



Crustacean classification: on-going controversies and unresolved problems*

GEOFF A. BOXSHALL

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom
E-mail: g.boxshall@nhm.ac.uk

*In: Zhang, Z.-Q. & Shear, W.A. (Eds) (2007) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. *Zootaxa*, 1668, 1–766.

Table of contents

Abstract	313
Introduction	313
Treatment of parasitic Crustacea	315
Affinities of the Remipedia	316
Validity of the Entomostraca	318
Exopodites and epipodites	319
Using of larval characters in estimating phylogenetic relationships	320
Fossils and the crustacean stem lineage	321
Acknowledgements	322
References	322

Abstract

The journey from Linnaeus's original treatment to modern crustacean systematics is briefly characterised. Progress in our understanding of phylogenetic relationships within the Crustacea is linked to continuing discoveries of new taxa, to advances in theory and to improvements in methodology. Six themes are discussed that serve to illustrate some of the major on-going controversies and unresolved problems in the field as well as to illustrate changes that have taken place since the time of Linnaeus. These themes are: 1. the treatment of parasitic Crustacea, 2. the affinities of the Remipedia, 3. the validity of the Entomostraca, 4. exopodites and epipodites, 5. using larval characters in estimating phylogenetic relationships, and 6. fossils and the crustacean stem-lineage. It is concluded that the development of the stem lineage concept for the Crustacea has been dominated by consideration of taxa known only from larval or immature stages. This has limited our understanding of key events in the origin of crown group Crustacea.

Key words: Crustacea, Linnaeus, taxonomy, phylogeny, morphology, fossils

Introduction

In the tenth edition of *Systema Naturae*, Linnaeus (1758) included 87 species of crustaceans that he placed in only six genera distributed through two of the classes that he recognised at the time (Table 1). The Linnaean genus *Cancer* was by far the largest of the Crustacea-containing genera, comprising 59 species, and, although dominated by brachyuran crabs, this genus was heterogeneous by modern standards as it incorporated stomatopods, amphipods and anostracan Branchiopoda, as well as representatives of five different infraorders of

decapods. The Linnaean genus *Monoculus* was even more heterogeneous, containing a xiphosuran chelicerate and a pteropod mollusc in addition to a variety of crustaceans which included a branchiuran fish louse, four branchiopods (one each from the Notostraca, Conchostraca, Anomopoda and Onychopoda), an ostracod and a copepod (see Damkaer 2002). *Monoculus* Linnaeus was eventually suppressed (Fox 1951) and is the only one of Linnaeus's original Crustacea-containing generic names no longer valid today. The third Linnaean genus classified in the class Insecta was *Oniscus*, which comprised eleven species, all but one of which are isopods. The exception is *Oniscus ceti* Linnaeus, an amphipod parasitic on cetaceans currently placed in the genus *Cyamus*. The three other Crustacea-containing genera were all classified by Linnaeus as members of the class Vermes but each was placed in a different order. The genus *Lernaea* contained just three species of parasitic copepods from fish hosts and was placed in the order Mollusca. Two other fish-parasitic copepods were included in the Linnaean genus *Pennatula*, belonging to the order Zoophyta. *Pennatula* is a valid genus of Cnidaria and the two copepod species included by Linnaeus are now classified within the siphonostomatoidan genus *Pennella*. Finally, the Linnaean genus *Lepas* comprised just five species of barnacles and was placed in the order Testacea.

TABLE 1. Classification of Crustacea-containing genera in Linnaeus (1758).

Class	Order	Genus	No. of species	Non-crustacean
Insecta	Aptera	<i>Cancer</i>	59	0
Insecta	Aptera	<i>Monoculus</i>	9	2
Insecta	Aptera	<i>Oniscus</i>	11	0
Vermes	Mollusca	<i>Lernaea</i>	3	0
Vermes	Testacea	<i>Lepas</i>	5	0
Vermes	Zoophyta	<i>Pennatula</i>	4	2

All of Linnaeus's Crustacea-containing genera are heterogeneous. *Monoculus* and *Pennatula*, for example, both contain representatives of more than one phylum. *Cancer* contains representatives of two classes within the subphylum Crustacea but the remaining three genera each comprise representatives of just a single superorder: *Oniscus* contains only peracaridans, *Lernaea*, only neocopepodan copepods, and *Lepas*, only thoracican cirripedes. The journey from these six genera to the modern classification of the Crustacea (cf. Martin & Davis 2001) is a fascinating one and can be seen as a search for natural order, set against a landscape of rapidly increasing knowledge, theoretical advances and changing methodology.

Progress was slow initially, with the century from the publication of the tenth edition in 1758 to the late 1850s being distinguished by the gradual accumulation of new knowledge on all aspects of metazoan diversity. The notable advances in crustacean systematics during this period were driven largely by discoveries of new taxa. The advent of the theory of evolution by natural selection (Darwin 1859) provided the theoretical basis for the continuing search for natural (i.e. monophyly-based) classification systems but had remarkably little immediate impact on crustacean classification. Gradually, however, it stimulated increased rigour through the application of concepts such as homology that provide the foundation for comparative morphology. The second century post-Linnaeus (1850s–1950s) is thus characterised by advances in theoretical understanding in combination with continuing discoveries of novel forms.

The pace of change from the 1950s to the present has increased dramatically and this period has been notable in the impact of two major methodological changes. Firstly, the widespread adoption of the methods of phylogenetic systematics (see Hennig 1979) has brought about an important revolution in the way relationships are estimated and is having a profound and continuing impact on crustacean classification. Secondly, the development of methods of extracting and analysing molecular sequence data has made a huge and potentially

informative dataset available for use in the study of crustacean systematics. In addition, the pace of discovery of novel forms has not slackened, with new higher taxa such as the Remipedia (Yager 1981), Tantulocarida (Boxshall & Lincoln 1983) and Mictacea (Bowman *et al.* 1985) all being based on newly discovered material. These methodological advances ensure that the study of crustacean systematics remains dynamic and in this paper I highlight a few of the major unresolved problems and on-going controversies in the field.

