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The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence

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Abstract Understanding the head is one of the great challenges in the fields of comparative anatomy, developmental biology, and palaeontology of arthropods. Numerous conflicting views and interpretations are based on an enormous variety of descriptive and experimental approaches. The interpretation of the head influences views on phylogenetic relationships within the Arthropoda as well as outgroup relationships. Here, we review current hypotheses about head segmentation and the nature of head structures from various perspectives, which we try to combine to gain a deeper understanding of the arthropod head. Though discussion about arthropod heads shows some progress, unquestioned concepts (e.g., a presegmental acron) are still a source of bias. Several interpretations are no longer tenable based on recent results from comparative molecular developmental studies, improved morphological investigations, and new fossils. Current data indicate that the anterior arthropod head comprises three elements: the protocerebral/ocular region, the deutocerebral/antennal/cheliceral segment, and the tritocerebral/pedipalpal/second antennal/intercalary segment. The labrum and the mouth are part of the protocerebral/ocular region. Whether the labrum derives from a former pair of limbs

remains an open question, but a majority of data support its broad homology across the Euarthropoda. From the alignment of head segments between onychophorans and euarthropods, we develop the concept of “primary” and “secondary antennae” in Recent and fossil arthropods, posit that “primary antennae” are retained in some fossil euarthropods below the crown group level, and propose that Trilobita are stem lineage representatives of the Mandibulata.

Keywords Segmentation · Labrum · Primary antennae · Secondary antennae · Trilobita · Cambrian

Introduction

For more than a century, the problems of the number and nature of segments and other elements constituting the arthropod head have been a hotly debated issue (e.g., Goodrich 1897; Weber 1952; Siewing 1963; Rempel 1975; Weygoldt 1985; Scholtz 1995; Scholtz and Edgecombe 2005). Models, theories, and hypothesis building have become an intellectual challenge unmatched by other problems of arthropod morphology. Numerous articles deal with head segmentation and even national schools or traditions of views on arthropod heads evolved. Accordingly, we find typical French (Chaudonneret 1987; Casanova 1996), German (Heymons 1901; Siewing 1969, Paulus and Weygoldt 1996) or Swedish (Holmgren 1916; Hanström 1928; Dahl 1956) heads (see Rempel 1975) with different segmental compositions which were, and sometimes still are, discussed in their respective traditional environment. The views on heads influenced reconstructions of arthropod phylogenetic relationships and our general views of arthropod evolution. This debate on heads finds an interesting parallel in the discussion about the vertebrate head where similar problems of segment numbers and nature and transformations of parts occur (e.g., Starck 1963; Kuratani 2003; Northcutt 2005; Olsson et al. 2005). Embryologists, anatomists, palaeontologists, and molecular developmental biologists are

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concerned by this problem, and in particular, the latter two groups revived the controversy in recent times, based on new fossil finds and new comparative molecular techniques (Schmidt-Ott et al. 1994a,b; Rogers and Kaufman 1997; Budd 2002, Urbach and Technau 2003a, Waloszek et al. 2005).

Why is this debate so long lasting and so vivid? What is so important about heads? In particular, the answer to the latter question is self-evident, if one thinks even cursorily about the meaning of a head. Furthermore, cephalization might be a clue to understand the evolutionary success of arthropods. Given this long-standing concerted multinational, multidisciplinary effort, the question arises, “Why has this discussion not come to an end or to a satisfying solution?” There are at least two reasons for this. On the one hand, the discussion is sometimes hampered by concepts based on assumed phylogenetic relationships or evolutionary scenarios that bias the interpretation of structures. On the other hand, there are real problems in the interpretation of certain structures in the head because we can rightly assume that the needs to form a head and a brain led to evolutionary transformations of structures to a degree that makes homologization very problematic. This effect is even amplified by the approach of some researchers dealing with the head problem, who do not integrate the available evidence but rely excessively upon a restricted set of data. In contrast, we want to propose a kind of “total evidence approach” to the arthropod head problem. The organization, combination, and interpretation of the diverse kinds of data from morphology, developmental biology, molecular biology, phylogenetics, and palaeontology form the intellectual challenge mentioned by Snodgrass (1960) because little tracks and traces have to be combined and interpreted as signs of a former structure and process. This is a kind of puzzle that resembles the indices that are used by a detective to reconstruct the course of a crime. Like all researchers struggling with the arthropod head problem, we are more or less “head detectives.”

The phylogenetic framework: Articulata vs Ecdysozoa, Mandibulata vs Paradoxopoda

To be meaningful, the discussion of the arthropod head has to be conducted with a combination of comparative developmental and phylogenetic perspectives. The developmental analysis of the head of only one model organism might lead to inconclusive solutions and hypotheses (see Page 2004; replies by Harzsch 2004; Scholtz and Edgecombe 2005). Hence, before we enter the discussion about arthropod heads, we have to set out the phylogenetic framework that forms the background for our considerations about head evolution. Arthropod phylogeny is a highly controversial field (Richter and Wirkner 2004) but not all differences influence our views on head evolution and organization. Two controversial levels of arthropod phylogeny seem most important to the following discussion: one is the question of the arthropod

sister group, the other concerns the phylogenetic relationships between the major euarthropod taxa.

Currently, there are two competing hypothesis for the placement of the arthropods within the Metazoa. One is the more traditional Articulata hypothesis, which favors a close relationship between Annelida and Arthropoda (Wägele and Misof 2001; Scholtz 2002; Jenner and Scholtz 2005). The other alternative is known as the Ecdysozoa hypothesis (Aguinaldo et al. 1997; Giribet 2003). According to this view, the Arthropoda are most closely related to the cycloneuralians, which include the Nematoida (nematodes and nematomorphs) and Scalidophora (Schmidt-Rhaesa et al. 1998). As the two hypotheses have a different impact on our understanding of what segmentation is and how it has evolved (Scholtz 2002, 2003), they are relevant to the discussion of head segmentation, as we will see below.

Based on molecular datasets, the monophyly of the Mandibulata, comprising myriapods, crustaceans, and hexapods, has been challenged by placing the Myriapoda as the sister group of the Chelicerata (Cook et al. 2001; Hwang et al. 2001; Mallatt et al. 2004; Negrisolo et al. 2004). This grouping has been named Paradoxopoda (Mallatt et al. 2004) or Myriochelata (Pisani et al. 2004). However, there is no convincing morphological support in favor of a sister group relationship between Chelicerata and Myriapoda. Only some characteristics of neurogenesis (Dove and Stollewerk 2003; Kadner and Stollewerk 2004) are shared between myriapods and chelicerates, and even if one were to discount mandibulate synapomorphies, the myriapod–chelicerate characters are as plausibly interpreted as symplesiomorphies. In contrast, there is ample evidence from development and morphology that supports the Mandibulata as a monophyletic group (see Edgecombe 2004; Harzsch et al. 2005a; Scholtz and Edgecombe 2005). Furthermore, some phylogenetic studies based on molecular data and combined datasets support Mandibulata as well (Edgecombe et al. 2000; Giribet et al. 2001, 2005; Kusche et al. 2003). Accordingly, the Mandibulata concept is used here for the discussion of head evolution and trilobite relationships.

The acron as an example for concept-based approaches to head segmentation

In most of the literature on arthropod heads, the authors assume the existence of an acron as the anteriormost non-segmental body part (Siewing 1969; Rempel 1975; Cohen and Jürgens 1991; Scholtz 1997). According to this view, the acron contains the ancestral brain (archicerebrum, supraesophageal ganglion, cerebral ganglion) which is inherited from the bilaterian stem species and which can be found plesiomorphically in animal groups such as Platyhelminthes, Nematoda, Mollusca, and Annelida (Siewing 1969; Lauterbach 1973). However, the existence of an acron has never been directly shown but rather it is an inference based on the assumption of a close relationship between annelids and arthropods, the Articulata hypothesis (Scholtz 2002). In the scenario based on this assumption,

the acron is homologized with the episphere of the trochophore larva and the prostomium of adult annelid worms (Fig. 1) (Nielsen 2001). The episphere is the region bearing the larval brain and the apical organ and lies anterior to the mouth. Its posterior boundary is marked by the first ciliary ring, the prototroch, of the trochophore (Fig. 1). As the episphere/prostomium contains only little (if any) mesoderm without coelomic sacs and nephridia, and as it is not formed by the ectodermal/mesodermal growth zone but derives from the micromeres (see Ackermann et al. 2005), it is considered to be asegmental in nature (e.g., Siewing 1969; Nielsen 2001). During development, the episphere becomes the prostomium (Hatschek 1878; Woltereck 1905; Nielsen 2005a,b), which lies anterior to the mouth and which bears the annelid brain (cerebral ganglion) and eyes (if present), and in some polychaetes, appendage-like sensory structures such as the antennae and palps (Bartolomaeus et al. 2005). As arthropods do not possess locomotory cilia, there is no prototroch in larvae or embryos, and accordingly, an episphere is not directly definable by structural criteria (Fig. 1). Mostly, the fact that the anteriormost region of arthropod embryos bears the eyes and the anterior part of the brain and lies in front of the mouth is taken as evidence to homologize this structure with the annelid episphere/prostomium. However, the position of the mouth in arthropod embryos is a problem in itself as there is an obvious migration posteriorly (e.g. Ungerer and Wolff 2005). Accordingly, even a position of the putative acronal structures anterior to the mouth cannot be unambiguously determined.

