovallius, 1887a: 13-14.
Paraphronima cuivis Stebbing, 1888: 1337-1342, pl. 157.

Type material

Type material of *P. crassipes* could not be found at the ZMB or ZMH and is considered lost. However, the description and figures provided by Claus (1879a) are sufficient to characterise this species. The type locality is the "Mediterranean". No specific locality is given by Claus (1879a).

Type material of synonyms

The holotype of *Hyperia pedestris* is in the ANSP (CA 2698, Guérin-Méneville Coll. No. 432) (see remarks).

Four syntypes of *P. clypeata* are in the ZMUC (CRU 449-452). Although this material is only in fair condition it is clearly conspecific with *P. crassipes*.

Two syntypes of *P. pectinata* are in the ZMUC (CRU 447 & 448). Both specimens are in good condition and readily identified as *P. crassipes*. Bovallius (1889) considers it a synonym of *P. clypeata*.

Syntype material of *P. cuivis* is in the BMNH (89.5.15.200). These specimens represent both *P. crassipes* and *P. gracilis*. However, the material described and illustrated by Stebbing (1888) represent *P. crassipes*.

Material examined

Types. Holotype of *Hyperia pedestris* from the coast off Chile: dried specimen in vial – almost destroyed. Four syntypes of *P. clypeata* from the North Atlantic; one male (CRU 449, 14 mm) captured 39°10'N 42°10'W, *Andrea*, 1863; one female (CRU 450, 11.2 mm) captured 30°34'N 30°50'W, *Andrea*, 1862; one female (CRU 451, 14 mm) captured 36°06'N 39° 28'W, "Warming", 1866; one female (CRU 452, 10.4 mm) captured 26°N 26°W, "Iversen", 1871: all in spirit. Two syntypes of *P. pectinata* from the North Atlantic; one female (CRU 451, 14 mm) captured 36°06'N 39°28'W, "Warming", 1866; one female (CRU 452, 10.4 mm) captured 26°N 26°W, "Iversen", 1871: in spirit, the latter one with mouthparts and A2 missing. Several syntypes of *P. cuivis* from between Japan and Honolulu, 35°N, surface, *Challenger*, July, 1875: several specimens in spirit and 8 microscope slides.

Other material examined. **Tasman Sea:** 16 lots (SAMA), 19 specimens. **North Atlantic:** 7 lots (BMNH), 7 lots (CMN), 22 lots (USNM), 3 lots (ZMB), several lots (ZMUC), numerous specimens. **South Atlantic:** 11 lots (BMNH), 24 specimens. **North Pacific:** 2 lots (CMN), several lots (LACM), 26 lots (USNM), numerous specimens. **South Pacific:** 1 lot (ZMB), 1 specimen. **Indian:** 1 lot (BMNH), 4 specimens. **Mediterranean:** 1 lot (BMNH), 2 specimens. **Arabian Sea:** 3 lots (BMNH), 3 specimens. **Philippines:** 3 lots (USNM), 3 specimens.

Diagnosis

Body length up to 31 mm, but usually 20-24 mm. Head slightly longer than deep. Pereonites 1-4 about equal in width. Pereopods 5-7; anterior margin of ischium to propodus with few or no robust setae. Pereopod 7 only slightly shorter than P6. Pleonite 1; ventral margin of epimeral plate evenly rounded, almost perpendicular to body axis anteriorly.

Remarks

The similarity of this species to the previous one has already been discussed under that species.

The recent discovery of the type of *Hyperia pedestris* Guérin-Méneville, 1836, and that it is most likely *P. crassipes* (Zeidler 1997a), posed the problem of whether or not Guérin-Méneville's specific name should be used for the species now known as *P. crassipes*. However, its replacement would create nomenclatural instability (Zeidler 1995b), because *P. crassipes*, as a scientific name, is well established in the scientific literature, and the type of *H. pedestris* is in very poor condition making specific identity uncertain, and it is a name that has not been used since Bovallius (1889). The proposal to conserve the specific name (Zeidler 1995b) was subsequently upheld by the ICZN (1997).

Paraphronima crassipes has been recorded as an associate of the siphonophores *Dyphies* and *Galeolaria* (Lo Bianco 1909) and *Rosacea cymbiformis* (Harbison *et al.* 1977, Laval 1980).

Distribution

This species is widely distributed in tropical and temperate regions including the Mediterranean Sea. In the southern Hemisphere it rarely penetrates up to the Antarctic Convergence (Vinogradov *et al.* 1982).

5.2 Superfamily CYSTISOMATOIDEA new superfamily

Diagnosis

Antennae 1 straight, inserted on anterior surface of head; peduncle of one short article; flagellum composed of slender, lanceolate first article and one or two tiny terminal articles; medial surface of first flagellar article with, or without, dense brush of aesthestascs. Antennae 2 reduced to small glandular spine on ventral surface of head. Pereopods 3-6 always simple. Pereopod 7 simple in male, subchelate, or prehensile in mature females, with distally expanded propodus, and curved dactylus. Developing eggs and young held in special brood sac (invagination) between second gnathopods.

One family: Cystisomatidae.

Remarks

The unusual method of brooding the young and the reduction of the second antennae to a remnant glandular spine in both sexes, are unique characters amongst the Hyperiidea.

Family **CYSTISOMATIDAE** Willemöes-Suhm, 1875

Diagnosis

Body very large, up to 150 mm, cuticle exceptionally transparent, pereonites and pleonites with short spines mid-dorsally and laterally. Head very large, as long as first 5-6 pereonites, rounded dorsally, flattened or slightly concave ventrally, with dentate border; ventral surface, anterior to mouthparts, with large anterior spine followed by glandular spine (A2), and sometimes row of up to 5 oral spines. Eyes comprise two oval areas dorsally and partly laterally. Pereonites 1 & 2 fused. Coxae fused with pereonites. Antennae 1 with small peduncular article and flagellum composed of one long, lanceolate proximal article, and one or two minute distal articles. Antennae 2 reduced to small spine on ventral surface. Mandibles without palp in both sexes, but with well developed molar. Maxillae 1 with palp and well developed outer lobe, inner lobe absent. Maxillae 2 with inner lobe reduced to small tubercle. Maxilliped well developed, with long inner lobe, widening distally with concave distal margin. Gnathopods distinctly chelate, relatively small. Pereopods 3-7 consist of long narrow articles. Pereopod 5 the longest. Pereopod 7 of mature females prehensile, with dactylus closing against concave distal margin of propodus. Uropod 2 absent. Uropods 1 and 3 having endopod fused with peduncle. Telson very small, rounded. Gills on pereonites 4-6. Oostegites on pereonites 2-5, those on pereonites 4 and 5 rudimentary.

One genus: *Cystisoma.*

Remarks

This family comprises some of the largest hyperiidean amphipods known, with females of some species reaching 140 mm and males almost 100 mm. They are rarely collected in good condition because of their fragile nature. No gelatinous hosts have been recorded and their association with gelatinous plankton remains to be confirmed.

Genus ***Cystisoma*** Guérin-Méneville

Cystisoma Guérin-Méneville, 1842: 215. – Dana 1852: 315. Dana 1853: 981 & 1442. Willemöes-Suhm, 1875: 24. Stebbing 1888: 1318. Barnard 1916: 286. Barnard 1932: 268. Pirlot 1938: 364. Pirlot 1939: 33. Bowman & Gruner 1973: 26. Vinogradov *et al.* 1982: 244. Vinogradov 1999a: 1176.

Cystosoma – Bate, 1862: 311. Willemöes-Suhm 1874a: 182. Gerstaecker 1886: 490.

Thaumops Willemöes-Suhm, 1873: 206. – Willemöes-Suhm 1874b: 634.

Thaumatops – Martens, 1873: 189. Bovallius 1886: 3. Bovallius 1887b: 557. Bovallius 1889: 40. Stephensen 1918: 56. Schellenberg 1927: 620. Spandl 1927: 170. Pirlot 1929: 89.

Cysteosoma Bovallius 1886: 3.

Thaumonectes Senna, 1903: 93.

Physosoma Woltereck, 1904: 553.

Type species

Cystisoma neptunus Guérin-Méneville, 1842, by monotypy. Type material could not be found at the MNHN, BMNH or ANSP and is considered lost. This is not an ideal situation since the true identity of *C. neptunus* is uncertain. However, there is no question that *C. neptunus* as described and figured by Guérin-Méneville (1842) belongs to the modern generic concept of *Cystisoma* (see note on major pre-20th century collections).

Synonyms

Cystosoma and *Cysteosoma* are variations in the spelling of *Cystisoma*.

Willemöes-Suhm (1873) proposed the genus *Thaumops* for his new species *T. pellucida*, unaware that this was a synonym of *Cystisoma*. He subsequently (1875) realised his error. Martens (1873) corrected the spelling to *Thaumatops*.

Thaumonectes and *Physosoma* are names given to larval forms.

Diagnosis

The characters of the family are also those of the genus.

Six species.

Sexual dimorphism

There are very few reliable morphological characters to distinguish the sexes of species of *Cystisoma*, and juveniles (<20 mm) are impossible to sex. The reproductive systems have been described by Brusca (1981) and provide the only reliable means to distinguish the sexes. Unfortunately these are sometimes difficult to see in damaged specimens. Briefly, the male reproductive system consists of paired testes, suspended in pereonites 1-3, with paired sperm ducts extending posteriorly to pereonite 7, where they terminate in the gonopores, each elevated in a small papilla. Generally the male gonopores are readily visible in all but juvenile (<20-30 mm) and damaged specimens. The female reproductive system is more complex. Ovaries are located in pereonites 3-4, and the oviducts terminate in gonopores on pereonite 5, which open on the medial side of small brood plates, which are pressed against the body. Mature specimens have a brood sac between the second gnathopods, which is covered by two pairs of brood plates arising posteriorly on pereonites 2 and 3. These brood plates are present as developing buds in immature specimens and provide a reliable character to distinguish females. Females as small as 30 mm can have the first two pairs of brood plates present as small buds. The presence of the gonopore is an additional character but is less obvious, especially in damaged specimens.

In addition to the above, in mature females, pereopod 7 is transformed into a prehensile appendage, with an expanded, gland-filled propodus and short hooked dactylus. Males possess a much narrower propodus without glands, and a longer straighter dactylus. As this character is only seen in mature females it is not very useful for distinguishing the sexes.

Various authors have also suggested other possible sexual differences such as the length of the first antennae; the head shape, the presence of glands in the antennae, pereopods and uropods, and the shape of the basis of pereopod 7. It is possible that the first antennae are relatively longer in smaller specimens but there is no evidence for males having slightly longer antennae than females. Woltereck (1903) and Vinogradov *et al.* (1982) suggest that males may have more wedge-shaped heads, but this could not be verified from the material examined. In fact the type male of the new species described here has a rather rounded head. Adult females of *C. pellucida* have highly developed glands in the distal part of the propodus of pereopods 3-7, and apically on the first antennae and the exopods of the uropods. These glands are not evident in the females of other species and males of *C. pellucida* are unknown, so it is impossible to determine whether or not these glands are present. The only record of males of *C. pellucida* are by Pirlot (1938), Brusca (1967b) and Vinogradov *et al.* (1982), but they do not provide a description or illustrations, and these specimens were not available for examination. The basis of pereopod 7 is relatively broad in the males of two species, *C. latipes* and *C.*

gershwinae **sp. nov**. for which the females are unknown. In all other species the basis of pereopod 7 is relatively slender, like the following articles, and there do not seem to be any sexual differences.

Remarks

Cystisoma is a readily recognisable genus, but distinguishing its species can be a frustrating process as they are surprisingly similar morphologically (Brusca 1981). Characters that might prove useful to distinguish species are as follows.

First antennae: The length of the first antennae seems to vary slightly with age, with juveniles tending to have relatively longer antennae. In adults the length of the first antennae seems to be a useful character. They are equal in length to about half of the head in *C. magna*; 0.5-0.7x the head in *C. longipes*; subequal to the head in *C. fabricii* and *C. pellucida,* much longer than the head, extending to the pleon, in *C. latipes,* and extending almost to pleonite 2 in *C. gershwinae* **sp. nov**. The latter two species are also the only ones to have antennae with a brush of aesthestascs on the inner surface. In all other species only a few scattered aesthestascs, or none at all, were found. The antennae of *C. pellucida* are swollen distally due to the presence of a gland, a distinguishing feature of this species.

Second antennae: The second antennae seem to be represented by small ventral spines posterior to the usually larger, anterior spines, on the ventral surface of the head. Stephensen (1918) who first classified the ventral spines concluded that the glandular spine is "undoubtedly a rudiment of ant. 2, and into which the antennal gland opens out". A number of specimens were examined in which a gland is clearly attached to the glandular spine, confirming that this is probably the remnant of the second antennae. In *C. latipes* and *C. gershwinae* **sp. nov**. the glandular spine is similar in size to, or slightly larger than, the anterior spine. In all other species the anterior spine is clearly the largest ventral spine.

Head shape: When viewed dorsally, the head can be rounded with a convex anterior margin as in *C. longipes* and *C. magna,* or it may be more rectangular in shape, with a relatively straight, or almost concave anterior margin as, in all other species.

Eye shape: When viewed dorsally, the eye facets of *C. latipes* occupy two obliquely oval areas almost touching anteriorly, and widely separated posteriorly. In all other species the eye facets occupy most of the dorsal head surface, consisting of two almost oval areas barely separated along the middle of the head.

Marginal spines on head: The number of marginal spines increase slightly with an increase in size, and vary from eleven in *C. gershwinae* **sp. nov**. to 14-18 in *C. longipes*. There is considerable overlap between species and this is not a useful character.

Ventral spines on head: The ventral spines consist of an anterior spine (usually the largest), followed by a glandular spine (most likely A2), and an arch of oral spines (in most species). The number of oral spines vary from 2-5, but are absent in *C. fabricii* and *C. gershwinae* **sp. nov**. Thus the absence of oral spines could be used to distinguish these two species. It seems that oral spines are always present in the other species, with a likely increase in number with increase in size, although one unidentifiable juvenile, measuring only 17 mm, had 2 and 3 oral spines ('Discovery' specimen, unregistered BMNH).

Mouthparts: The mouthparts are remarkably similar except for the number of mandibular teeth. Most species have only one prominent, medial tooth on the mandible, rarely with a small adjacent one (e.g. *C. fabricii*, SAM A42204). Additional lateral teeth occur in *C. latipes* (one only), and *C. longipes* (1-3), and this character can be used to distinguish these two species.

Female brood plates: The brood plates of mature specimens of all species, except for *C. latipes* and *C. gershwinae* **sp. nov**., species for which the female is unknown, were examined and no differences were found. Because brood plates are not fully developed except for mature specimens, and are restricted to females, they are not a useful character anyway.

Pereopod length: There is very little variation in the relative lengths of the pereopods across the whole range of species regardless of sex or size.

Pereopod articles: Only minor variations were found in the relative lengths of pereopod articles. In *C. fabricii* and *C. pellucida* the propodus of pereopod 5 is clearly longer than the carpus; in all other species the propodus is subequal in length to the carpus. In *C. gershwinae* **sp. nov**. the carpus and propodus of pereopod 5 are subequal in length to the basis; in all other species the basis is clearly the longest article. In *C. pellucida* the propodus of pereopod 6 is slightly longer than the carpus; in all other species the carpus and propodus are subequal in length.

Pereopod 7 of females: In mature females this pereopod is modified, presumably for the transfer of eggs from the oviduct to the brood chamber. The propodus is swollen distally, forming a concave distal margin, and the dactylus is curved, presumably to hold the egg against the concave surface of the propodus. Although limited to females, Vinogradov *et al.* (1982) suggested that this might be a useful character, but the morphology of pereopod 7 changes considerably as females mature, and appear to be similar at the same stage in all species examined thus, making it an unreliable character.

Uropods: There is very little variation in the relative lengths of the peduncle and the exopods or endopods. In most species the exopods are slightly longer than the endopods but in *C. pellucida* the exopods are considerably longer and swollen distally because of the presence of a gland, making it a readily recognisable character. In uropod 1 the exopod length relative to the peduncle is about one-third in *C. magna* and one-half in *C. pellucida*, with all other species inbetween (about 0.4x). In uropod 3 the exopod length relative to the peduncle is usually slightly more than half in most species, except for *C. magna* (slightly less than half) and *C. pellucida* (about two-thirds).

Woltereck (1903) made the first summary of known species, followed by Stephensen (1918) who noted mistakes made by previous authors, and added one new species.

Vinogradov *et al.* (1982) provided the first useful summary of the genus, together with a key, recognising five species. The information presented here is the first attempt to provide a taxonomic review of the genus.

There are twelve nominal species referable to *Cystisoma*. Of these, the type material of seven species has been confirmed as lost, but only two species, *C. spinosus* (Fabricius, 1775) and *C. neptunus* Guérin-Méneville, 1842, are insufficiently described, making determination impossible. In addition, two names have been given to larval forms, *Thaumonectes ducis aprutii* Senna, 1903 and *Physosoma* Woltereck, 1904 (see Fig. 34).

Six species are recognised in this review including one described as new. All appear to inhabit relatively shallow waters (200-1000 m) of the world's oceans, tending towards the temperate and tropical regions. Occasionally specimens are caught in surface waters, or are found washed up onshore after storms. Very little is known about their biology.

Because species of *Cystisoma* are very similar morphologically (Brusca 1981), detailed descriptions are not given, except for the species described here as new to science.

Key to the species of the genus *Cystisoma*

1. Ventral spines; only anterior and glandular spine present, oral spines absent.......... 2
   Ventral spines; in addition to anterior and glandular spine, 2-5 oral spines present in arched row 3

2. Antennae 1 about as long as head, without dense brush of aesthestascs. Pereopod 7; basis slender, not inflated proximally......................*C. fabricii* Stebbing, 1888
   Antennae 1 at least as long as head and pereon, with dense brush of aesthestascs. Pereopod 7; basis slightly inflated proximally .... *C. gershwinae* **sp. nov.**

3. Mandibles with one central tooth, lateral teeth absent. Antennae 1 as long as head, or less 4

Mandibles with one central tooth and 1-3 lateral teeth; if lateral teeth absent then A1 much longer than head 5

4. Antennae 1 as long as head. Uropods; exopod length about twice endopod. Uropod 1; exopod length about half peduncle. Adult females with glands distally on antennae, exopods of uropods and on propodus of P3-7 .... *C. pellucida* Willemöes-Suhm, 1873

Antennae 1 length, about half head. Uropods; exopods and endopods subequal in length. Uropod 1; exopod length about one-third peduncle. Adult females without glands as above .... *C. magna* Woltereck, 1903

5. Antennae 1 as long as head and pereon; aesthestascs present in dense brush. Pereopod 7; basis inflated proximally, pear-shaped, about 4x as wide proximally as distally .... *C. latipes* Stephensen, 1918

Antennae 1, shorter than head; aesthestascs absent or rare. Pereopod 7; basis slender, not inflated proximally .... *C. longipes* Bovallius, 1886

Cystisoma pellucida (Willemöes-Suhm)

(Figs 35-37)

Thaumops pellucida Willemöes-Suhm, 1873: 207-208. – Willemöes-Suhm, 1874a: 182. Willemöes-Suhm 1874b: 629-635, pl. 49, 50.

Cystosoma pellucida – Kingsley 1884: 73-74, fig. 99.

Thaumatops pellucida – Bovallius 1886: 8-10. Bovallius 1887a: 14. Woltereck 1903: 452-454, fig. 1. Stephensen 1918: 64-66, figs 19, 24-27. Schellenberg 1927: 622, fig. 31. Spandl 1927: 172-173, fig. 10.

Cystisoma pellucidum – Barnard 1932: 272 (spec. 1 & 6). Pirlot 1938: 364-365. Thorsteinson 1941: 92-93. Hurley 1956: 10. Brusca 1967a: 387. Brusca 1967b: 451. Brusca 1973: 14. Brusca 1981a: 19 (key), 39, fig. 5b. Brusca 1981b: 358.

Cystisoma pellucida – Vinogradov *et al.* 1982: 246-248, fig. 121. Zeidler 1992a: 96, fig. 9. Vinogradov 1999a: 1177, fig. 4.74.

Cystisoma spinosum [misidentification] – Stebbing 1888: 1325-1329, pl. 155 (spec. B).

Thaumatops spinosa [misidentification] – Vosseler 1901: 94. Woltereck 1903: 449-450, 453 (key).

Type material

The unique type, an ovigerous female measuring 84 mm, could not be found in the BMNH and is presumed lost. Fortunately the description and figures given by Willemöes-Suhm (1874b) are clearly of *C. pellucida* as understood by modern taxonomists. As the characteristic features of this species are very distinctive its status is not in doubt, despite the loss of the type. The type locality is off Cape St. Vincent, 35°47'N 8°23'W, in a trawl from 1090 fathoms.

Material examined

North Atlantic: 3 lots (BMNH), 2 lots (ZMUC), 5 specimens. **Tasman Sea:** lot (AM), 1 specimen. **Great Australian Bight:** 1 lot (SAMA), 1 specimen. **Philippines:** 2 lots (USNM), 3 specimens.

Diagnosis (female only)

Body length up to 85 mm. Head about as long as deep; almost as long as first six pereonites combined; oval when viewed laterally, with slightly convex anterior margin when viewed dorsally. Marginal spines, 10-15; anterior ventral spine larger than glandular spine, clearly the largest; oral spines, 3-5 in arched row. Eyes oval, barely separated medially. First antennae subequal in length to head, ending with swollen gland, with one or two tiny terminal articles. Mandibles with only one medial tooth. Pereopod 5 & 6; carpus distinctly shorter than propodus. Urosome (with uropods) slightly longer than pleon. Uropod 1; exopod length twice length endopod, and about half-length of peduncle, slightly swollen terminally with gland. Uropod 3 similar to U1, but exopod length about 0.6x length of peduncle.

Male unknown (see remarks)?

Remarks

There has been some confusion regarding the correct citation of this species (e.g. Vinogradov *et al.* 1982). Willemöes-Suhm's description of this species was received by the Royal Society of London on 27th February, 1873. An abbreviated version was published in the Societies' *Proceedings* in 1873 and a more detailed description with figures in the *Transactions* in 1874. Thus, the correct citation for this species is Willemöes-Suhm, 1873.

This is one of the most distinctive species of *Cystisoma,* readily distinguished by the characteristic shape of the first antennae and the exopods of the uropods, because of the presence of a swollen gland. The distal part of the propodus of pereopods 3-7 is also slightly swollen, because of the presence of a gland, but this is not always very obvious, except for pereopod 7 of mature females, in which the propodus becomes considerably swollen terminally, a feature also found in all other species of *Cystisoma*.

Males of this species could not be determined in any of the collections examined. Willemöes-Suhm (1874b), Pirlot (1938) and Brusca (1967b) refer to males of *C. pellucida* but do not provide any information as to how they differ from females, if at all! These authors may have mistaken immature females for males, or made an error in identification. However, Vinogradov *et al.* (1982) also refer to males, and provide some information on sexual differences. Unfortunately this material was not available for study.

Distribution

This species is known from widely separated records in tropical and temperate regions. It seems to be relatively common off southern California (Brusca 1981).

Cystisoma longipes (Bovallius)

(Figs 38-40)

Thaumatops longipes Bovallius, 1886: 13-16, figs 15-23. – Bovallius 1887a: 15. Bovallius 1889: 47-52, pl. 3, fig. 1-6 (spec. A, non B). Walker 1909: 50 (list), 52.

Cystisoma longipes – Chevreux 1935: 169. Vinogradov *et al.* 1982: 253-254, fig. 124. Vinogradov 1993b: 42, 43 (table). Vinogradov 1999a: 1176, fig. 4.72.

Thaumatops bovallii Woltereck, 1903: 457. – Stephensen 1918: 59-62, fig. 20. Schellenberg 1927: 621-622, fig. 30.

Cystisoma africanum Barnard, 1916: 287-289. – Dick 1970: 54.

Cystisoma magna [misidentification] – Shoemaker 1945: 233-234.

Type material

The unique type of *C. longipes*, measuring about 40 mm, is in the ZMUC (CRU 2829). It appears to be a young female as the second pereonites have a small bud ventrally, representing the developing brood plates. The type locality is "off the west coast of Australia", 30°S 90°E.

Type material of synonyms

The two female syntypes of *C. bovallii* could not be found at the ZMB or ZMH and are presumed lost. Woltereck's (1903) description is very brief and there are no figures. The species is characterised by having a mandible with one central and one lateral tooth, and antennae slightly shorter than the head; characters which apply only to *C. longipes*. Woltereck (1903) probably failed to appreciate this synonymy because Bovallius (1886) wrongly stated that the first two pereonite segments of his species were not fused.

The unique type of *C. africanum*, a female measuring in excess of 90 mm, is in the BMNH (1933.1.25.902 – previously SAM A239). It is not a moult as suggested by Dick (1970). Despite being in several pieces there is not problem identifying it as *C. longipes*.

Material examined

Types. Holotype female of *Thaumatops longipes*, approximately 40 mm: in spirit, damaged. Holotype female of *C. africanum*, approximately 90 mm, from the Indian Ocean, near South African coast, 33°S, "Buffalo River (East London) N.W. by N. distant 21 miles, 490 fathoms. S.S. "Pieter Faure". 22/4/01": in several pieces in spirit.

Other material examined. **North Atlantic:** 8 lots (USNM), 2 lots (ZMUC), 21 specimens. **South Atlantic:** 2 lots (SAM), 2 lots (USNM), 4 specimens. **South Indian:** 5 lots (SAM), 1lot (SAMA), 6 specimens.

Diagnosis

Body length of females up to 100 mm, of males up to 75 mm. Head almost as long as deep; about as long as first five pereonites combined; oval when viewed laterally, with evenly convex anterior margin when viewed dorsally. Marginal spines, 14-18; anterior ventral spine larger than glandular spine, clearly the largest; oral spines, 2-5 in arched row. Eyes oval, barely separated medially for anterior half, slightly wider apart posteriorly. First antennae as long as 0.7x length of head in immature specimens, but only about half length head, or less, in mature specimens, with two small terminal articles. Mandibles with one medial tooth and at least one lateral tooth, very large specimens with 2-3 lateral teeth. Pereopods 5 & 6 with articles slightly more slender than in other species. Pereopod 5; carpus subequal in length to propodus. Urosome (with uropods) about as long as pleon. Uropod 1; exopod slightly longer than endopod (slightly shorter than endopod in juveniles), about 0.4x length of peduncle. Uropod 3 similar to U1, but exopod length slightly more than half-length of peduncle.

Remarks

This species is similar to *C. magna* in that mature specimens have relatively short first antennae. In all other species the first antennae are as long or much longer than the head. Juvenile specimens often have longer antennae, and amongst the material examined there are two specimens in which the first antennae are slightly longer than the head (SAM A42196, male 26 mm; SAM A42197, female ~35 mm). These two specimens may have been identified with *C. latipes* on the basis of antennal length but, the shape of the head and pereopod articles are characteristic of *C. longipes*.

The shape of the eyes (Fig. 40) also tend to resemble *C. latipes* more than other species because they are slightly more separated medially towards the posterior part of the head (e.g. SAM A42198, female 99 mm).

Cystisoma longipes is the only species in which there is more than one lateral mandibular tooth (in large specimens) (Figs 38, 40). In all other species, except for *C. latipes*, lateral mandibular teeth are absent.

As the name suggests the pereopods seem to be relatively longer than in other species. But this is probably because the articles, particularly of pereopods 5 and 6, are slightly more slender. There are no differences in the relative lengths of pereopods, or pereopod articles, when compared to other species.

The type of *C. africanum* (Fig. 39) differs slightly from typical specimens in that the carpus of pereopod 6 is distinctly shorter than the propodus (as in *C. pellucida*).

Distribution

This species is known from widely separated records, mainly from the tropical or temperate regions of the world's oceans.

Cystisoma fabricii Stebbing
(Figs 41 & 42)

Cystisoma fabricii Stebbing, 1888: 1333-1334. – Barnard 1932: 272-273. Hurley 1956: 10. Brusca 1967a: 387. Brusca 1967b: 451. Brusca 1973: 9 (table), 13. Lorz & Pearcy 1975: 1444 (table). Brusca 1981a: 19 (key), 39, fig. 5c, e. Brusca 1981b:

358-375, figs 2-15. Vinogradov *et al.* 1982: 251-252, fig. 123. Vinogradov 1990a: 57. Vinogradov 1999a: 1176, fig. 4.71.

Thaumatops fabricii – Woltereck 1903: 457. Stephensen 1918: 63-64, figs 22, 23. Schellenberg 1927: 623, figs 32, 33. Pirlot 1929: 89.

Thaumatops loveni Bovallius, 1886: 10-13, figs 1-14. – Bovallius 1887a: 15. Bovallius 1889: 52-58, pl. 4, figs 1-25. Stephensen 1918: 59.

Thaumatops coalita Woltereck, 1903: 458, fig. 4.

Cystisoma coalitum – Siegfried 1963: 6 (list). Dick 1970: 55.

Cystisoma spinosum [misidentification] – Stebbing 1888: 1330-1331, pl. 156 (spec. D).

Type material

The unique type, a female measuring about 65 mm, is in the BMNH (1889.5.15.199). Stebbing (1888) originally described this species, referring to it as "*Cystisoma*. Specimen G", and proposed the name *C. fabricii* "should it be thought necessary to make this a separate species". Although Stebbing gives no illustrations, the absence of oral spines readily distinguished it from all its congeners, and thus it has been recognised as a valid species by subsequent authors. The type locality is "off the Meangis Islands, north of Papua", due south of Mindanao, the Philippines, 4°33'N 127°6'E; depth, 500 fathoms, trawled. (*Challenger* Stn. 214).

Type material of synonyms

The unique type of *C. lovenii*, a female measuring about 105 mm, appears lost. Stephensen (1918: 59) made a search for it in the ZMUC and all likely museums in Sweden without success. A recent search of the ZMUC and SMNH collections was also unsuccessful. The specimen figured by Bovallius (1886) is obviously a female, as the brood plates are clearly illustrated and the morphology of pereopod 7 is that of a mature female. As suggested by Stephensen (1918), Bovallius is wrong regarding pereonites 1 and 2 separate, as he had made this error with *C. longipes*. The mandible figured by Bovallius (1886, fig. 3) is most likely the second maxilliped, or part of the lower lip. He correctly illustrates the mandible later in his monograph (Bovallius 1889, pl. 4, fig. 4). It appears to have only one spine medially, although this is not clearly evident from his illustration. Regarding the presence of oral spines, Bovallius says "on the underside of the head there is no shorter row of spines as in *Th. neptunus* and *Th. pellucida*". This character, combined with the single mandibular spine, and the relatively short first antennae, confirms that *C. lovenii* is the same as *C. fabricii.* Although Bovallius' species has priority, it has not been mentioned in the literature since Stephensen (1918), and the type is lost. *Cystisoma fabricii* however, is a well-established, readily recognisable species. Consistent with nomenclatural stability Stebbing's (1888) name should continue to be used for this species (ICZN, article 79c amended).

The types of *C. coalita*, a female less than 40 mm long and four males measuring 26, 27, 32 and 40 mm, could not be found at the ZMB or ZMH and are presumed lost. The ventral spines consist of only one large anterior spine and the glandular spine. Oral spines are absent, and the first antennae are subequal in length to the head. The latter two characters apply only to *C. fabricii.* The fusion of pereonites is an unreliable character as the sutures are often difficult to see in all but adult specimens. Also, juveniles tend to have more anterior pereonites fused. Amongst the material examined was a larva (13 mm) with pereonites 1-5 fused, and juveniles of *C. fabricii* (25-30 mm) with pereonites 1-3 fused. Thus, *Cystisoma coalita* should be considered a synonym of *C. fabricii.*

Material examined

Types. Holotype female of *C. fabricii*, approximately 65 mm: in spirit, damaged.

Other material examined. **North Atlantic:** 5 lots (BMNH), 1 lot (ZMUC), 9 specimens. **South Atlantic:** 2 lots (BMNH), 2 lots (SAM), 4 specimens. **South Indian:** 1 lot (SAM), 1 specimen. **Philippines:** 1 lot (USNM), 1 specimen. **North Pacific:** 3 lots (CAS), 20 lots (LACM), 5 lots (SAMA), 9 lots (USNM), 46 specimens. **South Pacific:** 1 lot (BMNH), 7 lots (USNM), 9 specimens.

Diagnosis

Body length of females up to 90 mm; of males up to 50 mm. Head as long as deep; almost as long as first six pereonites combined; oval when viewed laterally, with evenly convex anterior margin when viewed dorsally. Marginal spines 10-14; anterior ventral spine larger than glandular spine, clearly the largest; oral spines absent. Eyes oval, barely separated medially. First antennae subequal in length to head, with one small terminal article. Mandibles with only one medial tooth. Pereopod 5; carpus distinctly shorter than propodus. Urosome (with uropods) slightly shorter than pleon. Uropod 1; exopod subequal in length to endopod, about 0.3-0.4x length of peduncle. Uropod 3 similar to U1, exopod length 0.4-0.5x peduncle.

Remarks

This species is readily distinguished by the lack of oral spines, a character shared only with *C. gershwinae* **sp. nov.**, but in that species the first antennae are considerably longer than the head. The anterior spine of *C. fabricii* is much larger than the glandular spine (A2), and usually relatively larger than found in other species.

In all of the material examined the carpus of pereopod 5 is distinctly shorter than the propodus, a character only shared with *C. pellucida*. In all other species these articles are subequal in length, or the propodus is slightly shorter than the carpus.

One specimen, a female measuring 66 mm (SAM A42204), has mandibles with a small tooth adjacent to the main medial one. It seems to be an abnormality of the medial tooth rather than an undeveloped lateral tooth. Lateral mandibular teeth are clearly absent in this species.

Cystisoma fabricii is an unusual species in that males seem to reach only half the maximum size of females.

Distribution

This species is found in the tropical and temperate regions of the Atlantic Ocean, the tropical part of the Indian Ocean and mainly in the tropical parts of the Pacific Ocean. It is relatively common off southern California where it is the most common species of *Cystisoma* (Brusca 1981b).

Cystisoma magna (Woltereck)

(Fig. 43)

Thaumatops magna Woltereck, 1903: 454-455, figs 2, 3. – Spandl 1927: 171-172, figs 8, 9a-d.
Cystisoma magna – Vinogradov *et al.* 1982: 248-250, fig. 122; Vinogradov 1990a: 57.
Cystisoma spinosum [misidentification] – Stebbing 1888: 1319-1325, pl. 154 (spec. A), 1331-1332 (spec. E).
Cystisoma pellucidum [misidentification] – Barnard 1932: 272 (spec. 2, 3, 5).

Type material

The two syntypes of *C. magna*, both females measuring about 80 mm (?) and 120 mm (photographed), could not be found at the ZMB or ZMH and are presumed lost. Despite the limited description and figures, the combined characteristic features of relatively short antennae, presence of oral spines (3), and mandibles with only one tooth, readily distinguish this species from all its congeners. The type locality is the tropical Indian Ocean, just west of the Cocos Islands, 10°8'S 97°15'E (*Valdivia* Stn. 182) and near the Seychelles, 4°35'S 53°43'E (*Valdivia* Stn. 235). The later is the locality of the figured specimen.

Material examined

North Atlantic: 4 lots (BMNH), 4 lots (USNM), 8 specimens. **South Atlantic:** 1 lot (BMNH), 1 lot (ZMB), 2 specimens. **South Indian:** 2 lots (SAM), 2 specimens. **North Pacific:** 1 lot (BMNH), 2 lots (CAS), 4 lots (LACM), 9 lots (USNM), 17 specimens.

Diagnosis

Body length of females up to 140 mm, of males up to 90 mm. Head as long as deep; as long as first 5.5 pereonites combined; oval when viewed laterally, with evenly convex anterior margin when viewed dorsally. Marginal spines 12-14; anterior ventral spine larger than glandular spine, clearly the largest; oral spines 2-4. Eyes oval, barely separated medially. First antennae only about half as long as head, with one small terminal article. Mandibles with only one medial tooth. Urosome (with uropods) slightly shorter than pleon. Uropod 1; exopod marginally shorter than endopod, about 0.3x length of peduncle. Uropod 3; exopod subequal in length to endopod, slightly less than half length of peduncle.

Remarks

This is the largest species of *Cystisoma* readily distinguished by the short first antennae, which are relatively shorter than in any other species. One of the *Challenger* specimens (specimen E, BMNH 1889.5.15.196), a juvenile male measuring 42 mm, has first antennae slightly longer than the head but it is identified with *C. magna*. Perhaps juvenile specimens have relatively longer first antennae as in *C. longipes*.

Cystisoma magna also differs from all other species in that the peduncle of uropod 1 is relatively longer, being about three times as long as the exopod.

Shoemaker (1945) recorded 15 specimens from Bermuda but an examination of this material proved that they are all *C. longipes*.

Distribution

This species is known from a few scattered records from the warm waters of the Indian, Atlantic and Pacific Oceans. It is also found off the southeast coast of South Africa.

Cystisoma latipes (Stephensen)

(Figs 44-47)

Thaumatops latipes Stephensen, 1918: 62-63, fig. 21. – Schellenberg 1927: 621, fig. 29.

Cystisoma latipes – Pirlot 1938: 377, 379, 380, 384, 386. Pirlot 1939: 34. Brusca 1973: 9 (table), 14. Brusca 1981a: 19 (key), 39, fig. 5d. Brusca 1981b: 358, fig. 12c. Vinogradov *et al.* 1982: 254-255, fig. 125.

?*Cystisoma parkinsonii* Stebbing, 1888: 1332-1333.

?*Thaumatops parkinsonii* – Stephensen 1918: 66-68, figs 28, 29. Schellenberg 1927: 623, fig. 32.

?*Thaumatops longipes* [misidentification] – Bovallius 1887b: 558. Bovallius 1889: 47-52 (spec. B, non A).

Type material

The unique type of *C. latipes*, a male measuring 44 mm, is in the ZMUC (CRU 2828). The type locality is the North Atlantic Ocean, south of Ireland, 49°22'N 12°52'W (*Thor* Stn. 81), 1350 m.

Type material of synonyms

The unique type of *C. parkinsonii*, a male measuring about 50 mm, is in the BM(NH) (1889.5.15.198). Stebbing (1888) originally described this species, referring to it as "*Cystisoma*. Specimen F", and proposed the name *C. parkinsonii* "if, in view of the great length of the upper antennae, it be necessary to separate this specimen from the others". The specimen is very similar to *C. latipes*, differing in having slightly shorter first antennae, mandibles with only a medial tooth, and the basis of pereopod 7 slightly narrower but still relatively inflated proximally. Despite these differences, it appears to be the same as *C. latipes*, as the length of the first antennae could not be determined accurately, because the specimen is in pieces. Amongst the material examined there are other specimens of *C. latipes* with mandibles without lateral teeth and the basis of pereopod 7 relatively inflated proximally, compared to other species.

Material examined

Types. Holotype male of *C. latipes*, approx. 44 mm: in spirit. Holotype male of *C. parkinsonii*, approx. 50 mm, specimen "F", *Challenger* Stn. 196, north of Amboina, 0°48'30"S 126°58'30"E, trawled 825 fathoms, 13th October, 1874: 3 microscope slides of head, mouthparts, Us, A1, G1 & 2 and P3-7 from right; remainder in spirit.

Other material examined. **North Atlantic:** 3 lots (ZMUC), 1 lot (USNM), 4 specimens. **South Atlantic:** 1 lot (SAM), 1 specimen. **South Indian:** 1 lot (SAM), 1 specimen. **North Pacific:** 2 lots (USNM), 2 specimens.

Diagnosis (males only)

Body length up to 50 mm. Head as long as depth posteriorly; as long as first 4.5 pereonites combined; wedge-shaped when viewed laterally, with slightly concave anterior margin when viewed dorsally. Marginal spines 14-15; anterior ventral spine sometimes smaller than glandular spine; oral spines 2-4. Eyes obliquely-oval, barely touching anteriorly, and widely separated posteriorly. First antennae as long as head and pereon combined, with one small terminal article, medial surface with dense brush of aesthestascs, slightly inflated proximally. Mandibles with one medial tooth and one lateral tooth (absent in some specimens). Pereopod 7 with pear-shaped basis, inflated proximally, maximum width about half length, or 4x width, near distal margin. Urosome (with uropods) slightly shorter than pleon. Uropod 1; exopod subequal in length to endopod, about 0.4x length of peduncle. Uropod 3 similar to U1, exopod length slightly more than half length of peduncle.

Female unknown.

Remarks

Unusual characters of this species are the relatively long first antennae with aesthestascs, and the wedge-shaped head. In all other species of *Cystisoma* the head is more oval and, except for *C. gershwinae* **sp. nov.**, the first antennae are without a brush of aesthestascs medially. The eye shape is also unusual, and the eyes occupy less of the lateral part of the head than other species, suggesting that this species may inhabit deeper water than its congeners.

Some specimens examined have all the characters of *C. latipes* except that the mandibles lack lateral teeth (e.g. USNM 39002). In this respect they are similar to the specimen described as *C. parkinsonii* by Stebbing (1888) (Fig. 46). Thus, it would seem that the presence or absence of a lateral mandibular tooth is variable in *C. latipes*. As these specimens are slightly larger than the type this character is not size dependent.

Amongst the material from the ZMUC, which was seen by Stephensen (1918), are three specimens with relatively long first antennae that are tentatively assigned to *C. latipes*.

The first of these (ZMUC CRU 2838), described by Stephensen as *Thaumatops bovalli* (=*C. longipes*), is a male measuring 46 mm from *Thor* Stn. 73. This specimen differs from *C. latipes* in having slightly shorter first antennae without aesthestascs, and pereopod 7 with a narrower basis. The medial surface of the first antennae have a broad white band which may represent developing aesthestascs. It is possible that this is a recently moulted specimen in which the aesthestascs have not yet developed (as found in other species of hyperiideans), and the basis of pereopod 7 has not differentiated.

A second specimen (ZMUC CRU 2833), described by Stephensen (1918) as *Thaumatops parkinsonii*, is a juvenile male measuring 38 mm from *Thor* Stn. 72. It is very similar to the previous specimen but the mandibles lack a lateral tooth.

The third specimen (ZMUC CRU 2834) is Bovallius' (1887b) "type" specimen B of *C. longipes* (Fig. 47), which Stephensen (1918) also refers to *T. parkinsonii*. This specimen, measuring 46 mm, seems to be a juvenile female with developing brood plates. Both Stephensen (1918) and Bovallius (1889) refer to it as a male, probably because pereonite 7 appears to have a pair of gonopores. However, the presence or absence of testes could not be determined as the specimen is in poor condition. It differs from *C. latipes* in that the mandibles lack lateral teeth and pereopod 7 has a narrow basis. In many respects it is similar to the type of *C. parkinsonii*, particularly in the generally more slender uropods and in the relatively longer exopods which are clearly longer than the endopods. This may be a female character of this species. If this specimen is *C. latipes* then it is the only confirmed female specimen of the species. The type of *C. parkinsonii* was re-examined but the sex could not be confirmed from the remains.

Distribution

This species has been recorded from the North Atlantic Ocean (ZMUC specimens, including the type), the South Atlantic Ocean, off South Africa, the southwest Indian Ocean off South Africa, the North Pacific Ocean near Amboina (type of *C. parkinsonii*), the Gulf of Mexico and off southern California (USNM specimens).

Cystisoma gershwinae sp. nov.

(Figs 48 & 49)

Material examined

Types. Holotype. Male, 43 mm (USNM Acc. No. 187538). Off Queen Charlotte Islands, British Columbia, Canada 51°57'N 131°05'W, 0-360 m, Halibut Commission, University of Washington, M.H. Pettibone: in spirit.

Paratypes. **1**. Male, approx. 53 mm (urosome missing) (USNM Acc. No. 233989). Baja California, Mexico, 39°00'N 121°00'W to 29°39'N 121°00'W, mid-water trawl 11409 fathoms, R. Wisner & Parby, 27 April 1951: in spirit. **2**. Male, approx. 53 mm (SAMA C5906), San Clemente Basin, California, 500-1000m, IKMT, A. Collins, December, 1997: in spirit.

Diagnosis (males only)

Body length up to 53 mm. Head as long as depth; as long as first 5 pereonites combined; oval when viewed laterally, with straight anterior margin when viewed dorsally. Marginal spines 11; anterior ventral spine shorter than, or subequal to, glandular spine; oral spines absent. Eyes oval, barely separated medially. First antennae slightly longer than head and pereon combined, with one tiny terminal article, medial surface with dense brush of aesthestascs. Mandibles with one medial tooth, lateral teeth absent. Pereopod 7 with basis slightly inflated proximally. Urosome (with uropods) about as long as pleon. Uropod 1; exopod slightly shorter than endopod, slightly less than half length of peduncle. Uropod 3 similar to U1, exopod length almost half length of peduncle.

Female unknown.

Description of holotype male

Body length 43 mm. Head as long as deep; as long as first 5 pereonites combined; oval laterally, with relatively straight anterior margin when viewed dorsally. Marginal spines 11, the anterior one the largest. Anterior ventral spine slightly shorter than glandular spine. Oral spines absent. Eyes oval, barely separated medially. First antennae as long as head, pereon and first 1.5 pleonites combined, with tiny terminal article, medial surface with dense brush of aesthestascs. Mandibles with one medial tooth, lateral teeth absent.

Gnathopod 1, relatively small, length slightly more than half G2, about 0.2x P3; distinctly chelate; basis about as long as remaining articles combined. Gnathopod 2, similar to G1, also relatively small, length about 0.4x P3; basis slightly longer than remaining articles combined. Pereopod 3, about half as long as P5; basis to propodus with denticulate posterior margin, denticles on propodus very small; merus, carpus and proximal half of propodus with transverse rows of setae, mainly medially; basis about as long as merus and carpus combined; carpus slightly longer than merus; propodus slightly shorter than carpus but slightly longer than merus. Pereopod 4, as long as 1.5x

P3 and 0.7x P5; ornamentation similar to P3 but merus with less, and propodus with more, rows of setae; basis slightly shorter than merus and carpus combined; carpus length about 1.3x merus, slightly shorter than propodus. Pereopod 5 is the longest pereopod; basis to propodus with denticulate anterior margin, denticles on propodus very small; basis to carpus also with row of denticles posteriorly; basis only slightly longer than carpus; merus length nearly 0.7x basis; propodus slightly longer than basis. Pereopod 6, similar to P5, length about 0.8x P5; basis slightly longer than carpus; merus length nearly 0.6x basis; propodus slightly longer than carpus but shorter than basis. Pereopod 7; length slightly less than half P5; basis to propodus with denticulate anterior margin, denticles on propodus smaller; basis and merus also with row of denticles posteriorly; basis pear-shaped, maximum width proximally almost 3x width near distal margin, 0.4x length; basis as long as merus and carpus combined; merus marginally longer than carpus; carpus with fringe of long setae along distal margin; propodus slightly longer than carpus, with transverse rows of setae medially and along distal margin; distal margin concave with anterior tooth; dactylus curved, closing against distal margin of propodus, slightly longer than width of propodus.

