

New ideas about the euchelicerate stem-lineage

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Abstract: Historically, various early Palaeozoic arthropods have been assigned to the fossil stem-lineage of Chelicerata. These include Trilobita and/or a number of extinct taxa belonging to the Arachnomorpha; most of which resemble Xiphosura (horseshoe crabs). However, many of the characters supporting Arachnomorpha fail when applied to Arachnida or Pycnogonida (sea spiders). Pycnogonida resolve either as basal Chelicerata or as sister-group to all other Euarthropoda. Furthermore, a new palaeontological hypotheses is reviewed here which identifies an assemblage of Cambrian ‘great-appendage’ arthropods (alternatively named protochelicerates or megacherians) as potential stem-group chelicerates. Significantly, these fossils have a robust pair of anterior head appendages and show a possible trend by which they became increasingly raptorial – approaching the condition of the chelate chelicerae. Homology of appendages at the ‘head’ end of arthropods remains highly controversial, but recent data suggests that chelicerae are homologous with the (a1) antennae. Thus in the scenario presented here euchelicerates did not lose (and indeed never had) long, sensory antennae, but probably evolved their chelicerae from a leg-like pair of uniramous appendages. The head region of the ‘great-appendage’ arthropods is not a prosoma, but may be segmentally homologous with an anterior body region associated with four pairs of appendages occurring in pycnogonids, many mites (Acari) and in arachnids with a divided carapace, or propeltidium.

Key words: Arthropoda, Chelicerata, stem-lineage, fossil, phylogeny, tagmosis

Introduction

Textbook accounts of Chelicerata usually recognise three major clades (or classes): Arachnida, Merostomata and Pycnogonida. Arachnids and merostomes together form the Euchelicerata WEYGOLDT, PAULUS, 1979; the monophyly of which seems to be one of the most stable and convincing results in arthropod phylogeny (GIRIBET, RIBERA 2000). Resolving euchelicerate ancestors from the fossil record has proven more challenging. Extinct arthropods like trilobites, and a number of other early Palaeozoic fossils which resemble both trilobites and horseshoe crabs, have often been proposed either as the oldest record of chelicerates, or as members of their immediate stem-lineage. Well preserved examples of these fossils often bear antennae – as opposed to chelicerae – leading to the assumption that chelicerates must have lost their antennae in the course of evolution (e.g. STÜRMER, BERGSTRÖM 1978). These putative stem-lineage chelicerates include Trilobita (in particular the Olenellida group), Aglaspidida and Cheloniellida (see below). Some of these fossils were traditionally grouped with chelicerates under the names Arachnomorpha HEIDER, 1913 or Arachnata LAUTERBACH, 1980. Nevertheless, the monophyly of Arachnomorpha has proven difficult to justify, since many of its putative synapomorphies are at best only applicable to trilobites (and similar-looking creatures) and horseshoe crabs – and not to arachnids and pycnogonids (SCHOLTZ, EDGECOMBE 2005).

Euchelicerata must have a sister-group. Among living taxa, Pycnogonida (sea spiders) remain the strongest candidate by virtue of their chelate chelifores. However, recent studies (summarised by DUNLOP, ARANGO 2005) have reduced the number of synapomorphies supporting the traditional

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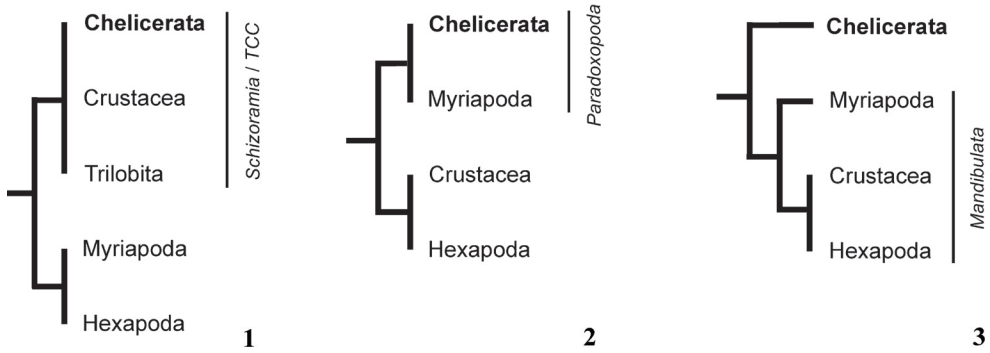
concept of Chelicerata (see below). Other authors resolved pycnogonids as sister-group to all other (living) arthropods (e.g. ZRZAVÝ *et al.* 1998). With respect to fossil arthropods, an important new hypothesis – reviewed here – has emerged (BOUSFIELD 1995, CHEN *et al.* 2004, COTTON, BRADY 2004) which recognises a number of so-called ‘great-appendage’ fossil arthropods as potential members of the chelicerate stem-lineage. The attractiveness of this new proposal is that if recent data (see e.g. SCHOLTZ 2001, MITTMANN, SCHOLTZ 2003) showing the chelicerae and (a1) antennae to be homologous appendages is correct, there is no need to invoke the loss of antennae during chelicerate evolution. Nor must we assume the transformation of a long, flagelliform, sensory limb into a short, claw-like feeding limb. Starting from an ancestor with a fairly generalised anterior head limb (cf. WALOSZEK *et al.* 2005), a logical sequence can be traced among these ‘great-appendage’ fossils whereby the first (a1) head limb reduces or consolidates the number of articles and becomes more compact and raptorial; eventually approaching the chelate condition seen in horseshoe crabs and (basal) arachnids.