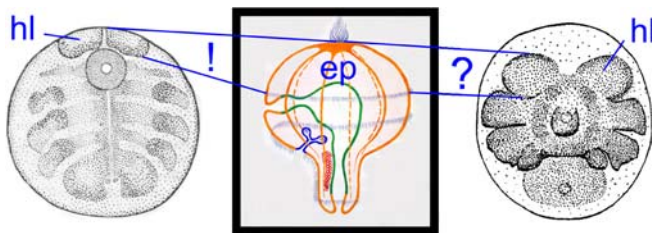


Fig. 1 The concept of the acron. *Middle*: a schematic representation (*lateral view*) of an annelid trochophore larva with the episphere (*ep*) as the anterior region in front the mouth and the first ciliary ring (prototroch). The *blue lines* indicate the suggested homology and transformation of the larval episphere (the prostomium in the adult worm) and the acron in arthropods according to the Articulata hypothesis. *Right*: a crustacean germ band (*ventral view*) with no direct evidence for a homologue of the episphere (?) (modified after Oishi 1959). The head lobes (*hl*) are interpreted as the acron which is the equivalent of the episphere/prostomium of annelids. *Left*: in polychaete worms (*ventral view*) with a more direct development, head lobes (*hl*) are formed similar to those of arthropods (modified after von Wistinghausen 1891). However, the homology to the episphere is beyond doubt (!) (see von Wistinghausen 1891; Seaver et al. 2005; Seaver and Kaneshige 2006). This shows that the interpretation of the arthropod head lobes and acron as equivalent to the episphere/prostomium might be appropriate and could be taken as additional evidence in favor of the Articulata hypothesis (Scholtz 2002, 2003)

The underlying concept of segmentation forms a bias for the interpretation of the head

If one accepts the Ecdysozoa hypothesis (Giribet 2003), the concept of an acron may no longer be necessary (see Budd 2002) and one can assume homonomous segments to have occurred from the anterior to the posterior region in the stem lineage of arthropods. We remain doubtful because the terminal regions in bilaterians are something special by bearing the mouth (not always) and the anus (if present), as well as by being terminal, i.e., many cells have no anterior or posterior neighbours. In addition, the anterior terminal region is characterized by the possession of a concentrated dorsal or preoral nerve plexus or brain (Fig. 2). These terminal regions including an anterior dorsal brain were present before segmentation evolved, e.g., in Platyhelminthes, Nematoda or Mollusca, but the transition to the trunk is not well defined. The difference between the unsegmented and segmented conditions is that, in the latter, there are developmental and morphological boundaries between the terminal regions and the adjacent segments (Fig. 2). Hence, only after segmentation had occurred did the anterior body region become morphologically distinct and separated from the subsequent segments. This is a meaningful assumption even if one believes in a segmented stem species of the Bilateria, often called “Urbilateria” (e.g., Prud’homme et al. 2003) because neither cnidarians nor ctenophores are segmented, and accordingly, segmentation must have evolved in the stem lineage leading to the crown group Bilateria. The evolutionary scenario of a specified terminal region before segmentation had evolved is reflected in the expression of the anterior homeobox genes of the orthodenticle (*otd/Otx*) group. Expression of *otd/Otx*-related genes has been described in various unsegmented and segmented bilaterians (e.g., Hirth et al. 1995; Li et al. 1996; Bruce and Shankland 1998; Tomsa and Langeland 1999; Umesono et al. 1999; Harada et al. 2000; Arendt et al. 2001; Nederbragt et al. 2002; Urbach and Technau 2003b). In all cases, the expression is related to the brain, and accordingly, it is found in the anterior region (but not in the extreme anterior area) of the animals studied. For instance, in the trochophore larvae of the mollusc, *Patella vulgata*, and the polychaete annelid, *Platynereis dumerilii*, *otd/Otx* is expressed in the posterior region of the episphere, in brain nerve cells, and in the mouth area (Arendt et al. 2001; Nederbragt et al. 2002). Likewise, in the leech, *Helobdella triserialis*, which lacks a trochophore larva, the expression is found in the prostomium, the cerebral ganglion, and the mouth region (Bruce and Shankland 1998). From several studies, it is obvious that the *otd/Otx* expression in hexapod arthropods is mainly found in the ocular/protocerebral region (but again not in the anteriormost area and not in the labrum), and to a minor extent, in the deutocerebral segment (Hirth et al. 1995; Li et al. 1996; Urbach and Technau 2003b). This similarity in the expression patterns between arthropods and other bilaterian taxa may be interpreted as an indication that the arthropod protocerebrum and the associated body unit corresponds to the anterior terminal

region of other Bilateria, and the boundary between the ocular/protocerebral region and the segment of the deutocerebrum corresponds to the posterior region of the ancestral bilaterian brain, supporting the views of Siewing (1969) and Lauterbach (1973) (Fig. 2). Consequently, this idea implies that the dorsal cerebral ganglion of arthropods is not a serial homologue of the ventral segmental ganglia. Taken together, these ontogenetic and phylogenetic aspects indicate the special conditions governing the anterior terminal region—and accordingly, a special term such as “acron” might be appropriate irrespective of the Articulata or Ecdysozoa perspectives of arthropod origins. Interestingly, in the segmented annelids and arthropods, this boundary seems to be established using a similar mechanism to the differentiation of undisputed segmental boundaries, namely, the action and interaction of segment polarity genes *engrailed* (*en*) and *wingless* (*wg*) (Schmidt-Ott and Technau 1992; Scholtz 1995; Prud’homme et al. 2003).

In summary on the one hand, the correspondence in the expression of *otd/Otx*, the dorsal brain and other peculiarities of the anterior region between arthropods and other bilaterians can be taken as evidence for an acron in arthropods, whereas, on the other hand, depending on the definition of a segment (Scholtz 2002; Seaver 2003; Minelli and Fusco 2004; Tautz 2004), it can be seen as the anteriormost (or an anterior) segment, the ocular segment

in arthropods (see Schmidt-Ott et al. 1994b; Rogers and Kaufman 1997). Hence, this terminal region is called an “acron,” mainly for phylogenetic reasons, and a “segment,” based on the fact that its posterior boundary is formed like that of segments in more posterior body regions (Rogers and Kaufman 1997). The latter approach reveals the problems of a reductionist view or definition of segmentation based on molecular gene expression alone because this neglects the structural characteristics of the various body regions. To avoid this ambiguity, we adhere to the term “ocular/protocerebral region” coined by Scholtz (1995).

Traditionally, the occurrence of sometimes only transitory coelomic sacs, appendages or their rudiments, ganglia and nerves, and nephridia and their derivatives, either in various combinations or alone, have been taken as evidence for segments or their vestigial appearance. Nowadays, we have, in addition, gene expression data for the specification of segments, and these new data should be seen in concert with the morphogenetic and morphological characteristics of segments (Scholtz 2002). According to the Articulata hypothesis, the whole set of segment characteristics was, more or less, present in the arthropod lineage right from the beginning. In the context of the Ecdysozoa hypothesis, this is not necessarily the case. Irrespective of this, it seems plausible that segmentation did not evolve as a whole complex at once but rather by a stepwise inclusion of characters repeated along the body axis (Scholtz 2003). Accordingly, the full complement of segmental components may never have been present in all metameric units. Furthermore, some metameric structures such as limbs might have undergone specialization before the full segmentation complex was achieved.

Given that the terminal body regions already showed some peculiarities before the evolutionary advent of segmentation, they are privileged for various specializations older than segmentation. This may be true for the following adjacent body parts as well. In other words, we probably pose the wrong questions when we assume that every unit in the head is derived from a complete former segment and that the segmental structures were alike in every respect. For instance, the anterior appendages such as antennae might have been derived from leg-like appendages before the hard segmented exoskeleton and the articulated arthropodia of euarthropods have evolved (see Minelli 2003). Furthermore, it is likely that the cerebral ganglion was a distinct structure before segmentation occurred in evolution. Accordingly, the brain was never a serial homologue of a segmental ganglion. The model of a strictly homonomous segmentation as the evolutionary starting point seems clearly wrong, and there is no example of an arthropod, be it Recent or fossil, crown group or stem lineage, showing homonomous segmentation throughout. The last but not the least, the interpretation of head structures is complicated by the problem that the embryonic anlage of a structure or character does not necessarily mean that the adult structure was present in the ancestor (Scholtz 2004, 2005).

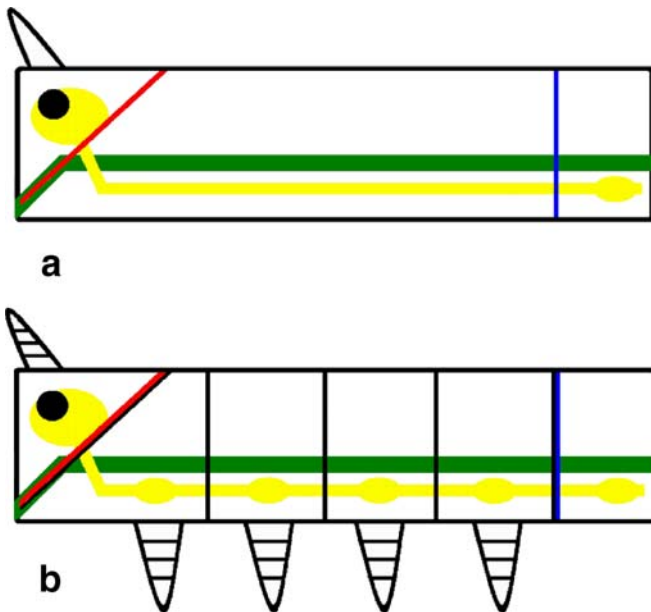


Fig. 2 Terminal regions were specific and differentiated before segmentation evolved. *Anterior to the left, yellow: CNS, green: digestive system.* **a** Depicts a hypothetical unsegmented bilaterian with specified and differentiated terminal regions. These terminal regions are characterized by specializations of the nervous system (dorsal brain, terminal ganglion), photoreceptor, sensory appendages, and gene expressions such as *otd/otx* in the anterior region (*red line*) and *caudal* (e.g. de Rosa et al. 2005) in the posterior region (*blue line*). **b** Shows a segmented bilaterian which evolved from an ancestor as shown in **a**. The segmentation overlies the ancestral differentiation of the terminal regions. The question arises whether the terminal regions and their characteristics are serially homologous to segments in the middle of the body

The current consensus: a tripartite anterior brain/head

The use of genetic markers, in particular, segment-polarity genes such as *en* and *wg*, led to a high resolution of head segmentation in the major part of the head. These data are available for a number of chelicerates, crustaceans, myriapods, and hexapods (Fleig 1994; Scholtz 1995; Rogers and Kaufman 1997; Telford and Thomas 1998; Damen 2002; Hughes and Kaufman 2002; Chipman et al. 2004; Janssen et al. 2004). Other segment polarity gene expression data such as *paxIII* and *hedgehog* (*hh*) are available for chelicerates, myriapods, hexapods, crustaceans, albeit to a lesser extent (Simonnet et al. 2004; Davis et al. 2005; Osborne and Dearden 2005). All these results point in the same direction. There is a tripartite anterior brain (comprising the protocerebrum, the deutocerebrum, and the tritocerebrum) and three anterior morphological units. For the Mandibulata these are: the ocular/protocerebral region, and the segments of the first and second antennae in crustaceans and the antennal and intercalary segments in myriapods and hexapods (Fig. 3). There is no corresponding cephalization at the external morphological level in the Chelicerata (see below). However, the close association of the tritocerebrum with anterior brain parts (Hanström 1928; Mittmann and Scholtz 2003; Harzsch et al. 2005b) shows that a tripartite brain is present as in

Mandibulata. In the latter group, the degree of fusion of the tritocerebrum to the more anterior brain regions varies, but in all cases, its status as a brain neuromere is evident (e.g., Hanström 1928; Harzsch 2004).