Treatment of parasitic Crustacea

Numerous Crustacea have entered into symbiotic associations with host organisms and many have adopted a fully parasitic mode of life. The Linnaean genus *Lernaea* was based on parasitic copepods and was placed in a different class from the only free-living copepod included by Linnaeus, the unrecognisable *Monoculus quadricornis*. Such arrangements, with parasitic forms treated as representing a distinct higher taxon from their free-living relatives, have remained common practice since Linnaeus's time. Classifications of this type were based primarily on differences and derived support from the morphological gaps that often exist between free-living taxa and their highly specialised parasitic relatives. The Epicaridea, for example, comprises parasites of crustacean hosts and has long been treated as a separate suborder within the Isopoda (see Bowman & Abele 1982; Martin & Davis 2001). New molecular evidence (Dreyer & Wägele 2002) now confirms Wägele's (1989) proposal that the epicarideans are closely related to cymothoids. Epicarideans are no longer treated as a distinct suborder characterised in part by their adaptations to parasitism, instead they have been placed within a revised Flabellifera by Wilson (2003), and within the suborder Cymothoidea by Dreyer & Wägele (2002) and by Brandt & Poore (2003). The latter authors also commented that the monophyly of the epicarideans has not yet been unequivocally established. On the basis of both molecular and morphological evidence it is now recognised that the epicarideans represent a specialised terminal branch of parasitic forms that has arisen within a primitively free-living clade.

The cyamids or whale lice, were known to Linnaeus who included a single species of these dorso-ventrally flattened amphipods in his otherwise isopod-based genus *Oniscus*. Cyamids were traditionally treated as a wholly parasitic infraorder of the amphipod suborder Caprellidea (cf. Martin & Davis 2001). Now, however, they are classified only as a family of parasites contained within a much larger clade (suborder Corophidea, infraorder Caprellida) of free-living amphipods that are predominantly detritivores (Myers & Lowry 2003).

In the case of copepods, parasitic forms tended to be even more artificially grouped together. The inconsistencies generated by the recognition of the higher taxon "Copepoda Parasitica" were outlined by Kabata (1979) and have now been successfully resolved so that symbiotic and free-living copepods are all integrated into a unified classification system (Kabata 1979; Huys & Boxshall 1991). A parasitic mode of life has evolved several times, in different lineages within three of the large orders within the Copepoda, all of which also contain basal free-living taxa, or in the case of the Siphonostomatoidea, at least loosely symbiotic rather than parasitic taxa. As a further example, Huys *et al.* (2007) recently demonstrated that the small parasitic order Monstrilloidea, characterised by its extreme reduction (loss of all mouthparts in the adult) and by its pro-telean life cycle, arose from within the order Siphonostomatoidea as sister group to a lineage of much less modified fish parasites.

Even in the decapods, the adoption of a symbiotic mode of life has generated uncertainty in systematic arrangement. The members of the brachyuran family Eumedonidae, for example, are obligate symbionts of echinoderm hosts, and have been regularly treated as a distinct family, although this treatment is not stable (cf. Martin & Davis 2001). Based on both larval and adult morphology, Ng & Clark (2000a) argued that the eumedonids should be placed within the otherwise free-living family Pilumnidae. They concluded that there are "no arguments for retaining the Eumedonidae as a distinct family, other than the fact that all its members are symbionts on echinoderms". In addition, Ng & Clark (2000a) recognised that the eumedonid genus *Hapa-*

lonotus is not closely related to other eumedonids, so the symbiosis with echinoderms is probably convergently derived within the large pilumnid group.

For more than two centuries since Linnaeus, parasitic crustaceans were commonly treated as representing distinct higher taxa. Recent phylogenetic studies, however, have revealed that crustaceans have repeatedly moved from a free-living life style into symbiotic and parasitic relationships, and this is now reflected by the disappearance of many of these higher taxa. Epicaridean isopods, cyamid amphipods, eumedonid brachyurans, and copepods such as the cyclopoid family Lernaeidae (based on the Linnaean genus *Lernaea*) are all now treated as terminal branches within higher taxa that are predominantly free-living. Wholly parasitic higher taxa, such as the Rhizocephala (a superorder within the infraclass Cirripedia), are still recognised within the Crustacea. Indeed the maxillopodan assemblage currently contains three subclasses (Tantulocarida, Branchiura and Pentastomida) that are exclusively parasitic and the subclass Thecostraca contains other parasitic taxa in addition to the rhizocephalans. Even in these cases uncertainty surrounds the placement of these taxa in the overall classification of the Crustacea.

The discovery of the dual sexual-asexual life cycle of the Tantulocarida (Boxshall & Lincoln 1987; Huys *et al.* 1993) and, in particular, the positioning of the gonopores in both sexes provided the strongest morphological evidence of the thecostracan affinities of tantulocarids. Their lack of a cyprid larval stage during development effectively excludes them from the Thecostraca as currently defined but the sister-group relationship has yet to be formally recognised in the classification hierarchy. As is often the case for highly reduced parasites, molecular sequence data are likely to be important in elucidating relationships and molecular data on tantulocarids should soon be available.

The relationship between the Branchiura, the fish lice, and the Pentastomida, the tongue worms, remains problematic. Both were treated as distinct subclasses of the class Maxillopoda by Martin & Davis (2001) who outlined the conflicting viewpoints on how to include the pentastomids. The controversy has been reviewed again recently by Waloszek *et al.* (2006). The traditional interpretation of pentastomids as stem-lineage derivatives of the Euarthropoda was based on their loose classification as “protoarthropods” together with taxa such as tardigrades and onychophorans, but received new support from the discovery of Cambrian fossils interpreted as pentastomids by Waloszek & Müller (1994) and by Waloszek *et al.* (2006). Evidence supporting a close affinity between branchiurans and pentastomids comes from comparative spermatology (Wingstrand 1972; Storch & Jamieson 1992), from molecular sequence data (Abele *et al.* 1989; Lavrov *et al.* 2004), and from gene order data (Lavrov *et al.* 2004). The analysis by Giribet *et al.* (2005) found support for both hypotheses, depending on whether they used morphological data alone, or a combination of both morphological and molecular data - a result that is hardly surprising. I regard this controversy as still unresolved although most molecular-based analyses, even if they do not recover a sister-group relationship between the Branchiura and Pentastomida place the latter within the Crustacea (e.g. Spears & Abele 1998; Giribet & Ribera 2000) or the Pancrustacea (or Tetraconata) (Regier *et al.* 2005; Mallat & Giribet 2006; Carapelli *et al.* 2007). The small number of available gene sequences and the restricted taxon sampling inside the pentastomids currently limit our ability to generate a robust molecular-based system of affinities.

