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Pycnogonid affinities: a review

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Abstract

Early authors regarded Pycnogonida (sea spiders) either as aquatic arachnids, 'degraded' crustaceans or as some sort of intermediate form between the two. Subsequently, pycnogonids were either placed among the Chelicerata or considered as an isolated group, unrelated to other arthropods. The latter model is untenable under phylogenetic systematics and recent cladistic studies have supported one of two alternative hypotheses. The first is the traditional Chelicerata *s.lat.* concept, i.e. (Pycnogonida + Euchelicerata). This, however, has only one really convincing synapomorphy: chelate chelicerae. The second hypothesis recognizes (Pycnogonida + all other Euarthropoda) and has been recovered in various 'total evidence' studies. Morphologically some characters – the presence of gonopores on the trunk and absence of a labrum, nephridia and intersegmental tendons – support Cormogonida (Euarthropoda excluding pycnogonids). Advances in developmental biology have proposed clear interpretations of segmentation homologies. However, so far there is also a confrontation of the two hypotheses depending on whether the last walking leg segment is considered part of the prosoma. In this case pycnogonids have too many prosomal segments compared with Euchelicerata; perhaps implying they are not sister groups. Alternatively, if part of the postprosomal region, the last leg pair could correspond to the chilarial segment in euchelicerates and its uniramous state could be apomorphic with respect to other euarthropods. Molecular phylogenies need to be more rigorously analysed, better supported by data from different sources and technique-sensitive aspects need to be explored. Chelicerata *s.lat.* may emerge as the more convincing model, yet even the putative autapomorphy of chelicerae needs to be treated with caution as there are fossil 'great appendage' arthropods in the early Palaeozoic which also have a robust, food-gathering, pair of head limbs and which may lie on the chelicerate, or even the euarthropod, stem lineage.

Key words: Pycnogonida – Chelicerata – Crustacea – Cormogonida – Acari – phylogeny

Introduction

Pycnogonids (sea spiders) are an unusual group of exclusively marine arthropods whose phylogenetic position has long been controversial. Some 1163 extant species are known (Munilla 1999) and these are usually divided among nine or 10 families (Child 1998; Munilla 1999, 2002; Arango 2002). As a group they have a cosmopolitan distribution and can be found from the shore down to deep water. They generally feed on sessile or slow-moving organisms and juvenile instars can be parasitic (Staples and Watson 1987; Miyazaki 2002a). Comprehensive accounts of pycnogonid biology can be found in King (1973) and Arnaud and Bamber (1987). A handful of fossil taxa are known dating back to the Upper Cambrian (Waloszek and Dunlop 2002) and the fossil sea spiders are significant in that some taxa preserve character states quite different from extant species (e.g. Bergström et al. 1980). Pycnogonids are best known for their bizarre, mostly autapomorphic, morphology (Fig. 1) and due to the paucity of convincing synapomorphies with other major euarthropod groups their affinities have proved difficult to resolve.

The common name 'sea spider' could suggest affinities with arachnids. This enduring hypothesis is reflected in the majority of textbooks that usually treat Pycnogonida as a class within Chelicerata. Despite this, a survey of the earlier literature reveals two other principal hypotheses: pycnogonids are related to crustaceans and pycnogonids are a distinct group, unrelated to all other arthropods. The relative merits of these alternatives have been debated since the early 19th century without achieving much progress [see e.g. the equivocal conclusions expressed in King's (1973) textbook]. The advent of cladistic studies, including the development of molecular data, has introduced testable hypotheses with clearly articulated synapomorphies (e.g. Ax 1984; Wheeler et al. 1993).

Recent work has found little support for crustacean affinities. On the contrary, under phylogenetic systematics pycnogonids cannot simply be unrelated to all other arthropods; they must have a sister group, however remote or extinct.

Phylogenetic analyses of arthropods which included pycnogonids have mostly recovered Chelicerata in the traditional textbook sense, i.e. (Pycnogonida + Euchelicerata) in which the euchelicerates, *sensu* Weygoldt and Paulus (1979), comprise the arachnids, xiphosurans and extinct eurypterids. This position has been corroborated in several morphological, molecular and combined analyses (e.g. Wheeler and Hayashi 1998). However, in all these models (Fig. 2) Chelicerata *sensu lato* was supported by at best only two or three morphological characters; typically chelate chelicerae, loss of antennae, and a prosoma–opisthosoma body tagmosis. Recent work throws serious doubt on the latter two characters (see Discussion), leaving the presence of chelicerae/chelifores as the best putative autapomorphy for Chelicerata (Waloszek and Dunlop 2002).

According to other combinations of morphological and molecular data, this traditional model has proved unstable, mostly depending on the gene sampled and the parameters used in the analysis (see e.g. Giribet et al. 2002). In consequence, an alternative hypothesis has emerged in which pycnogonids are sister group to all other (extant) Euarthropoda. The name Cormogonida Zrzavý, Hyspa and Vlášková 1998 was proposed for a taxon encompassing the euchelicerates plus the mandibulate euarthropods, i.e. myriapods, insects and crustaceans. A relationship of the form [Pycnogonida (Euchelicerata + Mandibulata)] implies that Chelicerata *s.lat.* is paraphyletic (Fig. 2). Furthermore, if recent Hox gene studies (Damen et al. 1998; Telford and Thomas 1998) are correct and chelicerae are homologous with the a1 antennae of

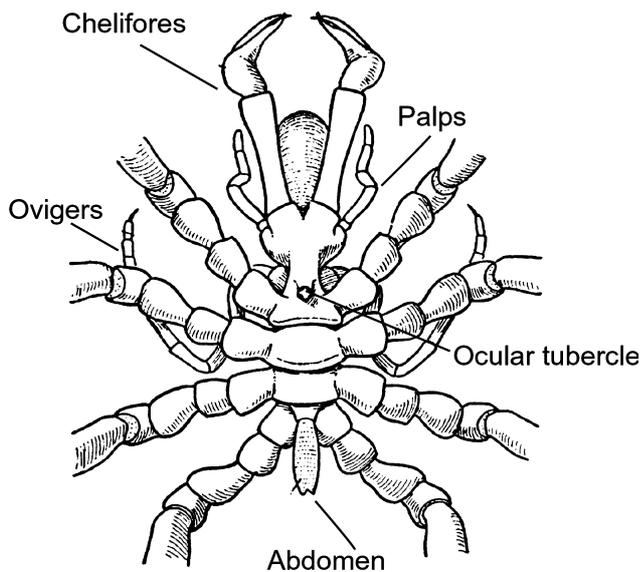


Fig. 1. Morphology of an extant pycnogonid. Modified from Snodgrass (1952)

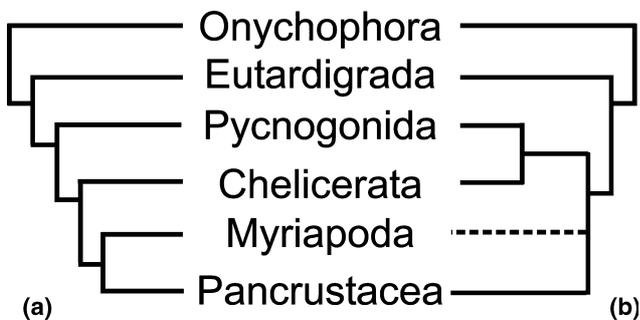


Fig. 2. Alternative hypotheses for the position of Pycnogonida based on recent phylogenetic analyses. (a) Total evidence analyses by Zrzavý et al. (1998) (305 non-sequence characters and sequences from six loci) and Giribet et al. (2001) (303 non-sequence characters, sequences from eight loci), and morphological data only (211 characters) in Edgecombe et al. (2000) all support pycnogonids as basal arthropods. (b) Total evidence analysis in Edgecombe et al. (2000) (morphology, H3 and U2), two nuclear loci (POL II and EF-1a) in Shultz and Regier (2000), EF-1a in Regier and Shultz (2001), and combined 18S and 28S in Mallatt et al. (2004) all support pycnogonids as sister group of euchelicerates or a lineage in the Chelicerata + Myriapoda clade

mandibulate arthropods then this begs the question which is the plesiomorphic character state (Chen et al. 2004) short, robust, food-gathering, chelicerae, or long, multi-segmented, sensorial antennae? Thus, are chelate chelicerae uniquely synapomorphic for (Pycnogonida + Euchelicerata) or are they simply a grade of raptorial feeding limb retained from a more basal euarthropod groundplan?