There is no indication for an additional preantennal segment between the ocular/protocerebral region and the antennal segment (see Heymons 1901; Siewing 1969; Lauterbach 1973). This pattern is consistent throughout the investigated species without exception. The only complication is the labral expression of some of these genes in some taxa (Schmidt-Ott and Technau 1992; Schmidt-Ott et al. 1994a; Urbach and Technau 2003b, see below). Posterior to the second antennae/intercalary segment, we find segment polarity gene stripes in the mandibular and the maxillary segments as in trunk segments. There is no indication of an additional segment between the mandibular and the second antennae/intercalary segments as postulated by Chaudonneret (1987). The question as to whether the ocular/protocerebral stripe indicates a true ocular segment or an acron seems not so important, rather, the neutral questions are whether this is the anteriormost body region which can be derived from the ancestral brain region of Bilateria and whether it represents only one unit or more than one (see above).

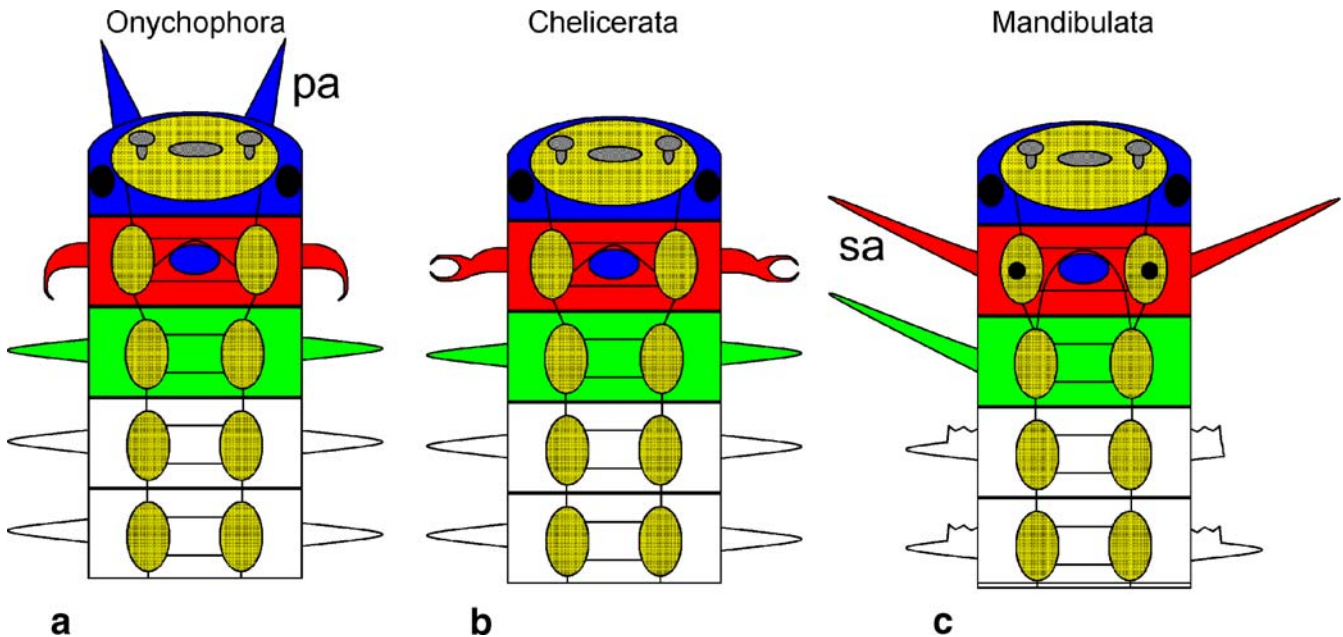


Fig. 3 Alignment of structures in the heads of Recent arthropods (see Fig. 6). **a** Onychophora with “primary antennae” (*pa*) in the ocular/protocerebral region (*blue*). **b** Chelicerata with chelicerae in the deutocerebral segment (*red*) **c** Mandibulata with “secondary antennae” (*sa*) in the deutocerebral segment (*red*). The *left side* shows the crustacean conditions with two pairs of antennae. The *right side* shows the situation in myriapods and hexapods with a limbless intercalary tritocerebral segment. The ocular/protocerebral region is shown in *blue*, the deutocerebral segment in *red*, the tritocerebral segment in *green*. The structures of the central nervous system are *shaded yellow with black connections*. The protocerebrum contains the mushroom bodies and the central body. In

Mandibulata, the deutocerebrum shows the olfactory lobe (*black spot*). The stomatogastric and labral nerves are depicted as a loop anterior to the mouth. In Onychophora and Chelicerata, they are connected to the deutocerebrum, in Mandibulata to the tritocerebrum. The mouth is depicted in *blue* to show its putative association with the ocular/protocerebral region. For the sake of segment alignment and a clearer picture, we generally put the tritocerebrum in a postoral position (the putative plesiomorphic condition as is found in Onychophora), although in most euarthropods, it occupies a preoral or paroral position. The *double line* in the Mandibulata marks the posterior margin of the head

The development of the labrum

A highly controversial head structure

The labrum always was (Weber 1952; Rempel 1975; Scholtz 1997, 2001) and still is the most controversial structure of the euarthropod head, and even the new molecular and morphological methods have not led to a conclusive answer about its nature. The interpretations of the labrum differ concerning its segmental affiliation ranging from the anteriormost segment via a preantennal segment to the tritocerebral/ intercalary segment and the question whether it represents a derived limb pair, a simple outgrowth (upper lip), a segment, or the anterior body terminus. Even the homology of the labrum among the Euarthropoda has been questioned (Walossek and Müller 1990). In the following, we describe the general characteristics of the labrum in terms of morphogenesis and gene expression.

Morphogenesis

The euarthropod labrum is formed at the anterior margin of the stomodaeum with or after the beginning of the stomodaeal invagination. In many representatives of chelicerates, myriapods, crustaceans, and hexapods the early anlage of the labrum is bilobed to different degrees (e.g., Brauer 1895; Scholl 1963, 1969; Dohle 1964; Ullmann 1964; Bruckmoser 1965; Pross 1966; Hertz 1984; Schoppmeier and Damen 2001; Simonnet et al. 2004; Abzhanov and Kaufman 2004; Ungerer and Wolff 2005) (see Fig. 4d). Even in pycnogonids with their extended proboscis, a transient bilobed labral anlage occurs which grows out to form the dorso-lateral part of the proboscis (Winter 1980). In all arthropods with an early bilobed labrum anlage, these two lobes fuse to form an unpaired outgrowth anterior to the mouth, later on. In contrast to this, there are also cases for a single undivided labrum anlage. Examples are some malacostracan and non-malacostracan crustaceans (Manton 1928; Benesch 1969; Olesen et al. 2001; Alwes and Scholtz 2006; Olesen 2004), hexapods (Rohrschneider 1968), myriapods (Heymons 1901; Tiegs 1940), and chelicerates (Scholl 1977; Thomas and Telford 1999).

As the investigations on the expression of the *Dll* gene show (see below), in cases such as the mite *Archegozetes longisetosus*, and the horseshoe crab *Limulus polyphemus*, there are two separate early gene expression areas which later fuse before the undivided labrum buds out (Thomas and Telford 1999; Mittmann and Scholtz 2001). Furthermore, ablation experiments conducted by Haget (1955) in the coleopteran *Leptinotarsa decemlineata*, reveal that even in this species with an undivided labral lobe, this lobe originates from two independent anlagen (Haget 1955), results which were confirmed by Wada (1965) in the grasshopper *Tachycines asymamorus*. The mesoderm of the labrum is always formed by a pair of cell masses irrespective of whether the labral bud is bilobed (Ullmann 1964) or undivided (Heymons 1901; Tiegs 1940;

Rohrschneider 1968). All this suggests that in general the labral bud derives from two separated anlagen. Accordingly, Scholtz (1997) suggested that a bilobed labrum anlage might be a euarthropod apomorphy.

The mesoderm of the labral region of euarthropods forms the labral, pharyngeal, and stomodaeal musculature, and sometimes, the anterior aorta (Scholl 1963, 1969, 1977; Dohle 1964; Benesch 1969; Siewing 1969; Anderson 1973; de Velasco et al. 2006). Sometimes a pair of transient coelomic cavities is formed (e.g., Tiegs 1940; Ullmann 1964; Rohrschneider 1968; Siewing 1969), but in most cases, the mesodermal masses stay compact (Scholl 1963, 1969; de Velasco et al. 2006). The mesoderm is sometimes restricted to the labrum itself, but there are also examples of a large mesoderm area that just shows processes (coelomic or massive) reaching into the labrum (Scholl 1963, 1969, 1977; Pross 1966; Rohrschneider 1968; Siewing 1969).

Gene expression

Data are available for the expression of two classes of genes in the labrum, appendage gap genes, namely, *Distal-less* (*Dll*), *dachshund* (*dac*), and *extradenticle* (*exd*) and segment polarity genes, *engrailed* (*en*) and *wingless* (*wg*). The most conspicuous gene expression in the labrum is that of *Dll*, which is found in all chelicerates (Popadic et al. 1998; Thomas and Telford 1999; Mittmann and Scholtz 2001; Schoppmeier and Damen 2001), myriapods (Scholtz et al. 1998; Prpic and Tautz 2003), crustaceans (e.g., Panganiban et al. 1995; Scholtz et al. 1998; Shiga et al. 2002; Olesen et al. 2001; Abzhanov and Kaufman 2004; Browne et al. 2005), and hexapods investigated, in this respect (e.g. Panganiban et al. 1995; Niwa et al. 1997; Scholtz et al. 1998; Prpic et al. 2001; Rogers and Kaufman 1997). Throughout euarthropods the overall pattern of *Dll* in the labrum resembles that of arthropod limbs: it is expressed in the distal area, and it is always present before the morphological buds are visible. As mentioned above, in some cases, it is found in two separate expression sites. *dac* is the second limb-related gene for which expression has been studied in the early labrum of some arthropod embryos. In hexapods, myriapods, and chelicerates, it is expressed in the anterior portion of the labral bud describing a half circle (Prpic et al. 2001, 2003; Prpic and Tautz 2003; Urbach and Technau 2003a). Unfortunately, the figures in Abzhanov and Kaufman (2000a) do not reveal whether a crustacean has a labral *dac* expression comparable to that of other arthropods. The third gene in this context is *exd*, though we lack sufficient data for a broader comparison. In the grasshopper *Schistocerca americana*, *exd* is expressed in the basal two-thirds of the labrum in a pattern comparable to that in the antennae and legs (Dong and Friedrich 2005).