Affinities of the Remipedia

The affinities of the class Remipedia within the Crustacea are unclear. They have often been treated as a basal taxon (Schram 1983; Wills 1998) or even outside of the Crustacea *sensu stricto* (Wills *et al.* 1995), primarily because of their multi-segmented and undifferentiated trunk. Remipedes, however, have also been considered as one of the more derived crustacean taxa (Boxshall 1998; Fanenbruck *et al.* 2004). Molecular data on remipedes have been slow to arrive and remain hard to interpret because of long branch attraction problems (e.g. Lavrov *et al.* 2004). The long awaited discovery of remipede larvae (Koenemann *et al.* 2007) has recently

shed some light on their phylogenetic relationships. The late appearance of the ventral flagellum on the antennule of the remipede post-larva is in accord with the discovery that the remipede antennule comprises a main dorsal axis consisting of segments provided with intrinsic muscles and a ventral annulated flagellum that lacks intrinsic musculature (Boxshall 2004). It confirms that the remipede antennule is fundamentally uniramous and bears an accessory flagellum. It should not be described as biramous and is also not homologous with the biflagellate antennule typical of malacostracans (Boxshall 2004).

The lecithotrophic nauplius larvae of remipedes share many characteristics with the nauplii of the Euphausiacea and dendrobranchiate Decapoda. The suite of characters associated with the adoption of lecithotrophy in these malacostracan nauplii includes a yolk-rich body, the absence of a labrum, the weakly invaginated stomodeum and proctodeum, the absence of the antennary naupliar process and mandibular gnathobase, the non-articulated naupliar appendages and an undifferentiated pre-anal growth zone (Scholtz 2000). Koenemann *et al.* (2007) discussed this shared character suite but did not unequivocally make inferences as to whether the similarity between remipede and malacostracan nauplii was symplesiomorphic, synapomorphic or convergent.

As with the branchiopods, the nauplii of most copepods are planktotrophic, but lecithotrophy has evolved repeatedly. For example, in the order Calanoida, the members of the family Euchaetidae have lecithotrophic nauplii whereas in closely related families they are planktotrophic. In the Harpacticoida, species of the genus *Pseudotachidius* have lecithotrophic nauplii and within the orders Cyclopoida and Siphonostomatoida many parasitic groups possess lecithotrophic nauplii (cf. Boxshall & Halsey 2004). Lecithotrophy has evolved independently in several different lineages and is characterised each time by shared characters from the suite, including a yolk-rich body, the absence of a labrum, the weakly invaginated stomodeum and proctodeum, the absence of the antennary naupliar process and of the mandibular gnathobase. Given the widespread and independent adoption of lecithotrophy across the Crustacea, I infer that the possession of lecithotrophic larvae by remipedes is another facet of their k-selected, large body size, predatory life style in an oligotrophic habitat and that the presence of lecithotrophic nauplii in remipedes and in malacostracans is probably derived independently from an ancestral planktotrophic type of larva, which is still retained in representatives of the Branchiopoda, Copepoda, Thecostraca and Cephalocarida.

The enormous, biramous mandibular palps of remipede nauplii are retained through into the post-larval phase (Koenemann *et al.* 2007) and presumably atrophy as the mandibular gnathobase develops. None of the naupliar limbs is involved in feeding but they are presumably responsible for locomotion. The few setae that they retain are located distally but remipede nauplii are probably weak swimmers since their ability to generate water flow will be reduced by the lack of well developed setal fans and by the apparently small angle through which the mandible can swing during its power stroke. Despite their small relative size, the antennae may be more important in swimming than the mandibular palps.

Detailed study of the “complex” remipede brain led Fanenbruck *et al.* (2004) to conclude that phylogenetic analysis based on brain anatomy strongly contradicts the hypothesis that remipedes are a basal crustacean group. Surprisingly, given the phylogenetic inferences they made, Fanenbruck *et al.* did not compare brain structure in remipedes with that of a cephalocarid, as elucidated by Elofsson & Hessler (1990). It is an obvious comparison since both groups lack any trace of eyes or associated optical centres in the brain. Key features of the cephalocarid brain include the presence of large olfactory lobes and of a tract between mushroom body 8 and the olfactory lobes which is homologous with the olfactory-globular tract of Malacostraca. Whilst large olfactory lobes are found in all three taxa, crossing over (chiasm) of fibres in the olfactory tract, as found in remipedes and malacostracans, is not found in cephalocarids. From their evidence, Fanenbruck *et al.* (2004) inferred a most likely sister-group relationship between the Remipedia and Malacostraca. The comparison with cephalocarids does not contradict this but could change the putative relationship with hexapods.

Validity of the Entomostraca

The Entomostraca, as a taxon comprising the non-malacostracan crustaceans, had fallen into disuse during the twentieth century and was not used by either Bowman & Abele (1982) or Martin & Davis (2001) in their comprehensive classification schemes for living Crustacea. Walossek (1999) attempted to resurrect the Entomostraca as a monophylum and as the sister taxon of the Malacostraca. The Remipedia were not considered in his analysis. Walossek's Entomostraca comprised the Cephalocarida, Branchiopoda and Maxillopoda, and were discussed only in comparison with the Malacostraca. He recognised three putative diagnostic character states (i.e. autapomorphies of the stem species of the Entomostraca): 1. mandible lacking palp in adult, 2. maxillule with four median enditic lobes, and 3. abdomen of at least four limb-less somites. None of these diagnostic character states is robust.

The first character state listed by Walossek is not simple to interpret given the presence of a mandibular palp in adult copepods and mystacocarids, and the loss of the palp in remipedes. Invoking heterochrony as an explanation for the retention of the larval palp in adults of copepods and mystacocarids requires an additional layer of assumptions but there is evidence to support such an assumption. Ostracods, however, also retain a mandibular palp in the adult and no robust evidence suggests that ostracods should be interpreted as paedomorphic. The second character relates to maxillary structure and is also difficult to interpret since the so-called entomostracans exhibit the malacostracan state identified by Walossek (protopod divided into coxa and basis) as well as the entomostracan state (presence of 4 endites on protopod). Boxshall (1998) inferred that a maxillule bearing 4 endites on a protopod that was divided into coxa and basis was present in the ancestral crustacean (i.e. this form of maxillule is an autapomorphy of the stem species of the Eucrustacea), so its retention in the Entomostraca is plesiomorphic. The third character state, the possession of an abdomen of at least four limb-less somites, is also problematic. It is probable that the differentiation of the trunk into thorax and limb-less abdomen is also a plesiomorphic trait and that the limb-less abdomen has been almost completely lost in the majority of malacostracans (see discussion in Gruner & Scholtz 2004). In addition, the abdomen of a cephalocarid comprises post-cephalic trunk segments 9 to 19, that of anostracans, trunk segments 13 to 19 (or 21 to 26 depending on family), and that of copepod, trunk segments 8 to 10. The abdomen of these three taxa is composed of different body segments and, in strict compositional terms, cannot be considered homologous although the genetic mechanism responsible for tagma differentiation (e.g. inhibition of limb development on abdominal segments) might be the same in all these taxa.