Although there are valuable reviews of early proposals, especially Dohrn (1881) and Wirén (1918), there have been no recent attempts to draw together the disparate literature on pycnogonid affinities. In the present paper the development of ideas is comprehensively reviewed and is integrated with new data from molecular phylogeny, palaeontology and cladistic studies of long-standing morphological characters. Sea spiders remain an enigmatic group, but may nonetheless have important bearings on our understanding of basal euarthropod relationships.

Nomenclature

The names Pycnogonida (Latreille 1810) and Pantopoda (Gerstaecker 1863) originally represented synonyms and were generally used on traditional, linguistic grounds; the latter predominant in the German literature. To resolve this issue Hedgpeth (1955) proposed recognizing Pycnogonida as the taxon name for all sea spiders, including fossil stem-group forms, while Pantopoda was restricted to the crown group and defined in the systematic context as all sea spiders in which the trunk region behind the limb-bearing segments has become reduced to a single segment bearing the anus. Pantopoda thus currently applies to one fossil and all extant species (Bergström et al. 1980). This scheme has generally been adopted in accounts of higher systematics (Arnaud and Bamber 1987; Munilla 1999, 2002; Waloszek and Dunlop 2002), but the traditional usage can still be found in the taxonomic literature. For consistency, we have transliterated references to Pantopoda into Pycnogonida unless the authors were specifically making a distinction between stem-group and crown group sea spiders.

Morphology

Detailed accounts of pycnogonid morphology can be found in classic treatises (Helfer and Schlotzke 1935) and more recent summaries (King 1973; Arnaud and Bamber 1987). Here we concentrate on the most salient features for resolving their phylogenetic position. As has long been recognized (see especially Wirén 1918), pycnogonids express many unusual, derived character states which are generally interpreted as autapomorphic; although there have been (mostly unsuccessful) attempts to identify homologues for some of these features among other arthropods. Widely accepted pycnogonid autapomorphies include the external, prominent proboscis used in feeding (Fig. 3a–f), genital openings involving multiple gonopores on preabdominal somites and modification of the third pair of appendages into ventral, egg-carrying ovigera (Fig. 3c–d). In crown group pycnogonids the abdomen is reduced to almost vestigial proportions (see below) and the organ systems are either apomorphically lacking (e.g. respiratory organs) or have become largely displaced into the legs (e.g. gonads, midgut diverticula).

Structurally, pycnogonids have a body divided into an anterior cephalosoma and a series of limb-bearing trunk segments (Fig. 1). The cephalosoma bears four eyes on a single tubercle and four pairs of appendages: (1) the (usually) chelate chelicerae or chelifores, (2) the palps, (3) the ovigera and (4) the first pair of legs. Chelicerae, palps and/or ovigera can be absent in some taxa and their reduction or loss in ingroup sea spiders is almost certainly derived (see Fig. 3) (see e.g. Cole 1905; Bain 1992; Munilla 1999; Arango 2002). All limbs are uniramous. In some Devonian taxa a longer trunk of three (*Palaeopantopus*) or four (*Palaeoisopus*) limbless segments is retained behind the last pair of walking legs (Bergström et al. 1980), and in the latter genus there is additionally a lanceolate telson bearing the anus midway along its length. Remarkably, as discovered by Eights (1835), some extant sea spider genera have either five or six pairs of walking legs as opposed to the usual four (Fig. 3e). Although Cole (1905, p. 410) regarded those genera with supernumerary legs to be basal, current phylogenetic models imply that they are derived.

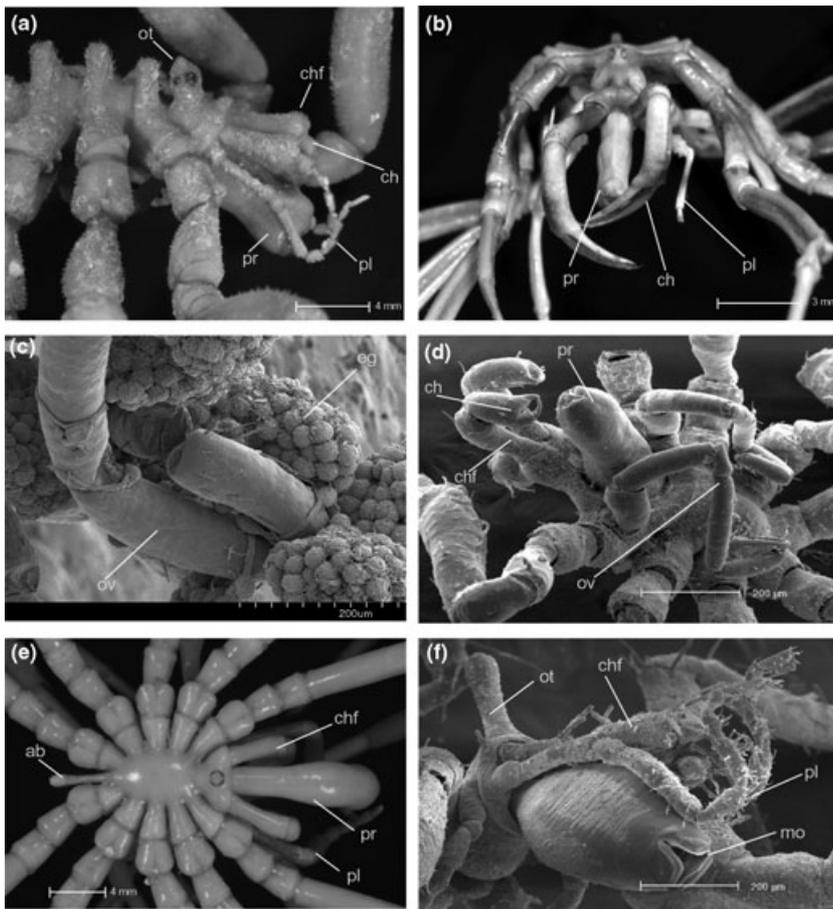


Fig. 3. (a) *Ammothea allopedes*, lateral view of cephalosoma and two anterior body segments, see chelae reduced. (b) *Nymphon uninguiculatum*, frontal view of cephalosoma, proboscis and chelifores with large, toothed chelae. (c) *Anoplodactylus californicus*, close-up of last segments of the oviger of male with masses of eggs attached by mucous rings (last segment of oviger loosen due to manipulation). (d) *Anoplodactylus proliferus*, ventral view ovigers in full length. (e) *Decolopoda australis* a 10-legged species, dorsal view of five-segmented trunk, proboscis and abdomen. (f) *Ammothella fistella*, frontal-lateral view of cephalosoma, and proboscis with detail of the mouth, chelae absent, eyes not visible. Ab, abdomen; ch, chelae; chf, chelifores; eg, eggs attached to male; mo, mouth; ot, ocular tubercle; ov, ovigers; pl, palp; pr, proboscis

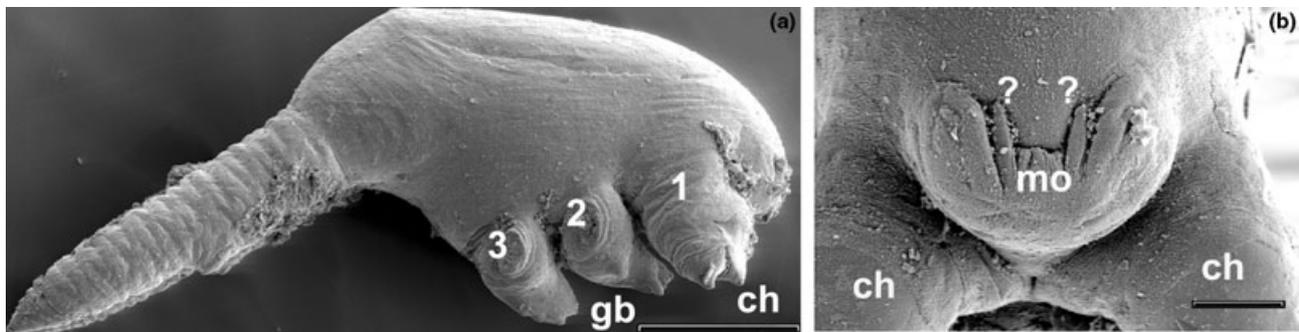


Fig. 4. The fossilized larva *Cambropycnogon klausmuelleri* Waloszek and Dunlop 2002 from the Upper Cambrian 'Orsten' of Sweden represents the oldest record of Pycnogonida. Probably at a postprotonymphal stage, these beautifully preserved fossils show the three head limbs (1–3) of the protonymph, the first of which is a chelicera (ch). They express characters not seen in recent sea spider larvae such as gnathobases on the appendages (gb: a putative plesiomorphy) and enigmatic precheliceral structures (?) either side of the mouth (mo). (a) Lateral view. Scale bar = 100 μ m. (b) Front view. Scale bar = 20 μ m. Images courtesy of Dieter Waloszek, Ulm