The widely studied segment polarity gene, *en*, is not expressed in the labrum of the crustaceans and myriapods studied so far (Patel et al. 1989; Scholtz et al. 1994; Scholtz 1995; Manzanares et al. 1996; Abzhanov and Kaufman 2000b; Browne et al. 2005; Janssen et al. 2004; Damen

2002; Hughes and Kaufman 2002; Chipman et al. 2004). Furthermore, *en* expression has not been found in most hexapods studied, such as representatives of Coleoptera, Diptera, Siphonaptera, Orthoptera, Hemiptera, Hymenoptera, Zygentoma (Patel et al. 1989; Fleig 1990, 1994; Brown et al. 1994; Schmidt-Ott et al. 1994b; Rogers and Kaufman 1997; Peterson et al. 1998). It is also not expressed in the chelicerate mite, *A. longisetosus* (Telford and Thomas 1998). The notable exceptions among hexapods are some Diptera including *Drosophila melanogaster* (Schmidt-Ott and Technau 1992; Schmidt-Ott et al. 1994a), the beetle *Tenebrio molitor* (Urbach et al. 2003) and the grasshopper *Schistocerca gregaria* (Boyan et al. 2002). Expression of *en* is also found in the anterior region of the labrum of the spider *Cupiennius salei* among the Chelicerata (Damen 2002). The interpretation of the *en* expression in the labrum of the hexapods is ambiguous. In *Drosophila*, there is an unpaired *en* expression on the ventral side and a paired expression at the dorsal margin (dorsal hemisphere) of the labrum (Schmidt-Ott and Technau 1992). However, whereas Schmidt-Ott and Technau (1992) and Urbach and Technau (2003a) interpret the ventral *en* expression as belonging to the foregut, and the dorsal expression as a marker of a labral segment, other authors take the ventral expression to be an indication of a labral segment (Cohen and Jürgens 1991). Similarly, Boyan et al. (2002) use the posterior labral expression in *Schistocerca* to prove that the labrum is an appendage of the intercalary segment. The anterior *en* expression in the labrum of *Tenebrio* is transient and restricted to early stages of labrum and stomodaeum formation (Urbach et al. 2003). The labral expression of *wg* has been studied in chelicerate, myriapod, hexapod, and crustacean representatives (Schmidt-Ott and Technau 1992; Nulsen and Nagy 1999; Damen 2002; Hughes and Kaufman 2002; Prpic et al. 2003; Janssen et al. 2004; Jockusch and Ober 2004; Dong and Friedrich 2005). In all instances, *wg* is found as a pair of expression domains at the lateral side of the labral buds.

The nature of the labrum?

The discussion about the nature of the labrum can be conducted from three perspectives. First, are the structures called a labrum homologous throughout euarthropods, at least the embryonic or larval anlagen? Second, is the labrum derived from a pair of appendages or is it a different structure? Third, what segmental affiliation does the labrum have?

Is the labrum homologous within Euarthropoda?

Several similarities with respect to labral development are shared by Euarthropoda. First of all is the close spatial and temporal association between the formation of the labrum and the stomodaeum. The labrum is always formed at the

anterior boundary of the stomodaeum and median to the central nervous system. Moreover, to our knowledge, there is no exception from the fact that the labrum is formed with or after the beginning of the stomodaeal invagination. Second, the labrum is formed by two anlagen (ectoderm and mesoderm), which earlier or later, fuse to form an undivided lobe. Third, the labral nerves form a complex with the stomatogastric nervous system (e.g., Hanström 1928; Younossi-Hartenstein et al. 1997; Harzsch and Glötzner 2002; Mittmann and Scholtz 2003). Fourth, the expression patterns of the leg gap genes and segmentation genes are largely similar in their spatial arrangement in relation to labrum morphogenesis throughout the euarthropod representatives studied. This concerns, at least, the expression patterns of *wg*, *dll*, and *dac* in the labral buds of myriapods, chelicerates, crustaceans, and hexapods. In summary, the similarities at the morphogenetic and the gene expression levels suggest that the labrum in all Euarthropoda is homologous. This relates, at least, to the embryonic structures. However, as homologous anlagen do not necessarily lead to homologous adult structures (for discussion see Scholtz 2005), it might be that labral structures of adult arthropods cannot be generally homologized. To clarify this, a comparative analysis of the adult structures called a labrum among euarthropods is needed.

Walossek and Müller (1990) (see also Waloszek 2003) redefined the labrum as the fleshy outgrowth equipped with glands present only in Crustacea. Accordingly, the suggestion was made to confine the term labrum exclusively to the structure found in Crustacea. With this usage, the labrum is formed behind a forehead sclerotization called a hypostome that is generally present in euarthropods. Such a hypostome can be identified in fossil arthropods (e.g., trilobites and other trilobitiforms, and the Cambrian “Orsten” stem lineage crustaceans/mandibulates) and is present in Early Cambrian taxa such as *Fuxianhuia* and *Chengjiangocaris* that are identified as stem lineage euarthropods (Hou and Bergström 1997; Waloszek et al. 2005). The evolution of the hypostome has been linked to the posterior recurvature of the mouth in the arthropod stem lineage (Dewel et al. 1999), with the mouth opening at the rear margin of the hypostome. This position of the mouth is well documented in the three-dimensionally preserved “Orsten” fossils (Walossek and Müller 1990; Stein et al. 2005). However, this need not necessarily be true for all fossil structures called a hypostome, and the homology of the hypostome in various fossils has not been tested by careful comparative analyses (see, e.g., Bergström and Hou 2005 for differences between the “hypostome” in agnostids and that of trilobites). Moreover, the term labrum has been traditionally used for the process anterior to the mouth opening in basically all anatomical and embryological literature. For the sake of clarity and in light of the putative homology of (at least embryonic) labral structures throughout euarthropods, we adhere to this use of the term labrum.

Is the labrum a fused pair of limbs?

The arguments in favor of an appendicular labrum

Even if one accepts the homology of the labrum among euarthropods, this is not automatically a clear evidence in favor of its limb nature. Several lines of evidence suggest that the labrum might be a derived pair of appendages. For example, it has a bilobed origin and is equipped with mesoderm which resembles the formation of appendages in the trunk (e.g. Siewing 1969; Lauterbach 1973; Rempel 1975). Furthermore, Boyan et al. (2002, 2003) claim that the pattern of nerve cells in the labrum of a grasshopper shows some correspondence to that in limbs and conclude that this supports the idea of the labrum being appendicular in nature. Haas et al. (2001b) discuss the interesting case of a seemingly homeotic transformation of the labrum in *Tribolium*. Here, the labrum is replaced by structures that resemble mandibles in several respects. From this, the authors conclude that the labrum represents the coxal portion of a limb. The strongest support, so far, for the limb nature of the labrum comes from gene expression patterns. This suggestion is mainly based on the patterns of *Dll*, *dac*, *exd*, *wg*, and *en* expression which show some resemblances to corresponding patterns in trunk limbs (see above). We need to ask whether this evidence really provides us with unambiguous support for the hypothesis that the labrum is derived from a pair of appendages.

Arguments disputing the limb nature of the labrum

The fact that the labrum is formed by two independent anlagen is not a convincing argument for the limb nature. Other paired structures that resemble early limb buds have been shown to have nothing to do with true limbs, i.e., paired segmental appendages. Examples are the paragnaths found in several crustaceans (Waloszek 2003; Wolff 2004), the paired lateral horns of the nauplius larvae of barnacles (which, e.g., Darwin 1854 interpreted as second antennae), and some of the paired terminal structures such as the furca and the anal valves in crustaceans, hexapods, and myriapods. Furthermore, the labrum is formed and situated between the central nervous system (CNS), whereas, limb buds have their origin lateral to the CNS. The correspondence of the patterns of nerve cells in the labrum and appendages (Boyan et al. 2002, 2003) is not very complex; basically, only a two-branched arrangement of a number of nerve cell clusters.

The expressions of the *dll*, *dac*, *exd*, *wg*, and *en* genes do not show the patterns which are characteristic for limbs. For instance, the *dac* expression is unlike that of the limbs, in that, it does not describe a full circle around the bud. The segment polarity genes, if expressed at all, show an inverted pattern, i.e., *wg* is expressed posterior to *en* (Schmidt-Ott and Technau 1992). As the mouth and labral region undergoes a migration towards the posterior, these expressions stem perhaps from different segmental rudiments, e.g., the *wg* expression from the antennal segment

and *en* from the ocular region. As *en*, *wg*, and *hh* are also expressed in the foregut of insects, the expression in the labrum might not be segmental at all but related to the origin of the labrum from the anterior stomodeal region (Inoue et al. 2002). In addition, the segment polarity genes are expressed in segmental structures in general, i.e., even an outgrowth of a sternite expresses *en* and *wg*. Accordingly, this does not indicate the limb character of a given morphological structure. Moreover, *Dll*, *wg*, and *en* are also expressed in other paired structures, most notably, terminal structures such as anal valves of myriapods, the furca in crustaceans or the posterior terminus of the chelicerate germ band (e.g., Peterson et al. 1998; Scholtz et al. 1998; Nulsen and Nagy 1999; Mittmann and Scholtz 2001; Schoppmeier and Damen 2001; Damen 2002; Shiga et al. 2002; Rogers et al. 2002).