The recent discovery of *Cinerocaris magnifica*, a phyllocarid from the Silurian fossil Lagerstätte of Herefordshire (Briggs *et al.* 2004), is highly significant in our understanding of malacostracan origins and the entomostracan-malacostracan divide. This remarkable fossil unequivocally displays malacostracan tagmosis and provides detailed information of the limbs of all three tagmata: cephalon, pereon and pleon. On the cephalon it carries stalked eyes, biflagellate antennules, biramous antennae, well developed mandibles with a uniramous palp, and a maxillule with a short uniramous palp. The fifth cephalic limb has been recruited as a feeding appendage, the maxilla, and differs markedly in structure from the pereopods. The protopodal part of the visualised maxillule (Briggs *et al.* 2004: Fig. 2(a)) lacks detail but appears to be bipartite, perhaps corresponding to the division into coxa and basis, each with an undivided medial enditic margin – a structure synapomorphic for malacostracans. The palp of the maxillule is short and not modified as an elongate grooming appendage as in modern leptostracans. The maxilla, with its series of well developed protopodal endites, closely resembles that of the Cambrian branchiopod *Rehbachella* (Walossek 1993), differing primarily in the apparent absence of an exopodite.

The pereopods of *Cinerocaris* are also a revelation because they retain a long protopod provided with a series of medial endites which continues onto the proximal segments of the endopodite. In the light of this, I interpret the setae present proximally on the medial surface of the developing pereopods in modern leptostracans (cf. Olesen & Walossek 2000) as representing vestiges of the enditic armature. This limb structure, with

its series of protopodal endites, was regarded by Walossek (1999) as characteristic of his Entomostraca, but is clearly also plesiomorphic for malacostracans, further weakening any support for retaining the Entomostraca as a monophylum within the Crustacea.

Exopodites and epipodites

The postantennular limbs of arthropods are primitively biramous (Boxshall 2004) and crustaceans display this original state more widely than other extant arthropods in which traces of exopodites can rarely be found. Boxshall tentatively suggested that exopodites were primitively two-segmented in euarthropods but the real significance of fossils such as the stem group chelicerate *Offacolus* and the marrellomorphan *Xylorkorys*, both of which have well developed, multi-segmented exopodites on the more anterior pairs of the postantennular limbs (Sutton *et al.* 2002; Siveter *et al.* 2007a), has yet to be assimilated. What these new fossils bring into focus is the identity of the exopodite as a ramus, carried distally on the basis and primitively supplied with intrinsic muscle insertions. This serves to distinguish an exopodite from trunk limb epipodites and other outer lobes which, to the best of my knowledge, lack any musculature in any crustaceans studied thus far. This criterion helps us to differentiate between an epipodite and, for example, the so-called pseudepipodite of cephalocarids. The pseudepipodite is provided with intrinsic musculature (Hessler 1964) and can be interpreted as a subdivided exopodite rather than a secondary exite or epipodite. Similarly the flagellum on the exopodite of branchiuran thoracopods 1 and 2 is provided with muscles that originate in the basis, supporting the interpretation of this enigmatic structure as part of a subdivided exopodite. No information is available on the musculature of the strongly bilobed exopodite found on the thoracopods of certain branchiopods (e.g. the laevicaudatan *Lynceus*). In all three of examples, however, the exopodite is likely to be subdivided, rather than displaying a novel marginal lobe.

The presence of large flap-like exites on the outer margin of the pereopods of *Cinerocaris* is the first documented example of epipodites in any Palaeozoic crustacean (Briggs *et al.* 2004). The origin of epipodites has been linked to the origin of insect wings (Averof & Cohen 1997) and their presence in the Silurian removes a potential timing incongruency identified by Boxshall (2004). The precise form of the pereopodal epipodites in *Cinerocaris* has yet to be determined because their relationship with the apparently foliaceous, and possibly subdivided, exopodite has yet to be confirmed. They are lamellate and appear to originate extremely close together on the lateral surface, so they almost completely overlap. In contrast, in the newly described *Tanzios* (see below), also from the Silurian, the trunk limbs also carry outer lobes (Siveter *et al.* 2007b) but each limb has two slender and tapering flattened lobes, one originating dorsal to the other. They do not resemble the epipodites of *Cinerocaris* and are separate from the well developed exopodite.

The recent report of “epipodites” in the Lower Cambrian *Yicaris dianensis* (Zhang *et al.* 2007) is questioned here. The structures interpreted as epipodites occur on the lateral margins of postmaxillary limbs. A maximum of three occurs on any one limb but the data presented by Zhang *et al.* (2007) indicated that these structures ontogenetically “develop from a single seta that widens into a bulb with a vestigial terminal spine and then into a subtriangular or subquadratic flap”. The described ontogeny raises serious doubt over the homology of these structures with the epipodites found in branchiopodan and malacostracan crustaceans, which commence development as expansions of the outer margin of the protopodal segment which will eventually carry them (e.g. Manton 1934). Although flattened, true epipodites are tissue-containing structures with, for example, the cellular margin at the outer edge expressing the *distalless* gene during development (Averof & Cohen 1997). They are not modified setae. Most epipodites lack setal armature but some are armed with setae, as in the case of the peracaridan oostegites which are modified epipodites. Crustacean setae are carried directly on limb segments, not on other setae, and the described development pattern indicates that the leaf-shaped structures in *Yicaris* are more likely modified setae than homologues of crustacean epipodites.

The possibility that the pseudepipodite of cephalocarids might represent a remnant of the distal-most of the three marginal structures on *Yicaris* trunk limbs, as suggested by Zhang *et al.* (2007) seems highly unlikely, given the setal origin of these structures compared to the origin of the pseudepipodite as a muscular subdivision of the cephalocaridan exopodite.