Larva

The hatching larva of pycnogonids is called the protonymph and a detailed recent account of ontogeny can be found in Vilpoux and Waloszek (2003). In contrast to the cephalosoma of the adult, the protonymph in extant Pantopoda has only *three* pairs of appendages (chelicerae plus two pairs of postcheliceral limbs) and additional appendages are added with subsequent moults. Later larval stages have been observed having different developmental sequences depending on the species, and in some cases related to their parasitic habits; a summary of observations recorded in the literature

can be found in Bain (2003). The oldest record of Pycnogonida are some fossilized larvae from the Upper Cambrian 'Orsten' of Sweden (Müller and Waloszek 1986). This remarkable material (Fig. 4) was formally named as *Cambropycnogon klausmuelleri* (Waloszek and Dunlop 2002). These minute, three-dimensional fossils, which may actually be at a postprotonymphal stage, have the same basic morphology as an early pantopod larva, but retain plesiomorphic characters such as gnathobases on the postcheliceral appendages and bear an enigmatic pair of precheliceral structures (Fig. 4b) which have been interpreted as either vestigial antennae (Waloszek and

Dunlop 2002), or as possible homologues of the so-called 'frontal organs' of crustaceans (Scholtz 2001). The later hypothesis is supported by Hox gene data (Damen et al. 1998; Telford and Thomas 1998) which imply that the chelicerae are homologous with insect antennae and the first (a1) antennae of crustaceans, and not with the second (a2) antennae of crustaceans, as suggested by traditional neuroanatomical investigations (e.g. Winter 1980). This alternative of chelicerae homologous to a1 has been recently supported by neurobiological data (Mittmann and Scholtz 2003) and is also preferred in the study of larval development of *Pycnogonum littorale* by Vilpoux and Waloszek (2003).

Degraded crustaceans and other hypotheses

The earliest descriptions of pycnogonids confused the relatively common *Pycnogonum* with the superficially similar whale louse crustaceans. Savigny (1816) thought that pycnogonids were more like crustaceans than arachnids, although his scheme involved interpreting the proboscis as a head! Milne-Edwards (1834–40) also noted similarities to whale lice and coined the name Araneiformes for sea spiders as an order of Crustacea. Both Johnston (1837) and Goodsir (1844) adopted this name and Johnston suggested that pycnogonids retained the basic crustacean body plan, but had somehow become 'degraded'; a sentiment shared by de Quatrefages (1845). Similarities between the pycnogonid protonymphon and the nauplius larva of crustaceans prompted Krøyer (1840) to support affinities between these groups; a recurring theme in subsequent discussions. Based on larval morphology, Meisenheimer (1902) concluded that pycnogonids were closer to crustaceans than either arachnids or tracheate arthropods. He argued that from a common ancestor possessing a larva with three pairs of appendages (but see below), crustaceans developed the free-swimming nauplius and pycnogonids specialized into the crawling protonymphon. Börner (1902) essentially recognized a phylogeny of the form {Euchelicerata [Pycnogonida (Trilobita + Crustacea)]}, while Richters (1912) inadvertently described a crustacean larva, albeit one with subchelate appendages, as a pycnogonid protonymphon.

In fact there is little evidence that pycnogonids are related to crustaceans. A short early larval instar with only a few pairs of appendages is clearly plesiomorphic for Euarthropoda. According to the head larva concept of Walossek and Müller (1998) and references therein the euarthropod groundplan (at least towards the crown of the arthropod stem lineage) is a larva with four pairs of appendages. Although both the nauplius and the protonymphon have only three pairs of appendages these are, in detail, evidently rather different (Lang 1889; Balfour 1880; Wirén 1918; Bouvier 1923; Vilpoux and Waloszek 2003). Through their papers on the exceptionally well-preserved 'Orsten' arthropod fossils Walossek and Müller (1998) summarized their hypothesis that four pairs of appendages are present in the larvae of stem-group crustaceans and argued that the nauplius is a specialized swimming larva and a derived, ingroup character defining the crown group Crustacea *s. str.* Thus, if a six-legged larva were to be proposed as a synapomorphy it would have to be for (Pycnogonida + crown group Crustacea). This hypothesis is easy to refute as pycnogonids do not express any of the characters in the crustacean groundplan (see especially Walossek 1999, p. 7) such as limbs with a proximal endite. Molecular data have not supported (Pycnogonida + Crustacea) and while the three

limb pairs in the protonymphon may yet prove to be significant (see Discussion), the 'degraded crustacean' hypothesis can be rejected.

Pentastomids and onychophorans

A number of early authors (Van Beneden 1849; Leuckart 1860) drew comparisons between the pycnogonid protonymphon and the larvae of Pentastomida (tongue worms), both of which hatch with a larva bearing two superficially similar pairs of claw-like appendages. This might reflect their parasitic mode of life. Pentastomids are also a highly problematic group of uncertain affinities, regarded by some authors as stem-group arthropods and by others as highly derived crustaceans. No explicit synapomorphies of (Pentastomida + Pycnogonida) have been identified. Tiegs and Manton (1958) speculated that the pycnogonids might be derived from forebears of the Onychophora (velvet worms), another stem-group arthropod taxon. These authors noted similarities between the round, suctorial lip of velvet worms and the pycnogonid proboscis (see Fig. 3f), but again this has not translated into unequivocal synapomorphies. The pycnogonid proboscis has also been tentatively homologized with the proboscis of polychaete worms (Henry 1953), a suggestion rejected by Hedgpeth (1954). Finally, Ihle (1898) bizarrely argued that as pycnogonids were not clearly related to either arachnids or crustaceans they must, by default, be derived from myriapods!

Aquatic arachnids

Lamarck (1802) included sea spiders among his Arachnides, as did Latreille (1810), who also proposed the name Pycnogonides, defining them partly on their distinct cephalon. Leach (1815) agreed that pycnogonids were arachnids and proposed an alternative taxon name, Podosomata, defining the group primarily on a body composed of four parts, i.e. the cephalon and three trunk segments. Latreille (1817) refuted crustacean affinities noting that arachnids and pycnogonids both lack a gill ramus on their limbs. Only later work would show the lungs of arachnids to be derived from gill-bearing appendages. An affinity between pycnogonids and tardigrades was suggested by von Siebold (1854), grouping them together in the same taxon Arachnoidae *sensu* von Siebold based on the presence of a multi-articulate cephalothorax and the absence of respiratory organs. Gerstaecker (1863) proposed the name Pantopoda specifically as an order of a broad class Arachnoidea, which also included groups such as tardigrades and pentastomids. Pycnogonid chelifores led Balfour (1880) to infer a common ancestor for sea spiders and arachnids – again a recurring theme in discussions of relationships.

The Chelicerata concept essentially dates back to Lankester (1881) who argued that xiphosurans were arachnids rather than crustaceans. He was not the first to propose this, but he argued the case most convincingly. Arachnida *sensu* Lankester also encompassed trilobites, but not, initially, pycnogonids. Schimkewitsch (1884) thought that pycnogonids shared a common ancestor with arachnids based on similarities in the structure of the gut and reproductive organs. Heymons (1901) introduced the name Chelicerata for arachnids and xiphosurans, but made no mention of the pycnogonids. His original definition of Chelicerata as arthropods with chelate chelicerae plus a series of (at least partly) gnathobasic limbs would exclude Pantopoda – which lack gnathobases – but not the

recently discovered Cambrian larva. Carpenter (1903, 1905) regarded pycnogonids as 'aberrant arachnids' and although homologizing the chelicerae with the chelifores, he recognized difficulties reconciling the tagmosis of the body in these two groups. Basically, pycnogonids have seven pairs of 'prosomal' appendages compared with the six in euchelicerates (see Discussion) and, as noted by Cole (1905), the extra pairs of limb-bearing segments in rare deep-sea species having five or six pairs of walking legs instead of the normal four only serve to confuse the homology issue further. Lankester (1905) now included pycnogonids among his 'arachnids', recognizing a *Nomomeristica* grade for arachnids with a fixed numbers of body segments, i.e. excluding trilobites. The *Nomomeristica* were subdivided into Pantopoda (=Pycnogonida) and Euarachnida (=Euchelicerata) and for Lankester (1905) the pycnogonids represented a 'degenerate offshoot' from the arachnids.