Results and Discussion

Major Issues in Arthropod Phylogeny

Arthropoda *sensu lato* is conventionally divided into the Euarthropoda and their stem. This stem-lineage includes the Recent Onychophora (velvet worms), Tardigrada (water bears) and, probably, Pentastomida (tongue worms). It also includes large, predatory extinct animals usually called anomalocaridids (cf. HOU *et al.* 1995, COLLINS 1996) and early onychophoran-like fossils usually known as lobopodians; see e.g. RAMSKÖLD, CHEN (1998) for an overview of the latter. Relationships among these stem-taxa remain largely unresolved, but there is clearly an accumulation of arthropod characters grading towards the euarthropod condition: i.e. a fully sclerotised body with legs attaching via a well-developed coxa (or basipod) and the beginnings of a recognisable head; see e.g. BUDD (2002), BERGSTRÖM, HOU (2003) and WALOSZEK *et al.* (2005) for recent discussions and alternative evolutionary scenarios. Euarthropoda thus includes Chelicerata, Myriapoda, Hexapoda and Crustacea, as well as many extinct, fossil forms. Of these, Trilobita are the most familiar by virtue of their high diversity (over 10,000 described species), long geological range (ca. 275 million years) and easily preserved, calcified exoskeleton. However, they are only one branch of a much wider group of extinct euarthropods, most of which lack a mineralised exoskeleton and are known primarily from a handful of localities yielding extraordinary preservation. Numerous names have been applied to trilobites plus these similar-looking forms, of which Trilobitomorpha STÖRMER, 1944 is probably the most widespread. The sub-group Arachnomorpha (see above) largely encompass the most horseshoe crab-like of these trilobitomorpha. Indeed some arachnomorpha were initially regarded as chelicerates and referred explicitly to Merostomata in their original description (see e.g. WALCOTT 1912).

Three main hypotheses concerning relationships among the Euarthropoda can be found in the current literature. In brief, a number of studies drawing heavily on palaeontological data have supported (Chelicerata + Crustacea). This TCC (trilobite-chelicerate-crustacean) or Schizoramia hypothesis (Fig. 1) (e.g. HOU, BERGSTRÖM 1997, EMERSON, SCHRAM 1997, WILLS *et al.* 1998) recognises the biramous limbs of chelicerates (and trilobitomorpha in general) and crustaceans, as well as some similarities in their embryological development. Alternatively, some molecular data supports (Chelicerata + Myriapoda). This Myriochelata or Paradoxopoda hypothesis (Fig. 2) (e.g. MALLATT *et al.* 2004 and references therein) has been recovered in a number of studies, but so far has relatively little morphological support. Probably the most widely accepted recent result based on combined morphological and molecular data (e.g. EDGECOMBE *et al.* 2000, GIRIBET *et al.* 2001) recognises (Euchelicerata + Mandibulata) (Fig. 3). The mandibulates encompass myriapods,



Figs 1-3. Alternative hypotheses in the recent literature for the position of the Chelicerata (see text for details): 1 - Trilobita + Chelicerata + Crustacea, (= Schizoramia or ‘TCC’ clade); 2 - Chelicerata + Myriapoda (= Paradoxopoda or Myriochelata); 3 - Chelicerata + Mandibulata. Hypothesis 3 seems to have the most widespread support based on current data, although its proponents have, in most cases, not tried to integrate fossil taxa into their analyses.

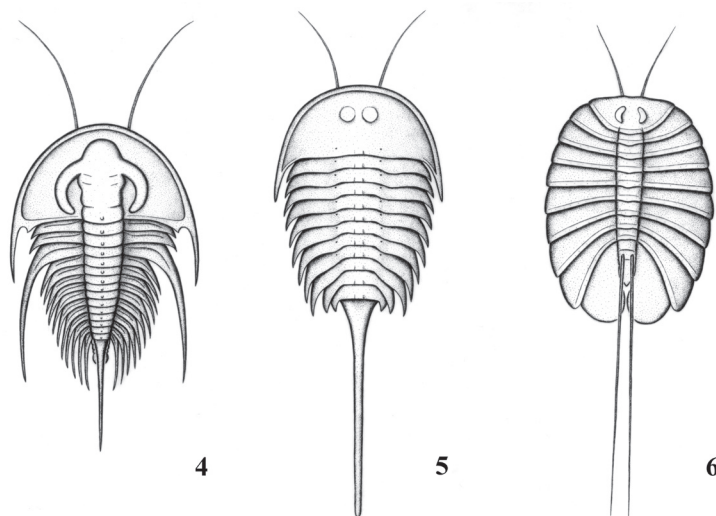
hexapods and crustaceans – all of which are united by a putatively homologous mandible (see e.g. SCHOLTZ 2001). The position of the Pycnogonida (sea spiders) relative to this scheme is discussed below, but it is also worth noting that most of the studies yielding (Euchelicerata + Mandibulata) or Myriochelata/Paradoxopoda have not tried to integrate fossil arthropods.

Trilobita and Chelicerata

Superficial similarities between trilobites (Fig. 4) and horseshoe crabs (Xiphosura) are self-evident. The fact that both the early instars of living horseshoe crabs and the adults of many fossil xiphosurans express trilobite-like segmentation has also long been recognised (e.g. LOCKWOOD 1870). Even today the hatching instar of horseshoe crabs is called the ‘trilobite larva’. LANKESTER’s (1881) classic paper firmly established the fact that horseshoe crabs were related to arachnids – and not crustaceans. In LANKESTER’s studies, both xiphosurans and trilobites were included within Arachnida; which he divided into a Nomomeristicia grade (euchelicerates and subsequently also pycnogonids) where the segmentation is fairly stable, and Anomomeristicia (trilobites) where segmentation is highly variable. LANKESTER’s scheme was not widely adopted, but trilobites continue to be implicitly grouped with chelicerates – even in modern zoological textbooks (e.g. GRÜNER 1993). Some cladistic analyses have also recovered (Chelicerata + Trilobita) (e.g. WHEELER *et al.* 1993), albeit when the diversity of fossil arthropods was ignored and trilobites were the only fossil terminal included.