The difficulties in interpreting these structures are partly a result of the lack of a clear understanding of what constitutes an epipodite and how it might be distinguished anatomically from any other of the nine named different types of outer lobes or exites that are found within the Crustacea (Boxshall 2004). Precise anatomical definitions of the different exites are required in order to make meaningful, homology-based comparisons. For example, the genes *pdm* and *app* were expressed only in cells of the distal epipodite in the thoracopods of *Artemia* (Averof & Cohen 1997), not in the proximal epipodite or in the exopodite. The inference Averof & Cohen made concerning the evolution of insect wings from crustacean “gills” presumably related to the dorsal epipodite as it was based on the gene expression evidence. Anatomical studies of the different exites on crustacean limbs should in future be combined with gene expression studies in order to improve our understanding of the origin and homology of these structures.

Using of larval characters in estimating phylogenetic relationships

Many crustaceans have complex life cycles comprising two or more different phases. Parasites, for example, may have free-living, infective and parasitic phases, and many free-living benthic crustaceans have a long planktonic, dispersal phase in their life cycle. Early descriptive studies on crustacean developmental stages captured in the marine plankton generated a plethora of “generic” names based on larval stages, including nauplius, zoea, megalopa, erichthus, glaucothoe, phyllosoma, alima, furcilia, calyptosis, etc. The confusion caused by these early misinterpretations has largely been resolved now and since the late nineteenth century the great majority of these names have remained in use in zoological literature only as names of stages or phases in crustacean life cycles. A few names remain in dual use: *Mysis*, for example, is a valid genus of Mysidacea while *mysis* is widely used for a phase in the development of dendrobranchiate shrimps.

In addition to elucidating life cycles, the study of larvae has been highly informative regarding phylogenetic relationships. The thoracican cirripedes, for example, were classified by Linnaeus in his order Testacea, along with many molluscs, and remained there until Thompson (1830) observed that they metamorphosed from planktonic cyprid larvae. On the basis of this larval evidence, Thompson was the first to conclude that the affinities of the barnacles lay with the Crustacea. Also among the barnacles, the discovery of the characteristic nauplii with paired lateral horns enabled Thompson (1836) to recognise the cirripede nature of the highly metamorphic, parasitic Rhizocephala. The later discovery of the cyprid larval stage in the rhizocephalan life cycle (Müller 1862) confirmed this placement. Remarkably, our knowledge of the related thecostracan infra-class Facteotecta is still based only on larvae. The Facetotecta comprises the y-nauplii and y-cyprids and is broadly distributed in coastal marine plankton from cold temperate to tropical seas. Adult facetotectans are widely thought to be endoparasites, probably in marine invertebrate hosts, but the adults have still not been discovered.

The characters exhibited by the first stage zoeal larvae of brachyuran crabs have provided valuable evidence relevant to resolving systematic problems. The coral-dwelling crab *Tanaocheles* had been placed in the family Trapeziidae but doubt had been raised over this treatment (cf. Ng & Clark 2000b). Consideration of zoeal characters in addition to adult characters led Ng & Clark (2000b) to recognise the pilumnid affinities of *Tanaocheles*. However, interpretation of larval characters and their use in phylogenetic analysis requires an in-depth understanding of developmental patterns in the taxa under study. Clark (2005) found robust evidence of mosaic heterochrony associated with abbreviated development in pilumnid crabs. Abbreviated development, in this case the shortening of the zoeal phase from four (in *Pilumnus hirtellus*), via three (in *Actumnus*

setifer), to two (in *Pilumnus sluiteri*) stages, can affect the timing of appearance and the rate of development of numerous characters. Clark showed that the presence, for example, of higher setal counts on the coxal and basal endites of the maxillule at a given zoeal stage of *P. sluiteri* than in *P. hirtellus* is indicative of heterochronic pre-displacement rather than of the retention of a relatively plesiomorphic state (as might be inferred under an assumed oligomerization scenario).

Fossils and the crustacean stem lineage

The bulk of Linnaeus's work was on living plants and animals but in the 12th edition of *Systema Naturae* - Tome III, the Stone Kingdom—he included descriptions of fossils (Linnaeus 1768). Among other fossil arthropods, Linnaeus briefly described *Entomolithus paradoxus pisiformis*, a name 'carried over into modern trilobite taxonomy as the name of the "type agnostid trilobite" *Agnostus pisiformis*' (see St John 2007). The affinities of this arthropod remain controversial: many workers treat agnostids as a trilobites (e.g. Cotton & Fortey 2005) while others place them near the base of the stem-lineage of the Crustacea (e.g. Stein *et al.* 2005). The application of the stem lineage concept in the Crustacea has been driven primarily by Waloszek and his colleagues (e.g. Waloszek & Müller 1990; Waloszek & Szaniawski 1991; Stein *et al.* 2005; Zhang *et al.* 2007) and has proved immensely valuable in understanding the relationships of Palaeozoic crustacean-like fossil taxa and in introducing rigour into our concept of what characterises the crown group Crustacea or Eucrustacea.

Future resolution of the stem-lineage needs to incorporate more data on a wider range of fossil taxa. The component taxa of the stem-lineage as most recently visualised by Stein *et al.* (2005) are *Agnostus*, *Oelandocaris*, *Henningsmoenicaris*, *Martinssonina*, *Cambrocaris*, *Cambropachycope*, *Goticaris* and the phosphatocopines. All of these 'Orsten' material taxa are small, with body length in the range of 100 µm to 1.0 mm (Stein *et al.* 2005), and are either larval or immature. Even in cases where probable adults are known, such as for *Agnostus*, information on limb structure is available only for larval and immature stages, not for adults. In addition, the earliest known fossil crustaceans within the crown group are the 'Orsten' branchiopods *Rehbachella* and *Bredocaris*, and these taxa are also based on developmental stages rather than adults (Waloszek 1993; see Boxshall 1998 for comments on *Bredocaris*). Comparing adults with larvae is always a risk given the major changes in limb structure that can occur during development, such as the change from an early, cephalic feeding mode to a later thoracopodal mode in some crustacean taxa. Such changes involve the loss of the antennary coxal feeding process, the loss of the mandibular palp during the post-larval phase, and ontogenetic changes in the form of the labrum. These characters are profoundly important in characterising successive steps along the stem-lineage but currently our interpretations are less robust because of the lack of adult data. For example, I regard the interpretation of short antennules with few podomeres as a total crustacean (stem-lineage plus crown) group feature (Waloszek 1999) as overly influenced by larval character states and not necessarily indicative of the adult state of the stem species of the entire Crustacea.