Pycnogonids and mites

Krøyer (1845), Leuckart (1848) and Zenker (1852) all drew comparisons between the pycnogonid protonymphon and the early (hexapodal) instar of mites. Fürstenberg (1861, p. 208) even went so far as to include pycnogonids as a family within the water mites, but apart from commenting that he regarded mites as more primitive than all other arachnids – a common view at that time (e.g. Abendroth 1868; Thorell 1877) – he did not discuss this scheme in detail. Weissenborn (1886) included pycnogonids among the arachnids and again noted that both pycnogonids and mites have an instar without the full complement of adult appendages. Jourdain (1892) made some superficial comparisons between the protonymphon, the larval instar of mites and the nauplius. All were claimed to have six legs, but Jourdain appears to have ignored the chelicerae and pedipalps of mites when counting appendages. Meinert (1899) and Bouvier (1923) tried to homologize the pycnogonid proboscis with the projecting labrum and lateral lips of mites, but detailed studies of the proboscis, its three constituent antimeres, movable lips and complex musculature (Dencker 1974) offer little support for this hypothesis. Functionally, the proboscis and structures such as the hypostome of ticks are quite similar, but this probably reflects their essentially parasitic mode of life.

The affinities, and even the monophyly, of the mites remains one of the most intractable problems in chelicerate phylogeny and pycnogonids as ingroup arachnids close to mites was recovered in the total data set of Giribet et al. (2002), albeit under conditions of extreme character conflict. An earlier model (Weygoldt and Paulus 1979) implied that mites are rather derived arachnids, expressing characters linked to miniaturization and special modes of feeding such as phytophagy and parasitism. Most recent authors have accepted the monophyly of Acari (see especially Lindquist 1984), and group them with the rare arachnid order Ricinulei, based primarily on the hexapodal larval instar – i.e. a juvenile stage with less appendages than the adult. This, of course, they share with pycnogonids. In fact one of the putative autapomorphies of Euchelicerata, to the exclusion of pycnogonids, is the absence of a larval instar (Waloszek and Müller 1998). Do mites and ricinuleids invalidate this character? Probably not. The hexapodal larva of mites and ricinuleids still closely resembles the final adult morphology and adds appendages rather than segments as per the anamorphic growth of sea spiders. The

protonymphon of the latter is a true larva, substantially different from an adult (e.g. Bain 2003; Vilpoux and Waloszek 2003). However, crude similarities between the early instars of both pycnogonids and mites (see also Delle Cave and Simonetta 1991, p. 213), and specifically their pattern of development in which appendages are added in later instars (although in some species of sea spiders at least one of the appendages can disappear and in some reappear in later stages, e.g. *P. litorale* in Vilpoux and Waloszek 2003), hint that both these taxa retain a similar, albeit plesiomorphic, mode of development.

Interestingly, many mites express a cephalosoma (=proterosoma) tagma with four pairs of appendages (see e.g. Bernini 1986 for a review). This is segmentally homologous with the cephalosoma of pycnogonids (cf. Vilpoux and Waloszek 2003, fig. 13). Solifuges, palpigrades and schizomids also express this character (Fig. 5), which has traditionally been scored in arachnids as an apomorphic 'divided carapace' (e.g. Shultz 1990). This four-segmented cephalosoma could in fact be a plesiomorphic expression of the original euarthropod head *sensu* Waloszek and Müller (1998); see also Scholtz (1998) for further support for this concept based on gene expression data. Thus we see no convincing morphological synapomorphies for (Pycnogonida + Acari), and gross morphological similarities between these taxa seem to be plesiomorphic.

Pycnogonida + Euchelicerata synapomorphies

Morgan's (1890, 1891) embryological studies led him to support arachnid affinities for pycnogonids and he recognized six characters in support of this hypothesis: (1) an endoderm constructed from multipolar delamination, (2) a possible homologue of the *Cumulus primitivus* – a transitory enlargement of the primary thickening of the germ disc during development (see e.g. Akiyama-Oda and Oda 2003) – in spiders, (3) similar 'Körperhöhle' or body cavities, (4) gut diverticula extending into the legs, (5) chelate chelicerae and (6) a similar eye morphology. Gaubert (1892) briefly mentioned that the limbs of pycnogonids and arachnids were similar. Meinert (1899) proposed five characters supporting a relationship between pycnogonids and arachnids: (1) that a homologue of the proboscis can be found in the so-called rostrum or epipharyngeal plate of the arachnid mouthparts, (2) tagmosis into a prosoma and opisthosoma, (3) chelate chelicerae, (4) a suggestion (rejected by Doigel) that the byssal gland in the chelicerae of pycnogonids was homologous with the cheliceral poison gland of arachnids such as spiders (note that pseudoscorpions have a cheliceral silk gland) and (5) the presence of auxiliary claws at the end of the legs which are absent in crustaceans. Of these, a homology between the proboscis and the arachnid mouthparts has never been satisfactorily demonstrated, the tagmosis question is addressed below, and auxiliary claws are probably plesiomorphic [see e.g. arthropod limb groundplans in Waloszek and Müller (1998), fig. 12.10].

Bouvier (1913) followed Lankester's basic hypothesis and differentiated pycnogonids from crustaceans on account of supposedly preoral appendages. He regarded pycnogonids as extremely primitive rather than degenerate forms. Wirén's (1918) detailed and important anatomical study rejected segmental homologies between the protonymphon and nauplius larva and strongly supported grouping pycnogonids with the chelicerates. Wirén regarded pycnogonids as the most

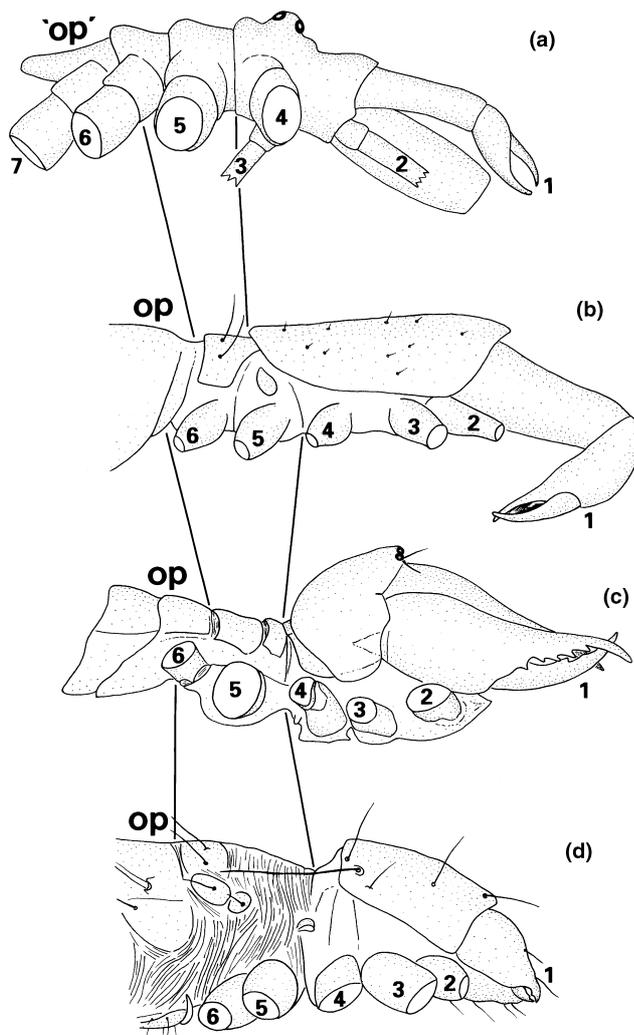


Fig. 5. Comparative tagmosis of pycnogonids and selected arachnids which also express a four-segmented head region. Distal limb podomeres removed for clarity. In this scheme – partly after Winter (1980) and Vilpoux and Waloszek (2003) – two things are of particular note. (1) The last limb-bearing trunk segment of Pantopoda correlates to the limbless first opisthosomal segment (OP) of arachnids. Thus Pantopoda do not exhibit a six-segmented prosoma or an unequivocal prosoma-opisthosoma tagmosis *sensu* Arachnida. Even in mites the opisthosoma boundary is often rather poorly defined, while the fossil xiphosuran *Weinbergina* (Stürmer and Bergström 1981) apparently has a ‘prosomal’ walking leg on the first opisthosomal segment, in place of the chilaria seen in Recent taxa. This last *Weinbergina* leg is conceivably homologous with the last walking leg of pycnogonids. (2) The four-segmented head region (=cephalosoma or propeltidium) in all these groups is conceivably a retention of the original four-segmented euarthropod head. See also Fig. 6. Redrawn from various sources. (a) Pantopoda (sea spiders). (b) Palpigradi (palpigrades). (c) Solifugae (camel spiders). (d) Acari: Palaeacariformes