Olenellid Trilobites

RAW (1957) considered chelicerates to be derived from a hypothetical ancestor of the so-called olenellid trilobites. Olenellids (olenellines in some classifications) (Fig. 4) are a Cambrian group whose most distinctive feature is the fact that the moulting, or facial, sutures of the cephalon (= head shield) run around its margin, and not across the cephalon to form the so-called free cheeks characteristic for other trilobite heads. Much of Raw’s evidence for his hypothesis has been superseded by recent work on head segmentation and the homology of the anterior appendages. His paper also relied on a rigid concept of ‘merocyclism’ in which the postcephalic regions of both trilobites and chelicerates could be characterised into regular patterns of either fifteen, twelve, nine or six segments. Enough deviations from this scheme can be observed among both euchelicerates and trilobites to regard this hypothesis with suspicion, but Raw did make some valid



Figs 4-6. Sketch reconstructions of some of the putative members of the chelicerate stem-lineage previously suggested in the literature: 4 - *Olenellus thompsoni* (Trilobita, Olenellida) after LAUTERBACH (1980, fig. 5a); 5 - *Aglaspis spinifer* (Aglaspidida) after HESSELBO (1992, fig. 26-1); 6 - *Cheloniellon calmani* (Cheloniellida) after STÜRMER, BERGSTRÖM (1978, fig. 2). Not to scale. These taxa form part of a wider group of arthropods usually referred to as Arachnomorpha or Arachnata; the monophyly of which has recently been drawn into question (SCHOLTZ, EDGEcombe 2005).

observations, such as the fact that chelicerates are more ‘primitive’ than mandibulate arthropods by virtue of the fact that they still use most of their head appendages for walking.

LAUTERBACH (1980, 1983, 1989) recognised an Arachnata clade comprising chelicerates and trilobites. Most controversially here, Trilobita was no longer considered monophyletic. Again the olenellids were the key group and were separated off from the remaining trilobites. LAUTERBACH’S Chelicerata was thus divided into (Olenellida + Chelicerata sensu stricto). Three rather complex synapomorphies were proposed in support of this hypothesis: (1) a ‘prothorax’ of 15 segments behind the cephalon, whereby if thoracic segments 1-2 have become incorporated into the chelicerate prosoma then this character could effectively be scored as a 13-segmented opisthosoma, (2) a macroplural third thoracic segment, i.e. the first opisthosomal segment in chelicerates should be noticeably wider, and (3) a long, median spine on the 15th trunk segment of these trilobites, implicitly homologous with the chelicerate telson. Lauterbach’s scheme – heavily based on his own hypothetical groundplan constructs – has found little support in the literature; but see AX (1987) and WEYGOLDT (1998). It was explicitly rejected by HAHN (1989), FORTEY, WHITTINGTON (1989) and RAMSKÖLD, EDGEcombe (1991), all of whom articulated numerous autapomorphies for Trilobita while drawing attention to the weakness of Lauterbach’s synapomorphies, such as the fact that axial spines and macropleural segments have evolved in different places in different trilobite taxa.

From a chelicerate perspective, the three proposed synapomorphies also deserve discussion. A thorax of 15 segments (= an opisthosoma of 13 segments) has some merit in that there are chelicerates, such as scorpions, apparently with 13 opisthosomal segments (DUNLOP, WEBSTER 1999). However, segment numbers are variable across the different euchelicerate orders and we have no obvious way to determine which of these patterns represents the ancestral condition. The median spine/telson homology is conceivable, but lacks explicit morphological support. Lots of arthropods have a telson. A macroplural third segment (= opisthosomal segment 1) is by far the weakest character. The trend, if anything, among chelicerates is to reduce or modify this segment;

the narrow pedicels of spiders and some other arachnids being a case in point. Lauterbach offered no clear example of an unequivocally ‘macroplural’ euchelicerate. In summary, none of his olenellid/chelicerate characters are particularly convincing and better evidence for a monophyletic Trilobita has been presented.

Aglaspidida

Aglaspidida (Fig. 5) are a group of mostly Cambrian arthropods, which (like trilobites) at least superficially resemble horseshoe crabs. HESSELBO (1992) provided a valuable overview. The monograph of RAASCH (1939) referred Aglaspidida to Merostomata based on one well-preserved specimen interpreted as showing six pairs of prosomal appendages, the first of which was supposedly chelate. For this reason it is still possible to read about horseshoe crabs being classic ‘living fossils’, unchanged since the Cambrian. In fact there are no unequivocal Cambrian horseshoe crabs and a putative Ordovician stem-xiphosuran (or stem-chelicerate according to DUNLOP, SELDEN 1998) turned out not to be an arthropod at all (MOORE, BRADY 2005). The oldest unequivocal Xiphosura are Silurian in age (e.g. MOORE *et al.* 2005), while the oldest modern-looking crown-group examples – assignable to the extant clade Xiphosurida – come from the Carboniferous (ANDERSON, SELDEN 1997). On current evidence some arachnid orders (Acari, Opiliones, Pseudoscorpiones) with modern-looking Devonian representatives are better examples of ‘living fossils’ than horseshoe crabs.

Raasch’s merostome interpretation of Aglaspidida was widely accepted in the subsequent literature (e.g. STÖRMER 1944). The hypothesis that Aglaspidida are specifically the sister-group of the remaining chelicerates owes much to the influential cladogram of WEYGOLDT, PAULUS (1979). In this paper they broadly accepted Lauterbach’s hypothesis (see above), recognising a scheme of the form (Trilobita (Olenellida (Aglaspidida + Euchelicerata))). Aglaspidids and euchelicerates were grouped together based on four putative synapomorphies: (1) reduced antennae, (2) chelate chelicerae, (3) two thoracic segments fused to the head to form a prosoma and (4) a predatory mode of life. However, in the same year BRIGGS *et al.* (1979) re-examined the key specimen of *Aglaspis spinifer* RAASCH, 1939 from the Late Cambrian of Wisconsin, which was supposed to show chelicerate characters. BRIGGS *et al.* concluded that in fact it had only four, or at most five, pairs of head appendages and that the first pair was not demonstrably chelate. HESSELBO (1992) confirmed this view, suggesting that the first pair of appendages were probably antenniform in life. These studies thus undermine the first three synapomorphies, while the fourth relates to behaviour and cannot be adequately tested in a fossil. Weygoldt and Paulus’s hypothesis still commands some support in the literature (AX 1987, WEYGOLDT 1998), while other authors have resolved aglaspidids fairly close to the chelicerates (e.g. WILLS 1996, WILLS *et al.* 1998, DUNLOP, SELDEN 1998). Despite this apparent consistency in phylogenetic analysis, robust and unequivocal synapomorphies exclusive to (Aglaspidida + Euchelicerata) are lacking.