Homeotic changes and the ectopic expression of structures, in this case, the formation of mandible-like structures in the labral area (Haas et al. 2001a,b), have to be interpreted with caution. Already, Bateson (1894) described a case of a lobster in which the eye of one side was replaced by a first antenna, but this example does not mean that the first antenna and the eye are homologous. Correspondingly, the impressive experiments by Gehring (2004) on ectopically expressed eyes in *Drosophila* do not indicate that, e.g., the margin of a wing or the tip of an antenna is homologous with an eye. Interestingly, Haas et al. (2001b) interpret their homeotic data in *Tribolium* as evidence for the labrum representing basal limb structures, whereas, Schoppmeier and Damen (2001), based on their RNAi experiments in the spider, *Cupiennius*, and Prpic et al. (2001), based on *dac* expression in *Tribolium*, came to the conclusion that the labrum can be only the distalmost limb part. Two aspects of homeotic changes speak against the limb character of the labrum. One is the fact that the labrum of adult *Drosophila* is not affected by ectopic *Antennapedia*, as are the other appendages, which are transformed toward thoracic legs (Schneuwly et al. 1987). The other is the ectopic expression of *Ultrabithorax (Ubx)* in *Drosophila*, which leads to the formation of abdominal structures in every head segment including the ocular region but not in the labrum (Rogers and Kaufman 1997).

In general, however, it is important to stress that differences in the corresponding patterns in limbs do not directly exclude the possibility of homology. Homology is not disproven if there is only a low degree of similarity, but the plausibility in favor of homology is low (Scholtz 2005). For instance, the absence of *Dll* expression in the mandibles of hexapods (e.g., Popadic et al. 1998; Scholtz et al. 1998) does not lead to doubts about the limb nature of the mandibles. This is also evident when one takes into account the great differences in the gene expression patterns between undisputedly homologous limbs (Angelini and Kaufman 2005). However, there has to be a distinct degree of similarity either of the developmental or the adult pattern. Homology can only be convincingly claimed based on a complex similarity.

In summary, it is questionable whether there is enough evidence to claim homology between the labrum and a pair

of limbs. All characteristics used in favor of the limb hypothesis are not really convincing as they are found in other non-appendiculate structures as well or they are not very complex. For instance, the close spatial and developmental association between the labrum and the stomodaeum could offer an alternative explanation for the involvement of the mentioned genes in labrum formation. The ancestry of the mouth region could be the reason that segmental mutants show only little effect on the labral region. More data are needed to reveal putative complex similarities between the labrum and appendages sensu stricto. One candidate is the gene, *decapentaplegic (dpp)*, which is known to play a major role in limb bud formation in concert with *wg* and *Dll* (Cohen 1993). There are some promising data, but all are restricted to hexapods and not specifically interpreted with respect to the labrum problem (Sanchez-Salazar et al. 1996; Friedrich and Benzer 2000; Giorgianni and Patel 2004; Jockusch and Ober 2004; Yamamoto et al. 2004). However, if the labrum should be derived from an appendage which was already specialized before segmentation evolved, we might never resolve the problem convincingly. Perhaps one should consider studying the ontogeny and gene expression of the onychophoran “antennae” in comparison to the labrum. As we will see below, these might be a corresponding structure with a shared common ancestral appendage.

What is the segmental affiliation of the labrum?

The labrum is not the pair of limbs of the tritocerebral/intercalary segment

The data presented by Haas et al. (2001a,b) and Boyan et al. (2002) in favor of an intercalary segmental origin of the labrum are not really substantiated. All evidence is based on the nervous connection between the labrum and the tritocerebrum as had already been argued by Butt (1960). More recently, de Velasco et al. (2006) interpret the partial derivation of the esophageal musculature from the intercalary segment as additional evidence for the interpretation of the labrum as appendages of the intercalary segment. In contrast to this view, a number of direct and comparative data suggest that the labrum may not be the appendage of the intercalary segment. It is apparent from all classical embryological studies that the labral mesoderm stems from regions anterior to the intercalary/tritocerebral segment (e.g., Tiegs 1940; Ullmann 1964; Rohrschneider 1968; Siewing 1969). Haget (1955) shows that the cells giving rise to the labrum have their origin from the anterior margin of the head lobes far in front of the intercalary/tritocerebral region. Recent scanning electron microscope (SEM) studies clearly reveal an origin of the labrum far more anterior to the tritocerebral segment (Ungerer and Wolff 2005). *Drosophila* embryos mutant for *empty spiracles (ems)* and *buttonhead (btd)* reveal that even the absence of the intercalary segment and the tritocerebrum does not affect the labrum (Schmidt-Ott et al. 1994b; Younoussi-Hartenstein et al. 1997). The only problem for the labral

nerves is that they find no target in the brain (Younoussi-Hartenstein et al. 1997). In addition, the *headless/hunchback (hb)* mutant of the wasp, *Nasonia vitripennis*, lacks all head and thoracic segments. Nevertheless, the labral structures are present (Pultz et al. 1999, 2005). The stomatogastric and labral nerves in Chelicerata are mainly connected to the deutocerebrum, i.e., the pattern with a tritocerebral labral innervation in the Mandibulata is derived and cannot indicate the origin of the labrum from the tritocerebrum (Mittmann and Scholtz 2003; Harzsch et al. 2005b; Scholtz and Edgecombe 2005). Moreover, Chelicerata and Crustacea possess a labrum and an appendage in the corresponding tritocerebral segment (pedipalp, second antenna), and in some hexapod embryos, transitory limb buds occur in the intercalary segment (e.g., Tamarelle 1984). Even if one argues that the labrum comprises only the endites of coxal or basal elements (Haas et al. 2001a,b; Boyan et al. 2002, 2003), this contradiction is not resolved. Both the second antennae of Crustacea and the pedipalps of chelicerates show strong endites (at least during the larval stages).

The labrum is not the appendage of the preantennal segment

The labrum as the appendage of a preantennal segment situated between the ocular region and the antennal segment (see Siewing 1969; Lauterbach 1973; Rempel 1975; Cohen and Jürgens 1991) is also unlikely, as based on segmental gene expression data, there is no indication for an additional segment between the eyes and the antennae (or chelicerae) (see above, Hirth et al. 1995; Scholtz 2001; Damen 2002). This is also evident from studies of *Drosophila* embryos mutant for the head gap gene, *ems* (Schmidt-Ott et al. 1994b). In these mutants, the ocular, antennal, and intercalary regions are reduced or absent. If there were an additional preantennal segment between the ocular region and the antennal segment, one would expect that the labrum is also deleted, which is not the case.

The labrum as part of the ocular/protocerebral region or as an independent anterior morphological structure

If these two segmental affinities of the labrum can be ruled out, only two possibilities are left. One is that the labrum is an independent morphological unit or segment anterior to the eye region (Wada 1965; Schmidt-Ott and Technau 1992; Urbach and Technau 2003a), the other is that it is part of the ocular/protocerebral region. Both possibilities allow that the labrum and the mouth occupy the anteriormost position of the body, and there are several indications that this is the case. One is the observation of the early anterior anlage and the posterior migration of labrum and mouth (e.g., Ungerer and Wolff 2005) and the experiments by Haget (1955) and Wada (1965). Furthermore, as mentioned above, the gene *otd/Otx* is not expressed in the anteriormost

body and brain region, including the labrum (Hirth et al. 1995; Li et al. 1996). Functional analyses of head gap genes by using mutants and RNAi experiments in *Drosophila*, *Tribolium*, and *Nasonia* indicate that the labrum occupies an anterior position in the head (Schmidt-Ott et al. 1994b; Pultz et al. 1999, 2005; Schröder 2003). In these cases, at least the ocular region and the antennal segment (in *ems* mutants also the intercalary segments) are suppressed but not the labrum.

Interestingly, Schmidt-Ott et al. (1994b) found that there are genes which obviously delete or reduce the labral and mouth area alone; this concerns genes that are expressed at the anterior pole of the embryo such as *torso* and *huckebein*. All this together leaves almost no doubt about the anterior position of the labrum, but it does not automatically mean that it represents its own segment as has been suggested by Schmidt Ott and Technau (1992), Schmidt-Ott et al. (1994b), Urbach and Technau (2003a) or perhaps the acron as discussed by Scholtz (2001). The lack of a proper *en* expression in the labrum of most euarthropods speaks against its segmental status. Furthermore, if *en* is expressed in the labral region as in *Drosophila* and *Cupiennius*, it is not clearly related to the posterior portion and the expression appears only after the morphogenetic appearance of the labrum; both characteristics are not found in any segment (see Scholtz 1995 for discussion). Likewise, the idea that the labrum represents the acron is problematic given the above discussed expression of *otd/Otx* genes in various Metazoa including arthropods which, instead, supports the hypothesis that the posterior boundary of the ocular region corresponds to the posterior boundary of the ancestral bilaterian brain and the terminal region. In contrast, the labrum does not contain a brain of any sort.

Interestingly, Urbach and Technau (2003a) adopt the classical subdivision of the protocerebrum into the archicerebrum (comprising the optical lobes and the mushroom bodies) and the prosocerebrum (comprising the central complex) (see Siewing 1969). Siewing (1969) interpreted the archicerebrum as the anteriormost brain part belonging to the acron and the prosocerebrum as the neuromere of the preantennal segment, which also bears the labrum (see above). In contrast to this view, Urbach and Technau (2003a) claim that the prosocerebrum and the labrum represent the anteriormost region. However, Hirth et al. (1995) showed that *otd* is required for the development of the protocerebral bridge, an important element of the central complex. Based on his meticulous teratological studies in *Tachycines*, Wada (1965) suggests that the optical lobes, the corpora pedunculata, and the central body form a morphological unit. These contradictions can best be resolved by the assumption of one large anteriormost body unit comprising all elements of the protocerebrum and the labrum—the ocular/protocerebral region.

In summary, it seems highly plausible that the labrum, in connection to the stomodaeum, occupies the anteriormost region of the body of arthropods. Furthermore, it seems

sensible to interpret the labrum as part of the first body unit comprising the protocerebrum with the eyes. The problem whether the labrum is the highly derived pair of limbs associated with this ocular/protocerebral region needs further clarification.