derived chelicerate group on the grounds of: (1) their reduced number of body segments, (2) the loss of gnathobases, (3) development of the proboscis, (4) loss of respiratory organs, (5) highly developed midgut diverticula, (6) gonopores on the legs and (7) cephalization of the anteriormost ganglia to a greater degree than in, for example, scorpions. Based mostly on neuroanatomical features, Wirén further concluded that pycnogonids were closer to arachnids than to xiphosurans. Similarities in the eyes were Loman’s (1924) principal reason

for favouring arachnid affinities and subsequently (Loman 1928) he placed pycnogonids as an order of the arachnids under the broad group ‘Arachnoidea’ in the *Tierwelt Deutschlands*. Snodgrass (1938) included pycnogonids among the chelicerates based on the chelate chelifores and the presence of a patella podomere in the legs, but noted that the unique features of sea spiders made it hard to ally them with any other group within Chelicerata.

The middle part of the 20th century was dominated by the view that pycnogonids were unrelated to other arthropods (see below). Chelicerate affinities were again supported by Firstman (1973) who, as part of a comparative study of arachnid endosternites, suggested that pycnogonids have a vascular septum, which is homologous with a hypothetical progenitor of the arachnid endosternite. He concluded by placing pycnogonids as the sister group of the Euchelicerata. Dencker (1974) studied the musculature and concluded that the chelifores and pedipalps of pycnogonids are very arachnid-like; an interesting observation in the light of Wirén’s hypothesis (see above) given that xiphosurans and eurypterids do not have a postchelicerate appendage modified into a pedipalp. In her polyphyletic theory of arthropod origins, Manton (1977) retained pycnogonids in the Chelicerata branch and subsequently (Manton 1978) recognized similarities between arachnid and pycnogonid limbs and concluded that pycnogonids could have been derived from an early arachnid group that remained in a marine environment. Grasshoff’s (1978) scheme regarded pycnogonids as a grade of basal chelicerates specialized in feeding on sessile organisms.

Cladistic studies

Weygoldt and Paulus (1979) were the first authors to try and reconstruct chelicerate phylogeny cladistically. In this classic study a basic phylogeny of the form (Aglaspida + Euchelicerata) was recognized. These authors also considered pycnogonids to be chelicerates, noting that they share no synapomorphies with any other arthropod group, and suggested that Pycnogonida were sister group either to Euchelicerata or to all Chelicerata, depending on the status of characters such as the eyes in the extinct Aglaspida. Pycnogonids have four median eyes while euchelicerates and (probably) aglaspids have only two. Weygoldt and Paulus also cited evidence for two more vestigial median eyes in extant Xiphosura, which supports the interpretation of four eyes (as in pycnogonids) as an ancestral character in chelicerates. Subsequent work (e.g. Walossek and Müller 1998) has disputed the inclusion of aglaspids among the chelicerates. Bergström et al. (1980) also accepted that pycnogonids were probably chelicerates and could have been derived from primitive merostomes. They also suggested that the lanceolate telson in the fossil sea spider *Palaeoisopus* might indicate an affinity between xiphosurans, scorpions and eurypterids – a group they interpreted as sharing this putatively apomorphic ‘tail spine’ character. Winter (1980) stated that pycnogonids and chelicerates were clearly sister taxa and described detailed homologies in their neuroanatomy.

(Pycnogonida + Euchelicerata) was first explicitly expressed in a cladogram by Ax (1984, fig. 67) who recognized three synapomorphies: (1) loss of antennae, (2) presence of chelate chelicerae and (3) tagmosis into a prosoma and opisthosoma. A similar cladogram was shown by Weygoldt (1986, fig. 8). The extensive, non-cladistic, studies of arachnid

relationships by van der Hammen (1989 and references therein) only mentioned sea spiders as possible chelicerate relatives while the seminal, but controversial, cladogram of arachnid ordinal relationships proposed by Shultz (1990) did not attempt to resolve the position of pycnogonids. Miyazaki and Makioka (1991 and references therein) argued that the pycnogonid pattern of oogenesis and their ovarian structure – in particular their protruding, stalked oocytes – is similar to that of euchelicerates, although the polarity of these characters remains unclear. In her thesis, Bain (1992) summarized various shared characters of arachnids and pycnogonids such as pedipalps, general limb musculature and similar nervous systems. Moritz (1993) summarized a number of potential synapomorphies of pycnogonids and euchelicerates including the (now strongly disputed) absence of antennae and a deutocerebrum. More robust characters here include chelicerae, arachnid-like walking-legs, form and histophysiology of the midgut, a circulatory system with a perineural and perivisceral sinus and construction of neuromeres with metameric paired ‘ventral organs’.

The first authors to empirically resolve the position of Pycnogonida through parsimony analysis were Wheeler et al. (1993) who combined morphological and molecular (18S rDNA and Polyubiquitin) data to produce a consensus cladogram including (Pycnogonida + Euchelicerata). Morphologically their synapomorphies for Chelicerata were: (1) prosoma–opisthosoma tagmosis, (2) chelicerae and (3) ‘typically’ four pairs of walking legs. Dunlop and Selden (1998) did not include pycnogonids in their attempt to resolve the stem line of Chelicerata – see also criticisms in Simonetta et al. (2000) – but Walossek and Müller (1998) did include pycnogonids as the sister group of the Euchelicerata; defining the latter as apomorphically lacking a true larval stage. Wheeler and Hayashi (1998) recovered (Pycnogonida + Euchelicerata) based on combined morphology and 18S and 28S rDNA, essentially recognizing Ax’s three morphological synapomorphies (see above) for this clade.

In phylogenetic analyses conducted using two nuclear genes, elongation factor-1 α (EF-1 α) and the largest subunit of RNA polymerase II (Pol II) to examine the relationships among the major arthropod groups (Pycnogonida + Euchelicerata) was again recovered and strongly supported (Fig. 2) (Shultz and Regier 2000; Regier and Shultz 2001). Recent molecular analysis of up to 43 taxa to reconstruct ecdysozoan phylogeny using nuclear ribosomal DNA was not definitive regarding pycnogonid position, but there was inclination towards pycnogonids as a lineage related to Chelicerates or the Chelicerata + Myriapoda clade (Mallatt et al. 2004). On the contrary, Waloszek and Dunlop (2002) supported the Chelicerata + Pycnogonida result, but argued that only the chelate chelicerae emerge as unequivocal morphological support for Chelicerata (see Discussion). Miyazaki (2002b) noted that all pycnogonid families have a ‘Y’-shaped pharyngeal lumen, a character also seen in whip spiders (Amblypygi) and parasitiform mites, but may not be a chelicerate autapomorphy, being present in potential outgroups such as tardigrades and onychophorans too. Additionally, a terminal mouth opening found in pycnogonids and in tardigrades and some extinct arthropods and lobopodians could be seen as a plesiomorphic state of Panarthropoda, when considering pycnogonids the putative sister group of Euarthropoda (see Giribet 2003). Miyazaki and Pass (2004) proposed the embracement of the brain by

the anterior part of the dorsal blood vessel as a putative synapomorphy of Pycnogonida + Euchelicerata, a character absent in onychophorans and the remaining euarthropod taxa.