Cheloniellida

Cheloniellida (Fig. 6) encompasses at least six Ordovician–Devonian arthropods which have also been resolved as possible members of the chelicerate stem-lineage (e.g. STÖRMER, BERGSTRÖM 1978, WILLS 1996, WILLS *et al.* 1998, DUNLOP, SELDEN 1998). All are oval arthropods which superficially resemble isopod crustaceans. Well preserved examples have both anterior antennae and posterior furcal rami. The best known example is *Cheloniellon calmani* BROILI, 1932 from the Early Devonian Hunsrück slates of Germany. It was redescribed in detail by STÖRMER, BERGSTRÖM (1978) who used radiographic techniques to reveal previously hidden characters, and who discussed its possible affinities. In brief, the anterior head region of *C. calmani* includes antennae, a pair of leg-like postantennal appendages and four pairs of strongly gnathobasic head limbs. This is fol-

lowed by a trunk of biramous limbs with well-defined exopods, presumably acting as gills. Thus *C. calmani* seems to approach the chelicerate condition of functional tagmosis into a ‘prosoma’ dominated by gnathobasic food-processing limbs and an ‘opisthosoma’ including respiratory appendage branches. However, *C. calmani* lacks chelicerae and in the homology scheme of Stürmer and Bergström has only five pairs of ‘prosomal’ limbs, not six as per euchelicerates, leading these authors to suggest that it may be late representative of the trilobitomorph branch which gave rise to the chelicerates.

Arachnomorphs and Their Antennae

Other arachnomorphs have also been proposed, usually rather speculatively, either as early chelicerates or their relatives; see e.g. COTTON, BRADY (2004) for a review. Yet there are difficulties with the general Arachnomorpha / Arachnata concept. First, the limits of what actually belongs within this group are not particularly stable. RAMSKÖLD *et al.* (1997, p. 19) attempted to resolve this by defining Arachnata as “...the most inclusive clade including Chelicerata but not Crustacea.” while WILLS *et al.* (1998, p. 74) stated that Arachnomorpha “...accommodates most non-bivalved Cambrian problematica in addition to trilobites and chelicerates”. This leads neatly into the second problem. For the most part arachnomorphs have not been characterised by unequivocal synapomorphies and were effectively defined as ‘not being crustaceans’. BRADY, COTTON (2004) did recover Arachnomorpha as a clade (rather than a paraphyletic grade), recognising three potential synapomorphies (their characters 12, 17 and 48). The first was absence of a multiannulate shaft of the exopod limb branch, with each article bearing setae; a reductive apomorphy, scored as present in crustaceans. Second, was the lack of medially directed exopod setae, scored as an arachnomorph plesiomorphy relative to their presence in crustaceans. Their final character was an anus opening at the base of the arachnomorph telson, rather than within the telson itself. An anus opening within the telson is, however, present in at least one fossil pycnogonid (cf. DUNLOP, ARANGO 2005), thus the latter character does not encompass all chelicerates as they are traditionally recognised.

Another problem is the fact that, unlike chelicerates, many fossil arachnomorphs preserve very obvious antennae. A widespread assumption in the older literature was that trilobites were the most ‘primitive’ arthropods, thus chelicerate ancestors were predicted to have had long, flagelliform, trilobite-like antennae. As part of this hypothesis, it was also assumed that the chelicerae represent the second (so-called a2) head appendage, innervated from the tritocerebrum of the brain, and that chelicerates had simply lost their (a1) antennae. All this changed in 1998 with studies of the distribution of Homeobox (Hox) genes in the head region of arthropods (DAMEN *et al.* 1998, TELFORD, THOMAS 1998, review by SCHOLTZ 2001). By lining up segmental expression patterns of homologous genes, these papers demonstrated that both the chelicerae and (first) antennae of mandibulate arthropods are in all likelihood expressions of the same (a1) head appendage. MITTMANN, SCHOLTZ (2003) found further evidence in the horseshoe crab brain to support this hypothesis. They described the commissure of the cheliceral ganglion as running primarily in front of the stomodaemum, which strongly implies that the chelicerae are innervated from the deutocerebrum – like the (a1) antennae of insects and crustaceans – and not the tritocerebrum as previously assumed. BOXSHALL (2004: 257-261) provided a further detailed review of the diversity of character states (and terminologies) observed for the uniramous (a1) appendage (ranging from antennae to chelicerae) in fossil and Recent arthropods, and current controversies in their interpretation. Further palaeontological work supports the idea that it is most parsimonious to assume that stem-chelicerates did not have antennae (MOORE 2005).

WALOSZEK, DUNLOP (2002) and COTTON, BRADY (2004) noted pycnogonid and arachnomorph fossils bearing putative precheliceral structures which might represent vestiges of the ‘missing’ (a1) antennae. However, SCHOLTZ (2001) mentioned potentially homologous frontal processes in front

of the (a1) antennae in some crustaceans. Developing this line of thought, SCHOLTZ, EDGECOMBE (2005) questioned the interpretation of at least some of the fossils reported to have precheliceral appendages while proposing a novel, but controversial, scheme of ‘primary’ and ‘secondary’ antennae. Here the ‘primary antennae’ are interpreted as homologous with the protocerebral antennae of Onychophora, which in their scheme became largely lost in the evolution towards the euarthropods. The ‘secondary’ (a1) antennae or chelicerae are, by contrast, demonstrably deuterocephalic in origin (see above) and thus not homologous with onychophoran antennae. If Scholtz and Edgecombe are correct, structures like crustacean frontal processes and precheliceral structures in fossil chelicerates and their stem-lineage could (when present) potentially be vestigial remnants of these protocerebral ‘primary’ antennae. Further discussion is beyond the scope of the present paper, but on current data the chelicerae = (secondary) antennae model appears the more robust hypothesis.