The dominance of this larval-based interpretation of possible stem-lineage taxa has, in my opinion, led to misinterpretation of key fossils. A good example is the recently described Silurian fossil *Tanazios dokeron* which was identified as a stem lineage crustacean by Siveter *et al.* (2007b). This is a large animal of about 30 mm body length with more than 60 post-cephalic trunk segments (i.e. presumably displaying adult limb morphology). The presence of a mandible with a well defined coxal gnathobase plus a large (in this case uniramous) palp was regarded as evidence possibly suggesting a placement of *Tanazios* within the Labrophora, close to the crown-group Eucrustacea but Siveter *et al.* (2007b) also commented that the lack of a defined coxa on the antenna would exclude it from the Labrophora. This demonstrates one of the potential dangers of comparing the adult of one taxon with larvae of others since in many recent crustacean taxa coxal processes are present in the earliest stages but are lost from the antenna during development. However, I consider that the misinterpretation of *Tanazios* is more profound.

Tanazios possesses a pair of tiny unsegmented structures on the frontal margin of the head located beneath the spiny margin of dorsal cephalic shield. For most crustaceans the antennules constitute an important sensory interface, but for those like *Tanazios* that lack compound eyes, the antennules effectively become the primary sensory interface, carrying an array of mechanosensors and chemosensors. The tiny structures of *Tanazios* are too small to extend beyond the margin of the cephalic shield, are unsegmented and lack evidence of setation. They appear ill-equipped, poorly developed and badly positioned for a primary sensory interface. They are much more reminiscent of the frontal organs of remipedes which are of a similar relative size and are located in a similar position. I think that the misinterpretation of these structures as antennules is another reflection of the larval-dominated stem-lineage reconstruction process. I consider these structures to be frontal organs, like those of the remipedes, rather than the paired antennules. The large uniramous limb interpreted by Siveter *et al.* (2007b) as the antenna becomes the antennule. Its uniramous, segmented construction and its far anterior origin are in accord with this reinterpretation.

I consider that the antenna of *Tanazios* is missing in the adult. Its absence is indicated by the marked gap in the limb series between the antennule and the mandible (see Siveter *et al.* 2007b: Fig. 1(k)) which is filled partly by the paired ventrolateral bulges adjacent to the hypostome. The mandible is as reconstructed by Siveter *et al.* (2007b) and the position of the mandibular coxal gnathobase just posterior to the labrum is typical of adult crustaceans. The alternative “absent-antenna” interpretation was briefly considered by Siveter *et al.* (2007b) but dismissed on the grounds that the two paired structures (their antennules and antennae) would represent a biramous limb but that there was no evidence for this as they did not arise from a common base. This objection is not relevant to the re-interpretation presented here.

Tanazios can thus be classified within the Labrophora but the lack of differentiation in the postmandibular limbs of *Tanazios* effectively excludes it from the Eucrustacea. The fourth and fifth limbs (maxillules and maxillae) closely resemble the post-cephalic trunk limbs and provide another example of the independence of the two processes involved in cephalisation (Boxshall 1983), namely the fusion of anterior segments to form a cephalon covered by a dorsal shield derived by fusion of the originally separate tergites, and the progressive specialization of the anterior limbs proceeding posteriorly from the maxillules, presumably under the control of Hox genes (cf. Averof & Patel 1997). The lack of paired antennae in a Silurian marine arthropod would be a major discovery of immense significance both to our understanding of deep mandibulate phylogeny, and to the emerging, but as yet unstable, picture of hexapod origins within the Pancrustacea.

Acknowledgements

I would like to thank Derek Siveter (Oxford University Zoological Museum) for his generosity in allowing me to study and generally enthuse over the virtual Silurian fossils on his hard disk. The series of magnificent reconstructions of these Silurian arthropods—*Tanazios*, the stem-group chelicerate *Offacolus*, the phyllocarid *Cinerocaris*, the myodocope ostracod *Colymbosathon*, the marrellomorph *Xylokorys* and the pycnogonid *Haliestes* – is of enormous importance. Not only do they fill a huge gap in the fossil record but they also provide a novel window on the Palaeozoic arthropods, helping us re-interpret both the effectively 2-dimensional adults of the Burgess Shale and Chenjiang faunas and 3-dimensional larval stages of the ‘Orsten’ type fauna. I think they will shift a few paradigms. I am also very grateful to the reviewers for suggesting significant improvements to this manuscript.

References

- Abele, L.G., Kim, W. & Felgenhauer, B.E. (1989) Molecular evidence for the inclusion of the phylum Pentastomida in the Crustacea. *Molecular Biology & Evolution*, 6, 685–691.