Urosome (with uropods) subequal in length to pleon. Uropod 1; peduncle length about 3x maximum width; exopod slightly shorter than endopod, slightly less than half length of peduncle. Uropod 3; peduncle length about 3x maximum width, about 0.8x length of peduncle of U2; exopod subequal in length to endopod, almost half length of peduncle. Telson very small, U-shaped, about 0.3x as long as third pleonite.

Etymology

Named for Lisa-ann Gershwin, Department of Integrative Biology, University of California, Berkeley, USA, for her continuous support and encouragement in my research of hyperiideans and for being responsible for locating paratype 2 of this unusual species.

Remarks

The paratypes are like the holotype, except for paratype 1, which has the urosome missing, and slightly shorter first antennae (as long as head and pereon combined), and anterior ventral spines slightly larger than the glandular spines.

The distal margin of the propodus of pereopod 7 is similar in shape to that found in juvenile females of other species. However, both the holotype and paratypes are clearly males, as they have distinct testes, and lack the developing brood plates usually found in females of a similar size.

The combination of characters of long first antennae with aesthestascs, the absence of oral spines, mandibles lacking lateral spines, and pereopod 7 with a pear-shaped basis, and subchelate propodus and dactylus, readily distinguish this species from all its congeners. It resembles *C. latipes* in the length of the first antennae, which have aesthestascs, and the shape of the basis of pereopod 7. It differs from *C. latipes* mainly in lacking an arched row of oral spines, a character that is only shared with *C. fabricii*. The shape of the head and eyes is also more like other congeners than *C. latipes*.

Distribution

This species is only known from the types, from off Queen Charlotte Islands, British Columbia, Canada, and San Clemente Basin, California and Baja California, Mexico. This species probably occurs along the entire western coast of northern America and perhaps in other oceans, having been mistaken for *C. latipes*.

Notes on the lost types of nomen dubia

Cystisoma spinosus (Fabricius)

Oniscus spinosus Fabricius, 1775: 298.

The description of this species is based on a drawing by Sydney Parkinson, while on board the *Endeavour*, and it is unlikely that Fabricius actually saw any specimens (Zeidler 1995a).

Although the figures are relatively detailed and accurate, some critical, characteristic features such as the mandibular teeth and ventral spines are not illustrated, thus making it difficult to determine which species is depicted.

The name *O. spinosus* of Fabricius (1775) is listed by Fabricius (1781, 1787 & 1793) and by Gmelin (1789) but the species is not mentioned again in the literature until Stebbing (1888). Stebbing regarded *C. neptunus* (Guérin-Méneville, 1842) and *C. pellucida* (Willemöes-Suhm, 1873) as junior synonyms. He describes a number of specimens under that name of *C. spinosum*, some of which cannot be determined from the literature. These specimens have been examined. Specimen "A", a male, is *C. magna* (Woltereck, 1903); specimen "B" is typical of *C. pellucida*; specimen "C" appears to be a juvenile *C. fabricii*; specimen "CC" is unidentifiable; specimen "D" is a juvenile *C. fabricii*; specimen "E" is a juvenile male *C. magna*; specimen "F" the type of *C. parkinsonii*, is most likely *C. latipes*, and specimen "G" is the type of *C. fabricii*. Subsequent taxonomists have accepted the synonymy of *C. neptunus* and *C. pellucida* with *C. spinosum*, but recent workers have not recognised Fabricius's species, and it has only been recorded four times this century. The records of Vosseler (1901) and Woltereck (1903) most likely refer to *C. pellucida*, and those of Tattersall (1906) and Yoo (1971b) cannot be confirmed from the literature.

Mature, female specimens of *C. pellucida* are relatively easy to distinguish by examining the antennae and the urosome. The antennae end in a diamond-shaped glandular swelling and the exopodites of the uropods are distinctly longer than the endopodites. These characteristic features are clearly not evident in Parkinson's drawings of *Onidium spinosum* (a mature female), and the above synonymy is not justified. Furthermore, Fabricius's species differs from *C. latipes* (Stephensen, 1918) by the head shape, antennal length and width of pereopod articles, and from *C. fabricii* by the antennal length. Also *C. fabricii* has a very large pair of anteroventral spines which would have been noticed by Parkinson, and would most likely have been illustrated if present. So, by process of elimination, we are left with *C. longipes* and *C. magna*. These two species are very similar but are separated on the basis of the mandibular spines, one in *C. magna* and two or three in *C. longipes*. Unfortunately Parkinson does not illustrate the mandibles so it is difficult to determine the species depicted with certainty. However, by comparing measurements made on specimens, it would seem that the length of pereopod 4 relative to pereopod 6 is most similar to *C. longipes*.

Cystisoma neptunus Guérin-Méneville

Cystisoma neptunus Guérin-Méneville, 1842: 215-216, pl. 1, fig. 1.

The type seems to be lost. It is not in the ANSP, which holds most of the Guérin-Méneville collection (Zeidler 1997a), and it is not present in the collections of the MNHN (checked personally by T. Laperousaz), or the BMNH.

In the past it has been considered a questionable synonym of *C. pellucida* (e.g. Vinogradov *et al.* 1982), but the antennae and uropods of *C. pellucida* are quite distinctive, and unlike that illustrated for *C. neptunus* by Guérin-Méneville (1842). The specimen illustrated by Guérin-Méneville appears to be male, as pereopod 7 would have differentiated at 80 mm if the specimen was female. The length of the antennae and pereopods resemble *C. longipes* (Bovallius, 1886), but in the absence of knowledge regarding the teeth on the mandible, this species cannot be determined with certainty.

5.3 Superfamily PHRONIMOIDEA Bowman & Gruner, 1973

Diagnosis

Antennae 1 inserted on anterior surface of head; flagellum of males long and filiform, composed of enlarged first article (callynophore), usually with dense brush of aesthestascs medially, and a series of shorter distal articles; flagellum of females one-articulate. Antennae 2 also inserted on anterior surface of head; reduced to few articles, rudimentary or absent in females; in males flagellum is long, multi-articulate, similar to A1 (rudimentary in male *Phronima sedentaria*). Pereopod 5 sometimes with large subchela. Developing eggs and young held in brood pouch underneath pereon, made up of oostegites on pereonites 2-5.

Seven families: Phronimidae, Phrosinidae, Hyperiidae, Dairellidae, Lestrigonidae **fam. nov.**, Bougisidae **fam. nov.** and Iulopididae **fam. nov.**

Remarks

This superfamily consists of families united by the morphology and positioning of the male antennae. The first antennae have a multi-articulate flagellum (except for *Themisto*) and are inserted on the anterior surface of the head. The second antennae are similar to the first (except for some species of *Phronima*, where A2 is reduced) and are also inserted on the anterior surface of the head.

Prior to the current review, the family Hyperiidae comprised fourteen genera which appeared morphologically similar, and presented considerable taxonomic difficulties. However, except for *Iulopis* and *Bougisia*, they are readily separated into two groups; 1) those with all pereonites separate, with coxae separate from pereonites, with a mandibular palp in both sexes and in which both antennae of females consist of four articles, and 2) those with some anterior pereonites fused (up to the first five), with coxae fused with pereonites, with the mandibular palp absent in females, and in which females have first antennae of two articles (2-3 in *Hyperioides*), and the second antennae are reduced to one article. The latter group comprises the genera *Lestrigonus,* *Phronimopsis, Themistella, Hyperioides, Hyperietta* and *Hyperionyx*. It is proposed that this group be placed in a new family, Lestrigonidae, derived from *Lestrigonus*, the oldest available generic name in the group. The remainder, which includes *Hyperia*, are retained in the family Hyperiidae.

Iulopis and *Bougisia* do not fit into either of the above families. *Iulopis* is similar to the Hyperiidae in having the pereonites and coxae separate, and the first antennae of females of four articles, but differs from both in that a mandibular palp is absent in both sexes, the mandibular molar is reduced to a broad plate with two small tubercles and a row of spines, the maxilliped is without inner lobes, the maxillae are not as well developed, and the second antennae of females are absent, or represented by a small knob on the cuticle. Therefore, it is proposed that *Iulopis* be accommodated in the new family, Iulopididae.

Bougisia shares characters with both the Hyperiidae and Lestrigonidae, **fam. nov.** It is similar to the Hyperiidae in having separate coxae and a mandibular palp in both sexes, and is like the Lestrigonidae in that pereonites 1-2 are fused, and the second antennae of females are one-articulate. However, it differs from both in that it is the only genus with the coxae separate from the pereonites in which pereonites (1-2) are fused. Additional differences are the relatively small eyes, the first antennae of females consist of only three articles, the inner lobe of the maxilliped is rudimentary and pereopod 5 is subchelate. Therefore, it is proposed that *Bougisia* be accommodated in the new family, Bougisidae.

The family Dairellidae is unusual in having a maxilliped with fused inner and out lobes, a character shared only with the Paraphronimidae. Retention of the Dairellidae within the Phronimoidea is thus questionable, but this family is similar to the Phronimidae and Iulopididae **fam. nov.**, in that the mandibles lack a palp in both sexes, and to the Phrosinidae and Phronimidae in that the second antennae are absent in females.

Family **PHRONIMIDAE** Dana, 1852

Diagnosis

Body length 10-40 mm, cuticle transparent. Head subconical, widest dorsally, narrowing and prolonged ventrally, about twice as deep as long. Eyes occupying most of head surface, divided into larger dorsal part and smaller ventrolateral part. Pereonites all separate (*Phronima*), or pereonites 1 & 2 partially fused (*Phronimella*). Coxae fused with pereonites. Antennae 1 reduced to two articles in females; in males composed of 3-articulate peduncle, large callynophore with dense, two-field brush of aesthestascs medially followed by multi-articulate flagellum. Antennae 2 reduced to small tubercle in females; in males reduced to two small articles in *P. sedentaria*, multi-articulate in all other species. Mandibles without palp in both sexes; molar well developed. Maxillae 1 with palp and well developed outer lobe; inner lobe absent. Maxillae 2 bilobed, well developed. Maxilliped with slender outer lobes; inner lobe very reduced in *Phronimella*, about half length (or longer) than outer lobes in *Phronima*. Gnathopods 1 & 2 weakly cheliform, or simple, with complex dactylus. Pereopods 3, 4, 6 & 7 simple; P3 & 4 usually the longest. Pereopod 5 ending in distinct, broad subchela (*Phronima*), or less perfect, slender subchela (*Phronimella*). Uropods slender with articulated endopods and exopods. Uropod 2 smaller than others, rudimentary in female *Phronimella*. Telson very small, rounded. Gills on pereonites 4-6. Oostegites on pereonites 2-5.

Two genera: *Phronima* and *Phronimella*.

Remarks

Shih (1969) has revised this family. Additions and modifications have been made by Laval (1968b, 1970) and Shih (1971a, 1971b, 1991), and additional taxonomic information for the Australian fauna is provided by Zeidler (1978, 1992a, 1998).

Key to the genera of the family PHRONIMIDAE

Pereonites 1 & 2 free. Pereopod 5 with distinct broad subchela. Uropod 2 well-developed .... *Phronima* Latreille, 1802

Pereonites 1 & 2 partially fused. Pereopod 5 with slender subchela. Uropod 2 rudimentary or absent.. *Phronimella* Claus, 1871

Genus ***Phronima*** Latreille, 1802

Phronima Latreille, 1802: 38.
Bivonia Cocco, 1832: 208.

Type species

Cancer sedentarius Forsskål, 1775, by monotypy. The holotype is in the ZMUC (Forsskål collection).

Diagnosis

Body moderately slender. Pereonites all separate. Pereonites 1 & 2 much narrower, and appreciably deeper, than following ones. Maxilliped with well developed inner lobe, length about half, or more, than that of outer lobes. Gnathopods 1 & 2 weakly cheliform. Pereopod 5 with carpus markedly widened distally, forming strong subchela with propodus; anterior margin of basis to carpus smooth. Uropod 2 present in both sexes; endopod sometimes reduced but never absent.

Ten species.

Remarks

Species of *Phronima*, especially immature specimens, can be difficult to identify. Shih (1969) provides basic keys, illustrations and biological information, and Shih (1991) provides the latest key to species. Zeidler (1992a, 1998) provides additional taxonomic information.

The phronimids are unusual amongst the Hyperiidea in that they are often found in transparent barrel-shaped "houses" that they have fashioned from tunicates (salps, doliolids and pyrosomes) and sometimes from siphonophores, or even heteropods (*Firoloida*). Laval (1968b, 1978, 1980) provides more information on Phronima and its association with gelatinous 'barrels'.

Additional biological information on *Phronima* is provided by Minkiewicz (1909a, b), Laval (1968b, 1980), Shih (1969), Repelin (1970, 1972), Laval and Lecher (1995), Land (1981, 1989, 1992), Vinogradov *et al.* (1982), Diebel (1988), Davenport (1994), Land *et al.* (1995) and Zelickman and Por (1996).

In view of all the above information that is available in the literature, only minimal additional information is provided here. The synonymy follows that justified by Shih (1969, 1991) and is not discussed further here.

Species of *Phronima* live in surface waters, and are relatively common in the tropical and subtropical regions of the world's oceans, and rarely cross the Subtropical Convergence. *Phronima sedentaria* is an exception, having a circum-global distribution between 60°N and 60°S, sometimes occurring just south of 60°S (Shih 1971a)

Phronima sedentaria (Forsskål)

Cancer sedentarius Forsskål, 1775: 95-96.
Gammarus sedentarius – Schousboe, 1802: 11, figs 1-6.
Phronima sedentaria - Latreille, 1803: 291.
Phronima custos Risso, 1816: 121, pl. 2, fig. 3.
Phronima borneensis Bate, 1862: 318, pl. 51, fig. 3.
Phronima novaezealandiae Powell, 1875: 294, pl. 21, figs 1 & 2.

Phronima neozelanica Thomson & Chilton, 1886: 150.
Phronima spinosa Bovallius, 1887a: 25.
Phronima tenella Stebbing, 1888: 1354-1356, pl. 161A.
Phronima affinis Vosseler, 1901: 20, pl. 1, figs 12-16.

Type material

The holotype of *Cancer sedentarius* is in the ZMUC (Forsskål coll.): in spirit.

Type material of synonyms

Type material of *P. custos* seems to be lost, although the ANSP has a female specimen embedded in a dried salp (CA 2689) from the Guérin-Méneville collection (No. 443) which may represent type material (see Zeidler 1997a).

Type material of *P. borneensis* could not be found at the BMNH or MNHN and is considered lost.

Type material of *P. novaezealandiae* could not be found in any museum in New Zealand, or at the BMNH and is considered lost.

Type material of *P. spinosa* could not be found at the SMNH, ZMUC or in Uppsala and is considered lost.

The holotype of *P. tenella* is in the BMNH (89.5.15.205): mounted whole on a microscope slide.

Type material of *P. affinis* could not be found at the ZMB or ZMH and is considered lost.

Remarks

This is the only species of *Phronima* in which the second antennae of the males are reduced. Females of this species can be confused with *P. atlantica*, especially when dealing with juveniles, but the pleonites of *P. sedentaria* possess a posterodistal spinose process which is absent in *P. atlantica*. It is also similar to *P. solitaria*, but males of that species have well developed second antennae, and in females the carpus of pereopod 5 has a strong medial tooth adjacent to the anterior tooth.

Phronima atlantica Guérin-Méneville

Phronima atlantica Guérin-Méneville, 1836a: 21, pl. 25, fig. 4.

Type material

Two syntype females of *P. atlantica* are in the ANSP (CA 2687), in the Guérin-Méneville collection (No. 444): once alcohol preserved, now dry.

Remarks

The current citation for the original description of this species is contentious. In the past most authors have cited Guérin-Méneville 1836c (p. 7-9; pl. 18, fig. 1) (e.g. Shih 1969; Spamer & Bogan 1992, 1994; Vinogradov *et al.* 1982), but next to *P. atlantica*, Guérin-Méneville refers to his 1836a publication (pl. 25, fig. 4). The figures in both publications are the same, but the fact that Guérin-Méneville refers to his 1836a publication in reference to *P. atlantica* indicates that this pre-dated his 1836c paper and should therefore become the original citation for this species. That 1836a was probably published well before 1836c is supported by the fact that other species described in his 1836c paper are not listed in 1836a.

Regarding the publication "Iconographie du Règne Animal de G. Cuvier…" (Guérin-Méneville 1836a), Stebbing (1888) says, "This work was published in *livraisons* between 1829 and 1844. The Plates containing Amphipoda probably all belong to the early part of 1836. An advertisement in the "Quarante-cinquième livraison. Crustacés. Pl. 35.," says, "La 46^e et dernière livraison se composera du Texte descriptif de l'Iconographhie et paraîtra fin mars 1838", but the promise was not, it appears, fulfilled till the end of 1843. The specific names, however, being given on the Plates, will carry the date 1836."

The similarity of this species to *P. sedentaria* has already been discussed under that species.

Phronima solitaria Guérin-Méneville

Phronima solitaria Guérin-Méneville, 1844: 21-22.
Phronima custos – Bate 1862: 318, pl. 51, fig. 2.
Phronima megalodus Stebbing, 1888: 1353-1354, pl. 162A.
Phronima atlantica var *solitaria* – Vosseler 1901: 23, pl. 2, fig. 5.

Type material

The holotype female of *P. solitaria* is in the ANSP (CA 2693) in the Guérin-Méneville collection (No. 446): once alcohol preserved, now dry.

Type material of synonyms

The holotype female of *P. megalodus* is in the BMNH (89.5.15.204): on two microscope slides.

Remarks

There is some doubt regarding the correct date for the citation of this species. Past reviewers (Vosseler 1901; Shih 1969, 1971) have cited Guérin-Méneville, 1836a, and, although this is the correct date for the plates, the text was not completed until the end of 1843 (see remarks on *P. atlantica*). *Phronima solitaria* was not figured in any of the plates, and was only described on p. 21 of the text, which was not published until 1844! This should therefore be the date used when citing this species (e.g. Spamer & Bogan 1992, 1994). Incidentally, the reference given by Shih (1969) for the original description of this species refers to *P. atlantica.*

Phronima solitaria was considered a mere variety of *P. atlantica* by Vosseler (1901) but Shih (1969) elevated it again to specific status, a decision which is supported by the examination of the type.

The similarity of this species to *P. sedentaria* has already been discussed under that species.

Phronima pacifica Streets

Phronima pacifica Streets, 1877: 128-130.

Type material

Type material of *P. pacifica* could not be found at the ANSP or USNM and is considered lost.

Remarks

The female of this species is easily distinguished from its congeners by the shape of pereopod 5. Males closely resemble *P. colletti* and in the past have been confused with it (Shih 1969), but the merus of pereopod 5 is distinctly wider than long, and the carpus is more trapezoid in shape.

Phronima bucephala Giles

Phronima bucephala Giles, 1887: 215-217, pl. 3, figs 1 & 2.

Type material

The type of *P. bucephala* could not be found at the BMNH and is considered lost.

Remarks

This species is most similar to *P. colletti* (Laval 1970) and *P. bowmani* (see Shih 1991).

Phronima colletti Bovallius

Phronima colletti Bovallius, 1887: 25.
Phronima diogenes Chun, 1889: 527-531, pl. 3, figs 5 & 6.
Phronima gasti Dudich, 1926: 134-137, figs 1-3.

Type material

Type material of *P. colletti* could not be found at the SMNH, ZMUC, or in Upsala and is considered lost.

Type material of synonyms

Type material of *P. diogenes* and *P. gasti* could not be found at the ZMB or ZMH and is considered lost.

Remarks

This species is most similar to *P. bucephala* (see Laval 1970) and *P. bowmani* (see Shih 1991). Its similarity to *P. pacifica* has already been discussed under that species.

Phronima curvipes Vosseler

Phronima curvipes Vosseler, 1901: 27-29, pl. 3, figs 1-3.

Type material

Type material of *P. curvipes* could not be found at the ZMB or ZMH and is considered lost.

Remarks

Females of this species can resemble *P. solitaria* but are readily distinguished by the characteristic reversed 'S' curvature of the basis of pereopod 5, in lateral view. Males are similar to *P. colletti* and *P. pacifica*, but are distinguished by the details in the shape of pereopod 5, and by the reduced numbers of flagella articles of antennae 2 (7-9 versus 12-13 for *P. colletti* and 15-17 for *P. pacifica*).

Phronima stebbingii Vosseler

Phronima stebbingii Vosseler, 1901: 36-39, pl. 4, figs 4-10.

Type material

Several syntypes of *P. stebbingii* are in the ZMB (17294): in spirit.

Remarks

This species is very similar to *P. dunbari* (see Shih 1991) but is readily distinguished from all other congeners by having pleonite 1 longer than pereonite 7.

Phronima bowmani Shih

Phronima bowmani Shih, 1991: 322, 327-328, figs 1a, 2a-h, 3a, 4a-h.

Type material

The holotype female, allotype male and four paratypes are in the USNM (Cat. No. 250351-53): in spirit.

Remarks

This species is very similar to *P. colletti* and *P. bucephala* (see Shih 1991). It seems to be restricted to the eastern tropical Pacific Ocean.

Phronima dunbari Shih

Phronima dunbari Shih, 1991: 328-332, figs 5a, b, 6a-p.

Type material

The holotype female, allotype male and 18 paratypes are in the USNM (Cat. No. 250354-56): in spirit.

Remarks

This species is very similar to *P. stebbingii* (see Shih 1991). It is found in the eastern tropical Pacific Ocean ranging westward to about 150°W.

Genus *Phronimella* Claus, 1871

Phronimella Claus, 1871: 149.
Anchylonyx Streets, 1877: 130.

Type species

Phronima elongata Claus, 1862. Type material could not be found at the ZMB or ZMH and is considered lost.

Diagnosis

Body and pereopods extremely slender. Pereonites 1 & 2 partly fused dorsally, not much deeper than following ones. Maxilliped with extremely reduced inner lobe, almost obsolete. Gnathopods 1 & 2 simple. Pereopod 5 with elongate carpus, only slightly widened distally, forming slender, imperfect subchela with propodus; anterior margin of basis to carpus dentate. Uropod 2 absent, or rudimentary in female; sometimes rudimentary in males, but usually with exopod and reduced endopod in mature specimens.

Monotypic.

Remarks

Phronimella makes ‘barrels’ from gelatinous plankton just like *Phronima* but the host species is not known (Laval 1980).

Phronimella is relatively common in the tropical regions of the world’s oceans and in the Mediterranean Sea.

Phronimella elongata (Claus)

Phronima elongata Claus, 1862: 193-195, pl. 19, figs 2, 3 & 7.
Anchylonyx hamatus Streets, 1877: 131-132.
Phronimella filiformis Bovallius, 1887a: 26.
Phronimella hippocephala Giles, 1887: 217-219, pl. 3, fig. 3.

Type material

Type material of *P. elongata* could not be found at the ZMB or ZMH and is considered lost.

Type material of synonyms

Type material of *A. hamatus* could not be found at the ANSP or USNM and is considered lost.

Type material of *P. hippocephala* could not be found at the BMNH and is considered lost.

Remarks

Phronimella is morphologically similar to *Phronima*, but the body is generally more slender, and the pereopods are much more slender and elongate. In addition, uropod 2 is reduced to a small pointed process in females and juvenile males. In adult males uropod 2 is usually present in a reduced form, with a relatively well developed exopod, but a small, or obsolete endopod. Occasionally adult males have uropod 2 reduced as in females.

Family **PHROSINIDAE** Dana, 1852

Diagnosis

Body length 10-30 mm, rather compact with relatively thick cuticle, relatively transparent. Head large, globular, height more than length. Eyes large, occupying most of head surface. Pereonites all separate, or pereonites 1 & 2 fused. Coxae separate from pereonites. Antenna 1 reduced to two articles in females; multi-articulate, in males with enlarged callynophore, with aesthetasc brush composed of two asymmetrical fields located ventromedially and ventrolaterally. Antennae 2 rudimentary, or absent in females; multi-articulate in males. Mandibles with palp in males, without palp in females; molar well developed. Maxillae 1 with palp and well developed outer lobe, inner lobe absent. Maxillae 2 bilobed, well developed. Maxilliped with slender outer lobes; inner lobe about half length outer lobes. Gnathopods 1 & 2 simple. Pereopods 3-6 prehensile, or subchelate. Pereopod 5 the longest with large, denticulate subchela. Pereopods 5-7 with broad basis. Pereopod 7 reduced in size, sometimes with reduced number of articles. Uropods composed of single, foliaceous article. Telson small, not longer than half length U3. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

Three genera: *Phrosina, Anchylomera* and *Primno.*

Remarks

Species of this family are very distinctive, and are often present in plankton collections, sometimes in very large numbers. *Phrosina* and *Anchylomera* are monotypic, and Bowman (1978) has revised *Primno*. Thus, only minimal additional information is provided here.

The structure of the uropods, each consisting of a single leaf-like article, is a unique feature amongst the Hyperiidea. They may serve as effective locomotory organs as phrosinids are known to be active swimmers, and sometimes occur in large swarms (Lobel & Randall 1986).

Key to the genera of the Family PHROSINIDAE

1. Pereopods 3 & 4 distinctly subchelate, with large teeth on distal margin of carpus. Pereopod 7 reduced to basis and one tiny additional article...*Phrosina* Risso, 1822

   Pereopods 3 & 4 simple, or if subchelate, with very small teeth, or bristles on distal margin of carpus. Pereopod 7 reduced, with at least 2 articles in addition to basis. 2

2. Pereopods 3 & 4 simple. Pereonites 1 & 2 separate ....*Primno* Guérin-Méneville, 1836

   Pereopods 3 & 4 distinctly subchelate. Pereonites 1 & 2 fused ....*Anchylomera* Milne-Edwards, 1830

Genus ***Phrosina*** Risso, 1822

Phrosina Risso, 1822: 244.
Dactylocera Latreille, 1829: 117.

Type species

Phrosina semilunata Risso, 1822. Type material could not be found in any major European or north American museum and is considered lost.

Diagnosis

Body length up to 30 mm for females; males usually smaller; average size about 8 mm. Head produced into two sharp, triangular, rostral points. Pereonites 1 & 2 fused. Pereopods 3 & 4 subchelate, with large tooth-like carpal process. Pereopod 5 broader than any other pereopod; carpus with anterodistal margin armed with large tooth-like processes, forming folding hand with dactyl-like propodus which is longer than carpus; dactylus absent, or fused with propodus. Pereopod 6 similar to, but much smaller than, P5. Pereopod 7 reduced to broad basis and sometimes one additional, tiny article. Gills without folds.

Monotypic.

Phrosina semilunata Risso

Phrosina semilunata Risso, 1822: 245.
Dactylocera nicaeensis Milne-Edwards, 1830: 393.
Phrosina longispina Bate, 1862: 320-321, pl. 51, fig. 7.
Phrosina pacifica Stebbing, 1888: 1430.
Phrosina australis Stebbing, 1888: 1431.

Type material

Type material of *P. semilunata* is considered lost (see above).

Type material of synonyms

The holotype female of *P. nicaeensis* is in the ANSP (CA 2682), in the Guérin-Méneville collection (number unknown): once alcohol preserved, now dry.

Type material of *P. longispina* could not be found at the BMNH or MNHN and is considered lost.

The two syntypes of *P. pacifica* are in the BMNH (89.5.15.238-239): in spirit.

The holotype of *P. australis* is in the BMNH (89.5.15.240): in spirit.

Remarks

An examination of the types of *P. nicaeensis, P. pacifica* and *P. australis* has confirmed the monotypy of this genus.

Whether or not this species is associated with gelatinous plankton has not been determined.

Distribution

A very common cosmopolitan species, favouring tropical and temperate regions. It often forms local concentrations near the surface but can occur down to 1000 m, rarely deeper (Vinogradov *et al.* 1982).

Genus ***Anchylomera*** Milne-Edwards, 1830

Anchylomera Milne-Edwards, 1830: 394.
Hieraconyx Guérin-Méneville, 1836c: 4-5.
Cheiropristis Natale, 1850a: 8.

Type species

Anchylomera blossevillii Milne-Edwards, 1830. Type material could not be found at the MNHN or ANSP and is considered lost.

Diagnosis

Body length up to 11 mm, but usually 6-8 mm. Head globular. Pereonites 1 & 2 fused. Pereopods 3 & 4 subchelate, with large tooth-like carpal process. Pereopod 5 with very broad articles; carpus with distal margin with short, rounded teeth, forming perfect folding hand with propodus. Pereopod 6 prehensile, with dilated carpus. Pereopod 7 reduced to basis and at least two additional articles, sometimes complete. Gills with folds.

Monotypic.

Anchylomera blossevillii Milne-Edwards

Anchylomera blossevillii Milne-Edwards, 1830: 394.
Anchylomera hunterii Milne-Edwards, 1830: 394.
Hieraconyx abbreviatus Guérin-Méneville, 1836c: 5-6, pl. 17, figs 2, 2a-f.
Cheiropristis messanensis Natale, 1850a: 8-12, pl. 1, fig. 2.
Anchylomera purpurea Dana, 1853: 1001-1004, pl. 68, figs 9a-m.
Anchylomera thyropoda Dana, 1853: 1004-1005, pl. 68, fig. 10.
Anchylomera antipodes Bate, 1862: 322-323, pl. 51, figs 9-10.

Type material

Type material of *A. blossevillei* could not be found at the MNHN or ANSP and is considered lost.

Type material of synonyms

Type material of *A. hunterii* could not be found at the MNHN or ANSP and is considered lost.

Three syntype females of *H. abbreviatus* are in the ANSP (CA2684), in the Guérin-Méneville collection (no. 440): once alcohol preserved, now dry.

Type material of *C. messanensis* could not be located at any major Italian museum (see acknowledgments) and is considered lost.

Type material of *A. purpurea* and *A. thyropoda* could not be located at the USNM and is considered lost.

Type material of *A. antipodes* could not be located at the BMNH or MNHN and is considered lost.

Remarks

This is a very distinctive species that is often found in great numbers and is known to form swarms (Lobel & Randall 1986, Young & Anderson 1987).

Its association with gelatinous plankton has not been confirmed. Risso (1826) recorded it as an associate of pyrosomes and Harbison *et al.* (1977) record it as prey, not as a parasite, for the siphonophore *Forskalia tholoides.*

Distribution

A very common cosmopolitan species favouring tropical and temperate regions.

Genus ***Primno*** Guérin-Méneville, 1836

Primno Guérin-Méneville, 1836c: 2.
Euprimno Bovallius, 1889: 397.

Type species

Primno macropa Guérin-Méneville, 1836 by monotypy. The holotype is in the ANSP (CA2685), in the Guérin-Méneville collection (No. 435): once alcohol preserved, now dry.

Diagnosis

Body length up to 21 mm, but usually about 10 mm. Head, quadrate with small rostrum. Pereonites 1 & 2 separate. Pereopods 3, 4 & 6 simple, with some teeth on margin of carpus and sometimes also merus. Pereopod 5 prehensile, entire anterior margin of carpus dentate, with several long teeth separated by groups of short teeth; propodus shorter than carpus; dactylus appears to be extension of propodus with limited articulation. Pereopod 7 with all articles present, but basis longer than remaining articles combined; dactylus digitiform, with ring of spinules at apex in female. Gills without folds.

Six species.

Remarks

Bowman (1978) revised this genus and recognised four species previously lumped as *P. macropa*. Additional species have been described subsequently by Bowman (1985) and Sheader (1986).

Species of *Primno* are often found in abundance in near-surface waters (e.g. Stephensen 1924, Yoo 1971a, Thurston 1976, Tranter 1977, Young & Anderson 1987, Vinogradov 1991).

Their association with gelatinous hosts remains to be established, and may be limited to juvenile stages. The adults are active swimmers, and larval development is more direct than in other hyperiideans, resulting in the release of active juveniles from the marsupium of females. Bowman (1978) suggests that the modified dactylus of pereopod 7 of females may be used to transfer juveniles from the marsupium to a gelatinous host, as has been observed in *Vibilia* (Laval 1963). The only record of an association with gelatinous plankton is that of Daniel (1973), who found "*Euprimno macropus*" within the posterior nectophores of the siphonophores *Abylopsis tetragona* and *Sulculeolaria chuni*. This record however, may not represent a true association as the position of the hyperiidean does not rule out the possibility of a passive introduction during sampling (Laval 1980).

Bowman (1978) provides a summary of biological information on *Primno* and Yoo (1972a), Ikeda (1995) and Sheader and Batten (1995) provide additional information.

Key to the species of the genus *Primno*

1. Pereopod 5; longer teeth on anterior margin of carpus nearly as long as width of carpus 2

   Pereopod 5; length of longer teeth on anterior margin of carpus about 0.3-0.5 x width of carpus 5

2. Pereopod 5; row of teeth on anterior margin of carpus with short tooth proximally 3

   Pereopod 5; row of teeth on anterior margin of carpus with one of the longer teeth proximally 4

3. Distribution restricted to southern hemisphere; subantarctic province. Rostrum conforming to contour of head, about 0.4x width of head .... *P. macropa* Guérin-Méneville, 1836

   Distribution restricted to North Pacific; subarctic province. Rostrum truncate, limited to space between first antennae .... *P. abyssalis* (Bowman, 1968)

4. Pereopod 7; basis length about 1.2 x length of remaining articles combined.............. ....*P. johnsoni* Bowman, 1978

   Pereopod 7; basis length more than 1.5x length of remaining articles combined ....*P. latreillei* Stebbing, 1888

5. Pereopod 5; length of longer teeth on anterior margin on carpus about 0.3x width of carpus. Pleon subequal in length to pereon..............*P. brevidens* Bowman, 1978

   Pereopod 5; length of longer teeth on anterior margin of carpus about 0.5x width of carpus. Pleon length about 1.4x length of pereon ....*P. evansi* Sheader, 1986

Primno macropa Guérin-Méneville

Primno macropa Guérin-Méneville, 1836c: 4, pl.17, fig. 1a-f.

Primno menevillei Stebbing, 1888: 1447-1448, pl.179B.

Primno antarctica Stebbing, 1888: 1448-1451, pl. 209B.

Type material

The holotype female of *P. macropa* is in the ANSP (CA 2685), in the Guérin-Méneville collection (No.435): once alcohol preserved, now dry (see Zeidler 1997a).

Type material of synonyms

The holotype female of *P. menevillei* is in the BMNH (89.5.15.244): on three microscope slides.

A syntype female of *P. antarctica* is in the BMNH (89.5.15.245): in spirit.

Remarks

This is one of larger species of *Primno*, attaining lengths of up to 15 mm. It is very similar to *P. abyssalis* which, until relatively recently (Bowman 1985), was considered a synonym. Although Bowman (1978) presumed the type of *P. macropa* was lost, his studies of this species are confirmed by the examination of the type, which probably came from the subantarctic waters off Chile. The distribution of this species is restricted to the subantarctic biotic province.

Primno latreillei Stebbing

Primno latreillei Stebbing, 1888: 1445-1447, pl.179A.

Type material

The three syntypes of *P. latreillei* are in the BMNH (89.5.15.243): on four microscope slides.

Remarks

This is one of the smaller species of *Primno*, with adults reaching only 6-10mm in length. It is very similar to *P. johnsoni*, and Vinogradov *et al.* (1982) regard *P. johnsoni* as a junior synonym of *P. latreillei*. Amongst the Australian material examined (Zeidler 1992a, 1998) there was considerable variation in the relative length of the basis of pereopod 7 compared to the remaining articles combined, ranging from slightly longer to about twice as long. This brings the specimens within the morphological range of *P. johnsoni* which is probably synonymous with *P. latreillei*. The morphological variation found in pereopod 7 appears to be ontogenetic.

Primno latreillei seems to have a scattered distribution having been recorded from the Tasman Sea, the North Pacific Ocean (off California), the Red Sea, the eastern Mediterranean Sea and the south-eastern part of the Gulf of Guinea.

Primno abyssalis Bowman

Primno abyssalis Bowman, in Fulton, 1968:104,109.

Type material

The holotype female is in the USNM (Cat. no. 213613), and two female paratypes are in the collections of Scripps Institution of Oceanography: in spirit.

Remarks

This is the largest species of *Primno*, with adults reaching 21 mm in length. Bowman (1985) suggests that this species was derived from *P. macropa*, or its progenitor, which was originally limited to the southern hemisphere, but during the ice age ranged into the North Pacific. When the oceans warmed again the continuity was broken, leaving the North Pacific population isolated. Its distribution is now restricted to the subarctic province of the North Pacific Ocean.

Primno brevidens Bowman

Primno brevidens Bowman, 1978: 8-10, figs 3d-j, 5-8.

Type material

The holotype and paratypes are in the USNM (Cat. no. 170203 & 4): in spirit.

Remarks

This is one of the medium sized species of *Primno* reaching lengths of 9 mm. It is distinguished (together with *P. evansi*) from its congeners by the short teeth in the anterior margin of the carpus of pereopod 5. It is very similar to *P. evansi* but seems to be restricted to the mid-Pacific. Bowman (1978) also records it from the southeastern part of the Gulf of Guinea, but this material may be referable to *P. evansi*, if these two species should be maintained as geographically isolated entities.

Primno johnsoni Bowman

Primno johnsoni Bowman, 1978:15, figs 11-13.

Type material

The holotype and paratypes are in the USNM (Cat. no. 170234-41): in spirit.

Remarks

This is also one of the medium sized species of *Primno*, reaching lengths of 9 mm. Its similarity to *P. latreillei* has already been discussed under that species. Vinogradov *et al*. (1982) regard it a synonym of *P. latreillei*.

Primno evansi Sheader

Primno evansi Sheader, 1986: 977-979, figs 1-3.

Type material

The holotype and paratypes are in the BMNH (1984: 298-302): in spirit.

Remarks

This is the smallest species of *Primno*, with adults of about 6 mm in length. It is very similar to *P. brevidens*, and it is possible that it represents a North Atlantic form of this species. However, until more material becomes available it seems prudent to recognise this North Atlantic form as a separate species.

Family **HYPERIIDAE** Dana, 1852

Diagnosis

Body length 5-30 mm, rarely longer, generally with pigmented cuticle. Head large, spherical, without projections except in *Pegohyperia*. Eyes large, occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antennae 1 composed of four articles in females; multi-articulate in males, sometimes same as in female (e.g. some species of *Themisto*), with enlarged callynophore with two-field brush of aesthestascs medially. Antennae 2 composed of four articles in females, multi-articulate in males. Mandibles with palp in both sexes. Maxillae 1 with palp and well developed outer lobe; inner lobe absent. Maxillae 2 bilobed, well developed. Maxilliped with relatively slender outer lobes; inner lobe well developed, often longer than half-length outer lobes. Gnathopod 1 ranging from barely chelate to distinctly chelate. Gnathopod 2 chelate. Pereopods 3-7 simple. Pereopods 3 & 4 sometimes prehensile. Pereopod 7 subequal in length to, or slightly shorter than, P6. Uropods with articulated endopods and exopods. Telson of moderate size but rarely longer than half of peduncle of U3. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

Six genera: *Hyperia*, *Themisto*, *Hyperiella*, *Hyperoche*, *Pegohyperia* and *Laxohyperia*.

Remarks

Only updated information is provided here as genera of this family have either been reviewed by previous authors (except for *Hyperoche*), or are monotypic.

Key to the genera of the Family HYPERIIDAE

1. Head produced anteriorly into prominent, sharp lobe between A1 & A2 .... *Pegohyperia* Barnard, 1931
   Head rounded, not produced between A1 & A2 2

2. Gnathopods 1 & 2; carpal process laterally compressed, knife-shaped, subequal in length to propodus .... *Hyperoche* Bovallius, 1887
   Gnathopods 1 & 2; carpal process spoon-shaped, or petaloid, length distinctly less than propodus, or if reaching limit of propodus, then G1 simple 3

3. Gnathopod 1 simple. Pereopods 3 & 4 prehensile, propodus closing against dilated carpus .... *Themisto* Guérin, 1825
   Gnathopod 1 subchelate, or chelate (carpal process sometimes short). Pereopods 3 & 4 not prehensile, without especially dilated carpus 4

4. Gnathopods 1 & 2 with similarly shaped, broad, flat, petaloid carpus and propodus .... *Laxohyperia* Vinogradov & Volkov, 1982
   Gnathopods 1 & 2 with spoon-shaped carpus; always more developed in G2 5

5. Pereopods 3 & 4 longer than P5 or P6 .... *Hyperia* Latreille in Desmarest, 1823
   Pereopods 3 & 4 shorter than P5 or P6 .... *Hyperiella* Bovallius, 1887

Genus ***Hyperia*** Latreille, in Desmarest, 1823

Remarks

This genus has been revised by Bowman (1973), who provides a key and very useful illustrations for each species. Bowman recognised eight species, one of which, *H. antarctica* Spandl, 1927, is now regarded a synonym of *H. spinigera* Bovallius, 1889 (Thurston 1977). More recently two additional species have been described; *H. bowmani* Vinogradov, 1976 and *H. curticephala* Vinogradov and Semenova, 1985.

Recently, I established that *Oniscus quadricornis* Fabricius, 1775 is most likely *H. medusarum* (Müller, 1776), and that the description of Fabricius is based solely on drawings by Sydney Parkinson held in the BMNH (Zeidler 1995a). This species was listed only once in the literature (Fabricius 1781) before Fabricius (1787) realised that his species might be the same as *H. medusarum*. This synonymy seems to have been accepted by later naturalists but, probably because *O. quadricornis* was an inadequately described species, it was not recognised as the senior synonym. Stebbing (1888) also accepted the above synonymy but, like his predecessors, did not realise that Fabricius's species was first published in 1775 and thus has priority. Similarly Bovallius (1889) gives a list of synonyms of *H. medusarum* but erroneously cites *O. quadricornis* Fabricius, 1781. Although Fabricius's name has priority his species cannot be determined with certainty and the name has not been in use since 1781 (Fabricius 1781). *Hyperia medusarum*, on the other hand, is a well-established species and the name should be maintained to conserve nomenclatural stability.

Subsequently a syntype of *Hyperia latreillii* Milne-Edwards, 1830 (later corrected to *H. latreillei*) was discovered in the ANSP (CA 2697), in the Guérin-Méneville collection (No. 431) (Zeidler 1997a). The specimen was identified tentatively as *H. galba* (Montagu, 1813), rather than the closely related species *H. medusarum*, with which *H. latreillei* has been synonymised in the past (Bowman 1973). Milne-Edwards (1830) gave the type locality of his species as the Bay of Biscay. But *H. medusarum* is a more northerly species than *H. galba*, being confined to the northern part of the North Sea (Schellenberg 1942), and extending south to about 52°N, off the west coast of Ireland, but with a single record at 48°N, southwest of Ireland (Stephensen 1924). *Hyperia galba*, on the other hand, extends farther south in the Atlantic than *H. medusarum*, reaching at least to the latitude of the coast of Spain (Alvarado 1955). Assuming that the locality data for *H. latreillei*, given by Milne-Edwards (1830), is correct then his species is more likely to be *H. galba*, as is supported by the examination of the syntype. Thus, in the absence of contrary evidence *H. latreillei* should be considered a synonym of *H. galba* rather than *H. medusarum* as has been assumed by Bowman (1973). Sars (1890), Norman (1900), Tattersall (1906) and Chevreux and Fage (1925) also regard *H. latreillei* a synonym of *H. galba*.

The gelatinous plankton associates of *Hyperia* are summarised by Thurston (1977) and Laval (1980). Most are with medusae, and Laval (1980) even suggests that records of associations with other gelatinous plantation such as salps and ctenophores may be erroneous. However, the association of *H. gaudichaudii* Milne-Edwards, 1840 with the ctenophore, *Beroe* sp. has been confirmed recently, and previous records of similar associations should not be dismissed (Zeidler & Gowlett-Holmes 1998).

Apart from Bowman (1973) and Laval (1980), additional biological information is provided for *H. galba* by Bowman *et al.* (1963), Metz (1967) and Dittrich (1987, 1988, 1992), for *H. macrocephala* by White and Bone (1972 – as *H. galba*), and for *H. spinigera* by Thurston (1977).

Bowman (1973) and Vinogradov et al. (1982) provide distributional data for the species.

Species: *Hyperia medusarum* (Müller, 1776); *H. galba* (Montagu, 1813); *H. gaudichaudii* Milne-Edwards, 1840; *H. macrocephala* (Dana, 1853); *H. spinigera* Bovallius, 1889; *H. crassa* Bowman, 1973; *H. leptura* Bowman, 1973; *H. bowmani* Vinogradov, 1976; *H. curticephala* Vinogradov & Semenova, 1985.

Genus *Themisto* Guérin 1825

Remarks

This genus has provided much taxonomic confusion in the past. Its status has been in question being known alternately as *Euthemisto* or *Parathemisto*, sometimes with subgenera. Bowman *et al.* (1982) restored the genus *Themisto*, which up until that time was considered a junior homonym of the nudibranch *Themisto* Oken, 1815; a work rejected for nomenclatural purposes by the ICZN (1956).

The uncertainty of the generic status combined with several ill-defined species, subspecies and varieties has made specific determination very difficult, despite the efforts of Bowman (1960), Sheader and Evans (1974) and Schneppenheim and Weigmann-Haass (1986). Vinogradov *et al.* (1982) recognise six species, but Schneppenheim and Weigmann-Haass (1986) demonstrated that northern hemisphere material, previously identified with *T. gaudichaudii* Guérin, 1825, is a separate species, *T. compressa* Goës, 1865. In view of the past confusion, and recent studies by Schneppenheim and Weigmann-Haass (1986), a new key to species is provided to assist future workers.

The holotype of *T. gaudichaudii* was discovered recently in the Guérin-Méneville collection (No. 438), in the ANSP (Zeidler 1997a). The correct citation for the original description of this species has been confused in the past with some authors citing Guérin, 1828 (eg. Schneppenheim & Weigmann-Haass 1986; Spamer & Bogan 1992, 1994). This has arisen because, although the genus and species was first described in 1825, Guérin (1828) more or less repeated his description in a separate memoir introducing them as new, and providing figures of the type.