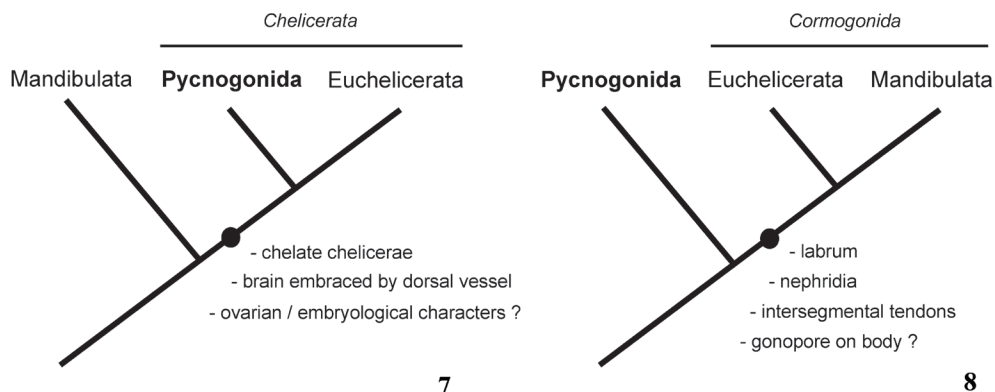
The End of Arachnomorpha?

SCHOLTZ, EDGECOMBE (2005) explicitly rejected Arachnomorpha as a clade, outlining arguments against the features traditionally used to ally trilobites (and certain other trilobitiforms) with chelicerates; see these authors for details. In summary, they argued that most of the proposed arachnomorph characters – including trilobation, a broad head shield with genal spines and a rather soft ventral side to the body – are at best relevant only to trilobites and horseshoe crabs and are largely absent (or inapplicable) in arachnids and pycnogonids. On these grounds trilobites, aglaspids, cheloniellids, etc. would have to be excluded from the stem-lineage of Chelicerata; an opinion which the present author largely supports. Scholtz and Edgecombe proposed (like BOUDREAU 1979) that trilobites, and related forms, actually belong on the mandibulate stem-lineage, whereby their sensorial (a1) antennae offers a potential synapomorphy for (Trilobita + Mandibulata); differing, in their hypothesis, from the short, raptorial (a1) chelicerae of the euchelicerates and pycnogonids.

Pycnogonida

Pycnogonid affinities were reviewed by DUNLOP, ARANGO (2005) who summarised the literature to date and recognised three main historical hypotheses: (1) chelicerates, (2) crustaceans, or (3) unrelated to all other arthropod groups. Affinities with crustaceans were mostly based on crude similarities in the larvae, and in detail the crustacean nauplius larva and pycnogonid protonymph are evidently rather different. There are no convincing synapomorphies for (Pycnogonida + Crustacea) and this relationship has not been recovered in any recent analyses. Other authors (e.g. HEDGPETH 1947) emphasised the uniqueness of pycnogonid morphology, using this as evidence against affinities with any other arthropod group. Characters like the pycnogonid proboscis and the reduced body with organ systems displaced into the legs are indeed unusual, but they are autapomorphies and tell us nothing about sister-group relationships.

Recent studies, including both morphological and/or molecular data, essentially favour one of two competing hypotheses. The first is the traditional (Pycnogonida + Euchelicerata) (Fig. 7), which was supported by three synapomorphies: (1) chelate chelicerae, (2) loss of antennae and (3) a body divided into a prosoma and opisthosoma. There are also further potential synapomorphies in the circulatory system and in embryology. Yet of the traditional characters, only chelicerae stand up to scrutiny; see e.g. WALOSZEK, DUNLOP (2002) for details. Loss of antennae is just an alternative character state for presence of chelicerae (see above). Yet even the homology of chelicerae (euchelicerates) and chelifores (in pycnogonid terminology) has recently been questioned based on neuroanatomical data (MAXMEN *et al.* 2005). These authors suggested that the pycnogonid chelifores are innervated from the protocerebrum and are thus topologically anterior



Figs 7-8. Alternative positions for the Pycnogonida (sea spiders) recovered in recent cladistic analyses: 7 - sister-group of Euchelicerata; 8 - sister group of Euarthropoda. Synapomorphies potentially supporting each of these models were discussed in detail by DUNLOP, ARANGO (2005).

to the position of the (a1) chelicerae (see above) which are innervated from the deuterocerebrum, as shown by MITTMANN, SCHOLTZ (2003). If Maxmen *et al.* are correct, one of the key characters supporting Chelicerata in its traditional sense would fail and pycnogonid chelifores would be in a homologous position to the 'primary' antennae postulated by SHOLTZ, EDGECOMBE (2005) and/or the protocerebral antennae of Onychophora (see above). Nevertheless, a recent test identifying Hox gene distributions in pycnogonids (JAGER *et al.* 2006) does not support the Maxmen *et al.* scenario, but rather supports the hypothesis that chelifores = chelicerae; both in the a1 position as elaborated above. Further comments on this controversial and rapidly evolving field are beyond the scope of the present paper.

The puzzling 'extra' (7th) limb pair in the pycnogonid prosoma is resolved by a simple count of appendages. This reveals that the 'prosoma' and 'opisthosoma' of pycnogonids are not segmentally homologous to those of euchelicerates (VILPOUX, WALOSZEK 2003, and references therein). Pycnogonids have a cephalosoma bearing four pairs of appendages (chelifores, palps, ovigers, walking leg 1) plus a trunk with three (rarely four or five) pairs of walking legs and a short tail end (abdomen) bearing the anus. Some fossil forms retain a few limbless segments, and in one case a telson, behind the legs. Thus a simple prosoma-opisthosoma division, in which the prosoma has six pairs of limbs, also fails to support the traditional concept of Chelicerata.