Emphasis on uniqueness

Although assigning a new pycnogonid to ‘Arachnides’, Eights (1835) suggested that sea spiders are transitional forms between crustaceans and arachnids. Costa (1836) and Krøyer (1845) broadly agreed. In an important treatise, Dohrn (1881) reviewed previous theories and, in contrast to some other authors, proposed that the proboscis of pycnogonids was truly autapomorphic and had no homologue among other arthropods. Dohrn was unconvinced by the proposed arachnid and crustacean characters and regarded pycnogonids as being derived directly from annelid ancestors, noting similarities between the protonymphon and the trochophore of annelid worms. Hoek (1881) agreed with Dohrn’s basic hypothesis, but further suggested that the similar early larvae of pycnogonids, crustaceans and annelids implied a distant common ancestor for these three groups. Oudemans (1886) treated pycnogonids as a separate arthropod lineage, unrelated to arachnids, and even separated the mites off from the other arachnids. Lang (1889) argued for an isolated position for pycnogonids, specifically rejecting the homology of the protonymphon and the crustacean nauplius larva.

Sars (1891) regarded pycnogonids as a distinct class of arthropod. Korschelt and Heider (1892) accepted that there were developmental similarities between pycnogonids and arachnids, but regarded arachnids as more like xiphosurans than pycnogonids. Their principal criticism of arachnid affinities was the ‘extra’ prosomal leg in pycnogonids. Kingsley (1893) placed sea spiders as one of his *incertae sedis* taxa in his scheme of arthropod classification and Cole (1905) found the position of pycnogonids almost impossible to resolve, noting how the studies of development by Meinert (1899) and Meisenheimer (1902) led to fundamentally different conclusions. Handlirsch (1906) regarded the pycnogonids as an isolated group, but speculated that they, and other arthropods, could have been derived from a trilobite-like ancestor.

Thompson (1909) in the *Cambridge Natural History* preferred to treat sea spiders as ‘remote’ from all other arthropods. Sokolow (1911) supported the isolated position of the pycnogonids based on their supposedly primitive eye structure. Dogiel’s (1913) exhaustive study of pycnogonid ontogeny rejected arachnid affinities, criticizing Meinert’s conclusions (see above) in particular. Doigiel noted the similarities in the larvae shared with crustaceans, but felt that because of the uniramous limbs and the presence of the proboscis the pycnogonids should be treated as a separate class of arthropods, again with possible origins among the annelids. In their comprehensive account of pycnogonid biology, Helfer and Schlotke (1935) also felt that pycnogonids should probably be regarded as an independent group. Similar sentiments were expressed in Størmer’s (1944) study of arachnomorph phylogeny in which he suggested raising Pycnogonida to a separate phylum.

Hedgpeth was probably the most vociferous critic of chelicerate affinities for pycnogonids (see e.g. Hedgpeth 1947, 1954, 1955; Schram and Hedgpeth 1978), recognizing sea spiders as an independent taxon and citing their numerous

autapomorphies (see Morphology) as evidence against a relationship with arachnids. For example, in the *Treatise on Invertebrate Paleontology* the Pycnogonida were introduced as ‘...superficially resembling the Chelicerata...’ (Hedgpeth 1955, p. 163). His opinions were highly influential, at least on pycnogonid taxonomists in the latter half of the 20th century, and recent work continues to express the idea that pycnogonids are a separate class within the arthropods (e.g. Child 1998). Comparisons between the proboscis in pycnogonids and polychaetes were used by Sharov (1966) to infer a basal position among arthropods. Similarly, in his textbook on pycnogonids King (1973) briefly reviewed the evidence for chelicerate and crustacean affinities, concluding that the general view at that time was to regard the sea spiders as a separate class or subphylum of arthropod, possibly with very primitive origins.

Pycnogonids as basal Euarthropoda

Accepting the widely supported monophyly of Arthropoda and Euarthropoda, the closest approximation of this ‘remote’ hypothesis (see above) under phylogenetic systematics is to place Pycnogonida as sister group to the remaining Euarthropoda. The first authors to formally propose this were Zrzavý et al. (1998) who recovered pycnogonids as basal euarthropods based on both morphology and sequence data from six different genes (Fig. 2). Their total evidence tree recognized pycnogonids as the sister group of all other extant arthropods, a clade containing euchelicerates, myriapods, crustaceans and hexapods. This (Euchelicerata + Mandibulata) clade they named Cormogonida, defining it on the putative autapomorphy of a gonopore on the trunk, as opposed to gonopores on the leg bases as in pycnogonids. Based on morphological data alone, Edgecombe et al. (2000) recovered pycnogonids as sister group to all other arthropods – effected by absences of nephridia, labrum, intersegmental tendons and gnathobasic endites – but when they combined the morphological data with histone H3 and U2 snRNA sequence data (see also Colgan et al. 1998) the more traditional (Pycnogonida + Euchelicerata) clade was recovered. Giribet and Ribera (2000) found the relationship between pycnogonids and euchelicerates to be unstable in their analysis using ribosomal gene data (18S and the D3 region of 28S rDNA). In the most inclusive analysis of arthropod relationships published so far (eight molecular loci, 303 morphological characters) Giribet et al. (2001) again recovered [Pycnogonida (Euchelicerata + Mandibulata)] (Fig. 2).

In the most comprehensive analysis of arachnid ordinal relationships to date, Giribet et al. (2002) found that under the optimal parameter set for a combined analysis of all data, including fossil taxa, Pycnogonida resolved *within* Arachnida, specifically (their fig. 6) in a clade with Acari and Palpigradi. However, this result was not repeated with morphological data restricted to extant taxa or with the molecular data alone, both of which resolved Pycnogonida in its more traditional position basal to the Euchelicerata. It should be added that Giribet et al. (2002) did not specifically set out to resolve the position of pycnogonids in this paper and they noted the alternative possibility that sea spiders might be sister group to all euarthropods as per Giribet et al. Interestingly, they mentioned that the addition of fossil pycnogonid taxa caused extreme character conflict in their analysis.

Arachnomorpha and Schizoramia

With respect to Mandibulata, there is an alternative Schizoramia hypothesis which unites arachnomorphs with crustaceans (see e.g. Hou and Bergström 1997). The Arachnomorpha, or Arachnata, concept essentially encompasses chelicerates, trilobites and numerous problematic fossils, mostly from early Palaeozoic Lagerstätte such as the Burgess Shale or Chengjiang which, at least superficially, resemble trilobites and/or xiphosurans. Many arachnate fossils express a horseshoe-shaped head shield and bear antennae followed by a series of biramous limbs. Nevertheless, the limits of this putative clade appear vague. There have been attempts at an explicit definition (e.g. Ramsköld et al. 1997), but unequivocal synapomorphies of chelicerates and the trilobite-like taxa are not particularly well-resolved. It is worth noting that analyses restricted to extant taxa tend to recover Mandibulata (e.g. Giribet et al. 2001) while analyses of early Palaeozoic arthropods – scoring only a few crown groups – tend to recover Schizoramia (e.g. Wills et al. 1998). There seems to be a methodological dichotomy here between neontological and palaeontological data and more integrative approaches scoring both fossil and recent terminal taxa together may be needed to resolve this issue.

Wills et al. (1998 and references therein) did not include Pycnogonida as a terminal taxon. Emerson and Schram (1997) did and recovered them within the Schizoramia, close to a clade including the euchelicerates and the famous Burgess Shale fossil *Sanctacaris*. Differences in embryological fate maps have been cited as one character differentiating schizoramians from atelocerates (i.e. insects and myriapods), but as Schram and Jenner (2001) noted, both pycnogonids and euchelicerates are equivocal for this character. Pycnogonids also clearly lack the most obvious schizoramian character, the biramous limb, although it should be added that in euchelicerates the biramous ancestry of the limbs is only revealed in characters such as the flabellum on limb VI and small endopods associated with gill-bearing opercula in xiphosurans (Walossek and Müller 1998, fig. 12.9). Further discussion of Mandibulata versus Schizoramia is beyond the scope of this review, but has been addressed in other papers (e.g. Edgecombe et al. 2000; Scholtz 2001; Schram and Jenner 2001).

Discussion

The morphological and molecular data analysed thus far, either independently or in combination, have yielded contradictory results. Despite the progress made and the increasing number of studies on arthropod phylogenetics the position of sea spiders remains uncertain, but can be narrowed down to two principal hypotheses: basal chelicerates or basal euarthropods? The degree of support for each of these is discussed in detail below.