All species of *Themisto* are mainly free-swimming, and can occur in large numbers, particularly in colder waters where, like krill, they play a significant role as food for plankton-feeding predators. Although considered mainly free-living, species of *Themisto* are known to be associated with medusae and salps (Madin & Harbison 1977; Laval 1980), and specimens of *T. australis* have been collected from *Salpa fusiformis* from Tasmanian waters. Additional biological and ecological information is given by the following; Bary (1959), Siegfried (1965), Gray (1967), Evans (1968), Semenova (1974), Sheader (1975, 1977, 1981, 1990), Sheader and Evans (1975), Williams and Robins (1981), Bowman *et al.* (1982), Hiroki (1988), Corey (1990), Semura *et al.* (1991), Percy (1993), Colombo and Vinas (1994), Koszteyn *et al.* (1995), Condon and Norman (1999), Vinogradov (1999b).

Themisto has a bi-polar distribution with species restricted to the colder waters of the Arctic and Antarctic regions and occasionally venturing into cool-temperature waters.

Species: as in the following key.

Key to the species of the genus *Themisto*

1. Pereopod 5 not longer than P6 or P7 2
   Pereopod 5 much longer than P6 or P7 5

2. Maxilliped without row of setae on distal margin of basal plate (arctic and subarctic of Atlantic) .... *T. abyssorum* (Boeck, 1871)
   Maxilliped with row of setae on distal margin of basal plate 3

3. Pereopods 5 & 6; dactylus smooth. Antenna 1 of female hooked, stout (colder waters of Australia and New Zealand) .... *T. australis* (Stebbing, 1888)
   Pereopods 5 & 6; dactylus with setae at base. Antennae 1 of female straight, tapering (North Pacific) 4

4. Antennae 2 of females longer than A1. Adult females reach 9-17 mm in length........ ....*T. japonica* Bovallius, 1887
   Antennae 2 of females equal in length to A1. Adult females reach 5-9 mm in length .... *T. pacifica* (Stebbing, 1888)

5. Pereopod 7 usually longer than P6, but shorter than P5. Gnathopod 2; merus with relatively straight distal margin, anterodistal corner produced into small tooth (North Atlantic) .... *T. compressa* Goës, 1865
Pereopod 6 & 7 subequal in length. Gnathopod 2; merus with rounded distal margin 6

6. Pereopods 3 – 7; dactylus with setae on basal part (arctic and subarctic) ....*T. libellula* (Lichtenstein in Mandt, 1822)
Pereopods 3 – 7; dactylus smooth (colder waters of southern oceans)........................ .... *T. gaudichaudii* Guérin, 1825

Genus ***Hyperiella*** Bovallius, 1887

Remarks

This genus has been revised by Bowman (1973) and Weigmann-Haass (1989), and includes three species, with a circumpolar distribution in the Antarctic Ocean. Very little is known about the biology of these species. To what extent adults are parasitic, or commensal, is not known although their morphology suggests a parasitic existence (Laval, 1980). Libertini and Lazzaretto (1993) provide some information on the karyotype morphology of *H. dilatata* Stebbing, 1888.

Species: *Hyperiella antarctica* Bovallius, 1887; *H. dilatata* Stebbing, 1888; *H. macronyx* (Walker, 1906).

Genus ***Hyperoche*** Bovallius, 1887

Remarks

This genus is in need of a thorough taxonomic revision. The most recent review is by Vinogradov *et al.* (1982) who recognised seven species. Weigmann-Haass (1991) also reviewed the taxonomy and geographical distribution of *H. luetkenides* Walker, 1906 and *H. capucinus* Barnard, 1930 in the Antarctic waters of the Atlantic.

The gelatinous plankton associates of *Hyperoche* are summarised by Laval (1980). Most are with ctenophores but *H. medusarum* (Kröyer, 1838) is mostly found with medusae. Additional biological information is provided by Bowman *et al.* (1963), Brusca (1970), Evans and Sheader (1972), Flores and Brusca (1975), Westerhagen (1976), Westerhagen and Rosenthal (1976), Harbison *et al.* (1977) and Cahoon *et al.*(1986).

Vinogradov et al. (1982) and Weigmann-Haass (1991) provide distributional data for the species.

Species (according to Vinogradov *et al.* (1982)): *Hyperoche medusarum* (Kröyer, 1838); *H. martinezi* (Müller, 1864); *H. cryptodactylus* Stebbing, 1888; *H. picta* Bovallius, 1889: *H. luetkenides* (Walker, 1906); *H. mediterranea* Senna, 1908; *H. capucinus* Barnard, 1930.

Genus ***Pegohyperia*** Barnard, 1931

Remarks

This is a very distinctive monotypic genus. Virtually nothing is known regarding its biology. It seems to be a relatively rare species having been recorded from the southeastern Atlantic Ocean (33°07'S 4°30'E) by Barnard (1931, 1932); the Antarctic (65°51'S 54°16'E) by Hurley (1960a); the North Pacific Ocean (28°N 155°W) by Shulenberger (1977), and the equatorial Pacific (13°35'N 101°145'W) by Vinogradov (1990a). Specimens from South Georgia (BMNH) and the North Pacific Ocean (USNM) have also been examined. In addition, the USNM also has several lots collected recently from Antarctic waters.

Species: *Pegohyperia princeps* Barnard, 1931.

Genus ***Laxohyperia*** Vinogradov and Volkov, 1982

Remarks

This monotypic genus is very similar to *Hyperoche* but is readily distinguished by the smaller size and the unique structure of the gnathopods. Virtually nothing is known regarding its biology, but its similarity to *Hyperoche* suggests that it may eventually be found in association with ctenophores. It seems to be a rare species having been recorded only twice in the literature. Vinogradov *et al.* (1982) had three females from the northern part of the South China Sea and Shih and Chen (1995) described a male, also from the South China Sea. There are also specimens from the Tasman Sea (SAMA), the South Atlantic, off Brazil (SAMA), the Gulf of Guinea (USNM), the North Pacific Ocean, off Baja California (USNM) and the Arabian Sea (USNM).

Species: *Laxohyperia vespuliformis* Vinogradov & Volkov, 1982.

Family **LESTRIGONIDAE**, new family

Diagnosis

Body length up to about 7 mm, but usually less than 5 mm. Integument generally pigmented but can be transparent. Head large, spherical to quadrate in shape. Eyes large, occupying most of head surface. Some anterior pereonites fused, usually 1-2 but sometimes up to 1-5; often more pereonites fused in female than male. Coxae fused with pereonites. Antennae 1 composed of two articles in females (2-3 in *Hyperioides*); multi-articulate in males with enlarged callynophore, with two-field brush of aesthestascs medially. Antennae 2 reduced to one article in females; multi-articulate in males. Mandibles with palp in males, without palp in females; molar sometimes reduced. Maxillae 1 with palp and well developed outer lobe (relatively less developed in species with maxilliped with reduced inner lobe); inner lobe absent. Maxillae 2 bilobed. Maxilliped with slender, or ovate outer lobes; inner lobe well developed, about half-length outer lobes, or rudimentary. Gnathopod 1 simple, barely chelate, subchelate, or moderately chelate. Gnathopod 2 chelate. Pereopods 3-7 simple (prehensile in *Phronimopsis*). Pereopod 7 subequal in length to, or slightly shorter than, P6. Uropods with articulated endopods and exopods. Telson rounded, often small, rarely as long as half of peduncle of U3. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

Six genera: *Lestrigonus*, *Phronimopsis*, *Themistella*, *Hyperioides*, *Hyperietta* and *Hyperionyx*.

Remarks

All of the genera of this family have been revised by Bowman (1973), except for *Phronimopsis*, which is considered to be monotypic. Thus only updated information is provided here.

Species of this family are difficult to identify with certainty without some specialist knowledge. The degree of fusion of the pereonites is a critical character used to distinguish species, and while this character is constant in adults, juveniles of some species may have more pereonites fused than adults. Thus, it is necessary to examine characters other than the fusion of pereonites, when dealing with immature specimens (see Zeidler 1998). While Bowman's (1973) keys work relatively well for females and most males, it is still difficult to identify species in which pereonites 1 and 2 are fused dorsally in males (i.e. the genera *Lestrigonus*, *Hyperioides* and *Hyperietta*). Thus, an additional key has been constructed to aid the identification of these species, but it should be used in conjunction with Bowman's (1973) keys and excellent illustrations.

Key to the genera of the family LESTRIGONIDAE

1. Gnathopod 2 chelate, dactylus closing against robust propodus. Pereopods 3-7 prehensile .... *Phronimopsis* Claus, 1879

   Gnathopod 2 chelate, propodus closing against spoon-shaped carpus. Pereopods 3-7 not prehensile 2

2. Pereopod 5 longer than P6 (1.1-1.2x). Pereopods 6 & 7; dactylus with distinct upward bend midway. Pereonites 1-5 fused in both sexes... *Themistella* Bovallius, 1887

   Pereopod 5 not longer than P6. Pereopods 6 & 7 with normal dactylus. Pereonites 1-5 rarely fused 3

3. Pereopod 5 about 0.8x length of P6 .... *Hyperionyx* Bowman, 1973

   Pereopod 5 subequal in length to P6 4

4. Pereopod 7 clearly shorter than P5 or P6; about 0.7x length of P6 ....*Hyperioides* Chevreux, 1900

   Pereopod 7 slightly shorter than P6 but similar in length to P5 5

5. Pereopods 5-7; carpus with at least one, relatively long, robust seta on anterior margin .... *Hyperietta* Bowman, 1973

   Pereopods 5-7; carpus with, or without, setae, these never very long or conspicuous .... *Lestrigonus* Milne-Edwards, 1830

Key to males of LESTRIGONIDAE with pereonites 1 – 2 fused (except *Phronimopsis*)

1. Eyes limited to dorsal surface of head .... *Hyperioides longipes* Chevreux, 1900

   Eyes occupying most of head surface 2

2. Pereopods 5-7; carpus with at least one strong spine on anterior margin................. 3

   Pereopods 5-7; carpus without strong spine 4

3. *Hyperietta parviceps*. *H. stephenseni* and *H. stebbingi* – consult Bowman (1973) to distinguish these species.

4. Pereopods 3 and 4; carpus with at least two conspicuous spines on posterior margin 5

Pereopods 3 and 4; carpus with only one conspicuous spine on posterior margin.. 10

5. Pereopods 5-7; propodus with recurved dentate hook overlapping dactylus .... *Lestrigonus crucipes* (Bovallius, 1889)

Pereopods 5-7; propodus with smooth spine overlapping dactylus.......................... 6

6. Gland cone pointed ventrally................ *Lestrigonus schizogeneios* (Stebbing, 1888)

Gland cone rounded ventrally.. 7

7. Gnathopod 1; basis deeply concave distally on anterior margin ....*Hyperietta luzoni* (Stebbing, 1888)

Gnathopod 1; basis with at most, an even bulge on anterior margin........................ 8

8. Pereopod 5; basis relatively broad, width about 0.8x length, overlapping anterior margin of ischium.. *Hyperietta vosseleri* (Stebbing, 1904)

Pereopod 5; basis narrow, width about 0.5x length, not overlapping ischium.......... 9

9. Gnathopod 1; propodus with one spine on anterior margin ....*Lestrigonus shoemakeri* Bowman, 1973

Gnathopod 1; propodus with two spines on anterior margin..................................... .... *Lestrigonus latissimus* (Bovallius, 1889)

10. Head with additional eye facets dorsally; forming small lobe over A1. Pereopod 7 much shorter than P6; dactylus long, almost half length of propodus................... .... *Hyperioides sibaginis* (Stebbing, 1888)

Head with evenly spread eye facets; evenly rounded anteriorly. Pereopod 7 subequal in length to P6; dactylus short, about 0.3x length of propodus .... *Lestrigonus macrophthalmus* (Vosseler, 1901)

Genus *Lestrigonus* Milne-Edwards, 1830

Remarks

Bowman (1973) recognised six species, one of which he described as new. One additional species has been described by Zeidler (1992b).

Very little is known about the biology of *Lestrigonus*. All records of associations with gelatinous plankton have been with medusae (Harbison *et al.* 1977, Laval 1980). Additional biological information is given for *L. schizogeneios* (Stebbing 1888) by Laval (1968a, 1972).

Distributional information for the species is provided by Bowman (1973), Bowman and McGuinness (1982) and Zeidler (1998).

Species: *Lestrigonus bengalensis* Giles, 1887; *L. schizogeneios* (Stebbing, 1888); *L. crucipes* (Bovallius, 1889); *L. latissimus* (Bovallius, 1889); *L. macrophthalmus* (Vosseler, 1901); *L. shoemakeri* Bowman, 1973; *L. ducrayi* Zeidler, 1992.

Genus *Phronimopsis* Claus, 1879

Remarks

This genus is monotypic. It is easily recognised by the distinctively chelate second gnathopods and by the phronimid type of body in females. Virtually nothing is known regarding its biology, other than that it seems to be an epipelagic species (Thurston 1976), found in surface layers down to a depth of 300-500m (Vinogradov *et al.* 1982). The only record of an association with gelatinous plankton is with the ctenophore *Beroe forskalii* (Krumbach 1911). The prehensile structure of pereopods 3–7 strongly suggests a parasitic existence. It is relatively uncommon, but widely distributed in tropical and temperate regions of the world's oceans.

Species: *Phronimopsis spinifera* Claus, 1879.

Genus ***Themistella*** Bovallius, 1887

Remarks

This genus is monotypic. It is characterised by the relatively long pereopod 5, the short telson and the upward bend of the dactylus of pereopods 6 and 7. Virtually nothing is known regarding its biology, and there are no records of associations with gelatinous plankton. It seems to be a relatively uncommon species, sparsely distributed in tropical waters of the world's oceans. Although it is mainly a surface water species, individuals have been caught as deep as 720 m (Thurston 1976).

Species: *Themistella fusca* Dana, 1853.

Genus ***Hyperioides*** Chevreux, 1900

Remarks

Bowman (1973) recognised two species for this relatively distinctive genus. Although both can be very abundant very little is known of their biology. Thurston (1976) provides some information on the vertical distribution and diurnal migration of *H. longipes*, and identified two size classes within a (presumed) single population. Shulenberger (1979) also provides some biological information for both species. *Hyperioides longipes* Chevreux, 1900 has been observed in association with the siphonophore *Lensia conoidea* (Laval 1980), but the host of the widespread, often abundant, *H. sibaginis* (Stebbing, 1888) is not known. It is suspected that it will prove to be a siphonophore that is also widespread and relatively common (Bowman & McGuinness 1982).

Distributional information for the species is provided by Bowman (1973), Bowman and McGuinness (1982), Vinogradov *et al.* (1982) and Zeidler (1998).

Species: *Hyperioides sibaginis* (Stebbing 1888); *H. longipes* Chevreux, 1900.

Genus ***Hyperietta*** Bowman, 1973

Remarks

Bowman (1973) recognised five species, three of which he described as new. Very little is known about their biology. Harbison *et al.* (1997) and Laval (1980) have found *Hyperietta* associated with polycystine radiolarians of the suborder Collodaria, and Brandt (1885) recorded hyperiids assigned to *Hyperia*, but referable to *Hyperietta*, as parasites of the radiolarians *Myxosphaera coerula* and *Collozoum pelagicum*.

Distributional information for the species is provided by Bowman (1973), Bowman and McGuinness (1982), Vinogradov *et al.* (1982) and Zeidler (1998).

Species: *Hyperietta luzoni* (Stebbing, 1888); *H. vosseleri* (Stebbing, 1904); *H. parviceps* Bowman, 1973; *H. stebbingi* Bowman, 1973; *H. stephenseni* Bowman, 1973.

Genus ***Hyperionyx*** Bowman 1973

Remarks

This genus is monotypic. It is readily distinguished by the relatively short pereopod 5, and in having pereonites 1–3 fused in both sexes. Virtually nothing is known regarding the biology, and there are not records of associations with gelatinous plankton.

It seems to be a rare circum-tropical genus. It has been recorded from the Mediterranean Sea (Stephensen, 1924), the tropical Atlantic Ocean, off Florida (Yang 1960), the South Atlantic Ocean, off South Africa (Dick, 1970), the Gulf of Mexico (Stuck *et al.* 1980), the tropical Pacific Ocean near Fiji (Hurley, 1960b) and the Indian Ocean (Bowman & McGuinness, 1982). There is also a specimen from the Tasman Sea, off eastern Tasmania (SAMA).

Species: *Hyperionyx macrodactylus* (Stephensen, 1924).

Family **IULOPIDIDAE**, new family

Diagnosis

Body length of 4-8 mm. Body and pereopods covered with fine setae. Head large, round. Eyes large, occupying most of the head surface. Pereon broad. Pereonites all separate. Pereonites 2-7 raised into transverse, rounded folds. Coxae separate from pereonites. Antennae 1 composed of four articles in females; multi-articulate in males, with enlarged callynophore, with two-field brush of aesthestascs medially. Antennae 2 absent, or reduced to small knob on cuticle in females; multi-articulate in males. Mandibles without palp in both sexes; molar reduced to broad plate with two small tubercles and row of small robust setae. Maxillae 1 with broad palp and slightly less-developed outer lobe; inner lobe absent. Maxillae 2 bilobed with robust setae. Maxilliped with slender, rounded outer lobes; inner lobe rudimentary, or absent. Gnathopod 1 weakly subchelate. Gnathopod 2 chelate. Pereopods 3-7 simple in males; in mature females P5-7 may be minutely subchelate. Pereopods 5-7 subequal in length. Uropods with articulated endopods and exopods. Telson triangular about as long as half of peduncle of U3. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Iulopis*.

Remarks

This family has been established to accommodate the genus *Iulopis* because it has characters that preclude it from the families Hyperiidae and Lestrigonidae, as defined here (see remarks under Phronimoidea).

According to the literature (e.g. Bovallius 1889, Bowman & Gruner 1973, Vinogradov *et al.* 1982) males have a mandibular palp which is absent in females. However, it seemed likely that if the are coxae free from the pereonites, and all pereonites are separate, that *Iulopis* should belong with the family Hyperiidae, and that the females probably possessed a mandibular palp which had been overlooked. Thus, some specimens of *I. loveni* Bovallius, 1887 (ZMUC Collection), which had previously been examined by Stephensen (1924) and Reid (1955) were examined to determine the presence or absence of a mandibular palp. Upon examining this material (27 females, 22 males) no mandibular palp could be found in either sex! The mouthparts of *Iulopis* are relatively large (Fig. 50), so it is relatively easy to determine this character without dissection. Careful dissection of a mature male confirmed that the mandibular palp is absent in this species. This finding is rather surprising, as Bovallius (1889) clearly illustrates a mandibular palp for the male of *I. loveni* (pl. 7, fig. 5), and says of the female (p.123) "the mouth-organs are like those in the male". One can only assume that Bovallius confused his preparations of mandibles and illustrated one from another genus. The absence of a mandibular palp in both sexes is a rare condition amongst the Physocephalata, occurring only in the Cystisomatidae, Paraphronimidae, Phronimidae and Dairellidae.

In all the female specimens of *I. loveni* examined, the second antennae are absent, or at most represented by a small knob on the cuticle. Bovallius (1889) records females with second antennae with two small articles, but provides no illustrations. It seems unlikely that this character is variable, or that it is dependent on maturity, as several ovigerous females were examined. Although it would be desirable to examine more material, it seems that Bovallius (1889) is incorrect in this regard, but his erroneous observation has unfortunately, been repeated in the literature. Amongst the Physocephalata the combination of mandibular palp absent in both sexes, and second antennae absent in females, is only found in the family Dairellidae.

Additional characters that distinguish *Iulopis* are the maxillipeds, which lack inner lobes, the mandibles, in which the molar is reduced to a broad plate and pereonites 2-7, which are raised into distinctive, transverse, rounded folds. The hirsute body is also unusual.

Genus ***Iulopis*** Bovallius, 1887

Iulopis Bovallius, 1887a: 17. – Barnard 1930: 418. Hurley 1955: 144. Bowman & Gruner 1973: 33. Vinogradov *et al.* 1982: 339. Vinogradov 1999a: 1186.

Euiulopis Bovallius, 1889: 116-117.
Euiulopsis – Pirlot, 1929: 120.

Type species

Iulopis loveni Bovallius, 1887, designated by Bowman and Gruner (1973). Type material could not be found at the SMNH, ZMUC or in Uppsala and is considered lost (but see later). However, *Iulopis* is a readily recognisable genus.

Diagnosis

The characters of the family are also those of the genus.

Two species.

Sexual dimorphism

As with most hyperiideans, the morphology of the antennae is the most useful means to differentiate the sexes. The antennae of males are multi-articulate, filiform, and much longer than the head and pereon, whereas in females the first antennae are much shorter than the head, and consist of only four articles, while the second antennae are absent. The pereon of females is also broader, and in mature females of *I. loveni* (and maybe also *I. mirabilis*) pereopods 5-7 are prehensile.

Remarks

Iulopis is a very distinctive genus. It is rarely found in plankton collections and consequently very little is known about the biology of species.

In the general structure of the gnathopods it occupies an intermediate position between *Hyperia* and *Hyperoche*.

Key to the species of the genus *Iulopis*

Gnathopod 1 weakly chelate, carpal process forming small, triangular lobe. Gnathopod 2 with slender carpal process, almost as long as propodus. Gnathopods 1 & 2; carpal process with single, robust seta terminally............*I. loveni* Bovallius, 1887

Gnathopod 1 subchelate, carpal process rounded, not produced. Gnathopod 2 with triangular carpal process, produced to about middle of propodus. Gnathopods 1 & 2; carpal process with scattered robust setae in addition to short, slender setae. ....*I. mirabilis* Bovallius, 1887

Iulopis loveni Bovallius
(Fig. 50)

Iulopis loveni Bovallius, 1887a: 17-18. – Barnard 1930: 418. Hurley 1955: 144. Reid 1955: 18-19. Harbison *et al.* 1977: 467-468. Shulenberger 1977: 378 (table). Tranter 1977: 647, 648 (table). Laval 1980: 16, 18 (table). Vinogradov *et al.* 1982: 278-280, fig. 140. Vinogradov 1990a: 61. Vinogradov 1991: 261 (table). Vinogradov 1999a: 1186, fig. 4.109.

Euiulopis loveni – Bovallius 1889: 118-124, pl. 8, figs 1-18. Senna 1908: 173, pl. 1, fig. 1-3. Stephensen 1924: 80. Spandl 1927: 159-161, fig. 4a-h. Bulycheva 1955: 1048 (table).

Euiulopsis loveni – Pirlot 1929: 120; Chevreux 1935: 191.

Type material

Type material of *I. loveni* could not be found at the SMNH, ZMUC or Uppsala and is considered lost. However, the description and figures provided by Bovallius (1889) readily characterise this species. The type locality is the "South Atlantic" according to Bovallius (1887a), but the only Atlantic record given for this species by Bovallius (1889) is 17°22'N 37°23'W!

Material examined

North Atlantic: 1 lot (BMNH), 2 lots (SMNH), 1 lot (USNM), 1 lot (ZMB), 2 lots (ZMUC), 9 specimens. **Mediterranean:** 1 lot (SMNH), 22 lots (ZMUC), numerous specimens. **South Pacific:** 10 lots (BMNH), 23 specimens.

Diagnosis

Body; length of sexually mature specimens 4-6 mm; very hirsute, even on head. Gnathopod 1 weakly chelate, carpal process forming small, triangular lobe, with single robust seta terminally. Gnathopod 2 with slender carpal process, almost as long as propodus, with single robust seta terminally. Pereopods 5-7 of mature females minutely subchelate.

Remarks

There is some confusion regarding the type locality for this species. Bovallius (1887a) says the "South Atlantic" but, in his monograph (Bovallius 1889), he gives two different localities for this species, one from the North Atlantic (17°22'N 37°23'W) and one from the Mediterranean Sea (36°20'N 4°30'W). In the SMNH there is a registered specimen (No. 1749) from "35°N 30°W" (a male with the gnathopods missing from the left), and also four unregistered microscope slide preparations; two without locality data, one labelled "27°N 45°W" and the other "Euiulopis 36°20'N 4°30'W ng.". None of this material can be confirmed as representing type material, but it is very likely that Bovallius used it for his monograph, particularly the specimens from the Mediterranean Sea.

This species closely resembles its only congener, *I. mirabilis*, but tends to be more hirsute, and in mature females pereopods 5-7 are prehensile, presumably for firm attachment to gelatinous hosts. As males and young females do not have these pereopods so transformed they may be free-living. The only record of a gelatinous association is by Harbison *et al.* (1977) who record a female from the medusa *Pandaea conica*.

Although this species is rarely collected, it has been captured in reasonable numbers in the Mediterranean Sea (Stephensen 1924).

Distribution

This species is known from scattered records in the tropical regions of the Atlantic Ocean and the Mediterranean Sea, and the warmer waters of the Pacific and Indian Oceans.

Iulopis mirabilis Bovallius

Iulopis mirabilis Bovallius, 1887a: 18. – Shoemaker 1945: 238-242, figs 36 & 37. Bowman & Gruner 1973: 33, fig. 41 (part). Brusca 1981: 20 (key), 42. Vinogradov *et al.* 1982: 280-282, fig. 141. Vinogradov 1990a: 61. Vinogradov 1991: 261 (table).

Euiulopis mirabilis – Bovallius 1889: 125-128, pl. 8, figs 19-33.

Type material

Type material of *I. mirabilis* is in the SMNH (No. 1750). The type locality is the "Pacific, Bay of Panama" according to Bovallius (1887a). Bovallius (1889) provides more detailed information: "in the Bay of Panama; taken in 1882 by the author among the Isles de las Perlas, at San Jose, and in the Bahia de Tychs, Isla del Reg."

Material examined

Types. Syntypic material from "Panama Bay 1882": male in spirit with G1 & 2 and P3 missing from the left; one microscope slide with mouthparts, antennae and G1.

Other material examined. **North Atlantic:** 2 lots (USNM), 3 specimens. **South China Sea:** 1 lot (ZMB), 1 specimen.

Diagnosis

Body; length of sexually mature specimens 6-8 mm; less hirsute than *I. loveni*, only sparsely hirsute on dorsal part of head. Gnathopod 1 subchelate, carpal process rounded, not produced, with scattered robust setae in addition to short, slender setae. Gnathopod 2 with triangular carpal process, produced to about middle of propodus, with scattered robust setae in addition to short, slender setae. Pereopods 5-7 of mature females simple.

Remarks

This is an extremely rare species, known from less than ten specimens worldwide. It is readily distinguished from its only congener, *I. loveni*, by the gnathopods. Judging by the material from Bermuda examined by Shoemaker (1945), who illustrated an ovigerous female, mature females do not seem to have pereopods 5-7 modified as in *I. loveni*. There are no records of this species in association with gelatinous plankton.

Distribution

This species is only known from the North Atlantic Ocean (Bermuda) and from the tropical Pacific Ocean (off California, Bay of Panama, approx. 20°S 81°W).

Family **BOUGISIDAE**, new family

Diagnosis

Body length 3-4 mm. Cuticle with polygonal markings. Head with small rostrum formed by dorsal, disc-like depression, and acute lateral process between A1 & A2. Eyes small. Pereonites 1 & 2 fused. Coxae separate from pereonites. Antennae 1 composed of three articles in females; multi-articulate in males with enlarged callynophore, with two-field brush of aesthestascs medially. Antennae 2 one-articulate in females; multi-articulate in males. Mandibles with palp in both sexes. Maxillae 1 with broad palp and slightly less-developed outer lobe; inner lobe absent. Maxillae 2 bilobed. Maxilliped with relatively short outer lobes; inner lobes very short, or rudimentary. Gnathopod 1 subchelate with short carpal process. Gnathopod 2 chelate. Pereopods 3, 4, 6 & 7 simple. Pereopod 5 prehensile, or subchelate. Pereopods 6 & 7 subequal in length. Uropods with articulated endopods and exopods. Telson triangular, slightly longer than half of peduncle of U3. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Bougisia*.

Remarks

This family has been established to accommodate the genus *Bougisia* because it has characters that preclude it from the families Hyperiidae, Lestrigonidae and Iulopidae as defined here (see remarks under Phronimoidea).

Genus ***Bougisia*** Laval, 1966

Bougisia Laval, 1966: 217.

Type species

Bougisia ornata Laval, 1966 by monotypy. Type material in MOM and collections of the Zoological Station, Villefranche-sur-Mer, France: in spirit.

Diagnosis

The characters of the family are also those of the genus.

Monotypic.

Sexual dimorphism

The sexes are very similar, but as with other Phronimoidea, males are distinguished by the filiform, multi-articulate antennae. Females have a slightly broader pereon, uropod 2 is relatively shorter than in males, and the telson is longer, about two-thirds the length of the peduncle of uropod 3, whereas in males the telson is slightly shorter than half of the peduncle of uropod 3.

Remarks

Bougisia is a very distinctive genus. It seems to be extremely rare and has been recorded only twice in the literature.

The morphology of the mouthparts, and the male antennae, are most similar to members of the family Hyperiidae.

The small eyes are a unique character amongst the Phronimoidea. They suggest that this is a deep-water form occasionally caught near the surface as a result of upwelling.

Bougisia ornata Laval

Bougisia ornata Laval, 1966: 210-216, figs 1-4. – Zeidler 1998: 43, figs 28 & 29.

Type material

The holotype male is in the MOM (No. 5296). The allotype female and a paratype male are in the collections of the Zoological Station, Villefranche-sur-Mer, France. The type locality is the Mediterranean Sea, near Villefranche-sur-Mer, France.

Material examined

North Atlantic: 1 lot (USNM), 1 lot (ZMB), 9 specimens. **Tasman Sea:** 1 lot

(SAMA), 1 specimen.

Diagnosis

Head slightly shorter than pereonites 1 & 2. Gnathopod 2 with carpal process extending to about middle of propodus (or slightly less). Pereopod 5 with long setae on anterior margin of basis to propodus. Pereopods 6 & 7 with relatively smooth margins.

Remarks

This is a very rare and distinctive species. Laval (1966) provides some biological information, and records it as an associate of *Phialidium* sp (Leptomedusae).

Distribution

This species has only been recorded from the Mediterranean Sea (near Villefranche-sur-Mer, France) and the Tasman Sea (off Jervis Bay, New South Wales). There are also specimens in the USNM and ZMB from off northwest Africa (24°N 17°W).

Family **DAIRELLIDAE** Bovallius, 1887

Diagnosis

Body length up to 10 mm; highly transparent. Head large, broad laterally. Eyes large, occupying most of head surface, divided into dorsal and ventral groups of ocelli. Pereon very broad with much narrower pleon tucked underneath. Pereonites 1 & 2 fused. Coxae fused with pereonites (suture sometimes visible). Antennae 1 composed of four articles in females; multi-articulate in males, with enlarged callynophore, with two-field brush of aesthestascs medially. Antennae 2 absent in females; multi-articulate in males. Mandibles without palp in both sexes; molar relatively well developed. Maxillae 1 with palp and reduced outer lobe; inner lobe absent. Maxillae 2 consist of a relatively large, single, pear-shaped plate. Maxilliped reduced to simple plate barely covering one-third of Mx2; inner and outer lobes fused or lost. Gnathopods and pereopods simple. Pereopods 3-7 subequal in length. Uropods with articulated endopods and exopods. Telson trapezoid, very small. Gills on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Dairella*.

Remarks

A most unusual feature of this family is the maxilliped, which is reduced to a single plate, a character shared only with the Paraphronimidae. However, the maxilliped only covers about one-third of the second maxillae, suggesting that the inner and outer lobes have been lost, and only the peduncle remains. In the Paraphronimidae there is a definite suture between the peduncle and the fused inner and outer lobes. Such a suture is absent in the Dairellidae.

Genus ***Dairella*** Bovallius, 1887

Dairella Bovallius, 1887a: 24. – Stebbing 1888: 1342-1343. Bovallius 1889: 332. Vosseler 1901: 51. Schellenberg 1927: 637. Pirlot 1929: 107. Bowman & Gruner 1973: 36-37. Vinogradov *et al.* 1982: 331. Vinogradov 1990a: 65. Vinogradov 1999a: 1181.

Type species

Paraphronima californica Bovallius, 1885. Type material could not be found at the SMNH, ZMUC or in Upsala and is considered lost. However, *Dairella* is a very distinctive genus, adequately characterised by Bovallius (1887a, 1889).

Diagnosis

The characters of the family are also those of the genus.

Two species.

Sexual dimorphism

The sexes are very similar, but the filiform, multi-articulate antennae readily distinguish males. Males also tend to have uropod 3 with relatively broader exopods and endopods, and the pereon is not as broad as in females.

Remarks

Dairella is a very distinctive genus, readily distinguished by the relatively broad, dorsoventrally compressed pereon, and the simple gnathopods and pereopods. The species seem to be uncommon, and very little is known about their biology.

Distinguishing between the two currently recognised species is extremely difficult as the characters used to separate them fall into the range of variation resulting from sex and age. Bovallius (1889), followed by Vinogradov *et al.* (1982), separate them as follows. In *D. californica,* pereopod 5 is only slightly longer than pereopod 4; the basis of pereopod 5 is slightly longer than the carpus, and uropod 3 has narrowly lanceolate exopods and endopods. In *D. latissima*, pereopod 5 is distinctly longer than pereopod 4; the basis of pereopod 5 is subequal in length to the carpus, and uropod 3 has broadly lanceolate exopods and endopods. These characters are subjective and have proved to be unreliable. In the material examined, which included both sexes of both species, pereopod 5 was always only slightly longer than pereopod 4 (1.1-1.2x). However, for most specimens identified as *D. californica*, the basis of pereopod 5 was about 1.3x as long as the carpus, whereas it was subequal in length to the carpus for most specimens identified as *D. latissima*. Thus, this may be a useful character. The endopods and exopods of uropod 3 vary considerably amongst females, but in juvenile males they are more like *D. californica*, whereas in mature males they are more like *D. latissima*, as illustrated by Bovallius (1889). Based on the figures of females by Bovallius, the width/length ratio of the rami of uropod 3 is 0.5 for *D. californica* and 0.6 for *D. latissima*; hardly sufficient to distinguish the two species. However, as specimens are relatively rare, it is difficult to determine the validity of specific characters. Therefore, until more material becomes available, it is prudent to accept the two species recognised by Bovallius (1887a, 1889) and Vinogradov *et al.* (1982).

Key to the species of the genus *Dairella*

Pereopod 5; basis about 1.3x length of carpus. ....*D. californica* (Bovallius, 1885)
Pereopod 5; basis subequal in length to carpus. ....*D. latissima* Bovallius, 1887

Dairella californica (Bovallius)

(Figs 51 & 52)

Paraphronima californica Bovallius, 1885: 11-12.
Dairella californica – Bovallius 1887a: 24. Bovallius 1889: 333-336, pl. 15, figs 21-33. Lorz & Percy 1975: 1444 (table). Brusca 1981a: 42, fig. 12. Vinogradov *et al.* 1982: 331-333, fig. 176. Vinogradov 1990a: 65. Vinogradov 1991: 261 (table).

Type material

Type material of *D. californica* could not be found at the SMNH, ZMUC or in Uppsala and is considered lost. In the SMNH there is one microscope slide of uropod 3 labelled "*Paraphronima californica*", without locality data, which may represent type material. The description and figures of Bovallius (1889) readily characterise this species. The type locality is "The Pacific", according to Bovallius (1885) and "off the coast of South California" (Bovallius 1887a).

Material examined

North Pacific: 3 lots (SAMA), 4 lots (USNM), 39 specimens. **South China Sea:** 1 lot (SMNH), 1 specimen.

Remarks

The male of this species has not been illustrated previously (Figs 51 & 52) and was unknown until relatively recently. It seems to be a rare species, although Lorz and Pearcy (1975) found about 60 specimens off the Oregon coast. Virtually nothing is known regarding its biology.

Distribution

It appears to be predominantly a northeast Pacific Ocean species, but Vinogradov (1990a) records a specimen from the equatorial southeast Pacific and there is a specimen in the SMNH from the South China Sea ("Palawan").

Dairella latissima Bovallius

Dairella latissima Bovallius, 1887a: 24. – Bovallius 1889: 336-340, pl. 15, figs 1-20. Vosseler 1901: 51. Tattersall 1906: 18. Chevreux 1913: 16. Stewart 1913: 254. Stephensen 1924: 112. Schellenberg 1927: 638, fig. 43. Spandl 1927: 169. Pirlot 1929: 107. Barnard 1932: 282. Chevreux 1935: 184. Barnard 1937: 184. Pirlot 1939: 41. Reid 1955: 19, fig. 5. Grice & Hart 1962: 300. Dick 1970: 59, fig. 7. Stuck *et al.* 1980: 363. Vinogradov *et al.* 1982: 333-335, fig. 177. Vinogradov 1988: fig. 2e. Vinogradov 1990a: 65. Vinogradov 1999a: 1181, fig. 4.92.

Dairella bovalli Stebbing, 1888: 1343-1346, pl. 158.

Type material

Type material of *D. latissima* could not be found at the SMNH, ZMUC, or Uppsala and is considered lost. The species is characterised by the description and figures of Bovallius (1889). The type locality is the "South Atlantic" according to Bovallius (1887a).

Type material of synonyms

Type material of *D. bovalli* is in the BMNH (89.5.15.201). It is in relatively good condition, and indistinguishable from that figured for *D. latissima* by Bovallius (1889). Bovallius's (1887a) description is misleading in regard to the relative lengths of the carpus and propodus of the gnathopods, and the peduncles of uropods 1 & 2; characters that Stebbing (1888) used to distinguish his species.

Material examined

Types. Syntypes of *D. bovalli* from "off St. Vincent, Cape Verde Islands", 16°49'N 25°14'W, *Challenger*, 26 April, 1876: on six microscope slides.

Other material examined. **North Atlantic:** 7 lots (USNM), 1 lot (ZMB), 3 lots (ZMUC), 12 specimens. **Mediterranean:** 4 lots (ZMUC), 4 specimens.

Remarks

This species is morphologically very similar to its only congener, and the two species may yet prove to be synonymous. For the time being though, and until more material becomes available, it is best to recognise this species because it seems to be geographically isolated from *D. californica*.

Very little is known about the biology of this species. Laval (1980) found a sub-adult female attached to the siphonophore *Forskalia edwardsi* and a sub-adult male attached to the narcomedusan *Cunina vitrea*, both caught near Villefranche, France. Vinogradov (1988) records it as penetrating the host tissue, and burying the abdomen in a manner reminiscent of the behaviour of hippoboscid flies.

Distribution

This is predominantly an Atlantic Ocean and Mediterranean Sea species. It has also been recorded from the Gulf of Aden (Barnard 1937) and a single specimen has been recorded from the south east equatorial Pacific Ocean (Vinogradov 1990a).

5.4 Superfamily LYCAEOPSOIDEA Bowman & Gruner, 1973

Diagnosis

Antennae 1 inserted on anterior surface of head, in small dorsally orientated cavity; flagellum of males with large, triangular first article (callynophore), with brush of aesthestascs ventrally and laterally, and row of stout setae along distal margin, with three small distal articles inserted subterminally; flagellum of females consists of tapering callynophore and one small terminal article. Antennae 2 inserted on ventral surface of head, very short, curved, composed of five short articles in both sexes. Pereopods 3-7 always simple. Pereopod 5 in mature males with extremely long and thin merus to dactylus. Developing eggs and young held in brood pouch underneath pereon made up of oostegites on pereonites 2-5.

One family: Lycaeopsidae.

Remarks

Bowman and Gruner (1973) proposed this superfamily to accommodate the family Lycaeopsidae as it differs sufficiently from the other families. A detailed examination of specimens of this family, particularly of the antennae, mouthparts and the extreme sexual dimorphism supports this view.

Family **LYCAEOPSIDAE** Chevreux, 1913.

Diagnosis

Body length up to 6 mm, but usually only 3-4 mm, slender, slightly compressed laterally. Head globular, as long as first three pereonites. Eyes large, occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antennae 1 short, slightly longer than half of head in males; less than half of head in females; in male, first flagellar article (callynophore) and 3-articulate peduncle, enlarged forming triangular-shaped structure, callynophore with brush of aesthestascs ventrally and anterodorsally on lateral surface, with row of robust setae on anterodorsally on medial surface, remainder of flagellum consists of three slender articles inserted sub-terminally on dorsal margin of callynophore; in females peduncle is 2-3 articulate, callynophore is elongate, tapering with one smaller elongate article forming remainder of flagellum. Antennae 2 inserted on ventral surface of head, just anterior to buccal mass; very short, curved 5-articulate, similar in both sexes. Mandibles with palp in males; without palp in females; palp relatively long with all articles usually fused; molar, spine row and lacina mobilis absent; incisor reduced to small bifid pincer. Maxillae 1 reduced to small, slender single lobe with 3-4 terminal teeth. Maxillae 2 reduced to single, slightly curved lobe; outer lobes curved, pointed, about twice as long as inner lobe. Gnathopods and pereopods simple. Pereopod 5 the longest in mature males as a result of extreme elongation of four distal articles; similar to, but shorter than, P6 in females. Pereopod 6 the longest in females; basis and merus especially broad in males. Pereopod 7 reduced in size, but all articles present. Uropods with articulated endopods and exopods. Telson triangular, sometimes bottle-shaped in males, exceeding peduncle of U3 in length. Gills on pereonites 5 & 6. Oostegites on pereonites 2-5.

One genus: *Lycaeopsis*.

Remarks

This family has several unusual characters that distinguish it from all other families of Hyperiidea. The morphology of the first antennae of males is unlike that of any other family. The second antennae are reduced in size, but similar in both sexes. In this respect, males of *Lycaeopsis* resemble those of *Thamneus*, whereas males of most other hyperiideans have longer second antennae. The mouthparts are styliform and relatively small and have not previously been described for females (Figs 53 & 55). The mandibular palp, which is absent in females, usually has all articles fused, a character not found in any other family. It is relatively long, filamentous, and projected forward between the second antennae. The mandible itself is reduced, with the only morphological feature being a small, pincer-like structure at the apex, probably all that remains of the incisor. The Platysceloidea are also noted for having reduced mandibles but all have a recognisable incisor with several teeth. However, the maxillae are like some families of the Platysceloidea. The sexual dimorphism of pereopod 5 is a character not observed in any other family. A reduction in the number of gills on the pereonites is also rare amongst the Hyperiidea.

Prior to this review, it was assumed that the second antennae were absent in females of *Lycaeopsis* (e.g. Bowman & Gruner 1973, Vinogradov *et al,* 1982), but second antennae were found in all specimens examined. In both sexes the second antennae are very short, curved medially, and composed of five short articles. Their small size might explain why previous authors thought they were absent in females, but they are no smaller in females than in males, and both Claus (1879) and Stebbing (1888) record females with second antennae of five articles.

Genus ***Lycaeopsis*** Claus, 1879

Lycaeopsis Claus, 1879b: 41-42. – Carus 1885: 426. Gerstaecker 1886: 486. Claus 1887: 66. Stebbing 1888: 1458. Spandl 1924: 27. Chevreux & Fage 1925: 417. Spandl 1927: 213. Pirlot 1939: 42. Hurley 1955: 179. Bowman & Gruner 1973: 41. Zeidler 1978: 20. Vinogradov *et al.* 1982: 358. Shih & Chen 1995: 140. Vinogradov 1999a: 1192.

Phorcus Milne-Edwards, 1830: 385, 391-392. – Milne-Edwards 1838: 304. Lucas 1840: 235. Milne-Edwards 1840: 79. Dana 1852: 316. Dana 1853: 1000. Bate 1862: 339. Gerstaecker 1886: 485. Claus 1887: 66.

Phorcorrhaphis Stebbing, 1888: 1451-1452.

Type species

Lycaeopsis themistoides Claus, 1879, by monotypy. Type material could not be found at the ZMB or ZMH and is considered lost. However, *Lycaeopsis* is a readily recognisable genus.

Type species of synonyms

The type species of *Phorcus* is *P. reynaudii* Milne-Edwards, 1830. Type material could not be found at the ANSP or MNHN and is considered lost. Although the description by Milne-Edwards (1830) is brief, he mentions the extremely long, thin pereopod 5 that is so characteristic of males of *Lycaeopsis*. However, *Phorcus* is preoccupied by a genus of Mollusca (Risso 1826). Thus, *Phorcorrhaphis* was introduced by Stebbing (1888) as a replacement name. At the time Stebbing did not appreciate that, because of the extreme sexual dimorphism, females were described as species of *Lycaeopsis*, a genus that has priority.

Diagnosis

The characters of the family are also those of the genus.

Two species.

Sexual dimorphism

This genus probably exhibits more extreme sexual dimorphism than any other hyperiidean. Apart from the structure of the first antennae, the extremely elongated articles of pereopod 5 distinguish males. Other differences are as follows; the body of males is more slender with the pereon being only about half as deep as the pleon, whereas in females they are of similar depth; females lack a mandibular palp; pereopod 6 of males has broader articles, especially the basis and merus; males of at least one species have the endopod of uropod 3 incised characteristically, and the telson is bottled-shaped.

Remarks

Two species are currently recognised in this distinctive genus. While males are readily identifiable, females of the two are more difficult to distinguish.

Although *Lycaeopsis* is moderately common in tropical and temperate regions, very little is known about its biology.

Key to the species of the genus *Lycaeopsis*

1. Pereopod 5; merus, carpus and propodus long and thin; propodus at least twice as long as basis (adult males) 2
   Pereopod 5; merus, carpus and propodus not especially long or thin; propodus shorter than basis (females and juveniles) 3

2. Uropod 3; endopod leaf-like, not modified. Telson triangular .... *L. themistoides* Claus, 1879
   Uropod 3; endopod incised on outer margin. Telson bottle-shaped .... *L. zamboangae* Stebbing, 1888

3. Pereopod 6; basis shorter than propodus. Double urosomite as broad as long........... .... *L. themistoides* Claus, 1879
   Pereopod 6; basis longer than propodus. Double urosomite longer than broad .... *L. zamboangae* Stebbing, 1888

Lycaeopsis themistoides Claus
(Figs 53-56)

?*Phorcus reynaudii* Milne-Edwards, 1830: 392. – Milne-Edwards 1838: 304. Milne-Edwards 1840: 79 ("*raynaudii*"). Lucas 1840: 235. Bate 1862: 339-340, pl. 53, fig. 9 ("*raynaudii*"). Bovallius 1887a: 28 ("*reynaudi*"). Claus 1887: 66 ("*raynaudii*").