The alternative model (Fig. 8) is (Pycnogonida + (Euchelicerata + Mandibulata)), a scheme first articulated by ZRVARÝ *et al.* (1998), who united euchelicerates and mandibulates in a clade called Cormogonida ZRVARÝ, HYPŠA, VLÁŠKOVÁ, 1998. This they defined on the synapomorphy of a gonopore on the body, rather than on the leg bases as in pycnogonids. The problem here is that appendicular gonopores have long been accepted as a convincing sea spider autapomorphy. Nevertheless, other studies have also recovered pycnogonids in a basal position relative to all other (living) euarthropods (EDGECOMBE *et al.* 2000, GIRIBET *et al.* 2001). Characters absent from pycnogonids and potentially synapomorphic for euchelicerates and mandibulates include a labrum, nephridia and intersegmental tendons. Yet, identifying 'missing' characters as plesiomorphic or apomorphic in pycnogonids is complicated by the numerous reductive trends seen in their body and organ systems.

VILPOUX, WALOSZEK (2003) also noted that the three-limbed protonymphon of pycnogonids is shorter than the four-limbed 'head larva' interpreted by these authors as characteristic for early Euarthropoda. This head larva is observable in, for example, trilobites and stem-group crustaceans, whereby the shorter nauplius is a later development of the crustacean crown-group. Perhaps pycno-

gonids represent a more plesiomorphic grade of organisation, hatching with a three-limbed larva? In this hypothesis the remaining, more derived, euarthropods would have in their ground pattern the synapomorphy of a four-limbed head larva – which was subsequently modified in modern arthropod groups. For example euchelicerates hatch more precociously. Their first instar closely resembles the adult form, thus they no longer express a true larval stage of development.

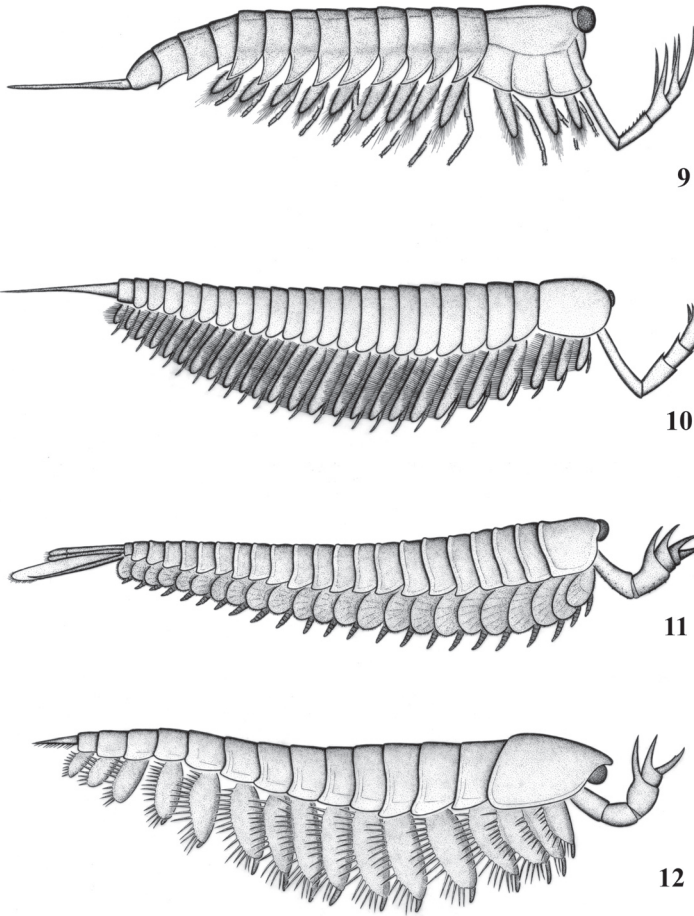
In summary, it is presently difficult to resolve between pycnogonids being basal chelicerates or basal euarthropods and further studies directed specifically at this question would be welcome.

‘Great-Appendage’ Arthropods: Stem-Chelicerates?

So what is the sister-group of Euchelicerata? Using a construction morphology approach GRASSHOFF (1978, p. 277) argued that the chelicerate grade of organisation must have arisen when their ancestors transformed the first appendage into something able to both detect and grasp food. In a rather obscure and poorly-known paper, BOUSFIELD (1995) compared feeding appendages in early fossil arthropods. He proposed that the distinctly raptorial head limbs in some specific arachnomorphs (see above) like *Yohoia tenuis* WALCOTT, 1912 (Fig. 9) from the famous Burgess Shale of Canada and *Jianfengia multisegmentalis* HOU, 1987 (Fig. 10) from the slightly older Chengjiang (or Maotianshan-Shale) fauna of China were effectively precursors of the chelicerae. These two genera were reassigned by Bousfield to the higher taxon Protochelicerata STØRMER, 1944 – although this name was originally proposed to encompass some quite different genera – redefined as animals with semi-chelate, preoral appendages composed of 4-5 articles, plus three more pairs of biramous head limbs used for walking. Protochelicerates sensu Bousfield were effectively placed on the lineage leading up to chelicerates (BOUSFIELD 1995, Fig. 7.), and indeed something similar was found by BRIGGS, FORTEY (1989) when one compares those arthropods which resolved close to chelicerates in their early cladistic analysis.

CHEN *et al.* (2004) and COTTON, BRADY (2004) recently arrived independently at essentially the same hypothesis. They recognised a series of so-called ‘great-appendage’ arthropods which they resolved cladistically on the direct stem-lineage leading towards chelicerates. Their examples of these ‘great-appendage’ arthropods include (as in Bousfield’s scheme) *Yohoia* and *Jianfengia* as well as other Maotianshan-Shale fossils like *Parapeytoia yunnanensis* HOU *et al.*, 1995, *Fortiforceps foliosa* HOU, BERGSTRÖM, 1997 (Fig. 11) and *Haikoucaris ercaiensis* CHEN *et al.*, 2004 (Fig. 12). It should be noted that interpretations of *Fortiforceps* are controversial, specifically in the Hou and Bergström description explicit antennae in front of the great-appendage were recognised; an interpretation not accepted by e.g. CHEN *et al.* (2004) who found no such structures in the nevertheless similar-looking *Haikoucaris*.