The chelicerate problem

The traditional text book view that the cheliceral segment in Chelicerata corresponds to the second antennal/intercalary segment of mandibulates was challenged by expression data of *Hox* genes and segment polarity genes (Damen et al. 1998; Telford and Thomas 1998). If the anterior boundary of a series of *Hox* genes is aligned with the anterior boundaries of the corresponding genes in Mandibulata, then the cheliceral segment aligns with the first antennal segment of crustaceans, the antennal segment of myriapods and hexapods. Moreover, *en* expression reveals that the ocular stripe, if present, lies directly anterior to the cheliceral expression (Damen 2002). The conclusions drawn from these results have been confirmed by neurogenetic data which show that the anlagen of the cheliceral and pedipalpal neuromeres are in the same position on the circumesophageal ring as the ganglia of the (first) antennae and second antennae/intercalary segments in mandibulates (Mittmann and Scholtz 2003) (Fig. 3). As well, the expression data of several neurotransmitters are in accordance with this view (Harzsch et al. 2005b). The post-cheliceral appendages accordingly align with the arachnid pedipalps being positionally equivalent to the second antennae/intercalary segment and the first three pairs of walking legs in arachnids being equivalent to the mandible, first and second maxillae, respectively, in mandibulates (Fig. 3).

The idea that the chelicerae are deutocerebral in all Chelicerata (s.l.) has not been universally accepted. In a recent paper on the brain in Pycnogonida, Maxmen et al. (2005) interpreted the chelifores of the nymphon larvae of *Anoplodactylus* sp. to be innervated by two lobes at the posterior margin of the protocerebrum, the anteriormost brain part. Accordingly, the authors suggest that the chelifores of Pycnogonida originate from the protocerebral segment, and are thus not homologous to the chelicerae of the Euchelicerata (Xiphosura and Arachnida). This is difficult to accept, in particular, based on the data presented from only one larval stage. Embryological studies on pycnogonids report a separate origin of the cheliforal neuromere in earlier stages (Meisenheimer 1902; Winter 1980). The deutocerebrum in other chelicerates, which innervates the chelicerae, is also relatively small and very closely attached to the protocerebrum (Babu 1965). Moreover, the anterior expression boundaries of the *Hox* genes *labial*, *proboscipedia*, and *deformed* in pycnogonids exactly match those in other chelicerates (Jager et al. 2006). In addition, structural resemblances support homology of chelifores and chelicerae (Dunlop and Arango 2004; Vilpoux and Waloszek 2003).

Table 1 This table summarises the different views of various authors about the alignment of fossil arthropod heads

	Budd 2002		Cotton and Braddy 2004		Chen et al. 2004; Waloszek et al. 2005		Scholtz and Edgecombe 2005/here	
	Euarthropod stem lineage	Euarthropod crown group	Euarthropod stem lineage	Chelicerate crown group	Euarthropod stem lineage	Euarthropod crown group	Euarthropod stem lineage	Euarthropod crown group
Protocerebrum	Frontal (“great”) appendage	Labrum	X	X	X	“Primary antenna” or transformation of “primary antenna”	“Primary antenna”	One or several losses or transformation of “primary antenna”
Deutocerebrum	Antenna (acquired in upper part of stem lineage)	Antenna	Antenna	X	Limb-like antenna	Antenna (modified to megacheiran great appendage/chelicera in chelicerate stem lineage)	Feeding great appendage (modified to chelicera in chelicerate stem lineage and to “secondary antenna” in mandibulate stem lineage)	Feeding great appendage (modified to chelicera in chelicerate stem lineage and to “secondary antenna” in mandibulate stem lineage)
Tritocerebrum	Trunk like limb	Trunk like limb	Megacheiran great appendage	Chelicera	Trunk like limb	Trunk like limb	Trunk like limb	Trunk like limb

Onychophora

Onychophora are together with the Tardigrada close relatives of the Euarthropoda. Depending on the position of the Tardigrada, Onychophora are either alone or together with Tardigrada, the sister group of the Euarthropoda, or the sister group to Tardigrada plus Euarthropoda (Dewel et al. 1999; Budd 2001; Giribet et al. 2001; Maas and Waloszek 2001; Nielsen 2001). As the heads of Tardigrada are difficult to analyze and need more investigations to gain a conclusive picture, we concentrate our discussion on the Onychophora. The organization of the onychophoran head has long been interpreted quite controversially. Attempts by Hanström (1928), Pflugfelder (1948), Manton (1949), and Butt (1960) led to very different results concerning segment number and arrangement and the relationship to euarthropod head segmentation. Recent studies by Eriksson and Budd (2000), Eriksson et al. (2003), and Mayer and Koch (2005) clarified some issues. From these studies, it is evident that the so-called antennae of onychophorans are formed and situated anterior to the eyes. Eyes and antennae are both parts of the anteriormost metameric unit. Based on the close association with a transitory nephridial structure, Mayer and Koch (2005) homologize the antennae with the onychophoran trunk limbs. Furthermore, Mayer and Koch (2005) suggest that the antennal ocular region corresponds to a true anteriormost segment and does not represent or include an acron. In contrast to this, the equipment of the anteriormost region with an annelid-like mushroom body connected to the antennae might indicate the prostomium-like nature of this body part (Scholtz and Edgecombe 2005). In any event, apart from these different interpretations (see above), and despite the lack of data of anterior *Hox* gene expression, the alignment of onychophoran head segments with those of euarthropods is most convincingly as depicted in Fig. 3.

“Primary” and “secondary antennae”

The alignment of the onychophoran and the euarthropod heads reveals that the so-called “antennae” of onychophorans are not homologous with those of the mandibulate taxa, namely, myriapods, crustaceans, and hexapods (Fig. 3) (Eriksson and Budd 2000; Scholtz and Edgecombe 2005; Mayer and Koch 2005). Onychophoran antennae are appendages of the anteriormost body unit comprising the eyes and the brain. Thus, these antennae are associated with the protocerebrum. In contrast, the antennae of myriapods, crustaceans, and hexapods are the limbs of the second brain part, the deutocerebrum. Based on this, Scholtz and Edgecombe (2005) developed the concept of “primary” and “secondary antennae.” The “primary antennae” are the original head sensory organs of the arthropods. These “primary antennae” are lost in the extant/crown group Euarthropoda. It is not clear whether this loss happened once or several times independently. The “primary antennae” are functionally replaced by the “secondary

antennae” of the mandibulate groups, which are connected to the deutocerebrum.

According to this view, the plesiomorphic condition for euarthropods is a mouthpart associated with the deutocerebral segment as is seen in Onychophora and Chelicerata. Of course, this does not necessarily mean that the euarthropod stem species possessed a chelicera. In any case, this deutocerebral mouthpart is apomorphically transformed into a sensory “secondary” antennal structure in the mandibulate lineage (Table 1, Fig. 3).

What happened to the “primary antennae?”

There are three possibilities for the fate of the “primary antennae” in Euarthropoda. One is a total loss without any traces left. Of course a loss cannot be directly proven. However, there are clear cases among arthropods where sensory antennae were reduced or entirely lost (see Scholtz and Edgecombe 2005). The most interesting case is the Protura among the Hexapoda. The loss of antennae led to a forward shift of the first pair of thoracic limbs which became sensory antenna-like structures (Fig. 4) and a fusion of the first thoracic ganglia with the subesophageal ganglion mass (François 1969; Janetschek 1970), a process that has to be considered as a neuronal cephalization.

The second is that the frontal filaments found in some Crustacea and similar structures such as the little protrusions in the fossil pycnogonid larva described by Waloszek and Dunlop (2002) are vestigial primary antennae. The frontal filaments are enigmatic sensory structures anteriorly on the head of Remipedia and Cirripedia larvae. Their outer appearance is very much limb-like, including articulation. This led Darwin (1854), for instance, to interpret them as the first antennae in his Cirripedia monograph. Moreover,

the nerves of the frontal filaments are clearly connected to the median region of the protocerebrum in Remipedia (Fanenbruck and Harzsch 2005) and Cirripedia (Semmler 2005) (Fig. 4).

The third possibility is that the euarthropod labrum might represent transformed primary antennae (Fig. 4) (see also Budd 2002; Eriksson et al. 2003, see below). This implies that the labrum is, in fact, a highly modified pair of appendages and not another structure such as a segment or an outgrowth of the anterior stomodeal area. This idea faces the problem that there is no real structural correspondence between the “primary antennae” of onychophorans or fossils or the “great appendages” and the labrum. Nevertheless, the idea of the labrum as the transformation product of primary antennae is a testable hypothesis. On the one hand, one would expect that the “antennae” of Onychophora are formed in the area anterior to the *otd/Otx* domain. On the other hand, if peculiarities of gene expression in the labrum, which are absent in trunk limbs of euarthropods, find their correspondence in that of onychophoran “antennae,” we could have direct evidence for homology between these two structures.

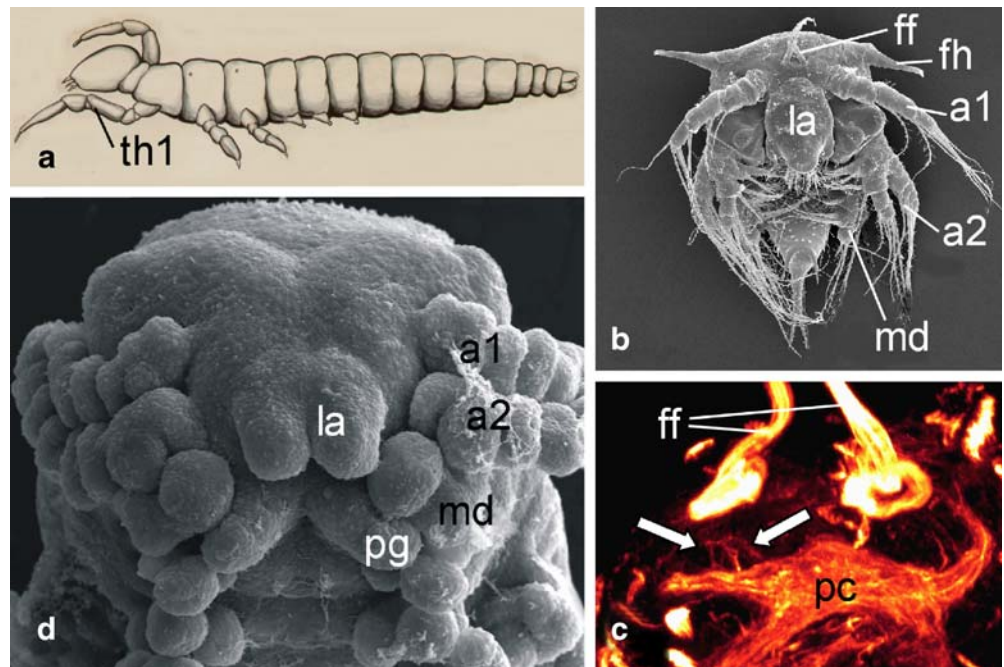
Possibilities one and three allow the assumption of a single loss in the stem lineage of crown group euarthropods, whereas, possibility two implies several independent losses of the “primary antennae.”