?*Phorcus hyalocephalus* Dana, 1853: 1006-1008, pl. 69, fig. 2a-c. – Bate 1862: 340, pl. 53, fig. 10. Bovallius 1887a: 29. Claus 1887: 66.

Lycaeopsis themistoides Claus, 1879b: 42(188). – Carus 1885: 426. Bovallius 1887a: 29. Claus 1887: 67, pl. 19, figs 11-24. Chevreux 1913: 16-22, figs 6-8. Chevreux

& Fage 1925: 417-418, fig. 412. Stephensen 1925: 153-155. Spandl 1927: 213-214, fig. 35. Pirlot 1929: 142-143. Pirlot 1930: 27-28, fig. 8. Barnard 1930: 425-426. Barnard 1931: 128. Chevreux 1935: 192-195, pl. 13, fig. 9, pl. 14, fig. 3, 7. Pirlot 1939: 42-43. Hurley 1955: 179. Reid 1955: 23. Irie 1959: table 4, 32 (table). Evans 1961: 201. Grice & Hart 1962: 300. Kane 1962: 310. Vinogradov 1962: 23. Siegfried 1963: 9. Laval 1965: 6198. Dick 1970: 64, fig. 10 (part). Yoo 1971b: 59-60. Thurston 1976: 432-433. Harbison *et al.* 1977: 470. Shulenberger 1977: 379 (table). Tranter 1977: 648 (table), 650. Zeidler 1978: 20-21 (part). Laval 1980: 19(table), 20. Brusca 1981a: 30 (key), 43, fig. 16a-d. Stuck *et al.* 1980: 365. Vinogradov *et al.* 1982: 358-359, fig. 192, Lin & Chen 1988: 328. Vinogradov 1990a: 71. Vinogradov 1991: 261 (table). Lin & Chen 1994: 118 (list). Montu 1994: 132 (list). Shih & Chen 1995: 140-143, figs 88, 89. Zeidler 1998: 70, fig. 39B,C. Vinogradov 1999a: 1192, fig. 4.132.

?*Phorcus loveni* Bovallius, 1887a: 29.

Phorcorrhaphis edwardsi Stebbing 1888: 1455-1458, pl. 181. – Stebbing 1910: 656.

Lycaeopsis edwardsi – Spandl 1924a: 28-30, fig. 4.

Type material

Type material of *L. themistoides* could not be found at the ZMB or ZMH and is considered lost. However, the description and figures provided by Claus (1879, 1887) are sufficient to characterise this species. The type locality is Messina Harbour, Mediterranean Sea.

Type material of synonyms

Despite the loss of type material of *P. reynaudii*, it is considered a likely synonym of *L. themistoides*, rather than *L. zamboangae*, because Milne-Edwards's (1830) description refers to a male, but he makes no mention of the peculiar endopod of uropod 3, or the telson, which characterise *L. zamboangae*. Likewise, Bate (1862) describes and illustrates a male, from material that he believed to be types, without mentioning the obvious characteristics of *L. zamboangae*.

Type material of *P. hyalocephalus* could not be found at the USNM, or in any other major North American museum, and is considered lost. It is considered a likely synonym of *L. themistoides* for the same reason as *P. reynaudii*.

Type material of *P. loveni* could not be found at the SMNH, ZMUC or in Uppsala and is considered lost. It is a likely synonym of *L. themistoides* based on Bovallius's (1887a) brief description. However, in the SMNH are two lots of specimens labelled "*Phorcus*". One of these (SMNH 1678) is from the mid-Atlantic and consists of a mixture of both species. The other one (SMNH 1679) is labelled "Caraibiska Sjon 17°58'N 67°33'W Balders Exp. No. 141" and may represent type material. It consists of two males, both of which are clearly *L. zamboangae*.

Two syntype males of *P. edwardsi* are in the BMNH (89.5.15.247). Both specimens are readily identifiable with *L. themistoides*. Because of the extreme sexual dimorphism, Stebbing (1888) did not appreciate that his species was merely the male of *L. themistoides*, the original description of which was based on a female.

Material examined

Types. Two syntype males of *Phorcorrhaphis edwardsi* from the North Pacific, 24°49'N 138°34'E, surface, *Challenger*, 3 April, 1875: one in spirit, the other on three microscope slides.

Other material examined. **Tasman Sea:** 14 lots (SAMA), 18 specimens. **Coral Sea:** 1 lot (BMNH), 3 specimens. **North Atlantic:** 2 lots (BMNH), 19 lots (CMN), 11 lots (USNM), 2 lots (ZMB), 4 lots (ZMUC), numerous specimens. **South Pacific:** 2 lots (BMNH), 2 specimens. **Philippines:** 2 lots (USNM), 2 specimens. **Indian:** 1 lot (BMNH), several lots (SAM), numerous specimens. **Mediterranean:** 1 lot (ZMH), 34 lots (ZMUC), numerous specimens.

Diagnosis

Head oval in vertical plane. Antennae 1 of female with peduncle of three articles (total 5 articles). Antennae 2 of male about half as long as mandibular palp. Pereopod 6 of male; basis sometimes with slightly concave posterior margin; merus with relatively evenly convex posterior margin. Pereopod 6 of female with merus shorter than carpus. Uropod 2; exopod reaches slightly beyond peduncle of U3. Uropod 3; peduncle length is about half length of exopod. Telson slightly exceeds peduncle of U3 in length.

Remarks

Morphologically this species is very similar to its only congener, *L. zamboangae*. It is most readily distinguished by the key and the diagnosis given above, especially the males. The best characters to distinguish females are the number of articles of the first antennae, the longer carpus and propodus of pereopod 6, the relative length of the double urosomite, and the telson length. Other useful characters are the larger and more rounded head (Fig. 55), and the more coarsely toothed rami of the uropods.

Lycaeopsis themistoides has been recorded as living in diphyid siphonophores. Stephensen (1925) recorded two specimens in *Diphyes*; Harbison *et al.* (1977) found it in the superior nectophore of *Diphyes dispar*, and Laval (1965) found it in the anterior nectophore of *Chelophyes appendiculata*.

Distribution

This is an uncommon, but widely distributed species, in tropical and temperate regions, usually found in surface waters. It is also relatively common in collections from off the southeastern coast of South Africa.

Lycaeopsis zamboangae (Stebbing)

(Figs 55 & 56)

Phorcorrhaphis zamboangae Stebbing, 1888: 1452-1455, pl. 180. – Chevreux 1900: 148-149, pl. 18, fig. 1a-d.

Lycaeopsis zamboangae – Chevreux 1913: 22-24, fig. 9. Spandl 1924a: 27-28, fig. 3. Spandl 1927: 213. Pirlot 1930: 28-30, fig. 9. Barnard 1930: 426. Barnard 1931: 129. Chevreux 1935: 195-196, pl. 14, fig. 9. Pirlot 1939: 43. Hurley 1956: 20. Hurley 1960b: 281. Pillai 1966b: 222-224, figs 13, 13a. Dick 1970: 64, fig. 10 (part). Thurston 1976: 433. Tranter 1977: 648 (table), 650. Stuck *et al.* 1980: 365. Brusca 1981a: 30 (key), 43, fig. 16 (part). Vinogradov *et al.* 1982: 360, fig. 193. Vinogradov 1990a: 71. Vinogradov 1991: 261 (table). Vinogradov 1993a: 48-51. Lin & Chen 1994: 115, 118 (list). Shih & Chen 1995: 143-145, figs 90, 91. Zeidler 1998: 70-72, fig. 39A.

Lycaeopsis lindbergi Bovallius, 1887a: 29. – Pirlot 1929: 143-144.

Lycaeopsis pauli Stebbing, 1888: 1459-1461, pl. 209C. **New synonymy**.

Lycaeopsis neglecta Pirlot, 1929: 144, fig. 8. – Pirlot 1939: 43. Shoemaker 1945: 242. Thurston 1976: 432.

Lycaeopsis themistoides [misidentification – in part]. – Zeidler 1978: 20-21, fig. 21. (SAMA C3678).

Type material

The holotype male of *Phorcorrhaphis zamboangae* is in the BMNH (89.5.15.246). The type locality is off Zamboanga, The Philippines.

Type material of synonyms

Type material of *L. lindbergi* could not be found at the SMNH, ZMUC or in Uppsala and is considered lost. Some authors have considered this species a probable synonym of *L. themistoides*. However, Bovallius's (1887a) description seems to be based on a female, and, although it is very brief, he describes the telson as "nearly twice longer than the peduncles of the last pair of uropods", which is characteristic of *L. zamboangae*.

The holotype of *L. pauli* is in the BMNH (89.5.15.248). Although the specimen is in poor condition, it is readily identified with *L. zamboangae*, based on the morphology of the first antennae, pereopod 6, and the double urosomite (assisted by Stebbing's description and figures). As with the previous species, Stebbing (1888) did not appreciate the sexual dimorphism in this genus, and that his species was merely the female of *L. zamboangae*, the original description of which was based on a male. Prior to this review, *L. pauli* was considered a synonym of *L. themistoides* (e.g. Vinogradov *et al.* 1982).

Type material of *L. neglecta* could not be found at the MNHN or MOM and is considered lost. Pirlot (1929) only had females, and like Stebbing (1888), probably did not appreciate the sexual dimorphism of this genus. It is regarded a synonym of *L. zamboangae* because Pirlot's figures and description are consistent with the characters given here for this species.

Material examined

Types. Holotype male of *Phorcorrhaphis zamboangae* from "off Samboangan, Philippine Islands", 8°32'N 121°55'E, surface, Challenger, 27 October, 1874: two microscope slides. The holotype female of *L. pauli*, from off St. Pauls' Rocks, 1°10'N 28°23'W, surface, *Challenger*, 27 August, 1873: one microscope slide.

Other material examined. **Tasman Sea:** 1 lot (SAMA), 1 specimen. **Coral Sea:** 1 lot (BMNH, 1 specimen. **North Atlantic:** 1 lot (BMNH), 5 lots (CMN), 5 lots (USNM), 4 lots (ZMB), 19 specimens. **South Atlantic:** 1 lot (BMNH) 1 specimen. **North Pacific:** 4 lots (USNM), 5 specimens. **Indian:** several lots (SAM), several specimens.

Diagnosis

Head obliquely oval in vertical plane, in males often almost horizontal with buccal mass aligned in horizontal plane. Antennae 1 of female with peduncle of two articles (total 4 articles). Antennae 2 of male about as long as mandibular palp. Pereopod 6 of male;

basis with evenly convex posterior margin; merus with posterodistal bulge, relatively wider than in *L. themistoides*. Pereopod 6 of females with merus longer than carpus. Uropod 2; exopod reaches to about the middle of the endopod of U3. Uropod 3; peduncle length is about one-third length of exopod. Telson about twice as long as peduncle of U3 in females; bottle-shaped in males extending past the exopod of U3.

Remarks

The similarity of this species to *L. themistoides* has already been discussed under that species. Generally it is more slender in appearance.

In the male illustrated here, the mandibular palp on the right mandible consists of two articles (Fig. 55E), but on the left all articles of the palp are fused. This observation supports the view that the mandibular palp in *Lycaeopsis* has not been reduced to one article, but that the articles are fused.

Virtually nothing is known about the biology of this species. Its association with a gelatinous host remains to be recorded, but like its congener, the host is most likely a siphonophore. Vinogradov (1993a) found five sexually mature males in deep-water collection trays near two hydrothermal vents in the eastern Pacific, at a depth of 2640 m. This is an unexpected find, as it is known as a surface-water species, and has not previously been recorded as associated with benthic communities.

Distribution

This is a relatively rare species widely distributed in tropical and temperate regions.

5.5 Superfamily PLATYSCELOIDEA Bowman & Gruner, 1973

Diagnosis

Antennae 1 inserted on ventral surface of head; flagellum of males with enlarged, curved first article (callynophore) with dense 1-2 field brush of aesthestascs medially and 1-3 shorter articles, usually inserted subterminally on callynophore; flagellum of females usually curved, the callynophore sometimes enlarged, with 0-2 smaller articles inserted terminally. Antennae 2 also inserted on ventral surface of head; in males usually composed of 5 slender, long articles (3 peduncular, 2 flagellar) folded back on one another in zigzag fashion; in female relatively short, composed of up to 5 slender articles, but often reduced in number or absent. Pereopods 3-7 always simple. Pereopods 5 & 6 often with enlarged basis. Pereopod 7 reduced in size, and sometimes in number of articles. Developing eggs and young held in brood pouch underneath pereon, made up of oostegites, usually on pereonites 2-5.

Eleven families: Pronoidae, Parapronoidae **fam. nov.**, Amphithyridae **fam. nov.**, Brachyscelidae, Lycaeidae, Anapronoidae, Thamneidae **fam. nov.**, Tryphanidae, Oxycephalidae, Platyscelidae and Parascelidae.

Remarks

A consistent character of families of this superfamily is the position of the antennae on the ventral surface of the head. In addition, males have second antennae of five articles (rarely six), which are folded back on one another, except in *Pronoe* and *Thamneus* and only partly in *Anapronoe*. The second antennae of males usually extend forwards, almost reaching the limit of the head, but can also extend backwards between the pereopods for most of the pereon (e.g. *Lycaea*). In *Anapronoe* they are positioned in a transverse groove underneath the head. Second antennae are often absent in females, but when they are present they are reduced in size and sometimes also in the number of articles.

This superfamily is also characterised by the extreme reduction of the mouthparts. The degree of reduction is probably correlated to the degree of dependence on gelatinous hosts, and is always more extreme in females. The mandible is often reduced, without a molar, and in females the palp is absent in all genera except *Pronoe* and *Tryphana*. Males all have a well developed mandibular palp (except *Glossocephalus*), which is often relatively long. The maxillae are reduced in size and usually consist of a single lobe. In some genera both maxillae are absent, or so reduced that they are not discernible, but usually both are present, or only the second maxillae are absent.

Families of this superfamily have provided the most taxonomic difficulties. Genera have often been grouped into families on general appearance and loosely defined characters that do not reflect phylogenetic relationships. A systematic revision of the families and genera using the taxonomic database program DELTA (Dalwitz *et al* 1999), and a phylogenetic analysis using PAUP (Swofford 2000) form the basis for a more detailed taxonomic revision of taxa in the future. The characters used (Appendix 2) were converted into an 'item descriptions' file (Appendix 3) to generate the generic descriptions, and the results of the phylogenetic analysis are presented in figures 57 and 58. The current study has resulted in significant taxonomic changes as summarised below.

Prior to this review the family Pronoidae comprised the genera *Pronoe, Eupronoe, Parapronoe* and *Paralycaea* (Vinogradov *et al.* 1982). Pronoidae is restricted here to the monotypic genus *Pronoe* that has some unique characters not found in any other platysceloidean. *Paralycaea* resembles *Amphithyrus* (Platyscelidae) in the broad basis of pereopods 5 and 6, but which is not transformed into a broad operculum, as is characteristic of the families Platyscelidae and Parascelidae. There are also other similarities and the two genera are placed in a new family, Amphithyridae, derived from *Amphithyrus*, which has page priority. This new family also includes a new genus, *Amphithyropsis*, erected for *Tetrathyrus pulchellus* Barnard, 1930, which links the other two genera. Zeidler (1998) mistakenly described it as a new species of *Paralycaea, P. platycephala*. *Eupronoe* resembles *Brachyscelus* in that males have an antennal pocket on the basis of gnathopod 1 to accommodate the posterior folds of the second antennae. This unique character, not found in any other genus of hyperiidean, would have united the two genera in the family Brachyscelidae. However, the morphology of the mouthparts, the antennae, and the gnathopods of *Eupronoe* are like those of *Parapronoe*. Also, in *Eupronoe*, the endopods and exopods of uropods 2 and 3 are foliaceous, a character sometimes found for uropod 3 in *Parapronoe*. Thus, *Eupronoe* and *Parapronoe* remain to form the new family, Parapronoidae.

The systematic limits of the family Lycaeidae have varied considerably in the past, but like Vinogradov *et al.* (1982) I restrict it here to *Lycaea* and *Simorhynchotus*. Similarly the family Brachyscelidae is recognised for *Brachyscelus*. However, *Thamneus*, previously included with *Brachyscelus*, has a number of characters that differ considerably from either *Brachyscelus* or *Lycaea* and thus, it is placed in a new family, Thamneidae.

The status of the family Anapronoidae is confirmed and now includes two species (Zeidler 1997b). In this family the second antennae lie in a diagonal groove on the ventral surface of the head, a character not found in any other hyperiidean.

The family Oxycephalidae may be polyphyletic. At the beginning of this study it was assumed that its systematics had been resolved by Bovallius (1890) and Fage (1960). However, more recently it has appeared that several genera have characters that may require their removal from the Oxycephalidae. The family currently consists of eight genera (Vinogradov *et al.*) but more detailed work is required to resolve their systematic status. Therefore, it has not been possible to reach a satisfactory conclusion during this study. *Metalycaea globosa*, referred to this family by Nair (1993), is considered to be a species of *Lycaea*. Its inclusion in the Oxycephalidae, and exclusion from the Lycaeidae, based on the absence of maxillae is not valid as *Lycaea* and most genera of Oxycephalidae have first maxillae that are reduced to a small, single plate and the second maxillae are absent or not discernible.

The family Platyscelidae is restricted to four genera, in which the basis of pereopod 6 has a distinct groove for the telson, and the basis of pereopods 5 and 6 lock together so that the whole forms a neat operculate covering for the other appendages (as in Parascelidae). *Amphithyrus* is removed to a new family, Amphithyridae (together with *Paralycaea* and a new genus, *Amphithyropsis*), because the basis of pereopods 5 and 6 does not lock in the same manner, and the basis of pereopod 6 is without a telsonic groove, so that it is unable to roll up into a protective ball, a characteristic of this family and the Parascelidae. *Tetrathyrus* is unusual in that the second antennae are absent in females, pereopod 6 has a basis without a fissure and the telsonic groove is very narrow. Thus, it links this family to the Amphithyridae.

The family Parascelidae is most similar to Platyscelidae in general morphology, but is distinguished by its mouthparts, which are styliform, resulting in a buccal mass that is in the form of a sharp, pointed cone instead of a broad, rounded cylinder as in Platyscelidae. In addition, pereopod 7, although reduced in size, always consists of the full compliment of articles. Four genera are recognised in this study. *Parascelus*, in which the basis of pereopod 6 is without a fissure; *Thyropus*, in which the basis of pereopod 6 has a fissure; *Schizoscelus*, in which gnathopod 1 is simple and gnathopod 2 is chelate, and *Euscelus*, in which both gnathopods are chelate. *Hemiscelus*, included in this family by Vinogradov *et al.* (1982), is regarded a synonym of *Hemityphis* (Zeidler 1998).

Family **PRONOIDAE** Claus, 1879

Diagnosis

Body length 10-14 mm, robust, slightly compressed laterally. Head bullet-shaped, slightly more pointed in males, as long as first four pereonites. Eyes large, occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antennae 1 of both sexes inserted in groove on ventral surface of head; peduncle 3-articulate; first flagellar article (callynophore) enlarged, with row of aesthestascs on ventral margin in females, in males aesthestascs are arranged in two-field brush medially, and in separate group anteroventrally; remainder of flagellum consists of two slender articles, inserted terminally. Antennae 2 inserted adjacent to buccal mass; in males consisting of large, quadrate basal article, followed by five elongate articles, folded only once and placed in groove next to mandibular palp, and partly under A1; in female reduced to basal article like that of male. Mandibles with palp in both sexes. Maxillae 1 consist of relatively well developed, curled, bifid lobes. Maxillae 2 also curled and relatively well developed, with rounded knobs terminally, and one-articulate palp medially, on the dorsal surface. Gnathopods and pereopods simple. Gnathopod 1 with enlarged basis, almost as broad as long. Pereopod 5 the longest, with slightly enlarged basis. Pereopod 6 with greatly enlarged basis, distinctly longer than remaining articles combined, which are inserted terminally. Pereopod 7 reduced to relatively large, quadrate basis and one tiny article, attached to anterodistal corner. Uropods with articulated endopods and exopods. Telson triangular, about two-thirds as long as peduncle of U3, not fused with double urosomite. Gills without folds on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Pronoe*.

Remarks

The family Pronoidae is restricted to the monotypic genus *Pronoe*, because it has some unique characters not found in any other platysceloidean.

Characters that distinguish *Pronoe* from other Platysceloidea are as follows. The antennae and mandibular palp are held in a narrow groove on the ventral surface of the head. The callynophore of the first antennae of males is spatulate, similar in shape to that found in *Vibilia*. The second antennae of males are reduced in size with a large, fleshy, quadrate basal article, attached for the most part to the buccal mass, and five slender articles, only folded once. Both sexes have a 3-articulate mandibular palp of similar proportions. The maxillae are relatively large and distinctly curled inwardly. The first maxillae are relatively simple and bifid. The second maxillae have, what appear to be, an inner palp, analogous to the inner plate found in the Gammaridea. Pereopod 7 is also unusual in that it is reduced to a relatively large, quadrate basis and one tiny, pointed article attached to the anterodistal corner.

None of the above characters are shared by *Eupronoe*, *Parapronoe* or *Paralycaea*, genera which have previously been included in the Pronoidae (Vinogradov *et al.* 1982). Thus, they are removed from the Pronoidae. *Eupronoe* and *Parapronoe* share a number of characters, and are placed in the new family Parapronoidae. On the other hand, *Paralycaea* differs from *Eupronoe* and *Parapronoe*, and is placed in a new family, Amphithyridae, together with *Amphithyrus* and *Amphithyropsis* **gen. nov.**

Genus *Pronoe* Guérin-Méneville, 1836
(Figs 59 & 60)

Pronoe Guérin-Méneville, 1836c: 6. – Milne-Edwards 1838: 307. Lucas 1840: 239-240. Milne-Edwards 1840: 98-99. Dana 1852: 316. Dana 1853: 1009, 1015. Bate 1860: 336-337. Claus 1879b: 23-25. Claus 1880: 588. Gerstaecker 1886: 484. Claus 1887: 48-50. Stebbing 1888: 1507. Pirlot 1929: 147. Bowman & Gruner 1973: 42-43. Vinogradov *et al.* 1982: 369. Shih & Chen 1995: 147. Vinogradov 1999a: 1204.

Type species

Pronoe capito Guérin-Méneville, 1836, by monotypy. A syntype male is in the ANSP (CA2674), Guérin-Méneville Collection no. 454 (Zeidler 1997a).

Diagnosis

Body shape robust or globular. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 3-articulate; flagellum with moderately enlarged oval callynophore and 1–3 articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with two flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 6-articulate; zig-zagged, with some articles folded back on each other; only extends forward under head. Antenna 2 females 1-articulate. Mandibular palp present in both sexes; females 3-articulate; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; curled, bifid; palp absent. Maxilla 2 reduced in size; curled, quadrate with medial palp. Maxilliped inner and outer lobes separate; inner lobes not fused; inner lobes well developed; medial margin of outer lobes without fringe of setae or membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 simple. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Monotypic: *Pronoe capito*.

Sexual dimorphism

The sexes are remarkably similar in gross morphology, differing mainly in the morphology of the antennae. Females tend to have a more rounded head, and in males the gnathopods are more robust, and armed with relatively more setae.

Remarks

Recently, a male specimen of *P. capito* (9.5 mm) was found in the Guérin-Méneville Collection, held by the ANSP, which was subsequently determined to be syntype material (Zeidler 1997a). Spamer and Bogan (1992, 1994) list this specimen as a holotype, and although this may be all that remains of Guérin-Méneville's original material, it is clear that he had more than one specimen at the time of description for he says, "Plusieurs individus de ces Crustacés nous ont été donnés par M. Gay". Therefore, the specimen must be regarded a syntype. It is also likely that the figures of this species, given by Guérin-Méneville (1836c), represent more than one specimen, because figure 3a could be that of a specimen with the head missing. Despite being dry, the specimen is in remarkably good condition, and there is no difficulty in determining the diagnostic features that characterise the genus *Pronoe*.

This is a very distinctive, monotypic genus. It differs most significantly from all other platysceloideans in that females have a 3-articulate mandibular palp. The only other platysceloidean genus in which females have a mandibular palp is *Tryphana*, but in that genus the palp is reduced to two articles. The maxillae are also relatively well developed, and their morphology is unique amongst the families of Platysceloidea, and hyperiideans in general. The medial palps on the second maxillae are extraordinary. At first it was thought that they might be an artefact of dissection, but careful manipulation revealed that they are indeed palps, attached medially near the base of the 'outer plate'. They are somewhat analogous to the inner plate found in the Gammaridea, but nothing like it has been found in any other hyperiidean. It seemed plausible that the maxillae might have been confused because first maxillae, with palps, occur in some hyperiidean families. However, careful manipulation of mouthparts, of intact specimens, confirmed the initial observation, which is supported by the illustrations of Claus (1887) and Stebbing (1888).

Pronoe also differs from most other Platysceloidea in that the second antennae of males are reduced in size, and the articles are not folded back on one another. In this respect it resembles *Thamneus*, but in that genus the second antennae of males are also reduced in the number of articles, and they are curved near the buccal mass, and do not extend forward underneath the head as in *Pronoe*.

Amongst the specimens examined there are small males and females (<6.0 mm) with the mandibular palp not fully developed. Also one large female (10.9 mm), has second antennae as illustrated here (Fig. 59), but with a small additional article on the anterior corner of the large, fleshy article.

Pronoe capito seems to be a rare species, and until recently (Shih & Chen 1995) no description or figure of the female existed and nothing is known regarding its biology. Most of the specimens in museum collections are males, suggesting that females may occupy a slightly different ecological niche, probably more closely associated with gelatinous plankton, as found for most other hyperiideans.

Pronoe has been found in the tropical warm-temperate parts of the Atlantic, Indian (including Arabian and Red Sea) and Pacific oceans. It seems to prefer surface waters (< 200 m).

Family **PARAPRONOIDAE** new family

Diagnosis

Body length up to about 20 mm but usually less than 10 mm. Head slightly pointed anteroventrally, particularly in males; sometimes rounded in females; as long as first 4-6 pereonites. Eyes large, occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antennae 1 with 3-articulate peduncle; in females first flagellar article (callynophore) enlarged with rows of aesthestascs on anterior margin, followed by two smaller, slender terminal articles; in males first flagellar article (callynophore) enlarged, curved, with dense brush of aesthestascs in posterior margin and on posterodistal corner, and three smaller, slender articles inserted on anterodistal corner. Antennae 2 of females of four slender articles and one small terminal article; in males of four long, slender articles folded back on one another, with 1-3 small articles in addition terminally, juncture of articles 2 & 3 supported in pocket of basis of G1 in some species (*Eupronoe*). Mandibles with palp in males, without palp in females. Maxillae 1 reduced to single lobes, with four teeth distally, on medial margin. Maxillae 2 reduced to single lobes, slightly curved and pointed laterally, with rounded bulge medially. Gnathopod 1 simple or weakly subchelate. Gnathopod 2 chelate. Pereopods 3-7 simple. Pereopod 5 the longest, with enlarged basis, and articles inserted terminally or subterminally. Pereopod 6 with greatly enlarged basis, distinctly longer than remaining articles combined, which are inserted subterminally. Pereopod 7 usually reduced to small, but relatively enlarged, basis and 1-2 additional tiny articles, sometimes all articles are present in abnormal specimens. Uropods with articulated endopods and exopods, those of U2, and/or, U3 sometimes foliaceous. Telson triangular, sometimes elongate, always much longer than peduncle of U3, not fused with double urosomite. Gills with folds on pereonites 2-6. Oostegites on pereonites 2-5.

Two genera: *Parapronoe* and *Eupronoe.*

Remarks

This new family has been established to accommodate *Parapronoe* and *Eupronoe*, which have several characters in common that differ significantly from *Pronoe*, and so could not be accommodated in the family Pronoidae, as defined here (see remarks on Pronoidae and compare diagnoses). The family name has been derived from *Parapronoe*, which has page priority.

Prior to this review, *Eupronoe* could have been placed with *Brachyscelus*, based on the antennal pocket of the first gnathopods in males, a unique character not found in any other hyperiidean. However, *Eupronoe* differs significantly from *Brachyscelus* in the morphology of the mouthparts, the antennae and the gnathopods, which are more like those of *Parapronoe*. The mouthparts of *Eupronoe* consist of a maxilliped with outer lobes with a medial fringe of hairs, the first maxillae are armed with four teeth terminally, the second maxillae consist of a curved plate with a medial bulge, and in males the mandibles have the incisor orientated at right angles to the palp. In *Brachyscelus* the outer lobes of the maxilliped have smooth margins, the first maxillae are reduced to a small rounded plate, the second maxillae are absent, and in males the mandibles have the incisor orientated parallel to the palp. In *Eupronoe* the first antennae have a peduncle of three articles in both sexes (only two in *Brachyscelus*) and the second antennae of females consist of five slender articles (absent in *Brachyscelus*). In males of *Brachyscelus* the second antennae consist of five long articles folded back on one another, with the juncture of articles 2/3 and 4/5 held in the antennal pocket of the first gnathopods. In males of *Eupronoe* the second antennae consist of only four long articles folded back on one another, plus one small terminal article (which is not folded), and only the juncture of articles 2/3 is held in the antennal pocket of the first gnathopods. The gnathopods of *Brachyscelus* are both strongly subchelate whereas in *Eupronoe* gnathopod 1 is weakly subchelate, almost simple, and gnathopod 2 is chelate. All of the above characters of *Eupronoe*, except for the antennal pocket of gnathopod 1, are shared with *Parapronoe*. In addition, the cuticular sculpture is similar, and pereopod 7 is reduced to the basis and few additional articles, whereas in *Brachyscelus* the full complement of articles is present.

A close relationship between *Parapronoe* and *Eupronoe* is strongly supported by the phylogenetic analysis, and it seems that the antennal pocket of the first gnathopods of males in *Eupronoe* has evolved independently in *Brachyscelus*.

This family resembles Anapronoidae, and some genera of Parascelidae and Platyscelidae, in the morphology of the female second antennae, and Lycaeidae and Oxycephalidae in the morphology of the male second antennae. The maxillae are most like those of Amphithyridae **fam. nov.**

Key to the genera of the family PARAPRONOIDAE new family

Pereopod 5; distal articles inserted subterminally on basis. Uropod 2; exopods and endopods with serrated margins. Uropod 3; exopod with serrated margins, endopod sometimes foliaceous .... *Parapronoe* Claus, 1879

Pereopod 5; distal articles inserted terminally on basis. Uropods 2 & 3 with foliaceous exopods and endopods .... *Eupronoe* Claus, 1879

Genus ***Parapronoe*** Claus, 1879

(Figs 61 & 62)

Amphipronoe Bate, 1862: 335-336.

Parapronoe Claus, 1879b: 29-31. – Gerstaecker 1886: 486. Claus 1887: 63-64. Stebbing 1888: 1521-1522. Schellenberg 1927: 651-652. Pirlot 1929: 135. Hurley 1955: 175. Bowman & Gruner 1973: 43-44. Zeidler 1978: 25. Vinogradov *et al.* 1982: 377-378. Shih & Chen 1995: 158. Vinogradov 1999a: 1203.

Sympronoe Stebbing, 1888: 1533. – Pirlot 1929: 151. Bowman & Gruner 1973: 44-45. Zeidler 1978: 24.

Type species

Parapronoe crustulum Claus, 1979. Type material could not be found at the ZMB or ZMH and is considered lost. However, the description and figures provided by Claus (1879b, 1887) readily characterise this genus.

Type species of synonyms

The type species of *Amphipronoe* is *A. cuspidata* Bate, 1862. Type material could not be found at the BMNH or MNHN and is considered lost. It appears to be a species of *Parapronoe*, judging by the description and figures. *Amphipronoe* has not been used in the scientific literature since Streets (1877), and is rejected as a senior synonym of *Parapronoe* in order to preserve nomenclatural stability (ICZN, Article 23.9).

The type species of *Sympronoe* is *Parapronoe parva* Claus, 1879. Type material could not be found at the ZMB or ZMH and is considered lost. Stebbing (1888) erected this genus for *S. parva*, and one other, that he described as new. However, Semenova (1981) described a new species of *Parapronoe* (*P. elongata*), and found that it had features in common with *Sympronoe*, and concluded that the generic status could not be maintained on the basis of the relatively short telson and carpal process of gnathopod 2.

Diagnosis

Body shape robust or globular. Head round. Rostrum present in both sexes; short and rounded. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 3-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in one-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 6-articulate; strongly zig-zagged, with most articles folded back on each other; only extends forward under head, or extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 2; basal article elongate, longer than following article, or elongate, about half length of following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly, or medially. Antenna 2 females 5-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated at right angles to palp. Maxilla 1 reduced in size; single lobes; single plate with four rounded teeth; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes incompletely fused, i.e., slightly separate terminally; inner lobes well developed; medial margin of outer lobes with fringe of closely packed slender setae. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, but not operculate; articles 3–7 inserted subterminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus anterodistal corner extended, distinctly overlapping carpus medially. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopod, and sometimes also exopod, leaf-like, foliaceous, with smooth margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Four species: *Parapronoe crustulum*, *P. parva*, *P. campbelli* and *P. elongata*.

Sexual dimorphism

The sexes are very similar in gross morphology, differing mainly in the morphology of the mandibles and the antennae. Females also tend to have a more rounded head than males, and reach a slightly larger size.

Remarks

Parapronoe resembles genera of the families Parascelidae and Platyscelidae in its ability to curl up into a ball. In all species, the coxa of pereopod 5 articulates proximally with the coxa/basis of pereopod 6, and, except for *P. campbelli*, the basis of pereopod 6 has a strong ridge/groove structure distally on the medial surface, which allows the opposing pereopods to lock together. This would enable the animal to enclose the pereopods with the broad basis of pereopods 5 and 6. *Parapronoe campbelli* lacks a locking mechanism on pereopod 6, but there is a thin ridge along the mid-medial surface of the basis which may enable the animal to hold the pereopods together. In *P. crustulum* the first epimeral plate has a posterodistal excavation which allows the pleon to curl up neatly, and the third epimeral plate has a distinct groove, that fits the basis of pereopod 6. In *P. parva* the pleonites have a strong lateral ridge that, when the pleon is curled up, lines up, and fits neatly with, the posterior margin of the basis of pereopod 6. In the few specimens of *P. elongata* that were examined, there was no evidence of any modification of the pleonites in relation to curling. In *P. campbelli* the third epimeral plate has a slight ridge, but this does not seem to be related to curling, and it is likely that this species, which also lacks the locking mechanism of pereopod 6, is unable to curl up into a ball.

Parapronoe crustulum differs significantly from all congeners in the morphology of the second antennae of males. They do not extend posteriorly underneath the pereon, the basal article is the longest, and the fourth article is relatively short, with 2-3 tiny terminal articles that together are orientated medially under the head. In all other species the second and third articles are longest and extend posteriorly to about pereonite 2, and the fourth article is about one-third the length of the preceding one, with two tiny terminal articles, which together are orientated parallel to the preceding articles.

During these studies, specimens from the collections of many museums were examined, including type material of *Typhis rapax* Milne-Edwards, 1830, held by the MNHN, which proved to be the same as *P. crustulum* (Zeidler 1996b). As this threatened the stability of some well-established scientific names an application to the ICZN was made to conserve the specific name of *Parapronoe crustulum* Claus, 1879 (Zeidler 1996a), which was subsequently upheld by the ICZN (1998).

Virtually nothing is known about its biology. Harbison *et al.* (1977) found *P. parva* associated with the siphonophore *Rosacea cymbiformis*.

Parapronoe appears to be widely distributed in tropical and temperate regions of the world's oceans. *Parapronoe elongata* is relatively rare, only known from the Tasman Sea (Semenova 1981), the Coral Sea (Zeidler 1998) and the China Sea (Shih & Chen 1995).

Four species are currently recognised (Vinogradov *et al.* 1982), but the genus is in need of revision.

Key to the species of the genus *Parapronoe*

1. Telson slightly shorter or longer than U3 2
   Telson length about half or less U3 3

2. Pereopod 6; basis with distal ridge/groove locking mechanism on medial surface for opposing pereopod. Epimeral plate 1 with distinct posterodistal excavation. Cuticular markings on body consist of circular pits ....*P. crustulum* Claus, 1879
   Pereopod 6; basis without distinct locking mechanism. Epimeral plate 1 without posterodistal excavation. Cuticular markings on body consist of longitudinal pits ....*P. campbelli* Stebbing, 1888

3. Gnathopod 2; carpal process rounded, barely reaching middle of propodus. Double urosomite; length much less than twice width. Uropod 3; endopods and exopods with rounded terminal margin..*P. parva* (Claus, 1879)

Gnathopod 2; carpal process pointed, reaching to about ¾ of propodus. Double urosomite; length about twice width. Uropod 3; endopods and exopods, lanceolate, pointed .... *P. elongata* Semenova, 1981.

Genus ***Eupronoe*** Claus, 1879

(Figs 63 & 64)

Eupronoe Claus, 1879b: 26. – Gerstaecker 1886: 484-485. Claus 1887: 50-52. Stebbing 1888: 1509. Chevreux & Fage 1925: 425. Pirlot 1929: 147. Hurley 1955: 175. Bowman & Gruner 1973: 43. Zeidler 1978: 21-22. Vinogradov *et al.* 1982: 362. Shih & Chen 1995: 148. Vinogradov 1999a: 1203.

Type species

Eupronoe maculata Claus, 1879. Type material could not be found at the ZMB or ZMH and is considered lost. However, the description and figures provided by Claus (1879b, 1887) readily characterise this genus.

Diagnosis

Body shape robust or globular. Head round. Rostrum present in males only; short and rounded. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 3-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in one-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head in groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward into antennal pocket of gnathopod 1; basal article elongate, subequal in length to following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Antenna 2 females 5-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated at right angles to palp. Maxilla 1 reduced in size; single lobes; single plate with four rounded teeth; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with fringe of closely packed slender setae. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 sub-chelate; basis with antennal pocket in male; antenna 2 males with fold of articles 2 & 3 held in pocket; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus anterodistal corner extended, distinctly overlapping carpus medially. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods leaf-like, foliaceous with smooth margins. Uropod 3 endopod articulated with peduncle; endopod, and sometimes also exopod, leaf-like, foliaceous, with smooth margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Five species: *Eupronoe maculata*, *E. armata*, *E. minuta*, *E. intermedia* and *E. laticarpa*.

Sexual dimorphism

Apart from the morphology of the mandibles, the antennae, and the antennal pocket of gnathopod 1, males differ from females in having a slightly more pointed head, the carpus of gnathopod 1 is generally broader, and the carpal process of gnathopod 2 ends in a sharper point. Females also tend to have a more robust pereon.

Remarks

In all species, the coxa of pereopod 5 articulates proximally with the coxa/basis of pereopod 6, as in *Parapronoe*. Similarly all species have a weak, ridge/groove locking mechanism near the proximal, anterior corner of the ischium, and pleonites 1-3 have a slight lateral ridge that lines up with the posterior margin of pereopod 6, when the animal is curled.

Virtually nothing is known about its biology, but it seems to be associated with salps, or siphonophores, or both. *Eupronoe maculata* has been recorded with salps (Spandl 1927), and *E. minuta* has been found associated with the siphonophores, *Agalma elegans* (Harbison *et al.* 1977), *Apolemia uvaria*, and *Sulculeolaria quadrivalvis* (Laval 1980), and has also been found with the salp *Thalia democratica* (Young & Anderson 1987 – misidentified as *E. armata*).

Eupronoe is widely distributed in tropical and warm-temperate regions of the world's oceans and can, at times, be relatively abundant in plankton hauls near the surface (Stephensen 1925, Pirlot 1939).

Species of *Eupronoe* are particularly difficult to determine with certainty because of the sexual dimorphism, morphological changes due to growth and moulting, and the lack of adequate illustrations in the literature. Zeidler (1992a, 1998) gives more information on all species, together with some illustrations. Vinogradov *et al.* (1982) recognise four species; to this should be added *E. intermedia* Stebbing, 1888, which Tashiro (1978) considers a valid species, separate from *E. armata* Claus, 1879.

Key to the species of the genus *Eupronoe*

1. Body sculpture consists of small semi-circular markings ....*E. minuta* Claus, 1879
   Body sculpture consists of dorso-ventral striations 2

2. Gnathopod 2; carpal process massive with almost straight terminal margin; dactylus attached to posterodistal corner of propodus, at right angles to posterior margin .... *E. laticarpa* Stephensen, 1925

   Gnathopod 2; carpal process tapering to point; dactylus curved, attached terminally to propodus in normal manner 3

3. Gnathopod 1; merus distinctly narrower than carpus. Telson ending in sharp point, margins slightly concave distally.................................... *E. maculata* Claus, 1879

   Gnathopod 1; merus distinctly wider than carpus. Telson evenly triangular, with rounded point 4

4. Head ending in small beak. Pereopod 5; basis with anterior margin convex in female, straight or slightly concave in males. Pereopod 7; terminal article oval, length at least twice width...................................... *E. intermedia* Stebbing, 1888

   Head without beak. Pereopod 5; basis with anterior margin concave in both sexes. Pereopod 7; terminal article circular, about as long as wide .... *E. armata* Claus, 1879

Family **AMPHITHYRIDAE** new family

Diagnosis

Body; length 3-5 mm, robust but not globular. Head usually rounded, sometimes flattened dorsally, relatively small, rarely longer than first 3 pereonites. Eyes large, occupying most of head surface. Pereonites all separate. Coxae 1-6 separate from pereonites; coxa 7 fused with pereonites. Antennae 1 of females reduced to two articles, or with 2-articulate peduncle, slightly enlarged first flagellar article (callynophore), and two smaller terminal articles; of males with 1-articulate peduncle and enlarged, curved first flagellar article (callynophore) with single brush of aesthestascs along posterior margin and covering most of posterodistal corner, and 2-3 smaller, slender articles inserted on anterodistal corner. Antennae 2 absent in females;

in males with short, enlarged basal article and four slender articles, folded back on one another underneath head and pereon, second article with slight bulge distally on dorsal margin. Mandibles with palp in males, without palp in females. Maxillae 1 reduced in size with four, rounded teeth distally on medial margin. Maxillae 2 very reduced in size, consisting of single lobes, slightly curved and pointed laterally, with rounded bulge medially. Gnathopods simple or complexly chelate, with carpus with pointed process forming chela, and propodus with concave distal margin forming subchela, or only propodus with rounded, thumb-like process. Pereopods 3-7 simple. Pereopod 5 the longest, with enlarged basis, distinctly shorter than remaining articles combined, which are inserted terminally. Pereopod 6 with enlarged basis, tending towards being operculiform, sometimes overlapping distally with opposing basis; with or without fissure; remaining articles inserted subterminally, together shorter than basis. Pereopod 7 reduced to basis, sometimes with some additional articles, rarely with full compliment of articles. Uropod 2, endopod sometimes fused with peduncle. Uropod 3; endopod fused with peduncle. Telson triangular, rounded terminally, almost reaching limit of U3, not fused with double urosomite. Gills without folds, on pereonites 2-6. Oostegites on pereonites 2-5.

Three genera: *Amphithyrus, Paralycaea* and *Amphithyropsis* **gen. nov.**

Remarks

This new family has been established to accommodate *Amphithyrus, Paralycaea* and *Amphithyropsis* **gen. nov.**, which have characters in common that differ from other families of Platysceloidea. Apart from being similar in general appearance, the three genera are united by the morphology of the male antennae, the absence of second antennae in females, the relatively long pereopod 5, which has a large rectangular basis, the large basis of pereopod 6, which is almost operculiform, but is without a telsonic groove, and coxa 7 which is fused with the pereonite. All species, except *Amphithyrus glaber*, also have a distinctive reticulate or striate cuticular sculpture. The family name has been derived from *Amphithyrus* which has page priority over *Paralycaea*.

Paralycaea could not be accommodated in the family Parapronoidae because it differs significantly from *Parapronoe* in the morphology of the antennae, mandibles and maxilliped. In addition, the second antennae are absent in females, the basis of pereopod 6 lacks the typical locking mechanism, and coxa 7 is fused with the pereonite.

The rediscovery of *Tetrathyrus pulchellus* Barnard, 1930 (Zeidler 1998 – as *Paralycaea platycephala*), and its similarity to *Amphithyrus*, suggested that *Amphithyrus* was not a platyscelid. A closer examination of characters, of all genera, of Platyscelidae and Parascelidae revealed that *Amphithyrus* has several characters that preclude it from either family (see later). In particular, *Amphithyrus* lacks the characteristic telsonic groove and locking mechanism on the basis of pereopod 6. However, *Amphithyrus* has characters in common with *Amphithyropsis pulchellus* **comb. nov.**, which in turn is very similar to *Paralycaea*. Thus, the three genera have been included together in this new family, and there is some support for this grouping from the phylogenetic analysis (Fig. 58).

This family shares characters with a number of other families of Platysceloidea. The first antennae of males are like *Thamneus* (Thamneidae **fam. nov.**), and *Thyropus* and *Euscelus* (Parascelidae), in that the peduncle is one-articulate, and the callynophore has a one-field brush of aesthestascs. The second antennae of males are similar to *Tetrathyrus* (Platyscelidae). A reduction in the number of articles of the first antennae of females, found in *Paralycaea*, also occurs in *Cranocephalus* and *Rhabdosoma* (Oxycephalidae). The second antennae of females are also absent in the family Oxycephalidae and *Tetrathyrus*. The maxillae are like those of the family Parapronoidae. *Amphithyrus* and *Amphithyropsis* **gen. nov.** are most similar to some genera of the families Platyscelidae and Parascelidae, in that the basis of pereopod 6 is operculiform and has a fissure. The family also resembles Platyscelidae and Parascelidae in the fusion of coxa 7 with the pereonite, and Platyscelidae in the reduction of articles of pereopod 7, which also occurs in *Rhabdosoma* and *Tullbergella*.

A unique character of *Amphithyrus* and *Amphithyropsis* **gen. nov.** is that the basis of the opposing sixth pereopods overlap distally, with the distal margin of the right fitting under a small flap (or into a groove) on the medial surface of the left (i.e. left overlaps right). There are no corresponding structures on the right pereopod. While there are several genera with a locking mechanism on pereopod 6, *Amphithyrus* and *Amphithyropsis* are the only genera in which a mechanism for overlapping has evolved.