- Averof, M. & Cohen, S.M. (1997) Evolutionary origin of insect wings from ancestral gills. *Nature*, 385, 627–630.
- Averof, M. & Patel, N.H. (1997) Crustacean appendage evolution associated with changes in Hox gene expression. *Nature*, 388, 682–686.
- Bowman, T.E. & Abele, L.G. (1982) Classification of the Recent Crustacea. In, L.G. Abele (Ed.), *Systematics, the fossil record, and biogeography*. Vol. 1, The Biology of Crustacea. (Ed. D. E. Bliss), Academic Press, New York, pp. 1–27.
- Bowman, T.E., Garner, S.P., Hessler, R.R., Iliffe, T.M. & Sanders, H.L. (1985) Mictacea, a new order of Crustacea Peracarida. *Journal of Crustacean Biology*, 5, 74–78.
- Boxshall, G.A. (1983) A comparative functional analysis of the major maxillopodan groups. In, F.R. Schram, (Ed.) *Crustacean Phylogeny*, A.A. Balkema, Rotterdam, pp. 121–143.
- Boxshall, G.A. (1998) Comparative Limb Morphology in Major Crustacean Groups: the coxa-basis joint in postmandibular limbs. In, R.A. Fortey & Thomas, R. (Eds), *Arthropod Phylogeny*, Chapman & Hall, London, pp. 155–167.
- Boxshall, G.A. (2004) The evolution of arthropod limbs. *Biological Reviews*, 79, 253–300.
- Boxshall, G.A. & Halsey, S.H. 2004 *An Introduction to Copepod Diversity*. The Ray Society, London, 966 pp.
- Boxshall, G.A. & Lincoln, R.J. (1983) Tantulocarida, a new class of Crustacea ectoparasitic on other crustaceans. *Journal of Crustacean Biology*, 3, 1–16.
- Boxshall, G.A. & Lincoln, R.J. (1987) The life cycle of the Tantulocarida (Crustacea). *Philosophical Transactions of the Royal Society of London*, B, 315, 267–303.
- Brandt, A. & Poore, G.C.B. (2003) Higher classification of the flabelliferan and related Isopoda based on a reappraisal of relationships. *Invertebrate Systematics*, 17, 893–923.
- Briggs, D.E.G., Sutton, M.D., Siveter, D.J. and Siveter, D.J. (2004) A new phyllocarid (Crustacea: Malacostraca) from the Silurian Fossil-Lagerstätte of Herefordshire, UK. *Proceedings of the Royal Society of London*, B, 271, 131–138.
- Carapelli, A., Lio, P., Nardi, F., van der Wath, E., & Frati, F. (2007) Phylogenetic analysis of mitochondrial protein coding genes confirms the reciprocal paraphyly of Hexapoda and Crustacea. *BMC Evolutionary Biology*, 7 (suppl.2), S8 (doi:10.1186/1471-2148-7-S2-S8).
- Clark, P.F. (2005) The evolutionary significance of heterochrony in the abbreviated zoeal development of pilumnine crabs (Crustacea: Brachyura: Xanthoidea). *Zoological Journal of the Linnean Society*, 143, 417–446.
- Cotton, T.J. & Fortey, R.A. (2005) Comparative morphology and relationships of the Agnostida. In, S. Koenemann & Jenner, R.A. (Eds), *Crustacea and Arthropod Relationships*. Taylor & Francis, London, pp. 95–136.
- Damkaer, D.M. (2002) *The Copepodologist's Cabinet. A Biographical and Bibliographical History*. American Philosophical Society, Philadelphia, 300 pp.
- Darwin, C. (1859) *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. John Murray, London, 502 pp.
- Dreyer, H. & Wägele, J.W. (2002) The Scutocoxifera tax. nov. and the information content of nuclear ssu rDNA sequences for reconstruction of isopod phylogeny (Peracarida: Isopoda). *Journal of Crustacean Biology*, 22, 217–234.
- Elofsson, R. & Hessler, R.R. (1990) Central nervous system of *Hutchinsoniella macracantha* (Cephalocarida). *Journal of Crustacean Biology*, 10, 423–439.
- Fanenbruck, M., Harzsch, S. & Wägele, J.W. (2004) The brain of the Remipedia (Crustacea) and an alternative hypothesis on their phylogenetic relationships. *Proceedings of the National Academy of Sciences*, 101, 3868–3873.
- Fox, H.M. (1951) Proposed suppression under the plenary powers of the generic name 'Monoculus' Linnaeus, 1758. *Bulletin of zoological Nomenclature*, 2, 37–39
- Giribet, G. & Ribera, C. (2000) A review of arthropod phylogeny: new data based on ribosomal DNA sequences and direct character optimization. *Cladistics*, 16, 204–231.
- Giribet, G., Richter, S., Edgecombe, G.D. & Wheeler, W. (2005) The position of crustaceans within Arthropoda – Evidence from nine molecular loci and morphology. In, S. Koenemann & Jenner, R.A. (Eds), *Crustacea and Arthropod Relationships*. Taylor & Francis, London, pp. 307–352.
- Gruner, H.-E. & Scholtz, G. (2004) Segmentation, tagmata, and appendages. In, J. Forest & von Vaupel Klein, J.C. (Eds), *The Crustacea revised and updated from the Traité de Zoologie*. Vol. 1. Brill, Leiden, pp. 13–57.
- Hennig, W. (1979) *Phylogenetic Systematics*. Urbana, University of Illinois Press, 263 pp. [Translated and revised edition of Hennig, W., 1950 *Grundzüge einer Theorie der phylogenetischen Systematik*].
- Hessler, R.R. (1964) The Cephalocarida. Comparative Skeletomusculature. *Memoirs of the Connecticut Academy of Arts & Sciences*, 16, 1–97.
- Huys, R., Llewellyn-Hughes, J., Conroy-Dalton, S., Spinks, J.N. & Johnston, D.A. (2007) Extraordinary host switching in siphonostomatoid copepods and the demise of the Monstrilloidea: Integrating molecular data, ontogeny and antennular morphology. *Molecular Phylogenetics and Evolution*, 43, 368–378.
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. London, The Ray Society, 468 pp.
- Huys, R., Boxshall, G.A. & Lincoln, R.J. (1993) The Tantulocaridan life cycle: the circle closed? *Journal of Crustacean Biology*, 13, 432–442.