Fossil arthropod heads

“Primary” and “secondary antennae” in fossils

Numerous fossil arthropods from the Cambrian have preserved anterior structures that allow for inferences on head segmentation. We find a variety of appendages

Fig. 4 The putative fate of “primary antennae.” **a** Entire loss exemplified by a proturan (*Eosentomon* sp.) showing the loss of hexapod antennae, which are functionally replaced by the first thoracic appendages (th1). **b, c** Frontal filaments in the nauplius larvae of cirripedes (photographs by Henrike Semmler). **b** SEM image of a stage 3 nauplius of *Balanus improvisus* revealing the limb-like appearance of the frontal filaments (ff). **c** The brain region of a nauplius larva of *B. improvisus* stained with the anti α -tubulin antibody. The frontal filaments (ff) are connected to the median protocerebrum (pc) via several nerve fibers (arrows). **d** SEM image of the head of the embryo of the amphipod crustacean *Orchestia cavimana* with bilobed labrum anlagen (la) (modified after Ungerer and Wolff 2005). a1 First antennae, a2 second antennae, fh frontal horns, la labrum, md mandibles, pg paragnaths



associated with the head and head shields covering different numbers of head segments. The most intriguing of these head appendages are the antennae and the so-called “great appendage” with putative raptorial or more general feeding function. Some of these antennae are attached near the anterior margin of the head, whereas, others are situated in a more ventral position lateral to the hypostome. Scholtz and Edgecombe (2005) take this as evidence for a discrimination of “primary antennae” (attached near the frontal margin) and “secondary antennae” (situated lateral to the hypostome). Interestingly, “primary antennae” are sometimes combined with a second pair of raptorial limbs/great appendages, whereas, “secondary antennae” are never associated with a great appendage (Fig. 5). The great appendage is interpreted as the limbs of the deutocerebral segment, i.e., they correspond to the chelicerae of Chelicerata and the first antennae of the Mandibulata (Fig. 5). The positional correspondence between “short” great appendages [those in the group Megacheira (Hou and Bergström 1997), best known from *Yohoia*, *Jiangfengia*, *Leanchoilia*, and *Alalcomenaeus*] and chelicerae is enhanced by structural similarities in the appendages themselves, which share a basal peduncle and a spine-bearing claw (Chen et al. 2004; Cotton and Braddy 2004).

Controversies about the interpretation of fossil heads

As with the heads of extant arthropods, a lively dispute concerns the heads of arthropod fossils. Accordingly, several recent hypotheses, summarized in Table 1 compete with our view.

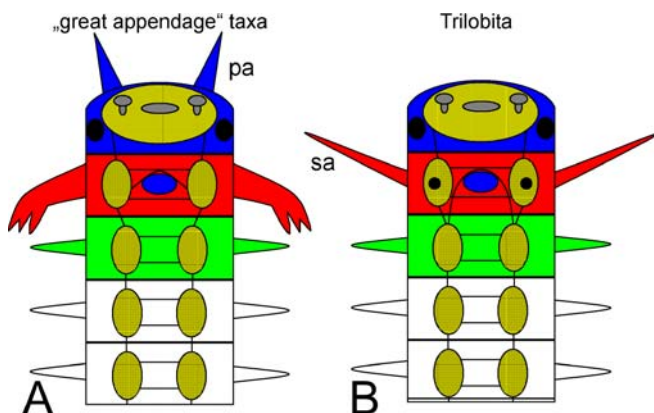


Fig. 5 Alignment of structures in the heads of fossil arthropods (see Fig. 3). **a** Great appendage taxa with “primary antennae” (*pa*). **b** Trilobita with “secondary antennae” (*sa*). The ocular/protocerebral region (*blue*), the deutocerebral segment (*red*), the tritocerebral segment (*green*). In **a** the deutocerebral region bears the great appendage which is transformed to the “secondary antennae” in the trilobites (**b**). The protocerebral primary antennae are lost in trilobites. The structures of the central nervous system (*yellow*) are inferred, and we do not know to what degree cephalization included the tritocerebrum. The *double line* in the posterior region of the trilobite head marks the posterior margin of the head shield. The mouth is depicted in *blue* to show its association with the ocular/protocerebral region

The protocerebral “great appendage” is transformed into the labrum

Budd (2002) derived the “great appendage” described in several Cambrian euarthropods such as *Occacaris*, *Fuxianhuia*, and *Branchiocaris* from the anteriormost appendage of some Cambrian lobopods such as *Kerygmachela* or *Aysheaia*. Accordingly, the great appendage in stem lineage euarthropods would also be the anteriormost appendage, the frontal appendage. This is a problematic homologization because the structural and topological correspondence between the frontal appendages of lobopods and euarthropods is very low. For instance, one could alternatively infer an antenniform structure on the head of *Kerygmachela* (Budd 1998) to be the anteriormost appendage. Nevertheless, the Megacheira-type great appendage is certainly the anteriormost limb, and Budd’s resolution of megacheirans low in the arthropod stem lineage was used as an argument on why this limb is a frontal appendage anatomically anterior to an antenna. The alternative, and in our opinion, better supported placement of Megacheira within the euarthropod crown group (Chen et al. 2004; Maas et al. 2004; Cotton and Braddy 2004) deflates this argument. The “frontal appendage” hypothesis faces the additional problem that in some instances, antennae are placed anterior to the raptorial limb/great appendage. An antenna is positioned anterior to an enlarged raptorial appendage in *Branchiocaris* (Briggs 1976), in *Occacaris* (Hou 1999; Hou et al. 2004), and in *Ovalicephalus* (Bergström and Hou 2005). Correspondingly, Budd had to suggest a ventral movement of the mouth and the great appendage to place the latter at the anterior position. The problem is that there is no example of a euarthropod stem lineage representative with a terminal mouth. Furthermore, the antennae of Recent Onychophora show that there is no necessary correlation between a ventral mouth position and a ventral position of the anteriormost antenna-like appendage.

The deutocerebral antenna is transformed into the great appendage which is transformed into the chelicera

Chen et al. (2004) and Waloszek et al. (2005) suggest a transformation series starting with a reconstructed euarthropod stem species with a limb-like antenna posterior to the eyes which in the lineage leading to Chelicerata is transformed into a “short” (Megacheira-type) great appendage which gives rise to the chelicerae of the crown group, Chelicerata. The Mandibulata retain the plesiomorphic limb-like antenna (secondarily modified into a sensorial antenna in crown group crustacean, myriapod, and hexapod lineages fide Chen et al. 2004). Waloszek et al. (2005) reconstruct the attachment of the antennae in the putative stem lineage arthropods, *Fuxianhuia*, *Chengjiangocaris*, and *Shankouia* as being at the sides of the hypostome and positioned close to the mouth. This positioning would be consistent with an

identity as “secondary antennae.” We are unaware of the evidence for an insertion of the antennae in fuxianhuids so far back at the sides of the hypostome. This is inconsistent with specimens that show the antennal peduncle to be situated close to the eye (Chen et al. 1995) and in specimens that preserve the hypostomal outline and show the antenna projecting from the front of the hypostome (Hou et al. 2004: Fig. 16.3a) rather than emerging from its lateral margins close to the mouth. The specimen of *Chengjiangocaris* noted by Waloszek et al. (2005), as displaying especially fine preservation of the hypostome, has its antennae originating just behind the eyes, near the front of the head (Hou et al. 2004: Fig. 16.5c). Accordingly, the positioning of the antenna in fuxianhuids is consistent with identity as a protocerebral (“primary”) antenna sensu Scholtz and Edgecombe (2005). *Fuxianhuia* had been interpreted as having a raptorial limb posterior to its antennae (Chen et al. 1995; Hou and Bergström 1997), a situation that resembles *Branchiocaris*, but Waloszek et al. (2005) instead argued that the alleged raptorial limb of *Fuxianhuia* is a pair of gut diverticulae. Some conflicting evidence leaves this in doubt. For example, the gut, itself, is not preserved anteriorly in *Fuxianhuia* and in the allied *Chengjiangocaris*; dark stains that represent diverticulae are in a more posterior position, behind the hypostome (Hou et al. 2004: Fig. 16.5c). The consistent geniculate shape of the structures and their preservation detached from the body (Chen et al. 1995) are anomalous for gut diverticulae. Furthermore, these structures seem to be covered by the same type of preserved cuticle as the tergites (Waloszek et al. 2005), whereas, gut diverticulae in Recent arthropods are formed by the mesodermal midgut, and thus, lack a cuticular cover.

The tritocerebral (second) antenna is transformed into the great appendage which is transformed into the chelicera

Cotton and Braddy (2004) agree with Chen et al. (2004) and Maas et al. (2004) in a homology between Megacheira-type great appendages and chelicerae, but they start from the traditional perspective of the segment of the chelicerae of Chelicerata corresponding to the segment of the second antennae of crustaceans or the intercalary segment of myriapods and hexapods. Cotton and Braddy (2004) used the supposed presence of an antenna anterior to the great appendage in the Cambrian *Fortiforceps* (Hou and Bergström 1997) to defend the likely tritocerebral innervation of the great appendage (assuming the antenna to be deutocerebral as in mandibulates). This alleged antenna is poorly preserved in a few specimens and is rejected in new reconstructions of *Fortiforceps* (Bergström and Hou 2003, 2005), which instead recognise the great appendage as the first cephalic limb. Furthermore, the recent developmental evidence from molecular and morphological studies for the new alignment of euarthropods heads (see above, Scholtz and Edgecombe 2005) disputes the fundamental assumption of Cotton and Braddy (2004) that the segment of the

chelicerae corresponds to the second antennal/intercalary segment.