Other species of Platysceloidea may be able to overlap the basis of opposing sixth pereopods, but no similar mechanism has been found that could facilitate this function.

Key to the genera of family AMPHITHYRIDAE new family

1. Pereopod 6; basis without fissure ....*Paralycaea* Claus, 1879
   Pereopod 6; basis with fissure 2

2. Gnathopods 1 & 2 with pointed carpal process; dactylus forming subchela with concave distal margin of propodus ....*Amphithyrus* Claus, 1879
   Gnathopods 1 & 2 without carpal process; propodus with rounded thumb-like, anterodistal projection..*Amphithyropsis* **gen. nov.**

Genus ***Amphithyrus*** Claus, 1879
(Figs 65 & 66)

Amphithyrus Claus, 1879b: 15. – Carus 1885: 425. Gerstaecker 1886: 483. Claus 1887: 41. Stebbing 1888: 1485. Spandl 1924a: 39. Spandl 1927: 246. Pirlot 1929: 158. Hurley 1955: 188. Bowman & Gruner 1973: 55. Zeidler 1978: 40. Vinogradov *et al.* 1982: 457-458. Shih & Chen 1995: 231-232. Vinogradov 1999a: 1200.

Type species

Amphithyrus bispinosus Claus, 1879. Type material could not be found at the ZMB or ZMH and is considered lost. However, the description and figures provided by Claus (1879b, 1887), for this and other species of *Amphithyrus*, readily characterise this genus.

Diagnosis

Body shape more or less spherical. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 5; basal article distinctly inflated, about half or less the length of following article; with terminal article subequal in length to preceding one, and folded back; last two articles subequal in length to preceding one; terminal articles pointing anteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with four rounded teeth; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 fused with pereonites. Gnathopod 1 chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process not armed, conspicuously smooth. Gnathopod 2 chelate; carpal process knife-shaped; carpal process not armed, conspicuously smooth. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, and operculate; articles 3–7 inserted terminally to basis; with simple knob and groove with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; with fissure; without telsonic groove; posterodistal corner without locking mechanism but opposing pereopod can overlap; distal margin without groove, but can overlap with opposing pereopod; merus anterodistal corner extended, distinctly overlapping carpus medially. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Five species: *Amphithyrus bispinosus*, *A. similis*, *A. sculpturatus*, *A. glaber* and *A. muratus*.

Sexual dimorphism

The sexes are very similar in gross morphology, differing mainly in the morphology of the mandibles and the antennae.

Remarks

This genus has been removed from the family Platyscelidae because it has a number of characters that are inconsistent with that family as follows. The first antennae of males have a callynophore with only a one-field brush of aesthestascs; the second antennae of males have a very short, thickened basal article, about one-third as long as the following article, which has a distal bulge dorsally, as found in *Paralycaea* and *Amphithyropsis* **gen. nov.**; the second antennae are absent in females (but also *Tetrathyrus*); the first maxillae are of a different structure, similar to those found in *Paralycaea* and *Amphithyropsis* **gen. nov.**; pereopod 5 is relatively long and the articles distal to the basis do not seem to be covered by the basis; the basis of pereopod 6 does not have a telsonic groove, or a ridge/groove locking mechanism, but merely overlaps with the opposing basis, and the distal margin does not have a groove to join with the opposing basis; the telson is not fused with the double urosomite.

Amphithyrus is most like *Amphithyropsis* **gen. nov.** in the morphology of pereopod 5, and in that the basis of pereopod 6 has a relatively large, semi-circular fissure.

Virtually nothing is known about its biology, but it has been found in association with siphonophores. *Amphithyrus bispinosus* and *A. glaber* have been found with *Agalma elegans* (Harbison *et al.* 1977), and *A. similis* has been found with *Chelophyes appendiculata* (Harbison *et al.* 1977, Laval 1980).

Amphithyrus is widely distributed in tropical and warm-temperate regions of the world's oceans, and some species such as *A. bispinosus* can be relatively abundant.

Five species are currently recognised (Vinogradov *et al.* 1982).

Key to the species of the genus *Amphithyrus*

1. Coxa 5 produced posterolaterally into spinous process .....*A. bispinosus* Claus, 1879
Coxa 5 normal, without any process.. 2

2. Body and appendages without cuticular sculpture. Pereopod 6; basis with relatively small, crescent-shaped fissure........................... *A. glaber* Spandl, 1924
Body and appendages with reticulate or striate cuticular sculpture. Pereopod 6; basis with relatively large U-shaped fissure, or if fissure is crescent-shaped, cuticular sculpture is prominent... 3

3. Pereopod 6; basis with relatively small crescent-shaped fissure. Cuticular sculpture extends to uropods ....*A. sculpturatus* Claus, 1879
Pereopod 6; basis with relatively large U-shaped fissure. Cuticular sculpture not present on uropods 4

4. Cuticular sculpture striate. Telson about twice as long as last urosomite, with nipple-like process terminally... *A. similis* Claus, 1879
Cuticular sculpture reticulate. Telson shorter than last urosomite, with rounded distal margin..*A. muratus* Volkov, 1982.

Genus *Paralycaea* Claus, 1879
(Figs 67-69)

Paralycaea Claus, 1879b: 40. – Gerstaecker 1886: 486. Claus 1887: 63-64. Stebbing 1888: 1567. Schellenberg 1927: 651-652. Pirlot 1929: 135. Hurley 1955: 175. Bowman & Gruner 1973: 43-44. Zeidler 1978: 25. Vinogradov *et al.* 1982: 377-378. Shih & Chen 1995: 158. Vinogradov 1999a: 1203.

Type species

Paralycaea gracilis Claus, 1879 by monotypy. Type material could not be found at the ZMB or ZMH and is considered lost. However, the description and figures provided by Claus (1879b, 1887) readily characterise this genus.

Diagnosis

Body shape robust or globular. Head round. Rostrum absent in both sexes. Eyes occupying part of lateral head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in one-field brush medially; with two flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 1 smaller article; peduncle absent; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 2; basal article distinctly inflated, about half or less the length of following article; with terminal article subequal in length to preceding one, and folded back; last two articles subequal in length to preceding one; terminal articles pointing anteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, without medial lobe; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with four rounded teeth;

palp absent. Maxilla 2 reduced in size; bilobed, with two terminal teeth or robust setae on each lobe. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 mostly fused with pereonite. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 simple. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus anterodistal corner extended, distinctly overlapping carpus medially. Pereopod 7 reduced in size with basis not particularly enlarged; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Two species: *Paralycaea gracilis* and *P. hoylei*.

Sexual dimorphism

Apart from the morphology of the mandibles and the antennae, no obvious sexual dimorphism could be determined.

Remarks

This genus differs from the other two in the family in that the basis of pereopod 6 lacks a fissure and opposing pereopods do not seem to overlap. Gnathopods 1 and 2 are also simple.

Very little is known about its biology. Stephensen (1925) recorded *P. gracilis* with a medusa, *Aglantha* (?), but most species seem to be associated with siphonophores, Harbison *et al.* (1977) having recorded *P. gracilis* from *Agalma clausi, Sulculeolaria chuni* and *S. monoica*; *P. hoylei* from *Nanomia bijuga* and *S. quadrivalvis*, and *P. newtoniana* from *S. chuni*, *S. monoica* and *S. quadrivalvis*.

Paralycaea seems to be relatively uncommon but widely distributed in tropical and temperate regions of the world's oceans, occurring mainly in near-surface waters.

The number of valid species in this genus is contentious. Vinogradov *et al.* (1982) consider it to be monotypic, but Harbison *et al.* (1977) argue for the recognition of at least two, if not all, of the three nominal species, viz. *P. gracilis* Claus, 1879; *P. newtoniana* Bovallius, 1887 and *P. hoylei* Stebbing, 1888. Clearly a thorough revision is long overdue.

The validity of *P. gracilis* and *P. hoylei* was established recently (Zeidler 1998), but the status of *P. newtoniana* is uncertain, as the description given by Bovallius is limited, the type material appears lost, and no figures are available. It seems to be very similar to *P. hoylei*, except for pereopod 6, in which the anterodistal corner of the merus does not overlap the carpus, and the two species may yet prove to be synonymous. The specimens mentioned by Harbison *et al.* (1977) were not available for examination, and until more material becomes available, only two species are currently recognised.

Key to species of the genus *Paralycaea*

Head obliquely oval when viewed laterally, with small beak ventrally. Uropod 2; endopod fused with peduncle..*P. gracilis* Claus, 1879

Head round when viewed laterally. Uropod 2; endopod articulated with peduncle.......... ....*P. hoylei* Stebbing, 1888

Genus *Amphithyropsis* gen. nov.

(Figs 70-72)

Type species

Amphithyropsis pulchellus (Barnard, 1930) **comb. nov.**, by present designation. The holotype male is in the BMNH (1930.8.1.861).

Diagnosis

Body shape robust or globular. Head round. Rostrum absent in both sexes. Eyes occupying part of lateral head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in 1.5-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 1 smaller article; peduncle absent; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 2; basal article distinctly inflated, about half or less the length of following article; with terminal article subequal in length to preceding one, and folded back; last two articles subequal in length to preceding one; terminal articles pointing anteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor reduced to 1–2 teeth; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with four rounded teeth; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes without fringe of setae or membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 fused with pereonite. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 simple. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; with fissure; without telsonic groove; posterodistal corner without locking mechanism but opposing pereopod can overlap; distal margin without groove, but can overlap with opposing pereopod; merus anterodistal corner extended, distinctly overlapping carpus medially. Pereopod 7 reduced in size with basis not particularly enlarged; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Monotypic: *Amphithyropsis pulchellus*.

Sexual dimorphism

Apart from the morphology of the antennae and the mandibles, males differ from females in having a rounded head, and the rounded thumb-like process of the propodus of the gnathopods is slightly longer, extending just beyond the base of the dactylus.

Remarks

This new genus has been established to accommodate *Amphithyropsis pulchellus* (Barnard, 1930) because this species does not belong to *Amphithyrus* or *Paralycaea* as defined here. It does not belong to *Amphithyrus* because the first antennae of females consist of only two articles, as found in *Paralycaea*; the shape of the basis of pereopod 6 is more like *Paralycaea*, and the gnathopods are not complexly chelate. It does not belong to *Paralycaea* because the basis of pereopod 6 is like that of *Amphithyrus*, although closer in shape to that of *Paralycaea*, and the gnathopods are not simple, with gnathopod 1 approaching that of *Amphithyrus similis*. Thus, this genus is intermediate between *Amphithyrus* and *Paralycaea*.

Recently I examined the unique type of *Tetrathyrus pulchellus* and found it to be the same as *Paralycaea platycephala* Zeidler, 1998. Barnard's (1930) description of this species is inadequate, and he only illustrated pereopods 6 and 7. He placed it in *Tetrathyrus*, probably on the basis of the thumb-like projection of the propodus of the gnathopods. However, the basis of pereopod 6 has a fissure (not illustrated or referred to by Barnard), which is absent in *Tetrathyrus*. The peculiar feature of the carpus of pereopod 6 being bent upwards led me to suspect that Barnard's species may be the same as mine. Apart from Hurley (1955), who repeats Barnard's (1930) record, this species has not been recorded in the literature since its description. This is not surprising, as it is clearly not a *Tetrathyrus*, or even a species of Platyscelidae. Curiously, Hurley (1955) illustrated this species from New Zealand waters, but identified it as *Paralycaea gracilis*.

The genus has been recorded from off Three Kings Islands, New Zealand (Barnard 1930); north of Stewart Island, New Zealand (Hurley 1955) and southeast of Cape Howe, Victoria, Australia (Zeidler 1998). There are also a number of specimens from the southeast coast of South Africa, which are indistinguishable from the Tasman Sea material. Thus, this genus is currently monotypic.

Family **BRACHYSCELIDAE** Stephensen, 1923

Diagnosis

Body length up to 20 mm, but usually about 10 mm. Head of females evenly rounded, usually slightly pointed anteroventrally in males; as long as first 4-5 pereonites. Eyes large, occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antennae 1 of females with 2-articulate peduncle, and enlarged first flagellar article (callynophore), followed by two small terminal articles; of males with 2-articulate peduncle, and enlarged, curved first flagellar article (callynophore), with two-field brush of aesthestascs medially, and three smaller, slender articles inserted on anterodistal corner. Antennae 2 absent in females; in males of five slender articles folded back on one another, juncture of articles 2 & 3 and 4 & 5 supported in pocket of basis of G1. Mandibles with palp in males, without palp in females. Maxillae 1 reduced to tiny, rounded lobes. Maxillae 2 extremely reduced, to barely discernible rounded lobes. Gnathopods 1 & 2 distinctly chelate, with dentate margins. Pereopods 3-7 simple. Pereopod 5 the longest. Pereopods 5 & 6 with greatly enlarged basis, slightly shorter than remaining articles combined, which are inserted terminally. Pereopod 7 reduced in size, but with full complement of articles, with enlarged basis, which is longer than remaining articles combined. Uropods with articulated endopods and exopods. Telson triangular, usually extending to limit of U3, not fused with double urosomite. Gills with folds on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Brachyscelus*.

Remarks

Bovallius (1890), in a footnote, divided the old family Tryphaenidae into two; Lycaeidae and Euthamneidae (for *Brachyscelus* and *Thamneus*) and changed *Thamneus* to *Euthamneus* to avoid confusion, and fit with the new family name. However, Stephensen (1932) quite rightly points out that *Brachyscelus* is the older generic name, and "the family must be named after the older genus and so be called Brachyscelidae". Not all subsequent authors have accepted this arrangement and have restored *Brachyscelus* and *Thamneus* to the family Lycaeidae (e.g. Bowman & Gruner 1973, Shih & Chen 1995), while others support the recognition of Brachyscelidae (e.g. Vinogradov *et al.* 1982, Vinogradov 1999a).

In this review the family Brachyscelidae is maintained for the genus *Brachyscelus* because it differs significantly from the family Lycaeidae in a number of characters as follows. The head of males is usually pointed (round in *Lycaea* and only slightly pointed in *Simorhynchotus*); the second antennae of males have the juncture of articles 2 & 3 and 4 & 5 supported in a pocket of the basis of gnathopod 1 (absent in Lycaeidae); the second antennae of males consist of a relatively long basal article, followed by three slightly longer articles, and one shorter one, all folded back on one another, the terminal one being about one-quarter as long as the preceding one, and orientated anteriorly (in Lycaeidae the basal article is only about one-third as long as the following article and the terminal article is minute, is not folded, and is orientated posteriorly); the basis of pereopods 5 and 6 is more operculiform, and in pereopod 6 the terminal articles are inserted subterminally to the basis; the endopods and exopods of the uropods are never fused with the peduncle; the telson is not fused with the double urosomite. In addition, newly hatched juveniles of *B. crusculum* have specialised appendages that differ from those of the adult. In particular, pereopod 5 is chelate, while in the adult it is simple. *Lycaea* lacks these specialised appendages, thus supporting the familial status for *Brachyscelus* (Harbison 1976). Some of the above characters, such as the morphology of the male head and the pereopods, are intermediate between the families Lycaeidae and Oxycephalidae. The morphology of the maxillae are also like those of Lycaeidae and Oxycephalidae.

Prior to this review this family included *Thamneus*, which has been removed to the new family, Thamneidae, because it has characters that are unique and inconsistent with *Brachyscelus* (or Lycaeidae).

Genus ***Brachyscelus*** Bate, 1861

(Figs 73 & 74)

Brachyscelus Bate, 1861: 7. – Bate 1862: 333. Stebbing 1888: 1543. Chevreux & Fage 1925: 427. Schellenberg 1927: 648-649. Pirlot 1929: 139. Hurley 1955: 181. Bowman & Gruner 1973: 47. Zeidler 1978: 28. Vinogradov *et al.* 1982: 395. Shih & Chen 1995: 178. Vinogradov 1999a: 1193.

Daira Dana, 1853: 981 (part).

Dairinia Dana, 1853: 1442 (part). – Bate 1862: 309.

Thamyris Bate, 1862: 335. – Claus 1879b: 32-36. Claus 1880: 588. Carus 1885: 426. Gerstaecker 1886: 485. Claus 1887: 56-59. Bovallius 1887b: 574.

Schnehagenia Claus 1871: 157.

Type species

Brachyscelus crusculum Bate, 1861 by monotypy. Type material could not be found at the BMNH or MNHN and is considered lost. However, the description and figures of Bate (1861) readily characterise this genus and its status is well established in the literature.

Type species of synonyms

The type species of *Thamyris* is *T. antipodes* Bate, 1862. Type material could not be located at the BMNH or MNHN and is considered lost. However, the description and figures of Bate (1862) are clearly those of a species of *Brachyscelus*, most likely *B. crusculum*.

The type species of *Schnehagenia* is *S. rapax* Claus, 1871. Type material could not be located at the ZMB or ZMH and is considered lost. It is not clear why Claus (1871) failed to appreciate that his species belonged to *Brachyscelus*. The figures and description of Claus (1887) are clearly those of a species of *Brachyscelus*.

Some of the species assigned to *Daira* or *Dairinia* by Dana (1853) are clearly species of *Brachyscelus*.

Diagnosis

Body shape robust or globular. Head round. Rostrum present in males only; short and rounded. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward into antennal pocket of gnathopod 1; basal article elongate, subequal in length to following article; with terminal article shorter than preceding one, and folded back; terminal articles pointing anteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single small rounded plate; palp absent.

Maxilla 2 reduced in size; small rounded lobe. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 sub-chelate; basis with antennal pocket in male; antenna 2 males with fold of articles 2 & 3 and 4 & 5 held in pocket; carpal process knife-shaped; carpal process armed with prominent teeth only. Gnathopod 2 sub-chelate; carpal process knife-shaped; carpal process armed with prominent teeth only. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Five species: *Brachyscelus crusculum*, *B. rapax*, *B. globiceps*, *B. macrocephalus* and *B. rapacoides*.

Sexual dimorphism

Apart from obvious differences in the morphology of the antennae, mandibles and gnathopod 1, males tend to be more slender in habit, and the head is more elongate, with a distinct point or beak in the majority of species. In some species the head is rounded in males, as in females, but is relatively smaller.

Remarks

This genus bears some similarities to the families Parapronoidae and Amphithyridae, especially in the enlarged basis of pereopods 5 and 6, but there is no evidence of a locking mechanism on the basis of pereopod 6, or that the basis of opposing sixth pereopods overlap. However, the ischium loosely overlaps the merus on both sixth pereopods and this may, in some way, enable the opposing pereopods to be held together. It also seems likely that all species are able to curl up into a ball, as the coxa of pereopod 5 articulates proximally with the coxa/basis of pereopod 6, and the pleonites have a lateral ridge which, when the pleon is curled, lines up with the posterior margin of the basis of pereopod 6.

This genus also resembles *Eupronoe* in the character of the male second antennae being held in a pocket on the basis of gnathopod 1, which has already been discussed under Parapronoidae.

Brachyscelus has been recorded from a variety of gelatinous plankton although most species seem to be preferentially associated with medusae. *Brachyscelus crusculum* has been recorded in association with salps (Stephensen 1923, 1925; Young & Anderson 1987) and medusae (Pirlot 1939), specifically the salps *Cyclosalpa affinis*, *Iasis zonaria*, *Pegea socia*, *Salpa maxima*, *Thalia democratica* (Harbison *et al.* 1977) and *Salpa fusiformis* (Laval 1980), and the medusa *Aequorea* sp., as well as Leptomedusae (Harbison *et al.* 1977). It has also been observed swimming around a heteropod, *Pterotrachea* sp., but the relationship, if any, is not clear (Harbison *et al.* 1977). *Brachyscelus rapacoides* has been recorded with Hydromedusae, and the medusae *Aequorea* sp., *Orchististoma* sp. and *Leuckartiara* sp., as well as with the pteropod *Cavolina longirostris* (Harbison *et al.* 1977).

Brachyscelus is widely distributed in tropical and warm-temperate regions of the world's oceans, and some species, such as *B. crusculum,* can be relatively abundant. Species, for which data are available, appear to be epipelagic to shallow-mesopelagic in habit (e.g. Thurston 1976).

This genus is in a state of considerable taxonomic confusion and a revision is long overdue. According to Madin and Harbison (1977) at least 17 species of *Brachyscelus* have been described, but only four of these are recognised as valid by Vinogradov *et al.* (1982). However, studies of Tasman Sea material (Zeidler 1992a, 1998), and limited examination of specimens in most major museums, have resulted in the recognition of at least five species.

Key to the species of the genus *Brachyscelus*

1. Head round in males (like female). Gnathopod 1; carpus with anterodistal corner developed into feeble lobe. Telson as long as wide 2

   Head pointed in males. Gnathopod 1; carpus with anterodistal corner developed into distinct lobe, partly overlapping propodus (especially in mature specimens). Telson longer than wide 3

2. Head as long as first five pereonites or less. Pereopod 6; basis with anterodistal lobe with rounded distal margin. Telson about as long as double urosomite .... *B. globiceps* (Claus 1879)

   Head as long as pereon. Pereopod 6; basis with anterodistal lobe pointed. Telson length about two-thirds double urosomite .... *B. macrocephalus* Stephensen, 1925

3. Pereopod 6; basis with anterodistal lobe reaching well beyond ischium, with straight distal margin. Double urosomite about as broad as long. Uropod 3 with broad exopods and endopods, particularly the endopod .... *B. crusculum* Bate, 1861

   Pereopod 6; basis with anterodistal lobe only reaching middle, or limit, of ischium, with round distal margin. Double urosomite distinctly broader than long. Uropod 3; exopods and endopods not especially broad..................................... 4

4. Gnathopods; carpal process with single row of large teeth. Pereopod 7; basis as long as following articles combined. Uropod 3; endopod slightly excised distally (as in *B. crusculum*). Male A2; terminal article very short, much less than half-length of preceding article .... *B. rapax* (Claus, 1871)

Gnathopods; carpal process with large teeth interspersed with smaller ones. Pereopod 7; basis slightly longer than following articles combined. Uropod 3; endopod tapers gradually. Male A2; terminal article about half-length of preceding article .... *B. rapacoides* Stephensen, 1925

Family **LYCAEIDAE** Claus, 1879

Diagnosis

Body length 5-10 mm, with slightly inflated pereon, especially in females. Head of females rounded, relatively large; slightly smaller in males but also rounded (*Lycaea*) or slightly pointed (*Simorhynchotus*); as long as first 3-5 pereonites. Eyes large, occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antennae 1 of females with 2-articulate peduncle, and enlarged first flagellar article (callynophore), followed by two small, terminal articles; of males with 2-articulate peduncle, and enlarged, curved first flagellar article (callynophore) with two-field brush of aesthestascs medially, and three smaller, slender articles inserted on, or near, anterodistal corner. Antennae 2 absent in females; in males with relatively short, slightly enlarged basal article, three slender articles folded back on one another and one short terminal article, tucked underneath head and pereon. Mandibles with palp in males, without palp in females. Maxillae 1 very reduced in size, consisting of tiny rounded lobes, or absent. Maxillae 2 absent. Gnathopods simple, weakly chelate or subchelate. Pereopods 3-7 simple. Pereopod 5 the longest. Pereopods 5 & 6 with moderately enlarged basis, distinctly shorter than remaining articles combined, which are inserted terminally. Pereopod 7 reduced in size, but with full complement of articles, with enlarged basis, which is longer than remaining articles combined. Uropod 1 with articulated endopods and exopods. Uropod 2, endopod sometimes fused with peduncle. Uropod 3, endopod always fused with peduncle. Telson triangular, with rounded apex, usually extending to near limit of U3, fused with double urosomite. Gills with folds on pereonites 2-6. Oostegites on pereonites 2-5.

Two genera: *Lycaea* and *Simorhynchotus*.

Remarks

The systematic limits of this family are in a state of flux, with some authors including such diverse genera as *Pseudolycaea* (=*Lycaea*), *Tryphana*, *Brachyscelus* and *Thamneus*, besides *Lycaea* (e.g. Bowman & Gruner 1973, Shih & Chen 1995). Authors who have accepted this arrangement usually place *Simorhynchotus* in the family Oxycephalidae, based on the erroneous assumption that the maxillae are present in Lycaeidae and absent in Oxycephalidae and *Simorhynchotus*. While the maxillae are not discernible in *Simorhynchotus*, this is only true for two genera of Oxycephalidae; *Oxycephalus* and *Rhabdosoma*. In all other genera of Oxycephalidae, the first maxillae are reduced to a small rounded lobe, and the second maxillae are absent, or so reduced that they cannot be distinguished from the buccal mass, as found in *Brachyscelus* and *Lycaea*. Thus, there is no valid reason to include *Simorhynchotus* in the family Oxycephalidae based on the absence of maxillae. In *Thamneus* the maxillae are present as small rounded lobes and in *Tryphana* the maxillae are relatively well developed.

In this review Lycaeidae is restricted to the genera *Lycaea* and *Simorhynchotus*. *Simorhynchotus* more closely resembles *Lycaea*, rather than any genus of Oxycephalidae, in the general habit and the morphology of the second antennae of males, and the gnathopods, pereopods, urosome and coxae. Also, in both *Lycaea* and *Simorhynchotus* the second antennae of males extend posteriorly for the entire length of the pereon. In Oxycephalidae the second antennae of males usually extend posteriorly to about pereonite 2, and only in *Tullbergella* do they extend beyond pereonite 2, to about pereonite 5. Similarly, in other families of Platysceloidea the second antennae of males do not extend posteriorly much further than about pereonite 5.

Justification for the removal of *Brachyscelus*, *Thamneus* and *Tryphana* from Lycaeidae is presented under the respective families Brachyscelidae, Thamneidae **fam. nov.** and Tryphanidae.

Clearly the family Lycaeidae is most closely related to Oxycephalidae, and this is supported by the phylogenetic analysis (Figs 57 & 58).

Key to the genera of the family LYCAEIDAE

Head rounded in both sexes. Gnathopods 1 & 2 both subchelate, or both simple .... *Lycaea* Dana, 1852

Head rounded in female, slightly produced and pointed in male. Gnathopod 1 simple. Gnathopod 2 subchelate .... *Simorhynchotus* Stebbing, 1888

Genus ***Lycaea*** Dana, 1852

(Figs 75-77)

Lycaea Dana, 1852: 316. – Dana 1853: 1017. Bate 1862: 338. Claus 1879b: 37-39. Carus 1885: 426. Gerstaecker 1886: 485-486. Claus 1887: 61-62. Stebbing 1888: 1563. Chevreux & Fage 1925: 429. Pirlot 1929: 136. Hurley 1955: 180. Bowman & Gruner 1973: 46. Zeidler 1978: 26. Vinogradov *et al.* 1982: 381-382. Shih & Chen 1995: 170-171. Vinogradov 1999a: 1194.

Pseudolycaea Claus, 1879b: 41. – Carus 1885: 426. Gerstaecker 1886: 486. Claus 1887: 64. Chevreux & Fage 1925: 430. Pirlot 1929: 138. Bowman & Gruner 1973: 47. Shih & Chen 1995: 183.

Metalycaea Stephensen, 1925: 183. Nair 1993: 1172.

Type species

Lycaea ochracea Dana, 1853 by subsequent designation. Type material could not be found in any major North American museum and is considered lost. Although the description and figures of Dana (1853) readily characterise this genus they are insufficient to determine the status of his species. The next oldest available species, *L. pulex* Marion, 1874, was therefore substituted to characterise the genus.

Type species of synonyms

The type species of *Pseudolycaea* is *P. pachypoda* Claus, 1879. Type material could not be found at the ZMB or ZMH and is considered lost. However, the description and figures of Claus (1879b, 1887) readily characterise this species, which is considered to be insufficiently different from other species of *Lycaea* to warrant generic recognition (see Remarks).

The type species of *Metalycaea* is *M. globosa* Stephensen, 1925. Three female syntypes are in the ZMUC (CRU 6567). This species is considered to be a species of *Lycaea*, near *L. serrata* (see Remarks).

Diagnosis

Body shape robust or globular. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 7; basal article distinctly inflated, about half or less the length of following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single small rounded plate; palp absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 sub-chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Gnathopod 2 sub-chelate; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Six to eight species of uncertain taxonomic status.

Sexual dimorphism

Apart from the morphology of the mandibles and the antennae, females are more robust than males, especially in the pereon. Males are generally more elongate, and have a relatively smaller head.

Remarks

This genus resembles *Tullbergella* in the morphology of the male antennae, mandibles and maxillae. Species of *Lycaea*, for which the morphology of the first antennae of males is known, fall into two groups. Those without a distal bulge on the anterior/dorsal margin of the callynophore (*L. pulex*, *L. serrata*, *L. nasuta* and *L. pachypoda*), and those with a slight distal bulge on the anterior/dorsal margin of the callynophore (*L. vincentii*, *L. bovalli* and *L. bajensis*). The latter approach the condition found in *Simorhynchotus*, and in all Oxycephalidae, except *Glossocephalus*. Thus, *Lycaea* may be closely related to the family Oxycephalidae.

In the past the genus *Pseudolycaea* has been considered monotypic amongst the family Lycaeidae, because of the almost simple gnathopods. In all other respects it resembles

Lycaea. As the gnathopods of *Lycaea* can vary from subchelate to almost simple (*L. serrata*), the validity of *Pseudolycaea* seems unjustified, and, like Vinogradov *et al.* (1982), I regard it as a synonym of *Lycaea*. Similarly, *Metalycaea*, which Nair (1993) resurrected as a valid genus of Oxycephalidae, is considered to be a species of *Lycaea*, similar to *L. serrata* (if not synonymous). Like *Simorhynchotus*, its inclusion in the Oxycephalidae on the presumed absence of the maxillae has been demonstrated to be invalid. An examination of the type material of *M. globosa* has confirmed that it is most probably the same as *L. serrata*, although it was not possible to examine the mouthparts for the presence or absence of maxillae. The specimens referred to by Nair (1993) have not been examined.

Lycaea is a well known associate of salps (Dana 1853, Marion 1974, Chevreux 1900), and Harbison (1976) even recorded the distribution of males, females and juveniles of *L. pulex* and *L. vincentii* on salp chains. From the available evidence, it seems that females may remain on the host, once settled, while males are more pelagic in habit, seeking out the settled females. The greater development of the pleon and urosome of the male supports this hypothesis.

Lycaea pulex and *L. pachypoda* have been recorded from *Salpa maxima* and pyrosomes (Chevreux 1892, 1900, Chevreux & Fage 1925, Laval 1980). *Lycaea pachypoda* has also been recorded from the medusa *Liriope tetraphylla* (Harbison *et al.* 1977), while *L. pulex* has been recorded in association with a variety of salps, *Cyclosalpa pinnata*, *Pegea confoederata* (Harbison 1976); *Cyclosalpa affinis*, *C. bakeri*, *C. pinnata*, *Helicosalpa komanii*, *Ihlea punctata*, *Pegea socia*, *P. bicaudata*, *P. confoederata*, *Salpa cylindrica*, *S. maxima*, *Transtedtra multitentaculata* (Madin & Harbison 1977). Similarly, *L. nasuta* has been recorded with *Cyclosalpa affinis*; *L. vincentii* with *Pegea confoederata* and *Salpa maxima*, and *L. 'bovallioides'* with *Cyclosalpa pinnata*, *Pegea socia*, *P. confoederata*, *Salpa cylindrica* and *S. maxima* (Madin & Harbison 1977). *Lycaea 'bovallioides'* has also been recorded with the pteropod *Corolla spectabilis* (Harbison *et al.* 1977).

Lycaea appears to be widespread in tropical and temperate regions of the world's oceans. Because of the confused taxonomy of species it is difficult to determine depth ranges for species, but most seem to be epipelagic in habit.

Species of *Lycaea* have always been difficult to determine and a thorough revision of the genus is required. Harbison and Madin (1976) provide a useful key to eight species, which they consider valid. Of these eight species, Vinogradov *et al* (1982) recognise three, but they regard *L. pauli* Stebbing, 1888, considered synonymous with *L. pulex* by Harbison and Madin, as valid, and include *L. pachypoda* and *L. lilia* Volkov (as a new species). Considering the state of taxonomic confusion of this genus it seems pointless to provide a key to species.

Genus ***Simorhynchotus*** Stebbing, 1888

(Figs 78 & 79)

Simorhynchus Claus 1871: 156. – Claus 1879b: 42-43. Gerstaecker 1886: 486. Claus 1887: 65.

Simorhynchotus Stebbing, 1888: 1572. – Bovallius 1890: 48. Pirlot 1929: 161. Hurley 1955: 182. Bowman & Gruner 1973: 53. Zeidler 1978: 31. Vinogradov *et al.* 1982: 390-391. Shih & Chen 1995: 212.

Type species

Simorhynchus antennarius Claus, 1871 by monotypy. Type material could not be found at the ZMB or ZMH and is considered lost. However, the description and figures provided for this species by Claus (1871, 1879b, 1887) readily characterise this genus.

Diagnosis

Body shape robust or globular. Head round. Rostrum present in both sexes; short and rounded. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with small anterodistal lobe; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted below anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 7; basal article distinctly inflated, about half or less the length of following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 sub-chelate; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Monotypic: *Simorhynchotus antennarius*.

Sexual dimorphism

Apart from the morphology of the mandibles and the antennae, females are more robust than males, especially in the pereon, as is found in *Lycaea*. In addition, the head of males is produced into a short, slightly pointed rostrum.

Remarks

In the past *Simorhynchotus* has often been placed in the family Oxycephalidae based on the slightly pointed head of males. However, the rostrum length is no greater than in males of Pronoidae or Brachyscelidae, and in general body shape, and especially in the form of gnathopod 2, *Simorhynchotus* resembles *Lycaea*. The pereopods, coxae and urosome are also more like lycaeids than oxycephalids. Thus, this genus links the families Lycaeidae and Oxycephalidae.

Very little is known about its biology. Laval (1980) recorded it in association with the medusa *Geryonia proboscidalis*.

Simorhynchotus is widely distributed, with a preference for near-surface, tropical waters.

Family **ANAPRONOIDAE** Bowman & Gruner, 1973

Diagnosis

Body length up to 8 mm, relatively plump, not laterally compressed. Head globular, with small 'beak' between antennae 1, as long as first 3-4 pereonites. Eyes large, occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antennae 1 of females with 3-articulate peduncle, first peduncular article the largest, flagellum of three slender articles, callynophore not enlarged; of males with 3-articulate peduncle, and enlarged, curved first flagellar article (callynophore), with single brush of aesthestascs along posterior margin, and three smaller, slender articles inserted on anterodistal corner. Antennae 2 of both sexes held in diagonal groove across ventral surface of head; of females of four slender articles, and one small terminal article; of males with three slender articles folded back on one another (the third slightly longer than the preceding two which are subequal in length), followed by three smaller articles that are not folded, together at about right angles to previous articles, directed towards head. Mouthparts styliform. Mandibles with palp in males, without palp in females. Maxillae 1 reduced to single lobes, with four bifid teeth distally on medial margin. Maxillae 2 reduced in size, bilobed, with two robust setae terminally on each lobe. Gnathopod 1 subchelate; gnathopod 2 chelate; basis of both very broad. Pereopods 3-7 simple. Pereopod 5 the longest with relatively broad basis. Pereopod 6 with broad basis but not operculate, distal articles inserted subterminally, together slightly shorter than basis. Pereopod 7 reduced in size, with full compliment of articles; basis slightly shorter than remaining articles combined. Uropods with articulated endopods and exopods. Telson triangular, rounded terminally, reaching limit of U3, not fused with double urosomite. Gills with folds on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Anapronoe*.

Remarks

The orientation of the antennae, especially antennae 2 of the male, is unique amongst the suborder Hyperiidea, justifying the establishment of the family Anapronoidae by Bowman and Gruner (1973). In the morphology of the antennae, females resemble those of the families Platyscelidae and Parascelidae, but differ in many other respects.

Zeidler (1997b) revised this family and corrected some errors made by previous authors, particularly in relation to the antennae and mandibular palp of males.

Genus *Anapronoe* Stephensen, 1925

(Figs 80-84)

Anapronoe Stephensen, 1925: 163. – Spandl 1927: 217. Bowman & Gruner 1973: 45. Vinogradov *et al.* 1982: 380. Shih & Chen 1995: 168. Zeidler 1997b: 139. Vinogradov 1999a: 1193.

Type species

Anapronoe reinhardti Stephensen, 1925 by monotypy. The unique male holotype is in the ZMUC (CRU 439) (Zeidler 1997b).

Diagnosis

Body shape robust or globular. Head round. Rostrum absent in both sexes. Eyes occupying part of lateral head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 3-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in one-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head in groove. Antenna 2 males 6-articulate; zig-zagged, with some articles folded back on each other; positioned in groove across head. Antenna 2 females 5-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with four bifid teeth; palp absent. Maxilla 2 reduced in size; bilobed, with two terminal teeth or robust setae on each lobe. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 sub-chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Gnathopod 2 chelate; carpal process spoon-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with basis not particularly enlarged; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Two species: *Anapronoe reinhardti* and *A. bowmani*.

Sexual dimorphism

The sexes are remarkably similar in gross morphology, differing mainly in the morphology of the antennae and the mandibles.

Remarks

Anapronoe is very rare in plankton collections. Material has been collected from the warm-temperate to tropical regions of the world's oceans, via vertical hauls from great depths (0-1000 m, 0-1500 m, 0-3000 m). Considering its rarity, one might speculate that *Anapronoe* is a deep-water genus, but other material was collected near the surface.

Nothing is known regarding its biology and there is no record of any association with gelatinous plankton.

Zeidler (1997b) redescribed *A. reinhardti* and described one new species.

Key to the species of the genus *Anapronoe*

Gnathopod 2; carpal process distally rounded, reaching to about middle of propodus, anterodistal margin smooth. Gnathopods and P3-6 with few, long setae on margins of articles... *A. reinhardti* Stephensen, 1925

Gnathopod 2; carpal process distally pointed, reaching to about limit of propodus, anterodistal margin with row of small teeth. Gnathopods and P3-6 with numerous, long setae on both margins of articles..........*A. bowmani* Zeidler, 1997

Family **THAMNEIDAE** new family

Diagnosis

Body length up to 10 mm, very plump, flattened dorsoventrally, especially in females. Head flattened, with slightly upturned, chisel-shaped rostrum in males, short and rounded in females, with slight depression dorsally. Eyes occupying most of head surface except for rostrum. Pereonites all separate. Coxae separate from pereonites. Antennae 1 of females with 2-articulate peduncle, and enlarged first flagellar article (callynophore), followed by two smaller terminal articles; of males with 1-articulate peduncle, and enlarged, curved first flagellar article (callynophore), with single brush of aesthestascs along posterior margin, and three smaller, slender articles inserted on anterodistal corner. Antennae 2 absent in females; in males reduced in size, about as long as A1, of four slender articles in a curve medially. Mandibles with palp in males, without palp in females. Maxillae 1 & 2 reduced to single, tiny rounded lobes. Gnathopods 1 & 2 subchelate. Pereopods 3-7 simple. Pereopod 5 the longest, with only slightly enlarged basis. Pereopod 6 similar to P5. Pereopod 7 reduced in size, with full compliment of articles; basis enlarged, about as long as remaining articles combined. Uropods with articulated endopods and exopods. Telson oval, reaching to about two-thirds of endopod of U3, not fused with double urosomite. Gills with folds on pereonites 2-6. Oostegites on pereonites 2-5.

One genus: *Thamneus.*

Remarks

This family has been established to accommodate *Thamneus* because it has characters that differ significantly from the family Brachyscelidae, and that are inconsistent with those of any other family.

Characters that distinguish *Thamneus* from other families of Platysceloidea are as follows. The head is relatively small, with a chisel-shaped rostrum, with bilateral, dorsal depressions. The body is subglobular, and dorsoventrally flattened, unlike any other platysceloidean. The second antennae of males consist of four shortened articles, which are not folded under the head, but arranged in a zigzag fashion, and together are much shorter than the head. The second maxillae consist of small, rounded lobes, whereas in all other Platysceloidea the second maxillae are absent, or if present, differ morphologically. The uropoda have relatively short, wide peduncles approaching the condition found in some members of the families Platyscelidae and Parascelidae.

This family resembles Amphithyridae, and the genera *Glossocephalus*, *Thyropus* and *Euscelus*, in the morphology of the male first antennae. In the absence of second antennae in females, it is like Brachyscelidae, Amphithyridae, Lycaeidae, Oxycephalidae and *Tetrathyrus*. The gnathopods resemble those of *Brachyscelus*, and pereopods 3-7 are most similar to those of Lycaeidae. Thus, Thamneidae shares characters with a number of families.

As mentioned under Brachyscelidae, Bovallius (1890) established the family Euthamneidae for *Brachyscelus* and *Thamneus*, and changed *Thamneus* to *Euthamneus* to avoid confusion, and fit with the new family name. However, as Stephensen (1923) points out, *Brachyscelus* is the older name and the family must be named after the older genus. In any case Bovallius's (1890) change of *Thamneus* to *Euthamneus* is invalid, and there is no reason why *Thamneus* should be rejected or changed in any way. Thus, the family name used here is derived from *Thamneus*. Bowman and Gruner (1973) also recognised the validity of Bovallius's earlier name, although some authors still use *Euthamneus* (e.g. Vinogradov *et al.* 1982, Vinogradov 1999a).

Genus ***Thamneus*** Bovallius, 1887

(Figs 85 & 86)

Thamneus Bovallius, 1887a: 31. – Stebbing 1888: 1558. Schellenberg 1927: 650. Bowman & Gruner 1973: 48. Shih & Chen 1995: 185.

Euthamneus Bovallius, 1890: 19. – Pirlot 1929: 153. Vinogradov *et al.* 1982: 401. Vinogradov 1999a: 1194.

Dairinia – (part), Bate 1862: 309. Bovallius 1885: 9.

Type species

Thamneus rostratus Bovallius, 1887 by monotypy. Type material could not be located at the SMNH, ZMUC or in Uppsala and is considered lost. However, *Thamneus* is a very distinctive genus.

Diagnosis

Body shape robust or globular. Head round. Rostrum present in both sexes; short and pointed. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in one-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 4-articulate; loosely zig-zagged or S-shaped, without any articles folded back on each other; only extends forward under head. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated at right angles to palp. Maxilla 1 reduced in size; single lobes; single small rounded plate; palp absent. Maxilla 2 reduced in size; small rounded lobe. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 sub-chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with prominent teeth only. Gnathopod 2 sub-chelate; carpal process knife-shaped; carpal process armed with prominent teeth only. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Monotypic: *Thamneus rostratus*.

Sexual dimorphism

Apart from the morphology of the antennae and mandibles, females are considerably more plump and wider than males, and the rostrum is much shorter, with an almost single, dorsal depression between the eyes.

Remarks

This is a very distinctive genus, easily distinguished by morphology of the head, body, pereopods and the second antennae of males.

It has been recorded in association with medusae (Stephensen 1925), and in particular *Pelagia noctiluca* (Harbison *et al.* 1977, Laval 1980). Otherwise very little is known about its biology. It is relatively uncommon, but widely distributed, known from records in tropical and temperate regions (Dick, 1970).

Family **TRYPHANIDAE** Boeck, 1871

Diagnosis

Body length up to 6 mm, relatively robust. Head rounded, relatively large, as long as first three pereonites. Eyes large, occupying most of head surface. Pereonites all separate. Coxae separate from pereonites. Antennae 1 of females with 2-articulate peduncle, and enlarged first flagellar article (callynophore), with about five aesthestascs grouped on diagonal posterodistal corner, followed by one slender, terminal article; of male with 2-articulate peduncle, and almost spherical, first flagellar article (callynophore), with single brush of aesthestascs on posterior margin; second flagellar article is slender and about as long as previous articles combined; third flagellar article is very slender and small, and is inserted subterminally, together with row of three aesthestascs. Antennae 2 of females consists of two, broad, slightly curved articles; of males with relatively short, enlarged basal article, followed by four slender articles of similar length, folded back on one another, the terminal article being more slender and slightly longer than any other; slender, folded articles held obliquely upwards in cavity of head. Mandibles with incisor with distal corner produced into rounded lobe medially; palp 3-articulate in males, 2-articulate in females. Maxillae 1 reduced to small quadrate lobes. Maxillae 2 reduced to small rounded lobes. Gnathopods and pereopods simple. Gnathopod 1, basis enlarged, almost as broad as long. Pereopods 3-6 with robust articles, dactylus closing against produced distal margin of propodus. Pereopod 5 the longest. Pereopod 7 reduced in size but with full compliment of articles; basis as long as remaining articles combined. Uropods with articulated endopods and exopods. Telson triangular, about a long as peduncle of U3, not fused with double urosomite. Gills without folds on pereonites 2-5, gill with fold on pereonite 6. Oostegites on pereonites 2-5.

One genus: *Tryphana*.

Remarks

This family has had a chequered history. It was proposed by Boeck (1871) for his new genus and species, *Tryphana malmi*. Bovallius (1887a) expanded it to include *Brachyscelus* (as *Thamyris*), *Thamneus*, *Lycaea*, *Paralycaea*, *Pseudolycaea* (=*Lycaea*) and *Simorhynchotus* (as *Simorhynchus*). Later (1890) he dispensed with the family altogether, placing *Lycaea* and *Pseudolycaea* in the family Lycaeidae, *Brachyscelus* and *Thamneus* (changed to *Euthamneus*) in a new family, Euthamneidae, *Paralycaea* is placed in the family Pronoidae and *Simorhynchotus* in the family Oxycephalidae. *Tryphana*, for some obscure reason, is considered to be like *Lycaeopsis*, and is placed with it in the family Phorcidae (=Lycaeopsidae). However, subsequent authors have included *Tryphana* in the family Lycaeidae (e.g. Chevreux & Fage 1925, Stephensen 1925, Bowman & Gruner 1973). Vinogradov *et al.* (1982) recognised the unique characters of *Tryphana* and reinstituted the family Tryphanidae, but mistakenly attribute it to Bovallius 1887. Not all subsequent authors have accepted this change (e.g. Shih & Chen 1995).

Tryphanidae, represented by *Tryphana*, has a number of unique characters that readily distinguish it from other families of Platysceloidea as follows. The morphology of the first antennae of males is unlike any other hyperiidean. The second antennae of males have a whip-like terminal article, which is longer than any preceding one, and the slender, folded articles are held obliquely upwards in a cavity in the head; a unique character only discovered recently while examining fresh specimens. The second antennae of females (absent in Lycaeidae) are unusual, and consist of two, broad, slightly curved articles, pressed closely to the side of the head. The mandibles have an incisor with the distal corner produced into a rounded lobe, which is unusually large. Females have a 2-articulate mandibular palp; *Pronoe* is the only other genus in which females have a mandibular palp (3-articulate). The inner lobes of the maxilliped are divided for about half their length. The morphology of the gnathopods is unusual but approach those of *Pronoe*. Pereopods 3-6 are almost prehensile, whereas they are simple in all other Platysceloidea.