Basal chelicerates?

The best character supporting (Pycnogonida + Euchelicerata) is the chelate chelicerae or chelifores. Although critics of chelicerate affinities have sought to dismiss this character as convergent, in both pycnogonids and euchelicerates the first functional pair of appendages (when present) are: (1) uniramous, (2) lack a gnathobase, even in fossil groups, (3) are composed of only a few articles and (4) end in an opposable,

chelate claw; subsequently modified into a fang in some arachnids and reduced in a few pycnogonid taxa. The number of cheliceral articles in the ancestral state of Pycnogonida remains unresolved as their phylogenetic position remains in conflict. In Euchelicerata the ancestral state is evidently three (e.g. Shultz 1990), but some Pantopoda unequivocally have four cheliceral articles (Helfer and Schlottke 1935, fig. 22). Furthermore, Bergström et al. (1980) reported five cheliceral articles in the Devonian fossil *Palaeoisopus*. Irrespective of the number of articles, Dencker (1974) described a similar cheliceral musculature in arachnids and pycnogonids and Winter (1980) demonstrated that the chelicerae and chelifores are innervated from the same 'Chelicerenneuromer'. There have been no convincing arguments to counter this homology. The problem is that the chelicerae currently appear to be the *only* morphological character that unequivocally supports (Pycnogonida + Euchelicerata) and criticisms of other putative chelicerate synapomorphies in the literature can be found in Waloszek and Dunlop (2002).

In brief, the problem of the 'extra' prosomal leg in the pycnogonid ancestral state has long been recognized (Korschelt and Heider 1891; Carpenter 1903). However, in the most logical scheme of segmentation and tagmosis (Winter 1980, fig. 26; Stürmer and Bergström 1981, fig. 7; Vilpoux and Waloszek 2003, fig. 13), the segments corresponding to the prosoma-opisthosoma boundary and the four pairs of walking legs in pycnogonids and euchelicerates do not represent serially homologous regions of the body (Fig. 5). This renders the tagmosis autapomorphy and 'typically' four pairs of legs (cf. Wheeler and Hayashi 1998) unconvincing. Secondly, if the Hox gene model is correct and chelicerae and antennae are homologous expressions of the same (a1) appendage, then the character of 'loss of antennae' is now simply subsumed into 'presence/absence of chelicerae'. Other putative chelicerate autapomorphies such as modification of the first postcheliceral appendage into a pedipalp (Munilla 1999) are undermined by the absence of such a modification in the limbs of xiphosurans and the extinct eurypterids.

There appear to be further potential synapomorphies of (Pycnogonida + Euchelicerata) in terms of embryology (Morgan 1890, 1891), oogenesis and ovarian morphology (Schimkewitsch 1884; Miyazaki and Makioka 1991), circulatory systems (Firstman 1973; Miyazaki and Pass 2004), neuroanatomy (Winter 1980) and, less convincingly, foregut structure (Schimkewitsch 1884; Miyazaki 2002b). Most are expressed in the older literature in somewhat vague terms such as 'similarities' and explicit investigations to establish statements of homology would be welcome. For example, the 'chelicerate' pattern of oocyte development on the outer wall of the ovary is also seen in onychophorans (see e.g. Edgecombe et al. 2000 and references therein), and may therefore be part of the arthropod groundplan rather than an explicit chelicerate autapomorphy.

Or basal euarthropods?

This relatively weak apomorphic support for Chelicerata has contributed to an increasing number of studies recovering (Pycnogonida + other Euarthropoda). It should also be added that in the Arachnata hypothesis (see above) pycnogonids as chelicerates sit uncomfortably as an ingroup taxon on a stem-line full of animals such as trilobites, xiphosurans and the various Burgess Shale-type 'trilobitormorph' fossils (Giribet

et al. 2002), most of which characteristically have a broad, well-developed, typically semicircular head shield with clearly developed compound lateral eyes. The only way to resolve this situation would be to make an *ad hoc* assumption that the lack of such a head shield in pycnogonids is autapomorphic (Waloszek and Dunlop 2002).

A number of combined morphological and molecular studies continue to resolve this Cormogonida clade for all extant arthropods excluding Pycnogonida. The problem with the 'cormogonid' concept from a morphological perspective is that the defining autapomorphy – gonopores on the trunk – is not obviously a derived character. Meinert (1899) commented on the uniqueness of the pycnogonid preabdominal genitalia among arthropods and even earlier Van der Hoeven (1850) proposed the name Polygonopoden for sea spiders in recognition of their multiple genital openings. Multiple gonopores on the leg bases (i.e. the second coxae) have been almost universally regarded as one of the best pycnogonid autapomorphies. Outgroup comparison with stem-group arthropod taxa (i.e. onychophorans, tardigrades and pentastomids) tends to support trunk gonopores as plesiomorphic for arthropods as a single gonopore opens on the body (and not the legs) in all three potential outgroups; the genitalia sharing a common opening with the gut in at least some tardigrades. However, if a polychaete annelid were to be used as an outgroup (see discussion in Wirén 1918, p. 169) as in the now disputed Articulata hypothesis of arthropod relationships (see Scholtz 2002 for a discussion and defence and Giribet 2003 for further details of Ecdyzoa versus Articulata), then multiple gonopores along the length of the body *could* be interpreted as plesiomorphic, supporting Cormogonida *sensu* Zrzavý et al. (1998).

This gonopore character clearly requires further investigation. Other putative morphological synapomorphies for (Euchelicerata + Mandibulata) mentioned in Edgecombe et al. (2000) include the presence of a labrum developing from a bilobed Anlage (cf. Scholtz 1998). Its absence in pycnogonids could not only be plesiomorphic, but could also relate to the terminal position of the mouth and the development of a specialized feeding device, namely the widely accepted autapomorphy of the proboscis. Arthropod-type intersegmental tendons (cf. Boudreaux 1979) and nephridia are also absent in pycnogonids. The latter character could, however, be argued as part of a general trend towards the reduction or loss of other organ systems such as the heart and respiratory organs. Vilpoux and Waloszek (2003) discuss one further point of interest. If the euarthropod ancestral state really is a head larva with four pairs of appendages, do the three pairs in the protonymphon represent a more plesiomorphic grade of organization (a hypothesis they favour) or an apomorphic reduction which parallels the crustacean nauplius? We can conceive a number of alternative scenarios in which a longer hatching larva is either acquired independently in both basal euchelicerates and mandibulates, or in which pycnogonids really *are* basal to all other euarthropods; the latter united by the addition of a segment to the hatching stage to form the four-segmented head larva. The absence of a true larva in euchelicerates makes it difficult to resolve this issue at present and we lack a clear series of stem-line euchelicerate fossils and/or their larvae (see Chen et al. 2004 and Cotton and Braddy in press for initial attempts). Among extant taxa, in the hexapodal mite larva it is the fourth pair of legs (appendage VI) which is missing, which suggests mites do hatch with a 'head larva' of sorts, i.e. a four-segmented tagmata bearing append-

ages I–IV; not a three-segmented one bearing appendages I–III as in pycnogonids.

Advances with molecular data

Sequences of eight genes, both nuclear and mitochondrial have been used in phylogenetic analyses of Arthropoda. When *only* molecular data are taken into account the clade (Pycnogonida + Euchelicerata) has been recovered in several of them (Colgan et al. 1998; Zrzavý et al. 1998; Edgecombe et al. 2000; Shultz and Regier 2000; Regier and Shultz 2001). However, in some cases this position of Pycnogonida has been shown to be unstable depending on the parameters and the partitions used in the analysis (Zrzavý et al. 1998; Giribet and Ribera 2000; Mallatt et al. 2004). Giribet and Ribera (2000) also cautioned that taxa which are difficult to place because of their unusual morphological characters – of which pycnogonids are a prime example – tend to show unusual sequence data as well. The conditions and parameters of analysis, usually arbitrarily chosen, and even the putative homologies established among the sequences affect the resulting topologies and the interpretation of relationships. When transforming nucleotide observations into homology statements and hypotheses of relationships among taxa, choices regarding means of optimizing homologies and the entities to be homologized are needed (Wheeler 2001). Multiple alignment of sequences is mostly used as the standard method to establish putative homologies among nucleotides preceding the cladogram analysis (as in Colgan et al. 1998; Zrzavý et al. 1998; Edgecombe et al. 2000). However, this method is problematic as some alignments are more favourably disposed to certain topologies than others (see discussions in Wheeler 1996, 2001). Alternative techniques implemented in POY (Wheeler et al. 2003) involve the creation of unique set of putative homologies for each topology. This is the Optimization Alignment or Direct Optimization method (Wheeler 1996) and has been implemented in arthropod phylogenies by Giribet and Ribera (2000) and Giribet et al. (2001, 2002). These different approaches have an effect on resulting optimal topologies, and the position of Pycnogonida within Arthropoda seems to be one of the ‘technique-sensitive’ elements of the analyses.