- Kabata, Z. (1979) *Parasitic Copepoda of British fishes*. The Ray Society, London, 468 pp.
- Koenemann, S., Schram, F.R., Bloechl, A., Iliffe, T.M., Hoenemann, M. & Held, C. (2007) Post-embryonic development of remipede crustaceans. *Evolution and Development*, 9, 117–121.
- Lavrov, D.V., Brown, W.M. & Boore, J.L. (2004) Phylogenetic position of the Pentastomida and (pan)crustacean relationships. *Proceedings of the Royal Society of London*, B, 271, 537–544.
- Linnaeus, C. (1758) *Systema Naturae Per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis*. Tomus I. (Editio Decima, Reformata). Laurentii Salvii, Holmiae, 823 pp.
- Linnaeus, C. (1768) *Systema Naturae Per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus & Differentiis*. Tomus III. *Regnum Lapideum*. (Editio Duodecima, Reformata), Lars Salvius, Stockholm, 236 pp.
- Mallat, J. & Giribet, G. (2006) Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. *Molecular Phylogenetics and Evolution*, 40, 772–794.
- Manton, S.M. (1934) On the embryology of the crustacean *Nebalia bipes*. *Philosophical Transactions of the Royal Society of London*, B, 223, 163–238.
- Martin J.W. & Davis, G.E. (2001) An Updated Classification of the Recent Crustacea. *Natural History Museum of Los Angeles County Science Series*, 39, 1–124.
- Müller, F. (862) Die Rhizocephalen, eine neue Gruppe Schmarotzender Kruster. *Archiv für Naturgeschichte*, 28, 1–9.
- Myers, A.A. & Lowry, J.K. (2003) A phylogeny and a new classification of the Corophidea Leach, 1814 (Amphipoda). *Journal of Crustacean Biology*, 23, 443–485.
- Ng, P.K.L. & Clark, P.F. (2000a) The eumedonid file: a case study of systematic compatibility using larval and adult characters (Crustacea: Decapoda: Brachyura). *Invertebrate Reproduction and Development*, 38, 225–252.
- Ng, P.K.L. & Clark, P.F. (2000b) The Indo-Pacific Pilumnidae XII. On the familial placement of *Chlorodiella bidentata* (Nobili, 1901) and *Tanaocheles stenochilus* Kropp, 1984 using adult and larval characters with the establishment of a new subfamily, Tanaochelinae (Crustacea: Decapoda: Brachyura). *Journal of Natural History*, 34, 207–245.
- Olesen, J. & Walossek, D. (2000) Limb ontogeny and trunk segmentation in *Nebalia* species (Crustacea, Malacostraca, Leptostraca). *Zoomorphology*, 120, 47–64.
- Regier, J.C., Shultz, J.W. & Kambic, R.E. (2005) Pancrustacean phylogeny: hexapods are terrestrial crustaceans and maxillopods are not monophyletic. *Proceedings of the Royal Society of London*, B, 272, 395–401.
- Scholtz, G. (2000) Evolution of the nauplius stage in malacostracan crustaceans. *Journal of Zoological Systematics and Evolutionary Research*, 38, 175–187.
- Schram, F.R. (1983) Remipedia and crustacean phylogeny. In, Schram, F.R. (Ed.) *Crustacean Phylogeny*, A.A. Balkema, Rotterdam, pp. 23–28.
- Siveter, D.J., Fortey, R.A., Sutton, M.D., Briggs, D.E.G. & Siveter, D.J. (2007a) A Silurian ‘marrellomorph’ arthropod. *Proceedings of the Royal Society of London*, B, 274, 2223–2229.
- Siveter, D.J., Sutton, M.D., Briggs, D.E.G. & Siveter, D.J. (2007b) A new probable stem lineage crustacean with three-dimensionally preserved soft parts from the Herefordshire (Silurian) Lagerstätte, UK. *Proceedings of the Royal Society of London*, B, 274, 2099–2107.
- Spears, T. & Abele, L.G. (1998) Crustacean phylogeny inferred from 18S rDNA. In, R.A. Fortey & Thomas, R. (Eds), *Arthropod Phylogeny*, Chapman & Hall, London, pp. 169–187.
- St John, J. (2007) The earliest trilobite research (Antiquity to the 1820s). In, D.G. Mikulic & Kluessendorf, J. (Eds), *Fabulous fossils – 300 years of worldwide research on trilobites*, New York State Museum Bulletin, 507, 201–211.
- Stein, M., Waloszek, D. & Maas, A. (2005) *Oelandocaris oelandica* and the stem lineage of Crustacea. In, S. Koenemann & Jenner, R.A. (Eds), *Crustacea and Arthropod Relationships*. Taylor & Francis, London, pp. 55–71.
- Storch, V. & Jamieson, B.G.M. (1992) Further spermatological evidence for including the Pentastomida (tongue worms) in the Crustacea. *International Journal of Parasitology*, 22, 95–108.
- Sutton, M.D., Briggs, D.E.G., Siveter, D.J., Siveter, D.J. & Orr, P.J. (2002) The arthropod *Offacolus kingi* (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological reconstructions and phylogenetic affinities. *Proceedings of the Royal Society of London*, B, 269, 1195–1203.
- Thompson, J.V. (1830) *Zoological Researches, and illustrations; or, natural history of nondescript or imperfectly known animals, in a series of memoirs illustrated by numerous figures*. Memoir IV. *On the Cirripedes or Barnacles; demonstrating their deceptive character; the extraordinary Metamorphosis they undergo, and the Class of Animals to which they indisputably belong*. King & Ridings; Cork, pp. 69–82, pls IX–X.
- Thompson, J.V. (1836) Natural history and metamorphosis of an anomalous crustacean parasite of *Carcinus maenas*, the *Sacculina carcini*. *Entomologists Magazine*, 3, 452–456.
- Wägele, J.W. (1989) Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. *Zoologica (Stuttgart)*, 140, 1–262.
- Walossek, D. (1993) The Upper Cambrian *Rehbachella* and the phylogeny of Branchiopoda and Crustacea. *Fossils & Strata*, 32, 1–202.

- Walossek, D. (1999) On the Cambrian diversity of Crustacea. In, F.R. Schram & von Vaupel Klein, J.C. (Eds), *Crustaceans and the biodiversity crisis: proceedings of the Fourth International Crustacean Congress, Amsterdam, 1998*. Vol. 1, Brill, Leiden, pp. 3–27.
- Walossek, D. & Müller, K.J. (1990) Upper Cambrian stem-lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus*. *Lethaia*, 23, 409–427.
- Walossek, D. & Müller, K.J. (1994) Pentastomid parasites from the Lower Palaeozoic of Sweden. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 85, 1–37.
- Waloszek, D., Repetski, J.E. & Maas, A. (2006) A new Late Cambrian pentastomid and a review of the relationships of this parasitic group. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 96, 163–176.
- Walossek, D. & Szaniawski, H. (1991) *Cambrocaris baltica* n. gen. n. sp., a possible stem-lineage crustacean from the Upper Cambrian of Poland. *Lethaia*, 24, 363–378.
- Wills, M.A. (1998) A phylogeny of recent and fossil Crustacea derived from morphological characters. In, R. A. Fortey & Thomas, R. (Eds), *Arthropod Phylogeny*, Chapman & Hall, London, pp. 189–209.
- Wills, M.A., Briggs, D.E.G., Fortey, R.A. & Wilkinson, M. (1995) The significance of fossils in understanding arthropod evolution. *Verhandlungen Deutsches zoologisches Gesellschaft*, 88, 203–215.
- Wilson, G.D.F. (2003) A new genus of Tainisopidae fam. nov. (Crustacea: Isopoda) from the Pilbara, Western Australia. *Zootaxa*, 245, 1–20.
- Wingstrand, K.G. (1972) Comparative spermatology of a pentastomid, *Raillietiella hemidactyli*, and a branchiuran crustacean, *Argulus foliaceus*, with a discussion of pentastomid relationships. *Kongelige Danske Videnskabernes Selskabs, Biologiske Skrifter*, 19, 1–72.
- Yager, J. (1981) Remipedia, a new class of Crustacea from a marine cave in the Bahamas. *Journal of Crustacean Biology*, 1, 328–333.
- Zhang, X-i., Siveter, D.J., Waloszek, D. & Maas, A. (2007) An epipodite-bearing crown-group crustacean from the Lower Cambrian. *Nature*, 449, 595–598.