Genus *Tryphana* Boeck, 1871

(Figs 87-90)

Tryphana Boeck, 1871: 9. – Gerstaecker 1886: 483. Bovallius 1887b: 572-573. Stebbing 1888: 1538. Sars 1890: 16. Schellenberg 1927: 653-654. Pirlot 1929: 135. Hurley 1955: 180. Bowman & Gruner 1973: 48. Vinogradov *et al.* 1982: 393. Shih & Chen 1995: 187. Vinogradov 1999a: 1204.

Type species

Tryphana malmi Boeck, 1871 by monotypy. Type material could not be found at the SMNH, ZMUC or in any major Norwegian Museum (Vader pers. comm.) and is considered lost. Although the description of Boeck (1871) is limited he later (Boeck 1872) provides some illustrations which readily characterise this genus.

Diagnosis

Body shape robust or globular. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with enlarged globular callynophore and 1–3 articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in one-field brush medially; with two flagellar articles terminally; subterminal article inserted on anterodorsal corner, terminal article inserted midway anteriorly on subterminal article. Antenna 1 female flagellum with narrowly rectangular callynophore and 1 smaller article; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; positioned obliquely up into head; basal article distinctly inflated, about half or less the length of following article; with terminal article subequal in length to preceding one, and folded back; last two articles subequal in length to preceding one; terminal articles pointing anteriorly. Antenna 2 females 2-articulate. Mandibular palp present in both sexes; females 2-articulate; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with relatively large distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; small quadrate plate; palp absent. Maxilla 2 reduced in size; curved, rounded with terminal denticles and with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes incompletely fused, i.e., slightly separate terminally; inner lobes well developed; medial margin of outer lobes without fringe of setae or membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 simple. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple, or with poorly developed subchela. Pereopod 5 simple, or with poorly developed subchela; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple, or with poorly developed subchela; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; some with fold on pereonite 5 or 6 or both.

Monotypic: *Tryphana malmi.*

Sexual dimorphism

The sexes are very similar in gross morphology, differing mainly in the morphology of the mandibles and the antennae. Males tend to have a slightly pointed head, which is also slightly narrowed anteriorly.

Remarks

This is a very distinctive genus, currently considered to be monotypic.

Virtually nothing is known regarding its biology. Laval (1980) recorded it from the siphonophore *Ceratocymba sagittata*, at Villefranche, France, Mediterranean Sea.

Tryphana is an uncommon but widely distributed genus, known mainly from records from temperate regions (Dick 1970). It seems to be epipelagic in habit (Thurston 1976).

Family **OXYCEPHALIDAE** Bate, 1862

Diagnosis

Body length up to 150 mm (mostly rostrum and telson in *Rhabdosoma*) but usually only 10-30 mm; body form variable, ranging from extremely elongate to relatively compact. Head usually produced into long rostrum, with distinct neck, sometimes globular, with relatively short rostrum. Eyes large, occupying most of head surface, except rostrum and neck. Pereonites all separate. Coxae totally fused, partly fused or not fused, with pereonites. Antennae 1 of females with 0-3 articulate peduncle, and enlarged first flagellar article (callynophore), followed by 0-2 smaller terminal articles; of males with 1-2 articulate peduncle, and enlarged, curved first flagellar article (callynophore), often with anterodistal corner transformed into distinct "horn", with 1-2 field brush of aesthestascs medially, and 1-3 smaller, slender articles inserted just below anterodistal corner of callynophore. Antennae 2 absent in females; in males of four slender articles, usually of similar length, folded back on one another, plus one tiny terminal article, all held underneath head and anterior part of pereon. Mandibles with palp in males, ranging from very elongate in species with long rostrum to one article in *Glossocephalus*; without palp in females. Maxillae 1 very reduced in size consisting of tiny rounded lobes, sometimes not discernible, or absent. Maxillae 2 absent. Gnathopods chelate or subchelate. Pereopods 3-7 simple. Pereopod 5 the longest. Pereopods 5 & 6 usually with moderately enlarged basis, distinctly shorter than remaining articles combined, which are inserted terminally. Pereopod 7 reduced in size, with full complement of articles, or distal articles sometimes reduced in number

(*Tullbergella*), or absent (*Rhabdosoma*), with enlarged basis which is longer than remaining articles combined. Uropod 1 with articulated endopods and exopods. Uropods 2 & 3; endopod sometimes fused with peduncle. Telson triangular and pointed, sometimes rounded, usually extending beyond limit of U3, usually fused with double urosomite. Gills with or without folds, usually on pereonites 2-6, sometimes rudimentary or absent on one or more of pereonites 2-4. Oostegites usually on pereonites 2-5, sometimes only on pereonites 3-5, sometimes reduced in size.

Eight genera: *Oxycephalus*, *Rhabdosoma*, *Leptocotis*, *Calamorhynchus*, *Glossocephalus*, *Tullbergella*, *Streetsia* and *Cranocephalus*.

Remarks

This family appears to be polyphyletic but a great deal more detailed taxonomic work is required to resolve the systematic status of the eight genera currently recognised. These genera are grouped together mainly on the basis of having a well developed rostrum, which may vary considerably in length and general morphology, but is generally much longer than found in any other family of Hyperiidea.

The family Oxycephalidae was reviewed by Bovallius (1890) and to some extent by Fage (1960). However, Fage was concerned only with material from the *Dana* expeditions (1928-1930) and his taxonomic treatment of the family is limited. Therefore, no thorough taxonomic revision of the family has appeared this century. Since the review of Fage (1960), the systematics of the family has changed little except for the exclusion of *Simorhynchotus*, which has been transferred to the family Lycaeidae. *Metalycaea*, which Nair (1993) argued should be recognised as a valid genus of Oxycephalidae, is regarded a synonym of *Lycaea*.

The phylogenetic analysis (Figs 57, 58) supports the view that *Rhabdosoma*, *Glossocephalus*, and *Tullbergella* vary considerably from other genera of Oxycephalidae (and each other) and may warrant removal from this family.

Most genera for which data are available are preferentially associated with ctenophores.

Key to the genera of the family OXYCEPHALIDAE

1. Body extremely slender, with long, needle-shaped rostrum. Pereopod 7 reduced to basis (sometimes with one or two additional articles) .... *Rhabdosoma* White, 1847

   Body only moderately slender, rostrum produced into sharp or blunt point, never needle-shaped. Pereopod 7 with all articles present or if reduced, body is robust 2

2. Rostrum with broad lateral flanges .... *Calamorhynchus* Streets, 1878

   Rostrum without lateral flanges 3

3. Double urosomite; length more than 3x width. Uropod 1 with very short exopod .... *Leptocotis* Streets, 1877

   Double urosomite; length less than 3x width. Uropods 1-3 with well developed exopods and endopods 4

4. Rostrum rounded. Pereopods 5 & 6 paddle-like; basis not much wider than following articles.. *Glossocephalus* Bovallius, 1887

   Rostrum pointed. Pereopods 5 & 6 with basis considerably wider than following articles 5

5. Pereopod 6; basis with posterodistal corner produced into distinct, almost upturned, triangular process. Pereopod 7 with reduced number of articles .... *Tullbergella* Bovallius, 1887

   Pereopod 6; basis with posterodistal corner not produced, rounded. Pereopod 7 with all articles present 6

6. Uropods 2 & 3; endopod fused with peduncle. Gnathopod 1 chelate .... *Oxycephalus* Milne-Edwards, 1830

   Uropods 2 & 3; endopod free. Gnathopod 1 subchelate 7

7. Head barrel-shaped. Coxae free, without processes .... *Streetsia* Stebbing, 1888

Head globular. Coxae fused with pereonites. Pereonite 5 (fused coxa) produced into backward-pointed process............................*Cranocephalus* Bovallius, 1890

Genus ***Oxycephalus*** Milne-Edwards, 1830

(Figs 91-95)

Oxycephalus Milne-Edwards, 1830: 396. – Guérin-Méneville 1836c: 9. Milne-Edwards 1838: 307. Lucas 1840: 240. Milne-Edwards 1840: 99. Nicolet 1849: 249. Dana 1852: 316. Dana 1853: 1009, 1443. Bate 1862: 342. Claus 1871: 155. Streets 1877: 136. Streets 1878: 278. Claus 1879b: 43. Claus 1880: 588. Claus 1884: 455. Carus 1885: 427. Gerstaecker 1886: 487. Bovallius 1887a: 35. Claus 1887: 68. Stebbing 1888: 1576. Bovallius 1890: 54. Spandl 1924a: 32. Spandl 1927: 179. Pirlot 1929: 162. Hurley 1955: 182. Fage 1960: 29. Pillai 1966a: 173. Bowman & Gruner 1973: 49. Zeidler 1978: 32. Vinogradov *et al.* 1982: 404. Zeidler 1992a: 120. Shih & Chen 1995: 190-191. Zeidler 1999: 392-393. Vinogradov 1999a: 1196.

Orio Cocco, 1832: 206. – Cocco 1833: 113 (in part). Prestandrea 1833: 11. Costa & Costa 1840: 5 (in part). Costa in Hope 1851: 21.

Ornithoramphus Natale, 1850a: 12. – Costa in Hope 1851: 21. Carus 1885: 428.

Erpetoramphus Natale, 1850b: 11. – Costa in Hope 1851: 22.

Natalius Costa, 1864: 87. – Carus 1885: 427.

Type species

Oxycephalus piscatoris Milne-Edwards, 1830 by monotypy. Type material could not be found at the BMNH, MNHN or ANSP (which has some types of Milne-Edwards) and is presumed lost. Despite the loss of type material, and the lack of illustrations at the time, *Oxycephalus* is a readily distinguished genus and is well established in the literature.

Type species of synonyms

The type species of *Orio* is *O. ornithoramphus* Cocco, 1832. Type material could not be located in any Italian or major European museum, and is considered lost. The description and figures of Cocco (1832) appear to resemble a male *Oxycephalus*, but are insufficient for a specific determination.

The type species of *Ornithoramphus* is *O. coccoi* Natale, 1850. Type material could not be located in any Italian or major European museum, and is considered lost. The figure by Natale (1850a) clearly resembles a male *Oxycephalus* but it, and the description, is insufficient for a specific determination.

The type species of *Erpetoramphus* is *E. costae* Natale, 1850. Type material could not be located in any Italian or major European museum, and is considered lost. The description and figure by Natale (1850b) are insufficient for a specific determination, but the species appears to belong to *Oxycephalus*, despite the fact that the first gnathopods are illustrated as subchelate.

The type species of *Natalius* is *N. candidissimus* Costa, 1864. Type material could not be located in any Italian or major European museum, and is considered lost. The descriptions of the genus and species by Costa (1864) seem to correspond to *Oxycephalus*, but the species description does not contain sufficient detail for a specific determination.

Diagnosis

Body shape elongate and narrow. Head oval. Rostrum present in both sexes; distinctly elongate. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with small anterodistal lobe; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted below anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 1; basal article elongate, subequal in length to following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all partly fused with pereonites. Gnathopod 1 chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with prominent teeth only. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with prominent teeth only. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, but not operculate; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with basis not particularly enlarged; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; some with fold on pereonite 5 or 6 or both.

Three species: *Oxycephalus piscator*, *O. latirostris* and *O. clausi*.

Sexual dimorphism

The sexes are very similar in appearance, and apart from the morphology of the antennae and mouthparts, are distinguished as follows. Females have a relatively smaller head and rostrum, and the head is slightly more bulbous around the eyes. In mature males the head is characteristically indented on the dorsal surface, above the eyes, with a slight keel anteriorly. The carpus of gnathopod 2 is relatively more slender in females. The basis of pereopod 7 is distinctly more narrowed distally in females, and sometimes the propodus can be relatively longer in mature females.

Remarks

This genus is distinguished from all others in the family by a combination of characters, mainly the morphology of the head, gnathopods, double urosomite, and uropods.

Oxycephalus does not closely resemble any other genus of Oxycephalidae. The shape of the cephalon vaguely resembles *Cranocephalus*, *Leptocotis* and *Streetsia*. *Oxycephalus* also resembles *Calamorhynchus*, *Cranocephalus* and *Rhabdosoma* in that the coxae are fused with the pereonites, and *Rhabdosoma* in having uropods 2 and 3 with endopods fused with the peduncle. The chelate gnathopods of *Oxycephalus* are very distinctive. Other oxycephalids that have both gnathopods chelate, although different from *Oxycephalus* in morphology, are *Calamorhynchus*, *Glossocephalus*, *Leptocotis*, and *Rhabdosoma*. Thus, *Oxycephalus* has characters in common with all other genera of Oxycephalidae, except perhaps for *Tullbergella*, but even that genus has uropod 3 with the endopod fused with the peduncle as in *Oxycephalus*.

Oxycephalus is a common component of plankton collections. Fage (1960) provides the most comprehensive biogeographical information available for this genus. Species seem to be preferentially associated with ctenophores, but have also been recorded with medusae and heteropods. *Oxycephalus piscator* has been recorded with medusae (Carus 1885) and the ctenophores *Leucothea multicornis* (Chun 1889) and *Mnemiopsis mccradyi* (Harbison *et al.* 1978). *Oxycephalus latirostris* has been recorded from the ctenophores *Cestum veneris* and *Eurhamphaea vexilligera* (Harbison *et al.* 1978). *Oxycephalus clausi* has been recorded with a variety of gelatinous plankton, including medusae, colonial radiolarians (Harbison *et al.* 1978), the heteropod *Pterotrachea hippocampus* (Harbison *et al.* 1977), the salps *Pegea socia* and *Salpa cylindrica* (Madin & Harbison 1977), but most frequently on ctenophores as follows; *Ocyropsis maculata* (Harbison *et al.* 1977, 1978), *Cestum veneris*, *Eurhamphaea vexilligera*, *Mnemiopsis mccradyi*, *Ocyropsis cristallina*, *O. maculata*, *Beroe* sp. (Harbison *et al.* 1978), *Ocyropsis maculata maculata*, *O. m. immaculata* and *O. crystata guttata* (Zeidler 1999).

Oxycephalus is a tropical genus although it sometimes occurs in temperate regions. It occurs worldwide and seems to prefer near-surface waters.

Key to species of the genus *Oxycephalus*

1. Pleonite 1, or pleonites 1-3, with sharp, medial tooth on ventral margin (and on posterodistal corner).. 2
   Pleonite without sharp medial projection on ventral margin.................................. 3

2. Pleonites 1-3 with medial tooth on ventral margin. Gnathopods 1 & 2; carpus with anterodistal corner produced into sharp point, above propodus (not always apparent in immature specimens) ....*O. clausi* Bovallius, 1887
   Only pleonite 1 with medial tooth on ventral margin (usually only in juvenile specimens less than 10 mm). Gnathopods 1 & 2; carpus without anterodistal corner produced.. *O. piscator* Milne-Edwards, 1830

3. Pereopod 7; propodus styliform, slightly longer than ischium to carpus combined (only in females) ....*O. latirostris* Claus, 1879
   Pereopod 7; propodus normal, only slightly longer, or shorter than carpus (in both sexes).. 4

4. Cutting edges of carpus and propodus of G1 & 2 with row of closely packed, relatively long, sharp teeth..*O. latirostris* Claus, 1879
   Cutting edges of carpus and propodus of G1 & 2 with few teeth, not in distinct row ....*O. piscator* Milne-Edwards, 1830

Genus ***Rhabdosoma*** White, 1847
(Figs 96 & 97)

Xyphicéphale Guérin-Méneville in Eydoux & Souleyet, 1842: 271.

Rhabdosoma White, 1847: 130. – Dana 1852: 316. Dana 1853: 1009. Bate 1862: 344. Claus 1871: 155. Streets 1878: 286. Claus 1879b: 49-51. Gerstaecker 1886: 487. Claus 1887: 73-74. Stebbing 1888: 1606. Stebbing 1895: 367. Spandl 1927: 207. Bowman & Gruner 1973: 52-53. Zeidler 1978: 36. Vinogradov *et al.* 1982: 431-432. Shih & Chen 1995: 206. Vinogradov 1999a: 1197.

Xiphocephalus Bovallius, 1890: 116. – Pirlot 1929: 168.

Macrocephalus Bate, 1858: 361-362.

Rhabdonectes Bovallius, 1887a: 39.

Pseudanurus Garbowski, 1895: 199.

Type species

Oxycephalus armatus Milne-Edwards, 1840. A probable syntype is in the ANSP, CA4200 (Guérin-Méneville Coll., no. 458) but the supposed type in the MNHN (Am 4807) is lost (see Zeidler 1997a). However, *Rhabdosoma* is a very distinctive genus.

Type species of synonyms

See Remarks for *Xyphicéphale* and *Xiphocephalus*.

The type species of *Macrocephalus* is *M. longirostris* Bate, 1858. Type material could not be located at the BMNH or MNHN and is considered lost. The brief description by Bate (1858) is suggestive of *Rhabdosoma*, and later (Bate 1862) he recognised the synonymy.

Rhabdonectes was proposed by Bovallius (1887a) as a replacement name for *Rhabdosoma* because he believed that it was preoccupied.

Pseudanurus was instituted by Garbowski (1895) for *R. brevicaudatum* Stebbing, 1888 because he believed that this species differed sufficiently to warrant a separate genus.

Diagnosis

Body shape elongate and narrow. Head oval. Rostrum present in both sexes; distinctly elongate. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with relatively large anterodistal lobe; with aesthestascs arranged in two-field brush medially; with one flagellar article terminally; distal articles inserted below anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 1 smaller article, or flagellum with narrowly rectangular callynophore and no additional articles; peduncle 1-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 1; basal article elongate, subequal in length to following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all fully fused with pereonites. Gnathopod 1 chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson articulated with double urosomite. Oostegites on pereonites 2–6. Gills on pereonites 2–6 or 5 and 6 in female, 4–6 or 5 and 6 in male; all without folds.

Four species: *Rhabdosoma armatum*, *R. whitei*, *R. brevicaudatum* and *R. minor*.

Sexual dimorphism

Sexually mature males of *R. brevicaudatum* and *R. minor* have not been recorded, and these species may be parthenogenic. In the other two currently recognised species, females have a relatively longer rostrum; the telson is longer relative to uropod 3; the gnathopods have a slightly longer carpal process, and gills occur on pereonites 2–6. In males, gills occur on pereonites 4–6, or 5 and 6.

Remarks

As suggested by Stebbing (1895), Guérin-Méneville (1842) merely gave an opinion on the taxonomic status of *Oxycephalus armatum* Milne-Edwards, 1840 (=*R. armatum*), and foreshadowed a suitable name, *Xyphicéphale*, but did not institute a new genus. Thus, Bovallius (1890) is wrong in accepting this, and changing it to *Xiphocephalus*. In rejecting this name we are left with *Rhabdosoma* as the earliest name for the genus and, except for Pirlot (1929), this has been accepted since Stebbing (1895).

Rhabdosoma is one of the most bizarre genera of Hyperiidea, easily characterised by the extremely slender, elongate body, and very long, needle-shaped rostrum. It seems to bear little resemblance to any other genus of Oxycephalidae, and it is the only one in which the telson is not fused with the double urosomite, although juveniles may have the telson fused (e.g. *R. brevicaudatum*). It resembles *Cranocephalus* in the reduction of the number of articles of the first antennae of females. The second antennae of males resemble those of *Leptocotis* and *Glossocephalus*, in that the juncture of articles 3/4 extends forward of the juncture of articles 1/2. In the absence of maxillae it resembles

Oxycephalus. The maxilliped is like that of *Oxycephalus* and *Cranocephalus*. The character of coxae fused with pereonites is shared with *Oxycephalus*, *Calamorhynchus* and *Cranocephalus*.

Fage (1960) provides the most comprehensive biogeographical information for this genus. Most species seem to be epipelagic in habit, preferring tropical and subtropical waters.

The only recorded association with gelatinous plankton is for juveniles of *R. whitei* and *Rhabdosoma* sp. with the ctenophore, *Beroe* sp. (Harbison *et al.* 1978).

Four species are currently recognised as valid (Fage 1960 , Vinogradov *et al.* 1982). Two large species, *R. armatum* and *R. whitei*, are distinguished by the morphology of the gnathopods, and uropods, and the two small species, *R. brevicaudatum* and *R. minor*, by the relative length of the telson. The two small species (< 30 mm) could be mistaken for juvenile *R. armatum*, in which the urosome is similar, and the telson is also reduced, but the presence of ovigerous females demonstrates the validity of these species. They appear to be parthenogenic, as mature males have not been found. Fage (1960) studied 643 specimens of *R. brevicaudatum* and 1921 specimens of *R. minor* without finding any males. It is sometimes difficult to distinguish between these two species as the length of the telson seems to vary, and Vinogradov *et al.* (1982) suspect that they may even be synonymous. However, in all the specimens that were examined the first antennae of *R. brevicaudatum* consist of the basal article, callynophore, and one small terminal article while in *R. minor* the first antennae are like those of female *R. whitei*, consisting of just the basal article, and callynophore, although, the callynophore seems to have an incomplete article proximally, thus approaching the condition found in female *R. armatum* (Fig. 97).

Key to species of the genus *Rhabdosoma*

1. Telson acute terminally, distinctly longer than U2, reaching beyond U3 in adults. Female with gills on pereonites 2-6. Body size 60-150 mm.............................. 2

Telson rounded terminally, distinctly shorter than U2. Female with gills on pereonites 5 & 6. Body size rarely exceeds 30 mm 3

2. Gnathopod 1; carpal process with additional tooth on posterior margin. Uropods 2 & 3 with minute exopods .... *R. armatum* (Milne-Edwards, 1840)

Gnathopod 1; carpal process simple, without additional tooth. Uropods 2 & 3 with relatively well developed exopods .... *R. whitei* Bate, 1862

3. Telson; length much less than half of double urosomite, not reaching limit of U2. Antennae 1 of female with small article terminally on callynophore .... *R. brevicaudatum* Stebbing, 1888

Telson; length slightly more than half of double urosomite, reaching limit of U2. Antennae 1 of female consists only of basal article and callynophore .... *R. minor* Fage, 1954

Genus ***Leptocotis*** Streets, 1877

(Figs 98 & 99)

Leptocotis Streets, 1877: 136-137. – Streets 1878: 283. Stebbing 1888: 1593. Bovallius 1890: 110. Spandl 1927: 204. Pirlot 1929: 168. Hurley 1955: 182. Bowman & Gruner 1973: 52. Zeidler 1978: 30. Vinogradov *et al.* 1982: 421. Shih & Chen 1995: 203-204.

Oxycephalus (part) – Claus 1879b: 48. Claus 1887: 71.

Dorycephalus Bovallius, 1890: 75. - Spandl 1927: 203.

Type species

Leptocotis spinifera Streets, 1877. Type material could not be found at any major North American museum and is considered lost. However, *Leptocotis* is a very distinctive genus, unlikely to be confused with any other of the Oxycephalidae. *Leptocotis spinifera* is currently considered to be synonymous with *Leptocotis tenuirostris* (Claus, 1871).

Type species of synonyms

The type species of *Dorycephalus* is *Leptocotis lindstroemi* Bovallius, 1887. Type material could not be found at the SMNH, ZMUC or in Uppsala and is considered lost. However, there is no doubt that it is synonymous with *Leptocotis*, although the validity of species attributed to this genus by Bovallius (1890) warrants further investigation. It is likely that the sexual dimorphism of uropod 2 may account for some of the confusion, as Bovallius separated the two genera on the basis of the morphology of the urosome and uropods.

Diagnosis

Body shape elongate and narrow. Head oval. Rostrum present in both sexes; distinctly elongate. Eyes occupying most of head surface, grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with relatively large anterodistal lobe; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted below anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antennae 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 1; basal article elongate, subequal in length to following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single small rounded plate; palp absent. Maxillae 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 sub-chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with prominent teeth and setae. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with prominent teeth and setae. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, but not operculate; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle in male; fused with peduncle in female; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Monotypic: *Leptocotis tenuirostris*.

Sexual dimorphism

This genus is unusual in the sexual dimorphism of uropod 2. In females the endopod is fused with the peduncle, while in males it is articulated with the peduncle, and the denticles on the outer margin are finely serrated. In addition, the head of females is more bulbous around the eyes, and in mature males the head is characteristically indented on the dorsal surface, above the eyes, anterior to the neck. The double urosomite is also relatively longer in males.

Remarks

This genus is readily distinguished by the morphology of the rostrum, gnathopods and urosome.

Leptocotis is similar to *Calamorhynchus* and *Oxycephalus* in general habit, and in the morphology of the pereopods, and the first antennae of females. The first antennae of males, with an anterodistal 'horn' on the callynophore, resemble those of *Calamorhynchus*, *Cranocephalus, Streetsia* and *Tullbergella.* The second antennae of males are like those of *Glossocephalus* and *Rhabdosoma*, in that the juncture of articles 3/4 extends forward of the juncture of articles 1/2. The first maxillae consist of small, rounded lobes as is found in all other genera of Oxycephalidae except for *Oxycephalus* and *Rhabdosoma*. The maxilliped is most similar to that of *Calamorhynchus*. In having coxae separate from the pereonites, it resembles *Glossocephalus*, *Streetsia* and *Tullbergella*, although in the former genus the seventh coxae are fused with the pereonite.

The fifth pereopods of *Leptocotis* have a relatively long, spinose structure on the medial surface of the coxae, which is analogous to similar structures found in most genera of Platysceloidea, allowing for the proximal articulation with the sixth pereopods. However, in *Leptocotis* the pereopods are sufficiently separated on the pereon so that articulation between pereopods 5 and 6 seems unlikely. Thus, the function of this spinose process is unclear. A similar structure is found in *Streetsia*.

Fage (1960) provides some information on the biology of *Leptocotis*, but there are no records of associations with gelatinous plankton. It seems to be epipelagic in habit, and is widely distributed in all of the world's oceans, with a preference for tropical waters, although it is apparently absent from the Mediterranean and Red Seas (Fage 1960).

Genus ***Calamorhynchus*** Streets, 1878

(Figs 100 & 101)

Calamorhynchus Streets, 1878: 285. – Stebbing 1888: 1599. Bovallius 1890: 72. Spandl 1927: 197. Pirlot 1929: 163. Hurley 1955: 182. Bowman & Gruner 1973: 50. Vinogradov *et al.* 1982: 423. Shih & Chen 1995: 198.

Type species

Calamorhynchus pellucidus Streets, 1878 by monotypy. Type material could not be found at any major North American museum and is considered lost. However, *Calamorhynchus* is a very distinctive genus, unlikely to be confused with any other of the Oxycephalidae.

Diagnosis

Body shape elongate and narrow. Head oval. Rostrum present in both sexes; distinctly elongate; with lateral flanges. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with relatively large anterodistal lobe; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted below anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 1; basal article elongate, subequal in length to following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, without medial lobe; in male orientated more or less parallel to palp. Maxilla 1 absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all partly fused with pereonites. Gnathopod 1 sub-chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with prominent teeth and setae. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with prominent teeth and setae. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, but not operculate;

articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Monotypic: *Calamorhynchus pellucidus*.

Sexual dimorphism

The sexes differ mainly in the morphology of the antennae and mandibles. Also, in males the dorsal keel on the head is often more developed than in females, and the lateral flanges are relatively feeble compared to females.

Remarks

This genus is readily distinguished by the morphology of the rostrum, gnathopods and urosome.

Calamorhynchus most closely resembles *Leptocotis* in general habit, and in the morphology of the pereopods, the first antennae of females, and the maxilliped. The first antennae of males resemble those of *Leptocotis*, *Cranocephalus*, *Streetsia* and *Tullbergella*. The second antennae of males are like those of *Oxycephalus* and *Streetsia*. The first maxillae consist of tiny, rounded lobes, similar to that found in all other Oxycephalidae except for *Oxycephalus* and *Rhabdosoma*. In having the coxae fused with the pereonites it resembles *Oxycephalus*, *Cranocephalus* and *Rhabdosoma*.

Fage (1960) provides some information on the biology of *Calamorhynchus*, but there are not records of associations with gelatinous plankton. It seems to be epipelagic in habit, occurring mainly in depths of 0-300 m (Fage 1960). It appears to be relatively uncommon, but is widely distributed, mainly in tropical regions of the world's oceans.

Genus ***Glossocephalus*** Bovallius, 1887

(Figs 102 & 103)

Glossocephalus Bovallius, 1887a: 35. – Bovallius 1890: 105. Chevreux & Fage 1925: 432-433. Spandl 1927: 196. Bowman & Gruner 1973: 51-52. Zeidler 1978: 34. Vinogradov *et al.* 1982: 427. Shih & Chen 1995: 200.

Elsia Giles, 1890: 249-250.

Type species

Glossocephalus milneedwardsi Bovallius, 1887. Type material could not be found at the SMNH, ZMUC or in Uppsala and is considered lost. However, *Glossocephalus* is a very distinctive genus whose status has been confirmed by Bovallius (1890).

Type species of synonyms

The type species of *Elsia* is *E. indica* Giles, 1890. Type material could not be found at the BMNH and is considered lost. However, the description and figures of Giles clearly represent *Glossocephalus*.

Diagnosis

Body shape elongate and narrow. Head round. Rostrum present in both sexes; short and rounded. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with small anterodistal lobe; with aesthestascs arranged in one-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 1; basal article elongate, subequal in length to following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 1-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single small rounded plate; palp absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae some fully fused or partly fused with pereonites. Gnathopod 1 chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process not armed, conspicuously smooth. Gnathopod 2 chelate; carpal process knife-shaped; carpal process not armed, conspicuously smooth. Pereopods 3 & 4 distinctly longer than pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 3–5. Gills on pereonites 2–6 in female, 3–6 in male; all without folds.

Monotypic: *Glossocephalus milneedwardsi*.

Sexual dimorphism

Apart from obvious morphological differences in the antennae and mandibles, males have a more elongate (less globular) head; gills are absent on pereonite 2, and pereopods 5 and 6 have slightly broader articles than in females.

Remarks

This genus is readily distinguished by the morphology of the rostrum, gnathopods, pereopods and urosome.

Glossocephalus has a number of unusual characters that support its removal from the family Oxycephalidae. In particular the mandibular palp in males consists of a single article, with a rounded lateral process. In all other genera of the superfamily Platysceloidea, males have a 3-articulate mandibular palp. The first antennae of males are similar to those of Amphithyridae and Thamneidae. The morphology of the maxilliped is unique, in that the peduncle has two small humps near the base of the outer lobes, and the inner lobe has a distinct, medial invagination. Pereopods 5 and 6 are paddle-like, and the basis is not especially enlarged, as is characteristic of other Platysceloidea. The seventh pairs of coxae are fused with the pereonite as in Amphithyridae, Parascelidae and most Platyscelidae. Gills are absent on pereonite 2 of males. Also the rostrum is not much longer than found in some other genera of Platysceloidea. However, until a thorough revision of this and other genera of Platysceloidea is undertaken, it is difficult to reassign *Glossocephalus*.

Amongst the family Oxycephalidae, *Glossocephalus* resembles *Oxycephalus*, *Leptocotis* and *Calamorhynchus* in the morphology of the first antennae of females; *Rhabdosoma* and *Leptocotis* in the morphology of the second antennae of males, and all other genera, except *Oxycephalus* and *Rhabdosoma*, in the presence of first maxillae.

Glossocephalus has, to date, only been recorded in association with the ctenophores *Deiopea kaloktenota* (Krambach 1911, Steuer 1911a, b), *Bolinopsis vitrea* (Harbison *et al.* 1977, 1978), *Leucothea multicornis*, *Cestum veneris* (Harbison *et al.* 1978), *L.*

multicornis, *Beroe ovata* (Laval 1980), *L. pulchra* and *Bolinopsis rubrapunctatus* (SAMA specimens).

Fage (1960) provides some information on the biology of *Glossocephalus*, and demonstrated that it occurred most frequently in the top 100 m, was fairly abundant down to 200 m, but very infrequent below that depth. It seems to be relatively uncommon, but is widely distributed in, mainly, tropical regions of the world's oceans.

Genus ***Tullbergella*** Bovallius, 1887

(Figs 104 & 105)

Tullbergella Bovallius, 1887a: 38. – Bovallius 1890: 68-69. Bowman & Gruner 1973: 53-54. Zeidler 1978: 33. Vinogradov *et al.* 1982: 425. Shih & Chen 1995: 223.

Type species

Tullbergella cuspidata Bovallius, 1887 by monotypy. Type material could not be found at the SMNH, ZMUC or in Uppsala and is considered lost. However, *Tullbergella* is a very distinctive genus whose status has been confirmed by the later work of Bovallius (1890).

Diagnosis

Body shape robust or globular. Head round. Rostrum present in both sexes; short and pointed. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with relatively large anterodistal lobe; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted below anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 5; basal article distinctly inflated, about half or less the length of following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single small rounded plate; palp absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 sub-chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with prominent teeth and setae. Gnathopod 2 sub-chelate; carpal process knife-shaped; carpal process armed with prominent teeth and setae. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis as wide or less than 5x as wide as following articles; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis as wide or less than 5x as wide as following articles; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Monotypic: *Tullbergella cuspidata*.

Sexual dimorphism

The sexes are remarkably similar in general morphology and, except for the antennae and mandibles, no additional sexual dimorphism could be determined amongst the limited material examined.

Remarks

This genus is readily distinguished by the morphology of the rostrum, gnathopods, pereopods and urosome. The relatively short, sharp rostrum, robust body, and thick cuticle are also unlike other members of Oxycephalidae.

Tullbergella has a number of unusual characters that support its removal from the family Oxycephalidae. The first antennae of females are like those of *Tetrathyrus* (and *Streetsia*) in that the callynophore has a proximal bulge. Other genera of Platyscelidae are also similar in this regard but the bulge on the callynophore is located distally. The first antennae of males are more like those of *Simorhynchotus* (Lycaeidae) than other Oxycephalidae. The second antennae of males are also like those of Lycaeidae in general morphology, and in that they extend under the body to pereonite 5. In all other genera of Oxycephalidae the second antennae of males are projected under the head for most of their length, and extend posteriorly only to pereonite 1, or rarely to pereonite 2. The mandibles are also more like those of Lycaeidae, while the maxillae resemble the families Brachyscelidae, Lycaeidae and most genera of Oxycephalidae.

Amongst the family Oxycephalidae, *Tullbergella* is most similar to *Streetsia* in the morphology of the first antennae of females and the maxilliped, and in that the head is without a neck (except for *S. mindanaonis*). In having the coxae separate from the pereonites, it resembles *Leptocotis*, *Glossocephalus* (fused with pereonite 7) and *Streetsia*.

Tullbergella is a relatively rare genus and consequently very little is known about its biology. Barnard (1931) recorded it on medusae, *Cotylorhiza* sp. (?), and some SAMA specimens, also from the outer Barrier Reef, were found “under medusae”. In this regard it is unlike most other Oxycephalidae, which are preferentially associated with ctenophores.

Tullbergella seems to prefer surface waters in tropical regions, and has been recorded from the South China Sea, the Java Sea, the Great Barrier Reef, the Indian Ocean southwest of India and the Atlantic Ocean near Barbados.

Genus ***Streetsia*** Stebbing, 1888

(Figs 106 & 107)

Streetsia Stebbing, 1888: 1603. – Bovallius 1890: 80. Spandl 1927: 184. Pirlot 1929: 164. Hurley 1955: 182. Bowman & Gruner 1973: 53. Zeidler 1978: 35. Vinogradov *et al*. 1982: 412-413. Shih & Chen 1995: 215. Vinogradov 1999a: 1198.

Oxycephalus (part) – Claus 1879b: 43. Claus 1887: 68.

Type species

Streetsia challengeri Stebbing, 1888 by monotypy. The unique, holotype female is in the BMNH (89.5.15.324): on three microscope slides.

Type species of synonyms

Some species assigned to *Oxycephalus* by Claus (1879b, 1887) clearly belong with *Streetsia*.

Diagnosis

Body shape elongate and narrow. Head oval. Rostrum present in both sexes; distinctly elongate. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with relatively large anterodistal lobe; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted below anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 1; basal article elongate, subequal in length to following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single rounded lobe with terminal denticles; palp absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 sub-chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with prominent teeth and setae. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with prominent teeth and setae. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, but not operculate; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Five species: *Streetsia steenstrupi*, *S. porcella*, *S. challengeri*, *S. mindanaonis* and *S. palmaspinosa*.

Sexual dimorphism

Some species exhibit more sexual dimorphism than do others. For example, mature females of *S. challengeri* have gnathopod 2 with the posterodistal corner of the basis expanded into a triangular lobe; a character not found in males or any other species of *Streetsia*. In *S. mindanaonis* the head of females has a slight neck, and in males the head has a slight dorsal depression, just posterior to the eyes, although it is not always well developed. Generally the head of males is relatively shorter, and there are minor variations in the setation of the gnathopods, and morphology of the pereopods.

Remarks

This genus is readily distinguished by the long, barrel-shaped head, which is produced into a sharp rostrum.

Streetsia most closely resembles *Leptocotis* in general habit, but in the morphology of the male antennae, mandibles, and maxilliped, it is more like *Calamorhynchus*. The first antennae of females are similar to *Tullbergella* in that the callynophore has a slight bulge. The first maxillae are relatively large with a group of tubercles terminally, unlike other genera of Oxycephalidae. In having the coxae separate from the pereonites, it resembles *Leptocotis*, *Glossocephalus* (fused with pereonite 7) and *Tullbergella*.

The fifth pereopods of *Streetsia* have a long, spinose structure on the medial surface of the coxae, similar to that found in *Leptocotis*. It does not seem to function as a means of articulation with the sixth pereopods, as the pereopods are too far apart on the pereon to allow for articulation between pereopods.

Fage (1960) provides considerable biogeographical information regarding this genus. Most species seem to be epipelagic in habit, preferring tropical and subtropical waters.

As with other genera of Oxycephalidae, *Streetsia* is preferentially associated with ctenophores, although recorded associations are few. Juveniles have been found with the ctenophore *Leucothea pulchra* (SAMA specimens), and *S. porcella* has been recorded with radiolarian colonies, marine snow, and the ctenophores, *Leucothea* sp. (Harbison *et al.* 1977), *L. multicornis* and *Eurhamphaea vexilligera* (Harbison *et al.* 1978).

Fage (1960) recognised four species, and one other has been described by Vinogradov (1990a).

Key to species of the genus *Streetsia*

1. Pereopod 6; basis with posterior margin produced into sharp lobe distally, projecting well beyond ischium. Gnathopod 2 of mature females; basis with posterodistal corner produced into rounded lobe .... *S. challengeri* Stebbing, 1888

   Pereopod 6; basis with posterior margin produced into rounded lobe distally, rarely projecting much beyond ischium. Gnathopod 2 of mature females; basis with normal posterodistal corner 2

2. Double urosomite almost twice as long as wide, or longer 3

   Double urosomite about as long as wide 4

3. Gnathopod 2; carpal process produced to base of dactylus. Epimeral plates without noticeable cuticular pore .... *S. steenstrupi* (Bovallius, 1887)

   Gnathopod 2; carpal process only reaching to about 0.7x length of propodus. Epimeral plates with large, central cuticular pore.. .... *S. mindanaonis* (Stebbing, 1888)

4. Gnathopod 2; carpal process with distal margin serrate...... *S. porcella* (Claus, 1879)

   Gnathopod 2; carpal process with distal margin armed with strong teeth.................. .... *S. palmaspinosa* Vinogradov, 1990

Genus ***Cranocephalus*** Bovallius, 1890

(Figs 108 & 109)

Cranocephalus Bovallius, 1890: 94-95. – Bowman & Gruner 1973: 51. Vinogradov *et al.* 1982: 429. Shih & Chen 1995: 202.
Stebbingella Bovallius, 1890: 97-98. – Pirlot 1929: 167.

Type species

Cranocephalus goesi Bovallius, 1890 by monotypy. Type material could not be found at the SMNH, ZMUC or in Uppsala and is considered lost. However, it is clear from Bovallius's (1890) description and figures that his species is synonymous with *Oxycephalus scleroticus* Streets, 1878. Never the less, *Cranocephalus* is maintained as a valid genus.

Type species of synonyms

Stebbingella was instituted by Bovallius (1890) for *Oxycephalus scleroticus* Streets, 1878, but this species is considered a senior synonym of *C. goesi*. Bovallius was most likely unaware of the variation in the morphology of the head, which is characteristic of this genus, thus adding to the confusion.

Diagnosis

Body shape robust or globular. Head oval. Rostrum present in both sexes; distinctly elongate. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore with relatively large anterodistal lobe; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted below anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle absent; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 2; basal article elongate, subequal in length to following article; with 1–3 small terminal articles not folded back on preceding article; terminal articles pointing posteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single small rounded plate; palp absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae all partly fused with pereonites; coxa 5 with lateral spinous process. Gnathopod 1 chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with prominent teeth only. Gnathopod 2 subchelate; carpal process knife-shaped; carpal process armed with prominent teeth only. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, but not operculate; articles 3–7 inserted terminally to basis; non-locking but may overlap with P6. Pereopod 6 simple; articles 3–7 inserted terminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, but not operculate; without fissure; without telsonic groove; posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together; distal margin without groove, pereopods not overlapping; merus with carpus attached terminally. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Monotypic: *Cranocephalus scleroticus*.

Sexual dimorphism

Apart from obvious morphological differences in the antennae and mandibles, males tend to have a slightly larger head, especially in mature specimens. Fage (1960) lists other differences in relative lengths of the body, and appendages, but these are minor.

Remarks

This genus is readily distinguished by the morphology of the head, body, gnathopods, pereopods and urosome. Additional distinctive characters are the strongly, calcified cuticle, and the distinctive pores found on the basis of pereopods 5-7, which also occur on the pereonites and pleonites. The fifth coxae also have a strong, backward projecting, spinous process, a character not found in any other oxycephalidean.

Cranocephalus is unusual in the development of the head. In juveniles the head is globular with a relatively short, sharp rostrum which becomes larger and longer in adults. A failure to appreciate these changes in development may have led to some past errors in identification.

Within the Oxycephalidae, *Cranocephalus* does not closely resemble any other genus. The morphology of the male antennae is most like that of *Calamorhynchus* and *Streetsia*. The first antennae of females are reduced to three articles, as is sometimes found in *Rhabdosoma*, but differ in their morphology. The first maxillae are very small, and the second maxillae are obsolete, as in *Calamorhynchus* and *Leptocotis*. The simple maxillipeds are most like those of *Rhabdosoma*, and also approach those of *Oxycephalus* and *Calamorhynchus*.

Fage (1960) provides some biogeographical information regarding this genus. It seems to be epipelagic in habit, and is widespread in tropical regions of the world's oceans, but has not been recorded from the Red Sea.

There are very few records of associations with gelatinous plankton. It has been found with the ctenophores, *Pleurobranchia* sp. (Harbison *et al.* 1977) and species of the order Cydippida (Harbison *et al.* 1978).

Cranocephalus is currently considered to be monotypic (Fage 1960, Vinogradov *et al.* 1982) and all nominal species are considered synonyms of *C. scleroticus* (Streets, 1878).

Family **PLATYSCELIDAE** Bate, 1862

Diagnosis

Body length up to 25 mm, rolled into ball, the enlarged basis of P5 & 6 completely covering other pereopods, with telson fitting neatly into telsonic groove of basis of P6, slightly flattened dorsoventrally. Head relatively short, with 'beak' between A1, fitting neatly between distal margins of basis of P6 when rolled up. Eyes in single (*Tetrathyrus*), or double groups, occupying most of head surface. Pereonites all separate. Coxae 1-6, or 1-7 (*Platyscelus*), separate from pereonites; coxa 7 almost totally fused with pereonite (except *Platyscelus*), with slight posterior notch between coxa and pereonite. Antennae 1 of females with 2-3 articulate peduncle, first flagellar article (callynophore) with slight bulge proximally (*Tetrathyrus*), or distally with two much narrower, smaller articles inserted terminally; of males with 1-2 articulate peduncle and enlarged, curved first flagellar article (callynophore), with two-field brush of aesthestascs medially, and three smaller, slender articles inserted on anterodistal corner. Antennae 2 of females absent (*Tetrathyrus*), or of five slender articles, the terminal one often very small; of males of five slender articles, folded back on one another underneath head and pereon, basal article the shortest and slightly more robust than following articles, articles 2 & 3 subequal in length; articles 4 & 5 are also subequal in length but distinctly shorter than previous pair, article 5 sometimes slightly shorter than article 4. Mouthparts in form of short, broad cylinder. Mandibles with palp in males, without palp in females, incisor relatively broad, with slightly enlarged tooth laterally. Maxillae 1 reduced in size, single lobes with oblique distal margin armed with few robust setae, or two, or four, bifid teeth. Maxilla 2 reduced to small, single lobes, slightly curved with rounded bulge medially. Gnathopods simple, subchelate, or chelate. Pereopods 3-7 simple. Pereopods 5 & 6 with basis transformed into broad operculum, always longer and larger in P6; distal articles inserted subterminally on basis of P5, more proximally in P6. Pereopod 6; basis with, or without (*Tetrathyrus*), fissure, posterodistal corner with ridge-groove locking mechanism with opposing P6, posterior margin with telsonic groove. Pereopod 7 reduced in size, usually consisting of basis and 1-2 tiny articles, rarely with full compliment of articles (abnormal). Uropod 3; endopod fused with peduncle, rarely articulated, or endopod of U2 also fused (*Tetrathyrus*). Telson triangular, relatively broad, fused with double urosomite. Gills with, or without, fold on pereonites 2-6. Oostegites on pereonites 2-5.

Four genera: *Platyscelus*, *Hemityphis*, *Paratyphis* and *Tetrathyrus*.