The posterior boundary of the head and the chelicerate problem

A true head tagma does not occur in crown group Chelicerata. The prosoma comprises the chelicerae and five additional pairs of limbs which, apart from the first pair, are mainly used for locomotion. The first pair, the pedipalps, is often modified for mating or feeding. In contrast, the opisthosoma is related to breathing. Based on the situation in Recent Chelicerata, there is no obvious reason to assume that the ancestors of Chelicerata ever possessed a head comparable to that of the Mandibulata. Chen et al. (2004) suggest that a head comprising eyes, antennae and three post-oral segments was present in the chelicerate stem species. This view is influenced by the resolution of Megacheira on the chelicerate stem lineage, with members of this group apparently having three biramous cephalic limbs behind the great appendages (Chen et al. 2004). Other authors have interpreted megacheiran heads as having only two pairs of postoral limbs (*Alalcomenaeus* fide Briggs and Collins 1999), though Chen et al. (2004) dispute this. From the fossil evidence, it is likely that a head shield was present in the chelicerate stem species, but it is not clear to what extent it was fused to the head segments and the number of segments covered (chelicera homologue + three postoral biramous limbs?) requires more conclusive documentation.

Trilobita as stem lineage representatives of the Mandibulata

With perhaps 20,000 species and a history that spanned 275 million years, the trilobites were an evolutionarily very successful arthropod group. Although a sound case can be made that trilobites are monophyletic (Fortey and Whittington 1989; Ramsköld and Edgecombe 1991; Hou and Bergström 1997), internal and external relationships are far from clear (Fortey 2001). Until recently, there was an almost universal agreement that Trilobita together with trilobite-like taxa, the Trilobitomorpha, are closely related to the Chelicerata. A notable exception was Boudreaux (1979), who put the trilobites as a sister group to the Mandibulata. Depending on the author and finer details on the internal relationships, the trilobitomorph–chelicerate grouping is called Arachnomorpha (Heider 1913 emend Størmer 1944) or Arachnata (Lauterbach 1980b). The characters interpreted as apomorphies supporting this relationship are critically discussed by Scholtz and Edgecombe (2005). They involve similarities in body shape such as trilobation/wide paratergal folds and an anterior widened body region, dorsal eyes, and the lamellipedian-type of setae (Hou and Bergström 1997) on the outer limb branches. These characters are problematic because, on the one hand, most Chelicerata (i.e., arachnids)

do not share them, and on the other hand, we find similar morphologies in other crown group arthropods, or even in likely stem lineage arthropods (e.g., trilobation; Waloszek et al. 2005). Homoplasy, in itself of course, does not rule out the relevance of a character as a potential synapomorphy, but polarity questions plague the putative arachnomorph synapomorphies. For example, two of the three characters that Cotton and Braddy (2004) optimized as synapomorphies of Arachnomorpha involve the absence of exopod structures that are present only in crustaceans and marrellomorphs. Given that trilobite–chelicerate affinities cannot be regarded as beyond question, Scholtz and Edgecombe (2005) drew attention to characters of the head that trilobites share with mandibulates, and hence, the possibility of a placement of trilobites on the mandibulate stem lineage. This line of argumentation is followed here. Trilobites possess a head shield that is fused to and covers the eye region, the antennal segment, and three post-oral segments. This head structure resembles what has been suggested on various grounds as the head in the ground pattern of Mandibulata (Lauterbach 1980a; Walossek 1993; Scholtz 1997).

According to the view of the discrimination of “primary” and “secondary antennae” by their position on the head, the Trilobita possess secondary antennae which are situated in an antennal notch at the lateral margin of the hypostome. Trilobites share the “secondary antennae” with the Mandibulata (Figs. 3, and 5). As the sensory antennae of Mandibulata are apparently apomorphic within the Euarthropoda (see above), the occurrence of “secondary antennae” in Trilobita and Mandibulata is interpreted as a synapomorphy. This places the Trilobita in the stem lineage of the Mandibulata and disputes the close affinity to the Chelicerata.

To test whether or not the “secondary antenna” transformation series is parsimonious, we incorporated trilobites and five additional fossil terminals into the morphological character set of Giribet et al. (2005). The expanded matrix (available as Electronic Supplementary Material includes new characters to accommodate the fossils. Trilobita is scored using the Cambrian *Olenoides*, known from soft-part preservation (Whittington 1975, 1980). Additional fossil terminals are the stem-crustacean or stem-mandibulate *Martinsonia* (Müller and Walossek 1986; Walossek and Müller 1990), *Alalcomenaeus* (Briggs and Collins 1999) as an exemplar of the Megacheira, the chelicerates, *Baltoerypterus* (Selden 1981) and *Proscorpius* (Kjellsvig-Waering 1986), and the Burgess Shale taxon *Emeraldella* (Bruton and Whittington 1983). Putative apomorphies of Arachnomorpha (e.g., lamellipedian-type outer limb branch setae) are included.

The result of the analysis is summarized in Fig. 6. Mandibulata is monophyletic, with Trilobita (*Olenoides*) and other taxa having “secondary antennae” (*Martinsonia*, *Emeraldella*) resolved in the mandibulate stem group. A deutocerebral raptorial appendage maps onto the cladogram as symplesiomorphic relative to a deutocerebral antenna because Pycnogonida (chelifores), Chelicerata (chelicerae), and Megacheira (*Alalcomenaeus*: great appendage) are

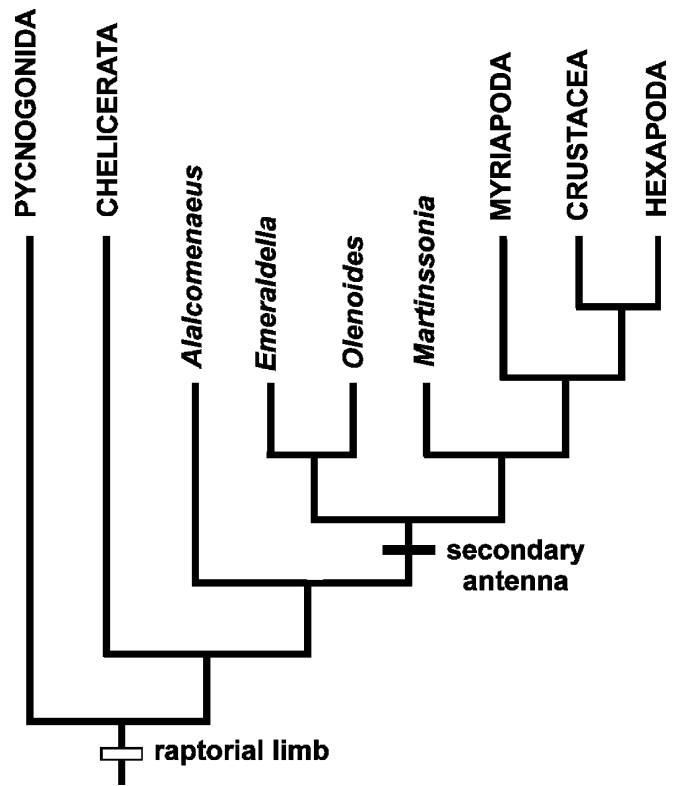


Fig. 6 Cladogram showing the phylogenetic relationships of fossil and Recent arthropods. Trilobita (here sampled by *Olenoides*) appear as stem lineage mandibulates. The 356 character, 74-taxon matrix was rooted between onychophorans and tardigrades and Euarthropoda including Pentastomida (cf. Maas et al. 2004). Heuristic searches with PAUP*4.0b10 using implied weights (Goloboff 1993) yield six shortest cladograms (strict consensus shown) that are stable across a range of concavity values ($k=1, 2, 3, 4, \text{ and } 5$). The internal resolution of extant Myriapoda, Hexapoda, and Euchelicerata is as in Giribet et al. (2005)

resolved as a grade rather than a monophyletic group. This topology needs testing with the inclusion of additional fossil terminals, but this analysis demonstrates that the hypothesis that a “secondary antenna” is apomorphic for trilobites and mandibulates is amenable to parsimony analysis.

Conclusion and perspective

From comparisons of Recent and fossil arthropods, two overlapping trends in the evolution of arthropod cephalization emerge. First, the specialization of head regions progresses from anterior to posterior, which is perhaps not too surprising. In fossils as well as in Recent Chelicerata, plesiomorphically only the anteriormost limbs (chelicerae) are modified and only apomorphically are subsequent appendages transformed to head structures such as pedipalps. This is also true for Mandibulata, in which we plesiomorphically find only one pair of maxillae as is exemplified by cephalocarid crustaceans (Lauterbach 1980a) as well as fossil representatives (see above). The second trend is not so obvious and more surprising in that

the dorsal differentiation precedes that on the ventral side. We always have more dorsal head segments fused than limbs differentiated to head structures, such as mouthparts or sensory organs, on the ventral side. A good example of this is the Trilobita, in which we find a head shield fused to the eye region and four segments, whereas, the post-antennal limbs covered by this head shield have, more or less, the same structure as the trunk limbs. The differentiation of these head limbs took place only later in the stem lineage leading to the crown group Mandibulata. The Crustacea, and in particular, the Decapoda among the Malacostraca reveal that cephalization has not come to an end. The head shield/carapace is fused to all eight thoracic segments in addition to the head segments. This so-called cephalothorax can be seen as an extremely elongated head comprising the ocular region and 13 segments. According to the stated trends, we find ventrally only up to three pairs of anterior thoracic appendages transformed to additional mouthparts, the maxillipedes (see Richter and Scholtz 2001). This condition is correlated with differences in the expression patterns of the *Hox* genes *Antennapedia*, *Ultrabithorax*, and *abdominal-A*, which show distinctively less overlap in decapod representatives than in other malacostracan crustaceans such as isopods (Abzhanov and Kaufman 2004).

As our review shows, a combination of modern and traditional approaches reduces the number of viable hypotheses about head segmentation; several of the older ideas are no longer tenable or can be seen in a new light. Nevertheless, the arthropod head remains a contentious issue, not the least because its study has been so theory laden. Investigators should be aware of and attempt to minimize the unwarranted assumptions that influence their views. Hypotheses about phylogenetic relationships and transformation series have an impact and the reconstruction of ancestors, assumed starting points, and definitions of segments. These problems start with the question over what a head is in the first place. Accordingly, it is not only a matter of better molecular resolution but also of basic theoretical underpinnings that determine whether we make progress in interpreting the head as a functionally and evolutionarily important part of the arthropods.

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