Yet, what these remarkable creatures all have in common is a ‘head’ region apparently bearing at least four pairs of appendages, the (?) first of which has around five articles and is relatively robust, somewhat raptorial and presumably played an active role in grasping prey. The other head limbs, and the limbs of the segmented trunk, are biramous with a leg-like endopod and a flap-like exopod bearing marginal spines or setae (Figs. 9-12). Chen *et al.* and Cotton and Brady differed slightly in the details – the latter also using the name Megacheria HOU, BERGSTRÖM, 1997 for these taxa – but their main conclusion was that these arthropods can be arranged in such a way on the chelicerate stem-lineage that they show a general trend towards a more claw-like head limb (Fig. 13). Thus ‘protochelicerates’ or ‘megacherians’ would probably represent a paraphyletic series of stem-taxa, rather than a monophyletic clade. Implicit in this hypothesis is of course the homology of the ‘great-appendage’ with the chelicera – but see BUDD (2002) and MAXMEN *et al.* (2005) for an alternative perspective whereby the ‘great-appendage’ and perhaps also the pycnogonid chelifore are effectively ‘prechelicerate’. If the ‘great-appendage’ is homologous with the chelicera



Figs 9-12. Sketch reconstructions of selected ‘great-appendage’, ‘protochelicerate’ or ‘megacherian’ arthropods recently suggested as members of the chelicerate stem-lineage: 9 - *Yohioia tenuis* after DUNLOP, ARANGO (2005, fig. 6); 10 - *Jianfengia multisegmentalis* modified from HOU 1987 (fig. 10); 11 - *Fortiforceps foliosa* modified from HOU, BERGSTRÖM (1997, figs 33C, 35); 12 - *Haikoucaris ercaiensis* after CHEN *et al.* (2004, fig. 3). Not to scale. Note that in some cases earlier descriptions were quite poor and/or other authors have reconstructed these taxa slightly differently; sometimes even with ‘prechelicerate’ appendages. Nevertheless a large, probably raptorial head appendage does seem to be a consistent and genuine feature of all of them.

then Chen *et al.* regarded the chelicerae and their forerunners as the (a1) appendage, while Cotton and Braddy preferred the traditional, but now less well-supported, (a2) interpretation.

The advantage of this ‘great-appendage’ = chelicerae hypothesis is that if the Hox gene and (most) neuroanatomical data is accepted, we have a scenario whereby the chelicerae evolved through a series of ancestors with increasingly chelate anterior head appendages. There is no need to invoke either the loss of antennae or the transformation of a long, sensory appendage into a short claw. Chelicerae need not be “...profoundly modified antennules.” sensu BOXSHALL (2004, p. 260) if they evolved from ambulatory rather than a sensorial first head limbs. This remains an area of much controversy since we do not know for sure what the original (a1) limb was like in the (eu)arthropod common ancestor: a leg, an antenna or a claw? The fossil data can be ambiguous or open to alternative interpretations. As a possible outgroup, the Maotianshan-Shale arthropod

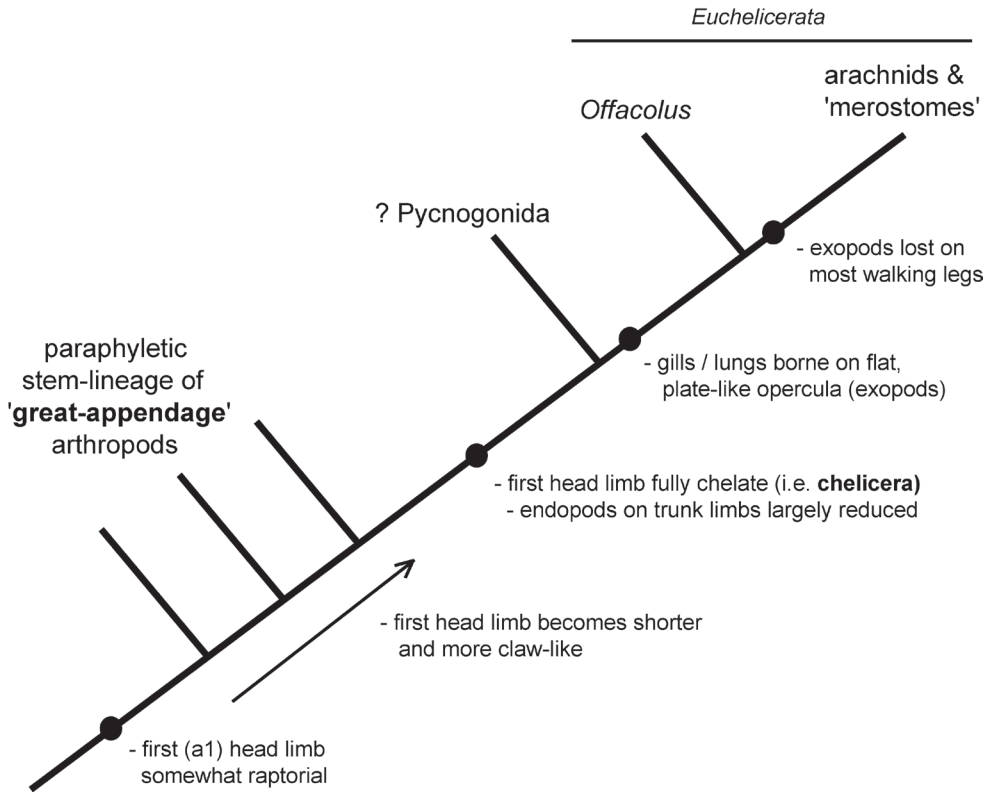


Fig. 13. A tentative scenario for euchelicerate origins illustrating the major transformations in limb morphology implied by the new ‘great-appendage’ arthropod hypothesis. See text for details.