Remarks

In the past this family has also been known as Typhidae Dana, 1853 (Claus 1879b, Stebbing 1888, Chevreux 1900, Chevreux & Fage 1925) and Eutyphidae Bovallius, 1887. The name Typhidae is derived from the genus *Typhis* Risso, 1816 which, although being an older name, is preoccupied by a genus of molluscs (Montfort 1810). Consequently Bate (1862) proposed the name Platyscelidae, derived from the next oldest available generic name, *Platyscelus* Bate, 1861. Claus (1879b) incorrectly proposed a new genus *Eutyphis* to encompass a number of older generic names including *Platyscelus*. Following Claus, Bovallius (1887a) proposed the family Eutyphidae but incorrectly attributed it to Dana (1853). Thus, *Platyscelus* is the oldest available generic name and the family should be known as Platyscelidae, as proposed by Bate (1862).

This family is very similar to Parascelidae, but is distinguished by the shape of the mouthparts, which are in the form of a broad, rounded cylinder (sharp, pointed cone in Parascelidae) and by pereopod 7, which is usually reduced to the basis and a few vestigial, terminal articles. Also, the basis of pereopod 5 is more elongate in Platyscelidae, and in Parascelidae the basis of pereopod 6 is more prominently narrowed for the distal half. A fissure is present on the basis of pereopod 6 in some genera of both families and can be a useful character to distinguish between them. In the Platyscelidae a fissure is present in all genera except *Tetrathyrus*, which is readily distinguished by the morphology of the gnathopods, and the shape of the basis of pereopod 6. The fissure is located just below the notch for the first urosomite (beginning of telsonic groove). In the Parascelidae a fissure is present in *Thyropus*, where it is located well above the telsonic groove, and in *Schizoscelus* where it is very long and extends above and below the notch for urosomite 1, but is absent in *Parascelus* and *Euscelus*.

Platyscelids are usually found rolled into a ball; the enlarged basis of pereopods 5 and 6 completely covering the gnathopods and other pereopods, with the telson fitting neatly into a telsonic groove on the basis of pereopod 6 (Fig. 110B). Although the ability to roll into a ball has evolved in other families of the Platysceloidea, none have perfected the habit to the extent found in Platyscelidae and Parascelidae. The morphological characters that allow individuals to achieve this have not been described in any detail previously. These characters vary slightly, in detail, at the generic and specific level but are basically the same for all members of both families. The basis of pereopod 5 is articulated proximally with the basis of pereopod 6 by means of a small knob, located medially, near the proximal anterior corner of the basis of pereopod 6, which articulates in a groove on pereopod 5, produced by an elongate process on the medial surface of the coxae and a small, adjacent knob on the basis. The basis of pereopod 5 has a bevelled anterior margin that fits under the coxae (1-4), and distally in a groove under the head, next to the second antennae. The posterior margin of the basis of pereopod 5 overlaps with the anterior margin of the basis of pereopod 6, which is bevelled to ensure a neat overlap. The basis of pereopod 6 has a posterior margin with a distinct notch (or shoulder) for urosomite 1, followed by a telsonic groove, which neatly accommodates the double urosomite and the telson. Distal to the telsonic groove is a locking mechanism for opposing pereopods, consisting of a ridge/groove arrangement, similar to the funnel locking mechanism found in squid, with the left usually overlapping the right (in 160 specimens of *Platyscelus ovoides* examined only three had the right overlapping the left). The distal margin of the basis of pereopod 6 (distal to the locking mechanism) is grooved so that the margins of opposing pereopods can interlock; usually the left over the right. The head has a central 'beak', which fits neatly with the anterodistal corner of the basis of pereopod 6. Finally the epimeral plates have lateral ridges, which fit neatly against the proximal part of the posterior margin of the basis of pereopod 6, when the animal is curled. Thus, these animals are able to achieve an almost smooth, tightly packed, globular shape. The reasons for adopting this habit are not known. A spherical shape would sink more rapidly, and this may assist in the avoidance of predators, or in diurnal migrations.

The family Platyscelidae has not been reviewed since the works of Claus (1879b, 1887) and all genera are in need of thorough taxonomic revision.

Prior to this review *Amphithyrus* was included in this family, but it differs significantly from the other genera of Platyscelidae, and is accommodated in the new family, Amphithyridae, together with *Paralycaea* and *Amphithyropsis*, with which it shares a number of characters. Thus, only four genera are recognised in this family.

Key to the genera of the family PLATYSCELIDAE

1. Gnathopods 1 & 2 without carpal process; dactylus closing against concave distal margin of propodus. Pereopod 6; basis without fissure ....*Tetrathyrus* Claus, 1879

   Gnathopods 1 & 2 usually with carpal process, sometimes absent on G1, and very reduced on G2; propodus and dactylus normal. Pereopod 6; basis with fissure (sometimes small) 2

2. Gnathopod 1 simple. Gnathopod 2 with small, or almost obsolete, carpal process ... .*Paratyphis* Claus, 1879

   Gnathopod 1 & 2 chelate. Gnathopod 2 with carpal process longer than half of propodus 3

3. Gnathopod 1; length of carpal process about half of propodus. Gnathopod 2; carpal process relatively slender, length about 0.7x propodus. Gnathopods 1 & 2; carpal process, and posterior margin of propodus, with very fine serrations. Antennae 2 of male; two distal articles each longer than half preceding article..... ....*Hemityphis* Claus, 1879

Gnathopod 1; carpal process usually longer than half of propodus. Gnathopod 2; carpal process as long, or almost as long, as propodus. Gnathopods 1 & 2; carpal process, and posterior margin of propodus, with distinct serrations. Antennae 2 of male; two distal articles each shorter than half preceding article.... ....*Platyscelus* Bate, 1862

Genus ***Platyscelus*** Bate, 1861

(Figs 110 & 111)

Typhis Risso, 1816: 122. – Guérin 1825: 755. Milne-Edwards 1830: 395. Lucas 1840: 239. Milne-Edwards 1840: 94-96. Lucas 1846: 57. Dana 1852: 316. Dana 1853: 1008.

Dithyrus Dana, 1852; 316. – Dana 1853: 1008-1010.

Platyscelus Bate, 1861: 4. – Bate 1862: 329. Thomson 1879: 244. Stebbing 1888: 1462. Spandl 1924a: 35. Chevreux & Fage 1925: 419. Schellenberg 1927: 646-647. Spandl 1927: 227-228. Hurley 1955: 189. Bowman & Gruner 1973: 55. Zeidler 1978: 39. Vinogradov *et al.* 1982: 439-440. Shih & Chen 1995: 226. Vinogradov 1999a: 1201.

Eutyphis Claus, 1879b: 5. – Claus 1880: 558. Carus 1885: 424. Claus 1887: 31-35. Gerstaecker 1886: 482. Pirlot 1929: 156.

Eutyphis – Bovallius 1887a: 45.

Type species

Typhis ovoides Risso, 1816 by monotypy. Type material could not be found at the MNHN or any other major European museum (see acknowledgments). Despite Risso's limited description and figure, *Platyscelus ovoides* is a well-established species in the literature.

Type species of synonyms

Bate (1861) instituted *Platyscelus* because *Typhis* is preoccupied by a genus of molluscs (Monfort 1810).

The type species of *Dithyrus* is *D. faba* Dana, 1853, by subsequent designation. Type material could not be located in any major North American museum and is considered lost. Despite the loss of type material it is clear from Dana's description and figures that *D. faba* is a species of *Platyscelus*, most likely *P. armatus*.

The type species of *Platyscelus* is *P. serratus* Bate, 1861 by monotypy. Type material could not be found at the BMNH or MNHN and is considered lost. However, it is clear from the description and figures of Bate that his species is synonymous with *P. ovoides*. Thus there is no problem with accepting *Typhis ovoides* Risso, 1816 as the type species of the genus. Claus (1879b) also designates *T. ovoides* as the type species of his genus *Eutyphis*.

Diagnosis

Body shape more or less spherical. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in two fields on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods to pereonite 2; basal article distinctly inflated, about half or less the length of following article; with terminal article subequal in length to preceding one, and folded back; last two articles shorter than preceding one; terminal articles pointing anteriorly. Antenna 2 females 5-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with few robust setae; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes without fringe of setae or membranous fringe. Pereonites all separate; simple. Coxae all separate from pereonites. Gnathopod 1 chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with prominent teeth only. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with prominent teeth only. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, and operculate; articles 3–7 inserted subterminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; with fissure; with telsonic groove; posterodistal corner with ridge-groove locking mechanism to join opposing pereopod; distal margin with groove connecting opposing pereopod; merus anterodistal corner slightly extended, overlapping carpus medially. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all with folds.

Four species: *Platyscelus ovoides*, *P. armatus*, *P. crustulatus* and *P. serratulus*.

Sexual dimorphism

The sexes are remarkably similar in general morphology, and except for the antennae and mandibles, there is no obvious sexual dimorphism.

Remarks

This genus is distinguished by the distinct serrations found on the carpus and propodus of the gnathopods. Also, in males, the last two articles of the second antennae are usually much less than half the length of the preceding article. However, it differs most significantly from all the other genera in that coxa 7 is not fused with the pereonite.

Very little is known about its biology. Stephensen (1925) and Thurston (1976) provide some limited biogeographical information. Most species seem to prefer tropical waters, and from the available data, appear to be epipelagic in habit.

Records of associations with gelatinous plankton are few. *Platyscelus ovoides* has been recorded with the medusa *Aequoria* sp. (Risso 1816), and *P. serratulus* with the siphonophore *Agalma elegans* (Laval 1980). An unidentified species of *Platyscelus* has also been found with the medusa *Pelagia noctiluca* (Laval 1980).

This genus is desperately in need of taxonomic revision. Only four species are currently recognised (Vinogradov *et al.* 1982).

Key to species of the genus *Platyscelus*

1. Gnathopod 1; propodus with serrated anterior margin .... *P. ovoides* (Risso, 1816)
   Gnathopod 1; propodus with smooth anterior margin 2

2. Gnathopod 1; carpal process short, not reaching mid-length of propodus. Pereopod 5; basis with undulated anterior margin. Pereopod 6; basis with proximal and distal notch on anterior margin .... *P. crustulatus* (Claus, 1879)
   Gnathopod 1; carpal process almost as long as propodus. Pereopod 5; basis with smooth anterior margin. Pereopod 6; basis without notches on anterior margin... 3

3. Gnathopod 1 almost subchelate. Pereopod 5; coxa with lateral knob, or spiniform process (not developed in juveniles). Pereopod 6; basis with relatively small fissure, only half as long as merus .... *P. armatus* (Claus, 1879)
   Gnathopod 1 distinctly chelate. Pereopod 5; coxa without lateral process. Pereopod 6; basis with relatively large fissure, about equal in length to merus .... *P. serratulus* Stebbing, 1888

Genus ***Hemityphis*** Claus, 1879
(Figs 112 & 113)

Hemityphis Claus, 1879b: 12. – Gerstaecker 1886: 482-483. Claus 1887: 38. Stebbing 1888: 1471. Spandl 1927: 233. Pirlot 1929: 159. Hurley 1955: 188. Bowman & Gruner 1973: 55. Vinogradov *et al.* 1982: 446. Shih & Chen 1995: 241. Vinogradov 1999a: 1201.

Hemiscelus Stewart 1913: 259-260. – Vinogradov *et al.* 1982: 474-475. Vinogradov 1999a: 1199.

Type species

Hemityphis tenuimanus Claus, 1879. Type material could not be found at the ZMB, but the ZMH has one lot of 13 male specimens from the Atlantic (K 8764) with "Schnehagen" as the collector. This dates the material to the time of Claus, because Claus (1871) proposed the genus *Schnehagenia* for his species *S. rapax* (= *Brachyscelus rapax*). One of the specimens has been dissected from the right, which is consistent with the figures of Claus (1887). Thus, these specimens are most likely syntypes, although one cannot be certain in the absence of more conclusive information.

Type species of synonyms

The type species of *Hemiscelus* is *H. diplochelatus* Stewart, 1913 by monotypy. The unique holotype female is in the BMNH (1914.2.25.122), on one microscope slide with remains in spirit. This specimen has been examined and is indistinguishable from juvenile specimens of *Hemityphis tenuimanus*, thus confirming the above synonymy, proposed by Zeidler (1998).

Diagnosis

Body shape more or less spherical. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in two fields on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 4; basal article distinctly inflated, about half or less the length of following article; with terminal article shorter than preceding one, and folded back; terminal articles pointing anteriorly. Antenna 2 females 5-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with few robust setae; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes without fringe of setae or membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 mostly fused with pereonite. Gnathopod 1 chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, but not operculate; articles 3–7 inserted terminally to basis, or subterminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; with fissure; with telsonic groove; posterodistal corner with ridge-groove locking mechanism to join opposing pereopod; distal margin with groove connecting opposing pereopod; merus anterodistal corner slightly extended, overlapping carpus medially. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Monotypic: *Hemityphis tenuimanus.*

Sexual dimorphism

The sexes are remarkably similar in general morphology, and except for the antennae and mandibles, there is no obvious sexual dimorphism.

Remarks

Hemityphis is currently considered to be monotypic (Zeidler 1998). In the past, *H. tenuimanus* Claus, 1879 has been considered a junior synonym of *Typhis rapax* Milne-Edwards, 1830. However, the description of *T. rapax* by Milne-Edwards (1830, 1840) refers to *Parapronoe crustulum* Claus, 1879, as has been confirmed by examination of type material in the MNHN (Zeidler 1996b). Thus, the type species of the genus is *H. tenuimanus* Claus, 1879.

Hemityphis bears some resemblance to *Platyscelus*, but is readily distinguished by the morphology of the gnathopods, the very small fissure on the basis of pereopod 6, and by the male second antennae, which have the last two articles considerably longer than half the length of the preceding one. The first maxillae differ from those of *Platyscelus* and *Paratyphis* in being armed with three tiny, stout setae, instead of bifid denticles. The second maxillae have a more denticulate inner lobe than other genera of the family.

Very little is known about its biology but Stephensen (1925) and Thurston (1976) provide some biogeographical information. It seems to be widespread in tropical and warm-temperate regions of the world's oceans and, from the limited available data, appears to be mainly epipelagic in habit.

There are no records of a parasitoid relationship with gelatinous plankton although Harbison *et al.* (1977) found *H. tenuimanus* inside a gastroid of a colony of the siphonophore *Forskalia tholoides*. "It was not appreciably digested, and so may have been recently capture and ingested. This siphonophore was also feeding on *Anchylomera blossevillei*" (Harbison *et al.* 1977).

Genus ***Paratyphis*** Claus, 1879

(Figs 114-116)

Paratyphis Claus, 1879b: 13-14. – Gerstaecker 1886: 483. Claus 1887: 39. Stebbing 1888: 1476. Spandl 1927: 243. Pirlot 1929: 157. Hurley 1955: 188. Bowman & Gruner 1973: 55-56. Zeidler 1978: 42. Vinogradov *et al.* 1982: 448. Shih & Chen 1995: 243. Vinogradov 1999a: 1201.

Type species

Paratyphis maculatus Claus, 1879 by monotypy. Type material could not be found at the ZMB or ZMH and is considered lost. However, the descriptions and figures of Claus (1879b, 1887) readily distinguish this genus.

Diagnosis

Body shape more or less spherical. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in two fields on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 4; basal article distinctly inflated, about half or less the length of following article; with terminal article subequal in length to preceding one, and folded back; last two articles shorter than preceding one; terminal articles pointing anteriorly. Antenna 2 females 5-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with four bifid teeth; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 mostly fused with pereonite. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 simple. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, and operculate; articles 3–7 inserted terminally to basis, or subterminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; with fissure; with telsonic groove; posterodistal corner with ridge-groove locking mechanism to join opposing pereopod; distal margin with groove connecting opposing pereopod; merus anterodistal corner slightly extended, overlapping carpus medially. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Four species: *Paratyphis maculatus*, *P. parvus*, *P. promontorii* and *P. spinosus*.

Sexual dimorphism

The sexes are remarkably similar in general morphology, and except for the antennae and mandibles, there is no obvious sexual dimorphism, although in some species the basis of pereopod 7 is more elongate in females.

Remarks

This genus is characterised by the simple first gnathopods, and the poorly developed chelae of the second gnathopods. In this respect it resembles *Parascelus* and *Thyropus*, of the family Parascelidae, in which the gnathopods are simple. However, in *Parascelus* the basis of pereopod 6 is without a fissure, and in *Thyropus* the fissure is located well above the telsonic groove.

Paratyphis seems to be relatively uncommon and very little is known about its biology, and there are no records of associations with gelatinous plankton. However, it seems to be widespread in tropical and warm-temperate regions of the world's oceans.

Species of *Paratyphis* are extremely difficult to determine with certainty and the genus is in need of revision. Pirlot (1930) and Vinogradov *et al.* (1982) recognise four species, for which the following tentative key is provided.

Key to species of the genus *Paratyphis*

1. Pereopod 5; ischium inserted subterminally on basis; basis without notch on distal margin. Pereopod 6; basis with relatively long fissure, extending above telsonic groove.. *P. spinosus* Spandl, 1924

   Pereopod 5; ischium inserted terminally on basis; basis with notch on distal margin, anterior to insertion of ischium. Pereopod 6; basis with moderate fissure located just below beginning of telsonic groove 2

2. Gnathopod 2; carpal process with fine serrations, pointed, extending to about one-third of propodus.. *P. parvus* Claus, 1887

   Gnathopod 2; carpal process without serrations, sometimes with setae, rounded or pointed, sometimes very small, never as long as one-third of propodus 3

3. Gnathopod 2; carpal process very small, angular. Pereopod 5; basis with smooth anterior margin. Pereopod 6; carpus length about 2.0-2.5x width........................ .... *P. maculatus* Claus, 1879

Gnathopod 2; carpal process rounded, very small, or absent. Pereopod 5; basis with slight undulation midway on anterior margin. Pereopod 6 carpus slightly longer than 3x width .... *P. promontorii* Stebbing, 1888

Genus ***Tetrathyrus*** Claus 1879
(Figs 117 & 118)

Tetrathyrus Claus, 1879b: 14. – Claus 1880: 588. Gerstaecker 1886: 483. Claus 1887: 40. Stebbing 1888: 1480. Chevreux & Fage 1925: 422. Spandl 1927: 240. Bowman & Gruner 1973: 56. Zeidler 1978: 43. Vinogradov *et al.* 1982: 454. Shih & Chen 1995: 248-249. Vinogradov 1999a: 1202.

Type species

Tetrathyrus forcipatus Claus, 1879 by monotypy. Type material could not be found at the ZMB or ZMH and is considered lost. However, the description and figures of Claus (1879b, 1887) readily characterise this genus.

Diagnosis

Body shape more or less spherical. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted terminally on callynophore. Antenna 2 absent in females; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 5; basal article distinctly inflated, about half or less the length of following article; with terminal article subequal in length to preceding one, and folded back; last two articles shorter than preceding one; terminal articles pointing anteriorly. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor relatively broad, straight with several teeth, with small distal lobe medially; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with few robust setae; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes incompletely fused, i.e., slightly separate terminally; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 mostly fused with pereonite. Gnathopod 1 sub-chelate; basis without antennal pocket in male; carpal process spoon-shaped; carpal process not armed, conspicuously smooth. Gnathopod 2 sub-chelate; carpal process spoon-shaped; carpal process not armed, conspicuously smooth. Pereopods 3 & 4 subequal in length to pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, and operculate; articles 3–7 inserted subterminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; without fissure; with telsonic groove; posterodistal corner with ridge-groove locking mechanism to join opposing pereopod; distal margin with groove connecting opposing pereopod; merus anterodistal corner slightly extended, overlapping carpus medially. Pereopod 7 reduced in size with large basis; only 1–3 articles terminal to basis. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Two species: *Tetrathyrus forcipatus* and *T. arafurae*.

Sexual dimorphism

The sexes are remarkably similar in general morphology, and except for the antennae and mandibles, there is no obvious sexual dimorphism.

Remarks

Tetrathyrus is readily distinguished by the morphology of the gnathopods and pereopod 6.

The inclusion of *Tetrathyrus* in the Platyscelidae is not entirely satisfactory as it has a number of characters that are not consistent with the other genera that currently make up the family. They eye facets are arranged in a single group on either side of the head (not double). The first maxillae are relatively simple, without teeth or setae. The inner lobe of the maxilliped is divided for about the distal third. The callynophore of the first antennae of females is bulged proximally, instead of distally. Females lack second antennae. The basis of pereopod 6 lacks a fissure, and the telsonic groove is relatively narrow. The endopod of uropod 2 is sometimes fused with the peduncle. Otherwise the characters of *Tetrathyrus* are like those of Platyscelidae, and it has all the characters that enable individuals to roll up into a ball, as detailed previously. Thus, *Tetrathyrus* is best kept in the family Platyscelidae until a thorough taxonomic revision is undertaken.

Although *Tetrathyrus* is relatively common in tropical and subtropical waters worldwide, very little is known regarding its biology. Stephensen (1925) provides limited biogeographical information, and judging from previous records, *Tetrathyrus* seems to be epipelagic in habit, preferring near-surface waters.

The only records of associations with gelatinous plankton are by Harbison *et al.* (1977) who record *T. forcipatus* from the siphonophores *Agalma clausi* and *Nanomia bijuga*.

Pirlot (1930) considers this genus to be monotypic and synonymises the six nominal species with *T. forcipatus*. Vinogradov *et al.* (1982) also recognise *T. arafurae* Stebbing, 1888 as a valid species, based mainly on that species having uropods 2 and 3 with endopods separate from the peduncle. However, studies of *T. forcipatus* (Zeidler 1978) revealed that the fusion of the endopod, with the peduncle of uropod 2, is variable and thus an unreliable character, although no specimen had the endopod of uropod 3 free. Thus, the genus is in need of further revision in order to determine the number of valid species. The following key, derived from Vinogradov et al. (1982) distinguishes the two currently recognised species.

Key to species of the genus *Tetrathyrus*

Uropods 2 & 3; endopod fused with peduncle. Telson shorter than double urosomite. Pereopod 5; basis oval, about twice as long as wide ...... *T. forcipatus* Claus, 1879

Uropods 2 & 3; endopod not fused with peduncle. Telson longer than double urosomite. Pereopod 5; basis elongate, 2.3-2.8x longer than wide........................ .... *T. arafurae* Stebbing, 1888

Family **PARASCELIDAE** Bovallius, 1887

Diagnosis

Body length 5-7 mm, rolled into ball, the enlarged basis of P5 & 6 completely covering other pereopods, with telson fitting neatly into telsonic groove of basis of P6, slightly flattened dorsoventrally. Head relatively short, with 'beak' between A1, fitting neatly between distal margins of basis of P6 when rolled up. Eyes in single, or double group, occupying most of head surface. Pereonites all separate. Coxae 1-6 separate from pereonites; coxa 7 almost totally fused with pereonite, with slight posterior notch between coxa and pereonite. Antennae 1 of females with 2-3 articulate peduncle, first flagellar article (callynophore) not particularly larger than peduncle articles, with two smaller articles inserted medially on anterodistal corner; of males with 1-2 articulate peduncle, and enlarged, curved first flagellar article (callynophore), with two-field brush of aesthestascs medially, and three smaller, slender articles inserted on anterodistal corner. Antennae 2 of females reduced in size consisting of 3-5 slender articles; of males of five slender articles folded back on one another underneath head and pereon, basal article the shortest, and slightly more robust than following articles, articles 2 & 3 subequal in length, the fourth is slightly shorter, and the fifth is slightly shorter than the fourth. Mouthparts styliform, forming buccal mass in shape of pointed cone. Mandibles with palp in males, without palp in females, with narrow incisor. Maxillae 1 reduced in size, single lobes, with oblique distal margin armed with few robust setae, or several in four groups. Maxillae 2 absent, or reduced to small, single lobes, slightly curved with rounded bulge medially, with minute denticles on rounded distal surface. Gnathopods simple or chelate. Pereopods 3-7 simple. Pereopods 5 & 6 with basis transformed into broad operculum, always longer and larger in P6; distal articles inserted subterminally on basis of P5, more proximally in P6. Pereopod 6, basis with, or without, fissure, posterodistal corner with ridge-groove locking mechanism with opposing P6, distal margin with groove to lock with opposing P6, posterior margin with telsonic groove. Pereopod 7 reduced in size but with full compliment of articles. Uropods 2 & 3; endopod sometimes fused with peduncle. Telson triangular, relatively broad, fused with double urosomite. Gills without folds on pereonites 2-6. Oostegites on pereonites 2-5.

Four genera: *Parascelus*, *Thyropus*, *Euscelus* and *Schizoscelus*.

Remarks

In the past this family has also been known as Scelidae Claus, 1879 (Stebbing 1888, Chevreux 1900, Chevreux & Fage 1925, Hurley 1955). However, there never was a genus *Scelus* and we must therefore use Parascelidae, a name introduced by Bovallius (1887a), which he incorrectly attributed to Claus (1879b), as do Vinogradov *et al.* (1982). Claus (1879b) does not refer to this family, so the name belongs to Bovallius.

Barnard (1930) proposed the name Thyropidae for this family, believing that the family name must be derived from the oldest genus, *Thyropus* Dana 1852. However, according to the ICZN the oldest generic name in a family need not be taken as the nomenclatural type (Opinion 141, ICZN 1950, 4: 138). Barnard's suggested substitution is therefore unnecessary.

This family is very similar to the previous one, as already discussed under that family. Bowman and Gruner (1973) recognise three genera, *Euscelus* Claus, 1879, *Schizoscelus* Claus, 1879 and *Thyropus* Dana, 1852. Vinogradov *et al.* (1982) also recognise these genera but make a case for removing *Parascelus* Claus, 1879 from the synonymy of *Thyropus*. They also include *Hemiscelus* Stewart, 1913, the type species of which is regarded a juvenile form of *Hemityphis tenuimanus* (Platyscelidae).

Vinogradov (1990a) described a new species of *Hemiscelus*, *H. setosus*, from the southeastern Pacific. Unfortunately it has not been possible to borrow any specimens of this species and so it is not possible to verify the taxonomic status. Judging from Vinogradov's description and figures, it seems to be a species of *Platyscelus*, near *P. crustulatus* (Claus, 1879), or *P. serratulus* Stebbing, 1888. Thus, only four genera are recognised in this review.

The four genera of Parascelidae are quite diverse in their morphology but fall into two main groups, *Parascelus* with *Thyropus* and *Schizoscelus* with *Euscelus*. *Parascelus* and *Thyropus* share the following characters that differ from *Schizoscelus* and *Euscelus*. The gnathopods are simple; the antennae of females are linear, the first consisting of six articles and the second of five articles; the first maxillae are armed with teeth, or groups of robust setae, and the second maxillae consist of a slightly curved lobe with a rounded medial bulge. In *Schizoscelus* and *Euscelus* the second gnathopods are chelate (also gnathopod 1 in *Euscelus*); the first antennae of females consist of five articles, with the terminal two articles reduced in size, and inserted dorsally on the medial corner of the callynophore; the second antennae of females are reduced and consist of only three or four articles; the first maxillae are armed with a few setae only, and the second maxillae are absent or not discernible. This grouping of these genera is also well supported by the phylogenetic analysis (Fig. 58).

The above grouping of genera might lead one to suggest that the family should be split but there are other characters shared by different combinations of genera. The first antennae of males have a two-articulate peduncle in *Paratyphis* and *Schizoscelus*, and a one-articulate peduncle in *Thyropus* and *Euscelus*. The basis of pereopod 6 has a fissure in *Thyropus* and *Schizoscelus*, which is absent in *Paratyphis* and *Euscelus*. *Thyropus* also differs from the other genera in having eyes grouped into two fields on either side of the head, and in having a less elongate maxilliped, with the inner lobe split distally. Thus, the phylogeny of genera of the family Parascelidae is not clear and requires further investigation.

Key to genera of the family PARASCELIDAE

1. Gnathopods 1 & 2 simple 2
   Gnathopods 1 simple, or chelate. Gnathopod 2 chelate 3

2. Pereopod 6; basis without fissure .... *Parascelus* Claus, 1879
   Pereopod 6; basis with fissure .... *Thyropus* Dana, 1852

3. Gnathopod 1 simple. Pereopod 6; basis with long fissure .... *Schizoscelus* Claus, 1879
   Gnathopod 1 chelate, similar to G2. Pereopod 6; basis without fissure .... *Euscelus* Claus, 1879.

Genus ***Parascelus*** Claus, 1879
(Figs 119 & 120)

Parascelus Claus, 1879b: 18. – Carus 1885: 425. Gerstaecker 1886: 483-484. Claus 1887: 45-46. Stebbing 1888: 1496. Spandl 1924a: 42. Chevreux & Fage 1925: 423. Spandl 1927: 262. Pirlot 1929: 155. Hurley 1955: 183. Vinogradov *et al.* 1982: 470-471. Vinogradov 1999a: 1200.

Type species

Parascelus edwardsii Claus, 1879. Type material could not be located at the ZMB or ZMH and is considered lost. However, the description and figures of Claus (1879b, 1887) readily distinguish this genus.

Diagnosis

Body shape more or less spherical. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially;

with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 5; basal article distinctly inflated, about half or less the length of following article; with terminal article shorter than preceding one, and folded back; terminal articles pointing anteriorly. Antenna 2 females 5-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor styliform, with reduced number of teeth; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with few robust setae; palp absent. Maxilla 2 reduced in size; curved, pointed with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 mostly fused with pereonite. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 simple. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, and operculate; articles 3–7 inserted subterminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; without fissure; with telsonic groove; posterodistal corner with ridge-groove locking mechanism to join opposing pereopod; distal margin with groove connecting opposing pereopod; merus anterodistal corner slightly extended, overlapping carpus medially. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Two species: *Parascelus edwardsii* and *P. parvus*.

Sexual dimorphism

This genus exhibits considerable minor sexual dimorphism, which may have contributed to some taxonomic confusion in the past. In males gnathopod 1 is slightly shorter than gnathopod 2; the basis of gnathopod 1 is slightly shorter than the following articles combined; the basis of pereopod 6 is more narrowed distally; the basis of pereopod 7 is crescent shaped, and the exopod of uropods 2 and 3 is slightly shorter than half of the length of the endopod. In females gnathopod 1 is relatively shorter than in males, and the basis is slightly longer than the following articles combined; gnathopod 2 is more slender than in males; the basis of pereopod 7 is very long and narrow, and the exopod of uropods 2 and 3 is slightly longer than half of the length of the endopod.

Remarks

This genus is very similar to *Thyropus* and in the past has been synonymised with it (e.g. Bowman & Gruner 1973). However, as suggested by Vinogradov *et al.* (1982), *Parascelus* and *Thyropus* should be recognised as separate genera as a number of characters readily distinguish them. *Parascelus* differs from *Thyropus* mainly in that the basis of pereopod 6 lacks a fissure. Other differences are as follows:- The eye facets are arranged in single (not double) fields on either side of the head; antennae 1 of males have a two-articulate peduncle (one-articulate in *Thyropus*); the first maxillae are armed with about six teeth distally, whereas in *Thyropus* there are four groups of stout setae, and the maxilliped is more slender, with the inner lobe completely fused.

Very little is known about its biology and it is difficult to extract information from the literature, because of the taxonomic difficulties in determining species, and its confusion with *Thyropus*. However, it seems to be preferentially associated with siphonophores, *P. edwardsii* having been recorded from *Bathyphysa sibogae* (Biggs & Harbison 1976, Harbison *et al.* 1977), *Agalma okeni*, *Diphyes dispar*, *Forskalia tholoides* (Harbison *et al.* 1977) and *F. edwardsi* (Laval 1980).

Parascelus is relatively uncommon, but is widely distributed in tropical and warm-temperate waters. From the available data it seems to be epipelagic, with a preference for the upper 200 m layer.

Harbison *et al.* (1977) provisionally recognise three species (all as *Thyropus*) one of which, *P. parvus* Claus, 1879, Vinogradov *et al.* (1982) regard a synonym of *P. edwardsii*. However, *P. parvus*, as illustrated by Claus (1887), has both gnathopods with serrations on the posterodistal corner of the carpus, a feature not found in any other described species of *Parascelus*. This species may therefore be valid. The other two species (also recognised by Vinogradov *et al.*) have recently been shown to represent the male and female of the same species, *P. edwardsii* (Zeidler 1998). Thus, this genus is currently restricted to two species, with the status of *P. parvus* being doubtful.

Key to the species of the genus *Parascelus*

Gnathopods 1 & 2; anterodistal corner of carpus with serrations ....
....*P. parvus* Claus, 1879

Gnathopods 1 & 2; anterodistal corner of carpus smooth........*P. edwardsii* Claus, 1879

Genus ***Thyropus*** Dana, 1852

(Figs 121 & 122)

Thyropus Dana, 1852: 316. – Dana 1853: 1008, 1012, 1013. Bate 1862: 326 (refers to *Platyscelus* and *Hemityphis*). Stebbing 1888: 1492. Spandl 1927: 258. Bowman & Gruner 1973: 57 (part). Zeidler 1978: 37 (part). Vinogradov *et al.* 1982: 468. Shih & Chen 1995: 254 (part). Vinogradov 1999a: 1200.

Tanyscelus Claus, 1879b: 17. – Gerstaecker 1886: 483. Claus 1887: 45.

Type species

Thyropus diaphanus Dana, 1853 by subsequent designation. Type material could not be located at any major North American museum and is considered lost. Dana's (1853) description and figures are inadequate to determine the specific status, but clearly refer to a species of Platyscelidae or Parascelidae. His figure of the male second antennae does not correspond to any genus of Platyscelidae and is most like *Parascelus*. However, his description of the eyes, "pigments of eye four in number", readily distinguish the genus *Thyropus* as defined here.

The diagnosis of *Thyropus*, presented here, is based on *T. sphaeroma*, as the specific status of *T. diaphanus* is uncertain, and *T. sphaeroma* is the next oldest available species.

Type species of synonyms

The type species of *Tanyscelus* is *T. sphaeroma* Claus, 1879 by monotypy. There are two lots of specimens in the ZMH which may represent type material; two males labelled "sansibar Tanyscelus" (K8757), and about 20 specimens labelled "Ombaistr" (K8755). This corresponds with the type localities, and the age of the material appears to correspond to the time of Claus. All of the specimens are in poor condition but are clearly *T. sphaeroma*, as described and figured by Claus (1879, 1887). *Tanyscelus* is clearly a synonym of *Thyropus*, based on the morphology of the eyes, second male antennae, and the basis of pereopod 6, and Claus (1879b) even suggested that his species may be the same as that of Dana (1853).

Diagnosis

Body shape more or less spherical. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in two fields on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 3-articulate; distal articles inserted terminally on callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 4; basal article distinctly inflated, about half or less the length of following article; with terminal article shorter than preceding one, and folded back; terminal articles pointing anteriorly. Antenna 2 females 5-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor styliform, with reduced number of teeth; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with robust setae in four groups; palp absent. Maxilla 2 reduced in size; curved, rounded with terminal denticles and with rounded medial bulge. Maxilliped inner and outer lobes separate; inner lobes incompletely fused, i.e., slightly separate terminally; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 mostly fused with pereonite. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 simple. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, and operculate; articles 3–7 inserted subterminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; with fissure; with telsonic groove; posterodistal corner with ridge-groove locking mechanism to join opposing pereopod; distal margin with groove connecting opposing pereopod; merus anterodistal corner slightly extended, overlapping carpus medially. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod articulated with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Two species: *Thyropus sphaeroma* and *T. similis*.

Sexual dimorphism

Sexual dimorphism in *Thyropus* is similar to that found in *Parascelus*.

Remarks

The similarity of this genus to *Parascelus* has already been discussed under that genus.

Very little is known about its biology. It is relatively uncommon, but widely distributed in the tropical and warm-temperate regions of the world's oceans. Although most records are from surface hauls, Thurston (1976) found *T. sphaeroma* down to 450 m.

Like *Parascelus*, *Thyropus* seems to be preferentially associated with siphonophores, *T. sphaeroma* having been recorded from *Stephanophyes superba* (Harbison *et al.* 1977), and *T. similis* from *Agalma okeni*, *Athorybia* sp., *A. rosacea* (Harbison *et al.* 1977), and *A. lucida* (Biggs 1978). Harbison *et al.* (1977) also record *Thyropus* sp. from the following siphonophores, but some of these records may be of *Parascelus* sp., as these authors synonymised the two genera; *Agalma okeni*, *Abyla* sp., *Athorybia* sp., *A. rosacea*, *Diphyes dispar*, *Forskalia* sp., *F. edwardsi* and *Stephanophyes superba*.

Vinogradov *et al.* (1982) consider this genus to be monotypic but *Parascelus similis* Stephensen, 1925 is recognised as a valid species of *Thyropus*, in addition to *T. sphaeroma* (Zeidler 1998).

Key to the species of the genus *Thyropus*

Pereopod 6; merus with short, anterodistal projection overlapping carpus .... *T. similis* (Stephensen, 1925)
Pereopod 6: merus without anterodistal projection .... *T. sphaeroma* (Claus, 1879)

Genus ***Schizoscelus*** Claus, 1879

(Figs 123 & 124)

Schizoscelus Claus 1879b: 20. – Gerstaecker 1886: 484. Claus 1887: 43-44. Stebbing 1888: 1503. Spandl 1927: 255. Bowman & Gruner 1973: 58. Vinogradov *et al.* 1982: 466. Shih & Chen 1995: 262. Vinogradov 1999a: 1200.

Type species

Schizoscelus ornatus Claus, 1879 by monotypy. Type material could not be located at the ZMB or ZMH and is considered lost. However, *Schizoscelus* is a very distinctive genus, adequately characterised by the description and figures of Claus (1879b, 1887).

Diagnosis

Body shape more or less spherical. Head round. Rostrum absent in both sexes. Eyes occupying most of head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 2-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in two-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted medially on anterodistal corner of callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 4; basal article distinctly inflated, about half or less the length of following article; with terminal article shorter than preceding one, and folded back; terminal articles pointing anteriorly. Antenna 2 females 4-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor styliform, with reduced number of teeth; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with few robust setae; palp absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 mostly fused with pereonite. Gnathopod 1 simple; basis without antennal pocket in male. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, and operculate; articles 3–7 inserted subterminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; with fissure; with telsonic groove; posterodistal corner with ridge-groove locking mechanism to join opposing pereopod; distal margin with groove connecting opposing pereopod; merus anterodistal corner extended, distinctly overlapping carpus medially. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Monotypic: *Schizoscelus ornatus*.

Sexual dimorphism

Apart from minor differences in the relative lengths of pereopods and pereopod articles, females have a more rounded head, and in males the basis of pereopod 7 is crescent-shaped, and relatively wide, as found in other genera of the family.

Remarks

This genus is readily distinguished by the morphology of the gnathopods and pereopod 6.

Schizoscelus is most similar to *Euscelus*, particularly in the morphology of the maxillae, antennae, gnathopod 2 and the urosome, and in that basis of pereopod 6 has an exceptionally, deep telsonic groove, and pereopod 7 has a hook-shaped, retractable dactylus. The close relationship of these two genera is strongly supported by the phylogenetic analysis (Fig. 58). *Schizoscelus* differs from *Euscelus* mainly in that the eyes are relatively larger, gnathopod 1 is simple, and the basis of pereopod 6 has an unusually long fissure.

This is a relatively rare genus and very little is known about its biology. It is known from widely separated records in tropical and subtropical regions (Dick 1970). Most records are from surface tows (Chevreux 1900, Dick 1970, Pirlot 1939, Stephensen 1925), but Thurston (1976) found a juvenile female in a night haul from 300 m.

Schizoscelus ornatus seems to be associated with the siphonophore *Bathyphysa sibogae* (Biggs & Harbison 1976). It has not been recorded from any other gelatinous plankton, and Biggs and Harbison found that it occurred with five of the eleven colonies of *B. sibogae* that they collected. Field and aquarium observations conducted by Biggs and Harbison (1976) "indicate that *S. ornatus* moves about freely on the pneumatophore and the smaller gastrozooids but avoids the gastrozooids with tentacles. If the amphipod's freedom of movement is restricted, as when it is enclosed in a jar with its host, it can be captured and quickly ingested".

Genus ***Euscelus*** Claus, 1879

(Figs 125-127)

Euscelus Claus, 1879b: 22. – Claus 1880: 588. Gerstaecker 1886: 484. Claus 1887: 43. Spandl 1927: 251. Bowman & Gruner 1973: 57. Vinogradov *et al.* 1982: 465.

Type species

Euscelus robustus Claus, 1879 by monotypy. Type material could not be found at the ZMB or ZMH and is considered lost. However, *Euscelus* is a very distinctive genus, adequately characterised by the description and figures of Claus (1879b, 1887).

Diagnosis

Body shape robust or globular. Head round. Rostrum absent in both sexes. Eyes occupying part of lateral head surface; grouped in one field on each side of head. Antenna 1 inserted on ventral surface of head. Antenna 1 male peduncle 1-articulate; flagellum with large, crescent-shaped callynophore and 1–3 small articles. Antenna 1 male callynophore without lobes; with aesthestascs arranged in 1.5-field brush medially; with three flagellar articles terminally; distal articles inserted on anterodorsal corner. Antenna 1 female flagellum with narrowly rectangular callynophore and 2 smaller articles; peduncle 2-articulate; distal articles inserted medially on anterodistal corner of callynophore. Antenna 2 present in both sexes; inserted on ventral surface of head, but lacking groove. Antenna 2 males 5-articulate; strongly zig-zagged, with most articles folded back on each other; extends forward under head and backward between gnathopods and pereopods; extend between gnathopods and pereopods to pereonite 3; basal article distinctly inflated, about half or less the length of following article; with terminal article shorter than preceding one, and folded back; terminal articles pointing anteriorly. Antenna 2 females 3-articulate. Mandibular palp absent in females; males 3-articulate. Mandibular molar reduced or absent. Mandibular incisor styliform, with reduced number of teeth; in male orientated more or less parallel to palp. Maxilla 1 reduced in size; single lobes; single plate with few robust setae; palp absent. Maxilla 2 absent. Maxilliped inner and outer lobes separate; inner lobes completely fused; inner lobes well developed; medial margin of outer lobes with membranous fringe. Pereonites all separate; simple. Coxae 1-6 separate from pereonites; coxa 7 mostly fused with pereonite. Gnathopod 1 chelate; basis without antennal pocket in male; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Gnathopod 2 chelate; carpal process knife-shaped; carpal process armed with microscopic teeth or setae. Pereopods 3 & 4 distinctly shorter than pereopods 5 & 6; simple. Pereopod 5 simple; basis very broad, more than 5x as wide as following articles, and operculate; articles 3–7 inserted subterminally to basis; with ball and socket locking mechanism with P6. Pereopod 6 simple; articles 3–7 inserted subterminally to basis. Pereopod 6 basis very broad, more than 5x as wide as following articles, and operculate; without fissure; with telsonic groove; posterodistal corner with ridge-groove locking mechanism to join opposing pereopod; distal margin with groove connecting opposing pereopod; merus anterodistal corner extended, distinctly overlapping carpus medially. Pereopod 7 reduced in size with large basis; all articles present; dactylus normal. Uropods normal, with peduncle, exopod, and endopod. Uropod 1 endopod articulated with peduncle. Uropod 2 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Uropod 3 endopod fused with peduncle; endopods and exopods lanceolate, usually with serrated margins. Telson fused with double urosomite. Oostegites on pereonites 2–5. Gills on pereonites 2–6; all without folds.

Monotypic: *Euscelus robustus*.

Sexual dimorphism

Females where unknown prior to this review. Although the available material is limited, males have relatively larger eyes, and the head is more produced than in females. Also, in common with other members of the family Parascelidae, the basis of pereopod 7 of males is more inflated.

Remarks

The morphology of the gnathopods and pereopod 6, and the relatively small eyes readily distinguish this genus.

Its similarity to *Schizoscelus* has already been discussed under that genus.

Euscelus is extremely rare and has only been recorded twice in the literature, initially from the Indian Ocean (Zanzibar) by Claus (1879b), and secondly from the Atlantic Ocean (Azores) by Spandl (1927). Both authors only record males. The record of *E. steueri* Spandl (1924b) is referable to *Hemityphis tenuimanus*, which has been confirmed by examination of the type (NMW 18337).

Recently, while examining the collections of the ZMB, more specimens of *Euscelus* were located, from the *Dana* expeditions of 1928-30, on loan from the ZMUC. This material represents the only specimens available for study, apart from the NMW material (Spandl 1927), which is on microscope slides. Most of the specimens are females, so it is possible to illustrate the female for the first time (Figs 125-127). The mouthparts are also illustrated for the first time (Fig. 125). Considering the rarity of this material, the following details of the *Dana* material, currently in the ZMB, is provided.

1. *Dana* Stn. 3556 VI, 2°52'N 87°38'W, North Pacific, just NE of Galapogos I., 4.IX.1928, MW 300 m, male 6.7 mm.
2. *Dana* Stn. 3556 VIII, as above, MW 50 m, male 6.7 mm.

3. *Dana* Stn. 3626 VIII, 27°00’S 177°41’W, South Pacific, just NW of Kermadec I., 31.XII.1928, MW 1500 m, female 6.5 mm.
4. *Dana* Stn. 3689 V, 7°13.5’N 111°49’E, South China Sea, 9.IV.1929, MW 1000 m, 19 females 6.9-9.2 mm.
5. *Dana* Stn. 4003 VIII, 8°26’N 15°11’W, North Atlantic, off W Africa, 9.III.1930, female 9.4 mm.

There are no records of *Euscelus* in association with gelatinous plankton.

Chapter 6

Discussion and Conclusion

This thesis addressed some of the systematic problems of the hyperiidean amphipod infraorder Physocephalata. The study, based on an examination of material held by the world's major museums, demonstrated that the Physocephalata are a fairly heterogeneous group. Although the phylogenetic relationship of many taxa remains unresolved, a sound taxonomic framework has been established to enable more rigorous studies in the future.

The family Vibiliidae proved to be the most speciose and taxonomically difficult of all the Physocephalata. Considering the amount of material examined, and that this family has never been revised thoroughly, it was disappointing that no new taxa were discovered. In the end, the systematics of the family changed little from that proposed by Vinogradov *et al.* (1982), but the systematic limits of the genera and species are now clarified.

The superfamily Cystisomatoidea, represented by the family Cystisomatidae, also proved to be a difficult group taxonomically, because of the uniformity of characters, the fragility of specimens, and the lack of material. The current revision is the first attempt to provide a comprehensive review of the family. Although limited by the availability of material, it forms the basis for further revision when more material becomes available.