The lack of robustness of the position of Pycnogonida among Arthropoda is also related to the conflict between the ‘taxonomic congruence’ and the ‘total evidence’ approaches. When data sets have been combined in total evidence analyses (i.e. morphology and DNA) the clade (Pycnogonida + other Euarthropoda) has been recovered (Zrzavý et al. 1998; Giribet et al. 2001), suggesting pycnogonids could be the sister group of all the other living arthropods. This is different from what molecular data alone have shown, but was also picked up in one purely morphological tree (Edgecombe et al. 2000). A total evidence approach should be preferred as all the available information included in the analysis should maximize the explanatory power of the data. It has even been stated that individual results become irrelevant (Kluge 1989). In that case, analyses in which available data are excluded or restricted to one or two DNA loci provide an incomplete insight into the evolutionary history of the organisms. More effort should be directed to expanding and analysing a comprehensive, total evidence data set to search for optimal topologies and propose robust phylogenetic hypotheses based on such a data set. Preliminary results after modifying parameters in the direct optimization analysis of Giribet et al.’s (2001) data set have

shown that (Pycnogonida + Euarthropoda) seems not to be stable. The Pycnogonida clade moves to the traditional position as sister group of Euchelicerata under certain parameters (C. P. Arango, unpublished data; L. Aegsen, pers. comm.).

Currently ongoing analyses indicate that the inclusion of molecular data representing eight families of pycnogonids into the Giribet et al. (2001) dataset (which included three pycnogonid taxa) could lead to the clade Pycnogonida + Euchelicerata as well (C. P. Arango, unpublished data). However, the issue of unbalanced taxon sampling needs to be considered given other arthropods are represented in the matrix by fewer taxa. Molecular systematics in a group such as Pycnogonida is in its infancy (see Arango 2003) and more complete and better analyses have to be set specifically to resolve their position. However, even if a large body of molecular data starts providing a stable position for Pycnogonida, we still have the task of proposing reliable morphological synapomorphies supporting either Pycnogonida + Euarthropoda or Pycnogonida + Euchelicerata. Work needs to be directed towards better taxon sampling for all arthropod groups, inclusion of more pycnogonid taxa following the exemplar approach (see Prendini 2001) filling the missing information for representative taxa from different lineages, in particular sets of morphological, anatomical and developmental characters that have not been examined in pycnogonids and other less studied groups.

A final palaeontological challenge

Chelicerata *s.str.* seems, on balance, to be the more robust hypothesis based on current data, but there is a final challenge to using chelicerata as its principal autapomorphy. At least some Palaeozoic Euarthropoda express robust, raptorial so-called ‘great appendages’ at the front of the head; i.e. potentially in the (a1) position. This is seen in, for example, fossils such as *Yohioia* from the Burgess Shale (Fig. 6). These raptorial ‘great appendages’ could conceivably be homologous with the chelicerata and represent their precursors in stem-group arthropods (Chen et al. 2004; Cotton and Braddy in press). However, Budd (2002) has developed an alternative model of homology in which the ‘great appendage’ is effectively a pre-a1 (or prechelicerata) element which is lost towards the crown of the Euarthropoda. Pycnogonida were not included in Budd’s scheme. This homology question must be tested against additional data, but if Chen et al. (2004) and Cotton and Braddy (in press) are right then the chelicerata in euchelicerates and pycnogonids could be interpreted as part of a grade of raptorial feeding appendage inherited from stem-group arthro-

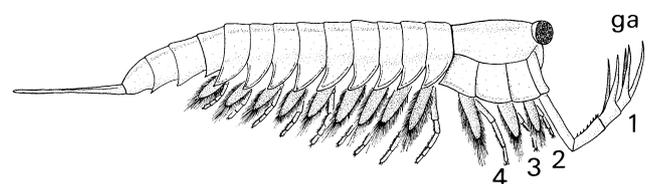


Fig. 6. The Burgess shale arthropod *Yohioia* (after Delle Cave and Simonetta 1991: Fig. 17A). One of a number of early Palaeozoic ‘great appendage’ (ga) arthropods which, according to Chen et al. (2004) and Cotton and Braddy (in press), could potentially lie on the chelicerate – or even the euarthropod – stem lineage. Like pycnogonids, and some arachnids, *Yohioia* expresses a four-segmented head region in which the anteriormost limb is a uniramous, (subchelate) raptorial, grasping appendage. Does a raptorial first leg define a clade among the arthropods or is it a plesiomorphic grade of organization?

Pods; appendages, which perhaps later become modified into the sensorial antennae in mandibulates. The question then would be: does the specific morphology of the cheliphore and the chelicera – three to (?)five articles ending in a distal, opposable claw – remain a valid synapomorphy for (Pycnogonida + Euchelicerata)?

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Zusammenfassung

Die Verwandtschaftsbeziehungen der Asselspinnen: Ein Überblick.

Frühere Autoren betrachteten die Pycnogonida (Asselspinnen) entweder als wasserbewohnende Spinnentiere oder als rückgebildete Krebstiere oder als eine Zwischenform zwischen den beiden Gruppen. Später wurden die Pycnogonida entweder den Chelicerata zugeordnet oder als eine isolierte Gruppe, die mit den anderen Arthropoden in keiner Verwandtschaftsbeziehung steht, betrachtet. Die letztere Annahme ist unter den Aspekten der phylogenetischen Systematik unbrauchbar. Neue cladistische Untersuchungen unterstützen zwei verschiedene, alternative Hypothesen: die erste Hypothese entspricht dem traditionellen Chelicerata s. lat.-Konzept, d.h. Pycnogonida + Euchelicerata bilden eine Gruppe. Hier gibt es aber nur eine einzige überzeugende Synapomorphie: klauenartige Cheliceren. Die zweite Hypothese anerkennt eine Gruppierung (Pycnogonida + alle anderen Euarthropoda), entsprechend den Ergebnissen verschiedener "Total Evidence-Analysen". Einige morphologische Merkmale, wie das Auftreten von Gonoporen am Rüssel, das Fehlen des Labrums, der Nephridien und der intersegmentalen Sehnen, unterstützt das Taxon Cormogonida (alle Euarthropoda mit Ausschluss der Pycnogonida). Fortschritte in der Entwicklungsbiologie erlauben jetzt eine klare Homologisierung der Segmente. Es besteht jedoch weiterhin ein Konflikt zwischen den beiden Hypothesen bezüglich der Frage, ob das letzte Laufbeinsegment ein Teil des Prosomas ist. In letzterem Fall hätten die Pycnogonida im Vergleich mit den Euchelicerata zu viele prosomale Segmente; vielleicht kann das als Hinweis angesehen werden, daß die beiden Taxa keine Schwestergruppen sind. Alternativ, wenn das letzte Laufbeinsegment ein Teil der post-prosomatischen Region ist, könnte es dem chilarialen Segment der Euchelicerata in seinem einstrahligen Zustand entsprechen und eine Apomorphie gegenüber den anderen Euarthropoden darstellen. Die molekularen Phylogeniestudien müssen strenger analysiert, besser durch Daten von anderer Seite unterstützt und die Aspekte der Empfindlichkeit der technischen Methoden besser untersucht werden. Das Chelicerata s. lat.-Modell mag als das mehr überzeugende erscheinen, doch müssen die vermutlichen Autoapomorphien der Chelicerata mit Vorsicht behandelt werden, denn es gibt da die fossilen Gliederfüßler aus dem frühen Paläozoikum, die sogenannten "great appendage" - Euarthropoden mit einem großen robusten Paar von Kopfgliedern als Fangapparat, die nahe bei den Chelicerata stehend oder sogar als Stammgruppe der Euarthropoden angesehen werden können.

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