Fuxianhuia protensa HOU, 1987 – itself once considered an early chelicerate (WILLS 1996) – was recently restudied by WALOSZEK *et al.* (2005) in combination with some similar fossils. These *Fuxianhuia*-like fossils may resolve just below the euarthropod grade of organisation, although different authors have disagreed quite fundamentally on the number and position of its head appendages (cf. WILLS 1996, HOU, BERGSTRÖM 1997, SCHOLTZ, EDGECOMBE 2005, WALOSZEK *et al.* 2005).

Fuxianhuia and its relatives have, at least in the WALOSZEK *et al.* (2005) hypothesis, a relatively short, somewhat leg-like (a1) appendage. If the same were true of the last common ancestor of the Euarthropoda, this fairly simple anterior limb could conceivably evolve in various directions: including a long, sensory structure, as per trilobites, or a more raptorial one, via the ‘great-appendage’ arthropods, to the chelicerae. Thus whether antennae evolved once (SCHOLTZ, EDGECOMBE 2005) or multiple times (WALOSZEK *et al.* 2005) remains to be resolved. Likewise, it is too early to rule out the possibility that claw-like limbs also developed in more than one lineage since this is clearly an adaptive character with a clear functional advantage – witness the almost certainly parallel development of (sub)raptorial pedipalpal claws for prey-capture in groups like scorpions and whipscorpions. Yet in the ‘great-appendage’ arthropods we now have one group of early fossil arthropods which (probably) lack antennae, which have raptorial feeding limbs instead, and thus appear to be excellent candidates for the animals which ultimately gave rise to the arachnids.

Missing Links?

These ‘great-appendage’ arthropods still differ in significant ways from euchelicerates, retaining for example plesiomorphic features like biramous limbs along the entire length of the body. If the

hypothesis that they are stem-lineage chelicerates is correct we would still expect to find some 'missing links' bridging this morphological gap, whereby the more anterior limbs lose the exopod and become primarily adapted for walking while the posterior ones are either lost completely or modified into plate-like, gill-bearing opercula. The enigmatic Silurian fossil *Offacolous kingi* ORR *et al.*, 2000 might be such a missing link. These authors reconstructed this probable early chelicerate from computer images of serial sections through the nodules which encase them and discovered that most of its prosomal appendages are still biramous. This suggests a more basal grade of organisation than xiphosurans which have only one biramous limb pair (the 6th) bearing the flabellum (Fig. 12).

Interestingly, the 'great-appendage' arthropods lack clear tagmosis into a prosoma and opisthosoma and express a head region probably bearing four pairs of appendages, including the raptorial pair. This 'head' in the chelicerate stem-lineage associated with four limb pairs is potentially segmentally homologous with the cephalosoma of pycnogonids (VILPOUX, WALOSZEK 2003, see also above), to the propeltidium of the carapace in some arachnids and the proterosoma region characteristic for many mites (see also DUNLOP, ARANGO 2005, fig. 5). Thus the 'great-appendage' hypothesis might alter interpretations of polarity for a number of arachnid characters.

A Final Word: *Sanctacaris*

Finally, one of the most famous candidates for the oldest chelicerate is *Sanctacaris uncata* BRIGGS, COLLINS, 1988 from the Burgess Shale; a fossil which has entered the popular literature (e.g. GOULD 1989) as an arachnid ancestor. In the original description it was specifically referred to Chelicerata on account of: (1) a head with at least six pairs of appendages, (2) a cardiac lobe, i.e. a swelling on the head shield such as that seen in horseshoe crabs, (3) division of the body into a putative prosoma and opisthosoma and (4) an anus on the last trunk segment. A common criticism of this interpretation is the fact that it lacks chelicerae (or antennae for that matter), although BOXSHALL (2004) suggested that chelicerae might be present, but indistinct. BUDD (2002) has even proposed that the 'six' pairs of prosomal limbs are just outgrowths from the articles comprising a single pair of 'great-appendages' (see above). Arachnomorph cladograms (e.g. WILLS *et al.* 1998) generally did not resolve *Sanctacaris* as sister-group of Chelicerata, drawing its affinities into question. Interestingly, what Wills *et al.* did recover was *Sanctacaris* close to *Yohoia*. Bearing in mind the new position proposed for *Yohoia* on the chelicerate stem-lineage, and the possibility that *Sanctacaris* has 'great-appendages' too, a new look at the affinities of *Sanctacaris* is clearly warranted. Its interpretation as a stem-lineage chelicerate may yet prove to be correct, albeit for different reasons to those proposed in the original description.

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Нови идеи за предшествениците на еухелицератите

Дж. Дънлоп

(Резюме)

В исторически план различни раннопалеозойски артроподи са били смятани за предшественици на хелицератите (Chelicerata). Сред тях са трилобитите (Trilobita) и фосилни видове, принадлежащи към Arachnomorpha, повечето от които наподобяващи ксифозурите (Xiphosura). Въпреки това, много от безезите, подкрепящи таксона Arachnomorpha, не издържат на проверка, когато са приложени към Arachnida и Pycnogonida (морските паяци). Пикногонидите се оказват или в основата на хелицератите или като сестринска група на всички останали еуартроподи (Euarthropoda). В настоящата статия е представена нова палеонтологична хипотеза, определяща групата от камбрийски „голямоиздатъчни” (great-appendage) артроподи (носещи наименованието протохелицерати или мегахериани), като потенциални предшественици на хелицератите. От значение е, че тези животни са имали двойка големи издатъци на предната част на главата, като се наблюдава тенденция, при която те се превръщат все повече в хватателни, така приближавайки се до състоянието на хелатните хелицери. Хомоложността на различните издатъци на края на главата на артроподите е много дискуссионен въпрос, но последните данни показват, че хелицерите са хомолжни с *a1* антените. В представения модел, еухелицератите никога не са загубвали дълги, сензорни антени (всъщност не са имали такива), а най-вероятно са развили хелицерите си от двойка кракоподобни, еднораменни издатъци. Главовата част на голямоиздатъчните артроподи не е прозома, а е вероятно сегментно хомоложна на тази предна част на тялото, която носи четирите двойки израстъци при пикногонидите, повечето акари и при арахнидите с разделен карапакс или пропелтидум.