The superfamily Phronimoidea is a very diverse group that has received little attention at the higher taxonomic levels. In this thesis, the systematic relationship of genera is examined in detail, resulting in the recognition of three new families. The genera seem to be well-defined taxonomic units, and many have been reviewed recently. However, some such as *Themisto* and *Hyperoche*, are in need of thorough taxonomic revision, while others, such as *Hyperia* and *Lestrigonus*, warrant further study because species of these genera are difficult to distinguish. Also, because of the taxonomic difficulty experienced with these genera, it is likely that more undescribed species remain to be discovered.

The unique status of the superfamily Lycaeopsoidea is confirmed by the present study. In addition, the two currently recognised species are reviewed in detail for the first time. The unique characters of *Lycaeopsis* support the hypothesis that the Hyperiidea are polyphyletic.

The superfamily Platysceloidea provided more taxonomic difficulties than any other, as was expected, and most of its families are in need of revision. This thesis addressed the systematic and phylogenetic relationships of the genera, thus providing a firm basis for more detailed taxonomic revisions in the future. Detailed revisions at the specific level remain to be done but were not tackled because of the large number of taxa involved. The current study resulted in the recognition of three new families, one new genus, and the reassignment of several genera. The generic descriptions, based on the type species, were generated using the taxonomic database program DELTA (Dalwitz *et al.* 1999). This method was used because the taxonomic complexity of the superfamily Platysceloidea provided the ideal opportunity to try out this program on hyperiideans, with the added advantage that the database could be used for phylogenetic analysis using PAUP (Swofford 2000). However, the maximum multiple parsimony analysis of the cladistic data matrix (Appendix 4) derived from the DELTA database (Appendix 2) is inconclusive. Three equally most parsimonious trees were found, but they do little to clarify the phylogenetic relationship of the genera of Platysceloidea (Figs 57 & 58). The strict consensus tree, derived from a summary of the three equally most parsimonious trees (Fig. 58), supports (from boot-strapping) the uniqueness of *Anapronoe* and *Pronoe*, and the close relationship of *Eupronoe* with *Parapronoe*, and *Euscelus* with *Schizoscelus*. Two main family groupings can also be identified, but do not have strong support from the boot-strapping analysis; Amphithyridae, Parascelidae, Platyscelidae and Tryphanidae and Oxycephalidae and Lycaeidae. These results are consistent with the taxonomic arrangement proposed here which was arrived at before carrying out the analysis.

The most logical explanation for the inconclusive results of the phylogenetic analysis lies in the bizarre adaptations of the Hyperiidea to planktonic life, which may have led to high rates of convergence of characters. The strong association with gelatinous plankton, exhibited by most Platysceloidea, has also resulted in the evolution of reduced mouthparts and antennae, thus reducing the number of phylogenetic characters for analysis. A more refined analysis of characters may produce a more meaningful result, and this will be attempted in the future. Material is also being collected for DNA analysis, which should help to resolve the phylogeny of the Hyperiidea.

The Hyperiidea are an interesting group because of their close relationship with gelatinous plankton. The precise nature of the relationship remains controversial. Some clearly eat the host tissue, or kill the host to fashion a floating "home" (e.g. *Phronima*), but others seem to utilise the host mainly for transport, or merely as a nursery for newly hatched young. However, the associates of many species are not known, and more field studies, such as those of Harbison *et al.* (1977) and Madin and Harbison (1977), need to be undertaken. Such studies might help to resolve the phylogeny and origins of this enigmatic group. A better understanding of the phylogeny and evolution of gelatinous plankton may also help to resolve that of the Hyperiidea.

Appendix 1

Revised Classification of the Infraorder Physocephalata

Infraorder PHYSOCEPHALATA Bowman & Gruner, 1973

Superfamily VIBILIOIDEA Bowman & Gruner, 1973
- Family VIBILIIDAE Dana, 1852
  - *Vibilia* Milne-Edwards, 1830
  - *Vibilioides* Chevreux, 1905
- Family CYLLOPODIDAE Bovallius, 1887
  - *Cyllopus* Dana, 1853
- Family PARAPHRONIMIDAE Bovallius, 1887
  - *Paraphronima* Claus, 1879

Superfamily CYSTISOMATOIDEA new superfamily
- Family CYSTISOMATIDAE Willemöes-Suhm, 1875
  - *Cystisoma* Guérin-Méneville, 1842

Superfamily PHRONIMOIDEA Bowman & Gruner, 1973
- Family PHRONIMIDAE Dana, 1852
  - *Phronima* Latreille, 1802
  - *Phronimella* Claus, 1871
- Family PHROSINIDAE Dana, 1852
  - *Phrosina* Risso, 1822
  - *Anchylomera* Milne-Edwards, 1830
  - *Primno* Guérin-Méneville, 1836
- Family HYPERIIDAE Dana, 1852
  - *Hyperia* Latreille in Desmarest, 1823
  - *Themisto* Guérin, 1825
  - *Hyperiella* Bovallius, 1887
  - *Hyperoche* Bovallius, 1887
  - *Pegohyperia* Barnard, 1932
  - *Laxohyperia* Vinogradov & Volkov in Vinogradov *et al.*, 1982

Family LESTRIGONIDAE new family
- *Lestrigonus* Milne-Edwards, 1830
- *Phronimopsis* Claus, 1879
- *Themistella* Bovallius, 1887
- *Hyperioides* Chevreux, 1900
- *Hyperietta* Bowman, 1973
- *Hyperionyx* Bowman, 1973

Family IULOPIDIDAE new family
- *Iulopis* Bovallius, 1887

Family BOUGISIDAE new family
- *Bougisia* Laval, 1966

Family DAIRELLIDAE Bovallius, 1887
- *Dairella* Bovallius, 1887

Superfamily LYCAEOPSOIDEA Bowman & Gruner, 1973

Family LYCAEOPSIDAE Chevreux, 1913
- *Lycaeopsis* Claus, 1879

Superfamily PLATYSCELOIDEA Bowman & Gruner, 1973

Family PRONOIDAE Claus, 1879
- *Pronoe* Guérin-Méneville, 1836

Family PARAPRONOIDAE new family
- *Parapronoe* Claus, 1879
- *Eupronoe* Claus, 1879

Family AMPHITHYRIDAE new family
- *Amphithyrus* Claus, 1879
- *Paralycaea* Claus, 1879
- *Amphithyropsis* new genus

Family BRACHYSCELIDAE Stephensen, 1923
- *Brachyscelus* Bate, 1861

Family LYCAEIDAE Claus, 1879
- *Lycaea* Dana, 1852
- *Simorhynchotus* Stebbing, 1888

Family ANAPRONOIDAE Bowman & Gruner, 1973
- *Anapronoe* Stephensen, 1925

Family THAMNEIDAE new family
- *Thamneus* Bovallius, 1887

Family TRYPHANIDAE Boeck, 1871
- *Tryphana* Boeck, 1871

Family OXYCEPHALIDAE Bate, 1861
- *Oxycephalus* Milne-Edwards, 1830
- *Rhabdosoma* White, 1847
- *Leptocotis* Streets, 1877
- *Calamorhynchus* Streets, 1878
- *Glossocephalus* Bovallius, 1887
- *Tullbergella* Bovallius, 1887
- *Streetsia* Stebbing, 1888
- *Cranocephalus* Bovallius, 1890

Family PLATYSCELIDAE Bate, 1862
- *Platyscelus* Bate, 1861
- *Hemityphis* Claus, 1879
- *Paratyphis* Claus, 1879
- *Tetrathyrus* Claus, 1879

Family PARASCELIDAE Bovallius, 1887
- *Parascelus* Claus, 1879
- *Thyropus* Dana, 1852
- *Schizoscelus* Claus, 1879
- *Euscelus* Claus, 1879

Appendix 2

Character List

#1. Body shape/
  1. robust or globular/
  2. more or less spherical/
  3. elongate and narrow/

#2. Head <shape>/
  1. quadrate/
  2. oval/
  3. round/

#3. Head <teeth>/
  1. with latero-ventral teeth/
  2. lacking latero-ventral teeth/

#4. Rostrum <presence/absence>/
  1. absent in both sexes/
  2. present in both sexes/
  3. present in males only/

#5. Rostrum <shape>/
  1. distinctly elongate/
  2. short and rounded/
  3. short and pointed/

#6. Eyes <position>/
  1. absent/
  2. occupying most of head surface/
  3. occupying part of lateral head surface/
  4. restricted to dorsal surface/

#7. Eyes <shape>/
  1. grouped in one field on each side of head/
  2. grouped in two fields on each side of head/

#8. Antenna 1 <position>/
  1. inserted on anterior surface of head in groove/
  2. inserted on anterior surface of head, but lacking groove/
  3. inserted on ventral surface of head/

#9. Antenna 1 male <peduncular articles>/
  1. peduncle 3-articulate/
  2. peduncle 2-articulate/
  3. peduncle 1-articulate/

#10. Antenna 1 male <shape>/
  1. flagellum with spatulate callynophore and 1-2 tiny articles/
  2. flagellum with long, narrowly conical callynophore and 1-2 tiny articles/
  3. flagellum with moderately enlarged callynophore and numerous small articles/
  4. flagellum with moderately enlarged oval callynophore and 1-3 articles/
  5. flagellum with large, crescent-shaped callynophore and 1-3 small articles/
  6. flagellum with enlarged globular callynophore and 1-3 articles/

#11. Antenna 1 male callynophore <shape of callynophore>/

1. without lobes/
2. with small anterodistal lobe <horn>/
3. with relatively large anterodistal lobe <horn>/

#12. Antenna 1 male callynophore <aesthestasc arrangement>/

1. with aesthestascs arranged in one-field brush medially/
2. with aesthestascs arranged in 1.5-field brush medially/
3. with aesthestascs arranged in two-field brush medially/

#13. Antenna 1 male callynophore <flagellar articles in addition to callynophore>/

1. with three flagellar articles terminally/
2. with two flagellar articles terminally/
3. with one flagellar article terminally/

#14. Antenna 1 male callynophore <insertion of terminal articles>/

1. distal articles inserted on anterodorsal corner/
2. distal articles inserted below anterodorsal corner <due to horn>/
3. distal articles inserted midway anteriorly/
4. subterminal article inserted on anterodorsal corner, terminal article inserted midway anteriorly on subterminal article/

#15. Antenna 1 female <shape>/

1. flagellum with spatulate callynophore and 1-2 tiny articles/
2. flagellum with long, narrowly conical callynophore and 1-2 tiny articles/
3. flagellum with narrowly rectangular callynophore and 2 smaller articles/
4. flagellum with narrowly rectangular callynophore and 1 smaller article/
5. flagellum with narrowly rectangular callynophore and no additional articles/

#16. Antenna 1 female <peduncular articles>/

1. peduncle 3-articulate/
2. peduncle 2-articulate/
3. peduncle 1-articulate/
4. peduncle absent/

#17. Antenna 1 female <terminal articles>/

1. distal articles inserted terminally on callynophore/
2. \tx720{}distal articles inserted medially on anterodistal corner of callynophore/

#18. Antenna 2 <presence/absence>/

1. present in both sexes/
2. absent in females/

#19. Antenna 2 <position>/

1. inserted on anterior surface of head in groove/
2. inserted on anterior surface of head, lacking groove/
3. inserted on ventral surface of head in groove/
4. inserted on ventral surface of head, but lacking groove/

#20. Antenna 2 males <number of articles>/
   1. multi-articulate, more than 6-articulate/
   2. 6-articulate/
   3. 5-articulate/
   4. 4-articulate/
   5. reduced to small spine/

#21. Antenna 2 males <shape>/
   1. greatly elongate, filiform and whip-like/
   2. moderately long and straight/
   3. short and curved/
   4. loosely zig-zagged or S-shaped, without any articles folded back on each other/
   5. zig-zagged, with some articles folded back on each other/
   6. strongly zig-zagged, with most articles folded back on each other/

#22. Antenna 2 males <position on head>/
   1. positioned in groove across head/
   2. positioned obliquely up into head/
   3. only extends forward under head/
   4. extends forward under head and backward between gnathopods and pereopods/
   5. extends forward under head and backward into antennal pocket of gnathopod 1/
   6. on anterior surface of head/

#23. Antenna 2 males <position, in relation to pereonites>/
   1. extend between gnathopods to pereonite 1/
   2. extend between gnathopods to pereonite 2/
   3. \tx720{}extend between gnathopods and pereopods to pereonite 3/
   4. extend between gnathopods and pereopods to pereonite 4/
   5. \tx720{}extend between gnathopods and pereopods to pereonite 5/
   6. \tx720{}extend between gnathopods and pereopods to pereonite 7/

#24. Antenna 2 males basal article <length>/
   1. elongate, longer than following article/
   2. elongate, subequal in length to following article/
   3. elongate, about half length of following article/
   4. distinctly inflated, about half or less the length of following article/

#25. Antenna 2 males <terminal articles>/
   1. with 1-3 small terminal articles not folded back on preceding article/
   2. with terminal article shorter than preceding one, and folded back/
   3. with terminal article subequal in length to preceding one, and folded back/

#26. Antenna 2 males <length of last two articles>/
   1. last two articles shorter than preceding one/
   2. last two articles subequal in length to preceding one/

#27. Antenna 2 males terminal articles pointing <orientation of terminal articles>/
   1. anteriorly/
   2. posteriorly/
   3. medially/

#28. Antenna 2 females <number of articles>/
  1. multi-articulate with more than 5 articles/
  2. 5-articulate/
  3. 4-articulate/
  4. 3-articulate/
  5. 2-articulate/
  6. 1-articulate/
  7. reduced to small spine/

#29. Mandibular palp <presence/absence>/
  1. present in both sexes/
  2. absent in females/

#30. Mandibular palp females/
  1. 3-articulate/
  2. 2-articulate/

#31. Mandibular palp males/
  1. 3-articulate/
  2. 1-articulate/

#32. Mandibular molar/
  1. well developed/
  2. reduced or absent/

#33. Mandibular incisor <shape>/
  1. relatively broad, straight with several teeth, without medial lobe/
  2. \tx720{}relatively broad, straight with several teeth, with small distal lobe medially/
  3. relatively broad, straight with several teeth, with relatively large distal lobe medially/
  4. styliform, with reduced number of teeth/
  5. reduced to 1-2 teeth/

#34. Mandibular incisor in male <orientation>/
  1. orientated more or less parallel to palp/
  2. orientated at right angles to palp/

#35. Maxilla 1/
  1. well developed/
  2. reduced in size/
  3. absent/

#36. Maxilla 1 <lobes>/
  1. bilobed/
  2. single lobes/

#37. Maxilla 1 <shape>/
  1. single plate with four rounded teeth/
  2. single plate with four bifid teeth/
  3. single plate with robust setae in four groups/
  4. single plate with few robust setae/
  5. single small rounded plate/
  6. small quadrate plate/
  7. curled, bifid/
  8. single rounded lobe with terminal denticles/

#38. Maxilla 1 <palp present or absent>/
    1. palp present/
    2. palp absent/

#39. Maxilla 2/
    1. well developed/
    2. reduced in size/
    3. absent/

#40. Maxilla 2 <shape>/
    1. bilobed, with numerous strong setae/
    2. bilobed, with two terminal teeth or robust setae on each lobe/
    3. curled, quadrate with medial palp/
    4. curved, rounded with terminal denticles and with rounded medial bulge/
    5. curved, pointed with rounded medial bulge/
    6. small rounded lobe/

#41. Maxilliped <fusion of inner and outer lobes>/
    1. inner and outer lobes fused/
    2. inner and outer lobes separate/

#42. Maxilliped inner lobes <fusion>/
    1. completely fused/
    2. incompletely fused, i.e., slightly separate terminally/
    3. not fused/

#43. Maxilliped inner lobes <development>/
    1. absent/
    2. rudimentary/
    3. well developed/

#44. Maxilliped medial margin of outer lobes <setae>/
    1. with fringe of closely packed slender setae/
    2. with membranous fringe/
    3. without fringe of setae or membranous fringe/

#45. Pereonites <fusion>/
    1. all separate/
    2. some anterior ones fused/

#46. Pereonites <form>/
    1. simple/
    2. with smoothly rounded transverse collars/
    3. with spiny transverse collars/

#47. Coxae <fusion>/
    1. all separate from pereonites/
    2. all partly fused with pereonites/
    3. some fully fused or partly fused with pereonites/
    4. all fully fused with pereonites/

#48. Gnathopod 1 <state>/
    1. simple /
    2. chelate/
    3. sub-chelate/

#49. Gnathopod 1 basis <with or without pocket>/
1. with antennal pocket in male/
2. without antennal pocket in male/

#50. Gnathopod 1 <basis> antenna 2 males <articles in G1 pocket>/
1. with fold of articles 2 & 3 held in pocket/
2. with fold of articles 2 & 3 and 4 & 5 held in pocket/

#51. Gnathopod 1 <shape of carpal process>/
1. carpal process knife-shaped/
2. carpal process spoon-shaped/

#52. Gnathopod 1 carpal process <to what extent toothed>/
1. not armed, conspicuously smooth/
2. armed with microscopic teeth or setae/
3. armed with prominent setae only/
4. armed with prominent teeth only/
5. armed with prominent teeth and setae/

#53. Gnathopod 2 <state>/
1. simple /
2. chelate/
3. sub-chelate/

#54. Gnathopod 2 carpal process <shape>/
1. knife-shaped/
2. spoon-shaped/

#55. Gnathopod 2 carpal process <to what extent toothed>/
1. not armed, conspicuously smooth/
2. armed with microscopic teeth or setae/
3. armed with prominent setae only/
4. armed with prominent teeth only/
5. armed with prominent teeth and setae/

#56. Pereopods 3 & 4 <length>/
1. distinctly longer than pereopods 5 & 6/
2. subequal in length to pereopods 5 & 6/
3. distinctly shorter than pereopods 5 & 6/

#57. Pereopods 3 & 4 <form>/
1. simple/
2. prehensile/
3. with distinct denticulate subchela/
4. with indistinct setose subchela/
5. with poorly developed subchela/

#58. Pereopod 5 <form>/
1. simple/
2. prehensile/
3. with poorly developed subchela/
4. with well developed subchela/

#59. Pereopod 5 basis <width>/
1. as wide or less than 5x as wide as following articles/
2. very broad, more than 5x as wide as following articles, but not operculate/
3. very broad, more than 5x as wide as following articles, and operculate/

#60. Pereopod 5 articles 3-7 inserted <insertion of articles terminal to basis>/
  1. terminally to basis/
  2. subterminally to basis/

#61. Pereopod 5 <locking mechanism with P6>/
  1. non-locking but may overlap with P6/
  2. with ball and socket locking mechanism with P6/
  3. with simple knob and groove with P6/

#62. Pereopod 6 <form>/
  1. simple/
  2. prehensile/
  3. with poorly developed subchela/
  4. with well developed subchela/

#63. Pereopod 6 <insertion of terminal articles on basis>/
  1. articles 3-7 inserted terminally to basis/
  2. articles 3-7 inserted subterminally to basis/

#64. Pereopod 6 basis <width>/
  1. as wide or less than 5x as wide as following articles/
  2. very broad, more than 5x as wide as following articles, but not operculate/
  3. very broad, more than 5x as wide as following articles, and operculate/

#65. Pereopod 6 basis <fissure>/
  1. with fissure/
  2. without fissure/

#66. Pereopod 6 basis <telsonic groove>/
  1. with telsonic groove/
  2. without telsonic groove/

#67. Pereopod 6 basis <posterodistal locking mechanism>/
  1. posterodistal corner with ridge-groove locking mechanism to join opposing pereopod/
  2. posterodistal corner without locking mechanism but opposing pereopod can overlap/
  3. posterodistal corner without locking mechanism, opposing pereopods do not overlap or join together/

#68. Pereopod 6 basis <groove on distal margin>/
  1. distal margin with groove connecting opposing pereopod/
  2. distal margin without groove, but can overlap with opposing pereopod/
  3. distal margin without groove, pereopods not overlapping/

#69. Pereopod 6 merus <anterodistal corner>/
  1. anterodistal corner extended, distinctly overlapping carpus medially/
  2. anterodistal corner slightly extended, overlapping carpus medially/
  3. with carpus attached terminally/

#70. Pereopod 7 <form>/
  1. similar in size and shape to P6/
  2. reduced in size with large basis/
  3. reduced in size with basis not particularly enlarged/

#71. Pereopod 7 <articles>/
   1. only 1-3 articles terminal to basis/
   2. all articles present /

#72. Pereopod 7 <dactylus>/
   1. dactylus normal/
   2. dactylus modified, rounded with microscopic scale-like structures/

#73. Uropods/
   1. normal, with peduncle, exopod, and endopod/
   2. peduncle broadened into single leaf-like article, exopod and endopod absent/

#74. Uropod 1 <fusion of endopod>/
   1. endopod fused with peduncle/
   2. endopod articulated with peduncle/

#75. Uropod 2 <fusion of endopod>/
   1. endopod fused with peduncle/
   2. endopod articulated with peduncle/

#76. Uropod 2 endopods and exopods <shape>/
   1. leaf-like, foliaceous with smooth margins/
   2. lanceolate, usually with serrated margins/

#77. Uropod 3 <fusion of endopod>/
   1. endopod fused with peduncle/
   2. endopod articulated with peduncle/

#78. Uropod 3 <endopods and exopods shape>/
   1. endopod, and sometimes also exopod, leaf-like, foliaceous, with smooth margins/
   2. endopods and exopods lanceolate, usually with serrated margins/

#79. Telson <fusion>/
   1. fused with double urosomite/
   2. articulated with double urosomite/

#80. Oostegites <position on pereonites>/
   1. on pereonites 2-5/
   2. on pereonites 3-5/
   3. on pereonites 2-6/

#81. Gills <position on pereonites>/
   1. on pereonites 2-6/
   2. on pereonites 2-6 in female, 3-6 in male/
   3. on pereonites 2-6 or 5 and 6 in female, 4-6 or 5 and 6 in male/

#82. Gills <shape>/
   1. all with folds/
   2. all without folds/
   3. some with fold on pereonite 5 or 6 or both/

Appendix 3

Item Descriptions

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# \i{}Amphithyropsis \i0{}gen. nov./
1,1 2,3 3,2 4,1 6,3 7,1 8,3 9,3 10,5 11,1 12,2 13,1 14,1 15,4 16,4 17,1 18,2
19,4 20,3 21,6 22,4 23,2 24,4 25,3 26,2 27,1 29,2 31,1 32,2 33,5 34,1 35,2 36,2
37,1 38,2 39,2 40,5 41,2 42,1 43,3 44,3 45,1 46,1 47,1 48,1 49,2 53,1 56,3 57,1
58,1 59,1 60,1 61,2 62,1 63,2 64,2 65,1 66,2 67,2 68,2 69,1 70,3 71,1 73,1 74,2
75,2 76,2 77,1 78,2 79,2 80,1 81,1 82,2

# \tx720\i{}Amphithyrus \i0{}Claus, 1879/
1,2 2,3 3,2 4,1 6,2 7,1 8,3 9,3 10,5 11,1 12,3 13,1 14,1 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,5 24,4 25,3 26,2 27,1 29,2 31,1 32,2 33,2 34,1 35,2 36,2
37,1 38,2 39,2 40,5 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,2 49,2 51,1 52,1 53,2
54,1 55,1 56,3 57,1 58,1 59,3 60,1 61,3 62,1 63,2 64,3 65,1 66,2 67,2 68,2 69,1
70,2 71,1 73,1 74,2 75,2 76,2 77,1 78,2 79,2 80,1 81,1 82,2

# \i{}Anapronoe \i0{}Stephensen, 1925/
1,1 2,3 3,2 4,1 6,3 7,1 8,3 9,1 10,5 11,1 12,1 13,1 14,1 15,3 16,1 17,1 18,1
19,3 20,2 21,5 22,1 28,2 29,2 31,1 32,2 33,2 34,1 35,2 36,2 37,2 38,2 39,2 40,2
41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,3 49,2 51,1 52,2 53,2 54,2 55,2 56,2 57,1
58,1 59,1 60,1 61,1 62,1 63,2 64,2 65,2 66,2 67,3 68,3 69,3 70,3 71,2 72,1 73,1
74,2 75,2 76,2 77,2 78,2 79,2 80,1 81,1 82,1

# \i{}Brachyscelus \i0{}Bate, 1861/
1,1 2,3 3,2 4,3 5,2 6,2 7,1 8,3 9,2 10,5 11,1 12,3 13,1 14,1 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,5 24,2 25,2 27,1 29,2 31,1 32,2 33,2 34,1 35,2 36,2 37,5 38,2
39,2 40,6 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,3 49,1 50,2 51,1 52,4 53,3 54,1
55,4 56,3 57,1 58,1 59,1 60,1 61,1 62,1 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2
71,2 72,1 73,1 74,2 75,2 76,2 77,2 78,2 79,2 80,1 81,1 82,1

# \i{}Calamorhynchus \i0{}Streets, 1878/
1,3 2,2 3,2 4,2 5,1 6,2 7,1 8,3 9,2 10,5 11,3 12,3 13,1 14,2 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,1 24,2 25,1 27,2 29,2 31,1 32,2 33,1 34,1 35,3 39,3 41,2
42,1 43,3 44,2 45,1 46,1 47,2 48,3 49,2 51,1 52,5 53,2 54,1 55,5 56,2 57,1 58,1
59,2 60,1 61,1 62,1 63,1 64,2 65,2 66,2 67,3 68,3 69,3 70,2 71,2 72,1 73,1 74,2
75,2 76,2 77,1 78,2 79,1 80,1 81,1 82,1

# \tx720\i{}Cranocephalus \i0{}Bovallius, 1890/
1,1 2,2 3,2 4,2 5,1 6,2 7,1 8,3 9,2 10,5 11,3 12,3 13,1 14,2 15,3 16,4 17,1 18,2
19,4 20,3 21,6 22,4 23,2 24,2 25,1 27,2 29,2 31,1 32,2 33,2 34,1 35,2 36,2 37,5
38,2 39,3 41,2 42,1 43,3 44,2 45,1 46,1 47,2 48,2 49,2 51,1 52,4 53,3 54,1 55,4
56,2 57,1 58,1 59,2 60,1 61,1 62,1 63,1 64,2 65,2 66,2 67,3 68,3 69,3 70,2 71,2
72,1 73,1 74,2 75,2 76,2 77,2 78,2 79,1 80,1 81,1 82,1

# \i{}Eupronoe \i0{}Claus, 1879/
1,1 2,3 3,2 4,3 5,2 6,2 7,1 8,3 9,1 10,5 11,1 12,1 13,1 14,1 15,3 16,1 17,1 18,1
19,3 20,3 21,6 22,5 24,2 25,1 27,2 28,2 29,2 31,1 32,2 33,2 34,2 35,2 36,2 37,1
38,2 39,2 40,5 41,2 42,1 43,3 44,1 45,1 46,1 47,1 48,3 49,1 50,1 51,1 52,2 53,2
54,1 55,2 56,3 57,1 58,1 59,1 60,1 61,1 62,1 63,2 64,2 65,2 66,2 67,3 68,3 69,1
70,2 71,1 73,1 74,2 75,2 76,1 77,2 78,1 79,2 80,1 81,1 82,1

# \i{}Euscelus \i0{}Claus, 1879/
1,1 2,3 3,2 4,1 6,3 7,1 8,3 9,3 10,5 11,1 12,2 13,1 14,1 15,3 16,2 17,2 18,1
19,4 20,3 21,6 22,4 23,3 24,4 25,2 27,1 28,4 29,2 31,1 32,2 33,4 34,1 35,2 36,2
37,4 38,2 39,3 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,2 49,2 51,1 52,2 53,2 54,1
55,2 56,3 57,1 58,1 59,3 60,2 61,2 62,1 63,2 64,3 65,2 66,1 67,1 68,1 69,1 70,2
71,2 72,1 73,1 74,2 75,1 76,2 77,1 78,2 79,1 80,1 81,1 82,2
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# \tx720\i{}Glossocephalus \i0{}Bovallius, 1887/
1,3 2,3 3,2 4,2 5,2 6,2 7,1 8,3 9,3 10,5 11,2 12,1 13,1 14,1 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,1 24,2 25,1 27,2 29,2 31,2 32,2 33,2 34,1 35,2 36,2 37,5
38,2 39,3 41,2 42,1 43,3 44,2 45,1 46,1 47,3 48,2 49,2 51,1 52,1 53,2 54,1 55,1
56,1 57,1 58,1 59,1 60,1 61,1 62,1 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2 71,2
72,1 73,1 74,2 75,2 76,2 77,2 78,2 79,1 80,2 81,2 82,2

# \i{}Hemityphis \i0{}Claus, 1879/
1,2 2,3 3,2 4,1 6,2 7,2 8,3 9,3 10,5 11,1 12,3 13,1 14,1 15,3 16,2 17,1 18,1
19,4 20,3 21,6 22,4 23,4 24,4 25,2 27,1 28,2 29,2 31,1 32,2 33,2 34,1 35,2 36,2
37,4 38,2 39,2 40,5 41,2 42,1 43,3 44,3 45,1 46,1 47,1 48,2 49,2 51,1 52,2 53,2
54,1 55,2 56,3 57,1 58,1 59,2 60,1/2 61,2 62,1 63,2 64,3 65,1 66,1 67,1 68,1
69,2 70,2 71,1 73,1 74,2 75,2 76,2 77,1 78,2 79,1 80,1 81,1 82,2

# \i{}Leptocotis \i0{}Streets, 1877/
1,3 2,2 3,2 4,2 5,1 6,2 7,1 8,3 9,2 10,5 11,3 12,3 13,1 14,2 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,1 24,2 25,1 27,2 29,2 31,1 32,2 33,2 34,1 35,2 36,2 37,5
38,2 39,3 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,3 49,2 51,1 52,5 53,2 54,1 55,5
56,2 57,1 58,1 59,2 60,1 61,1 62,1 63,1 64,2 65,2 66,2 67,3 68,3 69,3 70,2 71,2
72,1 73,1 74,2 75,2 76,2 77,1 78,2 79,1 80,1 81,1 82,2

# \i{}Lycaea \i0{}Dana, 1852/
1,1 2,3 3,2 4,1 6,2 7,1 8,3 9,2 10,5 11,1 12,3 13,1 14,1 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,6 24,4 25,1 27,2 29,2 31,1 32,2 33,2 34,1 35,2 36,2 37,5
38,2 39,3 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,3 49,2 51,1 52,2 53,3 54,1 55,2
56,3 57,1 58,1 59,1 60,1 61,1 62,1 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2 71,2
72,1 73,1 74,2 75,2 76,2 77,1 78,2 79,1 80,1 81,1 82,1

# \i{}Oxycephalus \i0{}Milne-Edwards, 1830/
1,3 2,2 3,2 4,2 5,1 6,2 7,1 8,3 9,2 10,5 11,2 12,3 13,1 14,2 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,1 24,2 25,1 27,2 29,2 31,1 32,2 33,2 34,1 35,3 39,3 41,2
42,1 43,3 44,2 45,1 46,1 47,2 48,2 49,2 51,1 52,4 53,2 54,1 55,4 56,2 57,1 58,1
59,2 60,1 61,1 62,1 63,1 64,2 65,2 66,2 67,3 68,3 69,3 70,3 71,2 72,1 73,1 74,2
75,1 76,2 77,1 78,2 79,1 80,1 81,1 82,3

# \tx720\i{}Paralycaea \i0{}Claus, 1879/
1,1 2,3 3,2 4,1 6,3 7,1 8,3 9,3 10,5 11,1 12,1 13,2 14,1 15,4 16,4 17,1 18,2
19,4 20,3 21,6 22,4 23,2 24,4 25,3 26,2 27,1 29,2 31,1 32,2 33,1 34,1 35,2 36,2
37,1 38,2 39,2 40,2 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,1 49,2 53,1 56,3 57,1
58,1 59,1 60,1 61,1 62,1 63,2 64,1 65,2 66,2 67,3 68,3 69,1 70,3 71,1 73,1 74,2
75,1 76,2 77,1 78,2 79,2 80,1 81,1 82,2

# \tx720\i{}Parapronoe \i0{}Claus, 1879/
1,1 2,3 3,2 4,2 5,2 6,2 7,1 8,3 9,1 10,5 11,1 12,1 13,1 14,1 15,3 16,1 17,1 18,1
19,4 20,2 21,6 22,3/4 23,2 24,1/3 25,1 27,2/3 28,2 29,2 31,1 32,2 33,2 34,2 35,2
36,2 37,1 38,2 39,2 40,5 41,2 42,2 43,3 44,1 45,1 46,1 47,1 48,1 49,2 53,2 54,1
55,2 56,3 57,1 58,1 59,2 60,2 61,1 62,1 63,2 64,2 65,2 66,2 67,3 68,3 69,1 70,2
71,1 73,1 74,2 75,2 76,2 77,2 78,1 79,2 80,1 81,1 82,1

# \tx720\i{}Parascelus \i0{}Claus, 1879/
1,2 2,3 3,2 4,1 6,2 7,1 8,3 9,2 10,5 11,1 12,3 13,1 14,1 15,3 16,1 17,1 18,1
19,4 20,3 21,6 22,4 23,5 24,4 25,2 27,1 28,2 29,2 31,1 32,2 33,4 34,1 35,2 36,2
37,4 38,2 39,2 40,5 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,1 49,2 53,1 56,3 57,1
58,1 59,3 60,2 61,2 62,1 63,2 64,3 65,2 66,1 67,1 68,1 69,2 70,2 71,2 72,1 73,1
74,2 75,2 76,2 77,2 78,2 79,1 80,1 81,1 82,2
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# \tx720\i{}Paratyphis \i0{}Claus, 1879/
1,2 2,3 3,2 4,1 6,2 7,2 8,3 9,3 10,5 11,1 12,3 13,1 14,1 15,3 16,2 17,1 18,1
19,4 20,3 21,6 22,4 23,4 24,4 25,3 26,1 27,1 28,2 29,2 31,1 32,2 33,2 34,1 35,2
36,2 37,2 38,2 39,2 40,5 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,1 49,2 53,1 56,3
57,1 58,1 59,3 60,1/2 61,2 62,1 63,2 64,3 65,1 66,1 67,1 68,1 69,2 70,2 71,1
73,1 74,2 75,2 76,2 77,1 78,2 79,1 80,1 81,1 82,2

# \i{}Platyscelus \i0{}Bate, 1861/
1,2 2,3 3,2 4,1 6,2 7,2 8,3 9,2 10,5 11,1 12,3 13,1 14,1 15,3 16,1 17,1 18,1
19,4 20,3 21,6 22,4 23,2 24,4 25,3 26,1 27,1 28,2 29,2 31,1 32,2 33,2 34,1 35,2
36,2 37,4 38,2 39,2 40,5 41,2 42,1 43,3 44,3 45,1 46,1 47,1 48,2 49,2 51,1 52,4
53,2 54,1 55,4 56,3 57,1 58,1 59,3 60,2 61,2 62,1 63,2 64,3 65,1 66,1 67,1 68,1
69,2 70,2 71,1 73,1 74,2 75,2 76,2 77,1 78,2 79,1 80,1 81,1 82,1

# \i{}Pronoe \i0{}Guerin-Meneville, 1836/
1,1 2,3 3,2 4,1 6,2 7,1 8,3 9,1 10,4 11,1 12,3 13,2 14,1 15,3 16,1 17,1 18,1
19,4 20,2 21,5 22,3 28,6 29,1 30,1 31,1 32,2 33,2 34,1 35,2 36,2 37,7 38,2 39,2
40,3 41,2 42,3 43,3 44,3 45,1 46,1 47,1 48,1 49,2 53,1 56,3 57,1 58,1 59,1 60,1
61,1 62,1 63,2 64,2 65,2 66,2 67,3 68,3 69,3 70,2 71,1 73,1 74,2 75,2 76,2 77,2
78,2 79,2 80,1 81,1 82,2

# \i{}Rhabdosoma \i0{}White, 1847/
1,3 2,2 3,2 4,2 5,1 6,2 7,1 8,3 9,2 10,5 11,3 12,3 13,3 14,2 15,4/5 16,3 17,1
18,2 19,4 20,3 21,6 22,4 23,1 24,2 25,1 27,2 29,2 31,1 32,2 33,2 34,1 35,3 39,3
41,2 42,1 43,3 44,2 45,1 46,1 47,4 48,2 49,2 51,1 52,2 53,2 54,1 55,2 56,2 57,1
58,1 59,1 60,1 61,1 62,1 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2 71,1 73,1 74,2
75,2 76,2 77,1 78,2 79,2 80,3 81,3 82,2

# \i{}Schizoscelus \i0{}Claus, 1879/
1,2 2,3 3,2 4,1 6,2 7,1 8,3 9,2 10,5 11,1 12,3 13,1 14,1 15,3 16,2 17,2 18,1
19,4 20,3 21,6 22,4 23,4 24,4 25,2 27,1 28,3 29,2 31,1 32,2 33,4 34,1 35,2 36,2
37,4 38,2 39,3 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,1 49,2 53,2 54,1 55,2 56,3
57,1 58,1 59,3 60,2 61,2 62,1 63,2 64,3 65,1 66,1 67,1 68,1 69,1 70,2 71,2 72,1
73,1 74,2 75,1 76,2 77,1 78,2 79,1 80,1 81,1 82,2

# \i{}Simorhynchotus \i0{}Stebbing, 1888/
1,1 2,3 3,2 4,2 5,2 6,2 7,1 8,3 9,2 10,5 11,2 12,3 13,1 14,2 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,6 24,4 25,1 27,2 29,2 31,1 32,2 33,2 34,1 35,3 39,3 41,2
42,1 43,3 44,2 45,1 46,1 47,1 48,1 49,2 53,3 54,1 55,2 56,3 57,1 58,1 59,1 60,1
61,1 62,1 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2 71,2 72,1 73,1 74,2 75,1 76,2
77,1 78,2 79,1 80,1 81,1 82,2

# \i{}Streetsia \i0{}Stebbing, 1888/
1,3 2,2 3,2 4,2 5,1 6,2 7,1 8,3 9,2 10,5 11,3 12,3 13,1 14,2 15,3 16,1 17,1 18,2
19,4 20,3 21,6 22,4 23,1 24,2 25,1 27,2 29,2 31,1 32,2 33,2 34,1 35,2 36,2 37,8
38,2 39,3 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,3 49,2 51,1 52,5 53,2 54,1 55,5
56,2 57,1 58,1 59,2 60,1 61,1 62,1 63,1 64,2 65,2 66,2 67,3 68,3 69,3 70,2 71,2
72,1 73,1 74,2 75,2 76,2 77,2 78,2 79,1 80,1 81,1 82,1

# \tx720\i{}Tetrathyrus \i0{}Claus, 1879/
1,2 2,3 3,2 4,1 6,2 7,1 8,3 9,3 10,5 11,1 12,3 13,1 14,1 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,5 24,4 25,3 26,1 27,1 29,2 31,1 32,2 33,2 34,1 35,2 36,2
37,4 38,2 39,2 40,5 41,2 42,2 43,3 44,2 45,1 46,1 47,1 48,3 49,2 51,2 52,1 53,3
54,2 55,1 56,2 57,1 58,1 59,3 60,2 61,2 62,1 63,2 64,3 65,2 66,1 67,1 68,1 69,2
70,2 71,1 73,1 74,2 75,1 76,2 77,1 78,2 79,1 80,1 81,1 82,2
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# \i{}Thamneus \i0{}Bovallius, 1887/
1,1 2,3 3,2 4,2 5,3 6,2 7,1 8,3 9,3 10,5 11,1 12,1 13,1 14,1 15,3 16,2 17,1 18,2
19,4 20,4 21,4 22,3 29,2 31,1 32,2 33,2 34,2 35,2 36,2 37,5 38,2 39,2 40,6 41,2
42,1 43,3 44,2 45,1 46,1 47,1 48,3 49,2 51,1 52,4 53,3 54,1 55,4 56,3 57,1 58,1
59,1 60,1 61,1 62,1 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2 71,2 72,1 73,1 74,2
75,2 76,2 77,2 78,2 79,2 80,1 81,1 82,1

# \i{}Thyropus \i0{}Dana, 1852/
1,2 2,3 3,2 4,1 6,2 7,2 8,3 9,3 10,5 11,1 12,3 13,1 14,1 15,3 16,1 17,1 18,1
19,4 20,3 21,6 22,4 23,4 24,4 25,2 27,1 28,2 29,2 31,1 32,2 33,4 34,1 35,2 36,2
37,3 38,2 39,2 40,4 41,2 42,2 43,3 44,2 45,1 46,1 47,1 48,1 49,2 53,1 56,3 57,1
58,1 59,3 60,2 61,2 62,1 63,2 64,3 65,1 66,1 67,1 68,1 69,2 70,2 71,2 72,1 73,1
74,2 75,2 76,2 77,2 78,2 79,1 80,1 81,1 82,2

# \i{}Tryphana \i0{}Boeck, 1871/
1,1 2,3 3,2 4,1 6,2 7,1 8,3 9,2 10,6 11,1 12,1 13,2 14,4 15,4 16,2 17,1 18,1
19,4 20,3 21,6 22,2 24,4 25,3 26,2 27,1 28,5 29,1 30,2 31,1 32,2 33,3 34,1 35,2
36,2 37,6 38,2 39,2 40,4 41,2 42,2 43,3 44,3 45,1 46,1 47,1 48,1 49,2 53,1 56,2
57,1/5 58,1/3 59,1 60,1 61,1 62,1/3 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2 71,2
72,1 73,1 74,2 75,2 76,2 77,2 78,2 79,2 80,1 81,1 82,3

# \tx720\i{}Tullbergella \i0{}Bovallius, 1887/
1,1 2,3 3,2 4,2 5,3 6,2 7,1 8,3 9,2 10,5 11,3 12,3 13,1 14,2 15,3 16,2 17,1 18,2
19,4 20,3 21,6 22,4 23,5 24,4 25,1 27,2 29,2 31,1 32,2 33,2 34,1 35,2 36,2 37,5
38,2 39,3 41,2 42,1 43,3 44,2 45,1 46,1 47,1 48,3 49,2 51,1 52,5 53,3 54,1 55,5
56,2 57,1 58,1 59,1 60,1 61,1 62,1 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2 71,1
73,1 74,2 75,2 76,2 77,1 78,2 79,1 80,1 81,1 82,1

# \i{}Vibilia \i0{}Milne-Edwards, 1830/
1,1 2,1 3,2 4,1 6,3 7,1 8,2 9,1 10,1 11,1 12,3 14,1 15,1 16,1 17,1 18,1 19,2
20,1 21,2 22,6 28,1 29,1 30,1 31,1 32,1 33,1 34,1 35,1 36,1 38,1 39,1 40,1 41,2
42,1 43,3 44,3 45,1 46,1 47,1 48,1 49,2 53,2 54,1/2 55,2 56,3 57,1 58,1 59,1
60,1 61,1 62,1 63,1 64,1 65,2 66,2 67,3 68,3 69,3 70,2 71,2 72,2 73,1 74,2 75,2
76,2 77,2 78,2 79,2 80,1 81,1 82,2
```

Appendix 4

Paupdata: Cladistic Data Matrix

```
!Hyperiid Genera 23:31 10-MAR-00
PARAMETERS NOTU=29 NCHAR=82;
SYMBOLS 1-8;
DATA (A8,A1/( 80A1));
Amphithy

1321?31335121144124364243 21?2?125122122521331111 2???1??311
1121221222131?12221221
12

Amphithy

2321?21335131132124364543 21?2?122122122521321112 2?11211311
313123122212 1?12221221
12

Anaprono

1321?3131511113111325 1?????22?1221222222213211132?12222211
1111222233332112222221
11

Brachysc

13232213251311321243 65?22?1?2?122122522621321113121431 4311
1111112233322112222221
11

Calamorh

32221213253312321243641 21?2?2?12113???3?213211232?15215211
2111122233322112221211
11

Cranocep

12221213253312341243642 21?2?2?122122523?213211222?14314211
2111122233322112222211
11

Eupronoe

132322131511113111336 5?21?222?12222212252131111311122 12311
11112222331 21?12212121
11
```

Euscelus

1321?313351211322143643 42?142?124122423?213211122?12212311
32212321111221121 21211
12

Glossoce

33222213352111321243641 21?2?2?222122523?213211322?11211111
11111122333221122222 12
22

Hemityph

2321?223351311321143644 42?122?122122422521331 1122?12212311
2?21231111221?12221211
12

Leptocot

322212132533123212436412 1?2?2?122122523?213211132?15215211
2111122233322112221211
12

Lycaea D

1321?2132513113212436464 1?2?2?122122523?213211132?12312311
1111112233322112221211
11

Oxycepha

322212132523123212436412 1?2?2?12213???3?213211222?14214211
2111122233332112121211
13

Paralyca

1321?31335112144124364243 21?2?121122122221321111 2???1??311
111121223313 1?12121221
12

Parapron

13222213151111311142632 11?222?1222221225223111112???212311
22112222331 21?12222121
11

```
Parascel

2321?21325131131114364542?122?124122422521321111 2???1??311
3221232111222112222211
12

Paratyph

2321?22335131132114364443112 2?1221222225213211112???1??311
3?2123111122 1?12221211
12

Platysce

2321?22325131131114364243112 2?12212242252133111 22?14214311
32212311112 21?12221211
11

Pronoe G

1321?2131413213111425 3????6111221227223233311112???1??311
1111222233321?12222221
12

Rhabdoso

32221213253332431243641 21?2?2?12213???3?2132114 22?12212211
11111122333 21?12221223
32

Schizosc

2321?213251311322143644 42?132?124122423?21321111 2???212311
3221231111122112121211
12

Simorhyn

1322221325231232124364641?2?2?12213???3?213211112???312311
11111122333221121 21211
12

Streetsi

32221213253312311243641 21?2?2?122122823?21321113 2?15215211
2111122233322112222211
11
```

```
Tetrathy

2321?2133513113212436454311?2?1221224225223211132?21321211
3221232111221?12121211
12

Thamneus

1322321335111132124443??????2?122222522621321113 2?14314311
1111112233322112222221
11

Thyropus

2321?22335131131114364442?122?124122322422321111 2???1??311
3221231111222112222211
12

Tryphana

1321?21326112442114362?43215121231226224223311112???1??211
1111112233322112222221
13

Tullberg

1322321325331232124364541?2?2?122122523?21321113 2?15315211
111111223332 1?12221211
11

Vibilia

1121?3121113?111112126?????111111111?1112133111 12???2?2311
1111112233322212222221
12

UNORDERED  1-2 4-6 8-16 19-25 27-28 33 35 37 39-40 42-44 4
6-48 52-53 55-59 61-62
64 67-70 80-82;
WEIGHTS 82*1;
GO ;
END ;
```

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