The Arthropod Head

10

Stefan Richter, Martin Stein, Thomas Frase
and Nikolaus U. Szucsich

Contents

S. Richter (✉) · T. Frase
Allgemeine und Spezielle Zoologie, Universität
Rostock, Universitätsplatz 2, 18055, Rostock,
Germany
e-mail: stefan.richter@uni-rostock.de

T. Frase
e-mail: thomas.frase@uni-rostock.de

M. Stein
Danish Museum of Natural History, University of
Copenhagen, Universitetsparken 15, 2100,
Copenhagen, Denmark
e-mail: martin.stein@snm.ku.dk

N. U. Szucsich
Department of Integrative Zoology, University of
Vienna, Althanstrasse 14, 1090, Vienna, Austria
e-mail: nikola.szucsich@univie.ac.at

The anterior region of arthropods is profoundly influenced by effects of condensation and integration that has taken place in various character complexes. Prominent examples are the cerebralization of the central nervous system, the integration of anterior appendages to encompass sensory function and food uptake, the integration of anterior segments covered by a continuous dorsal shield, and a condensation of the endoskeleton which has resulted in the partial obscuring of the segmental organization. The borders between these different complexes, however, do not necessarily correspond. The exact composition and origin of the 'arthropod head' is an enduring problem in arthropod evolution. The discussion is heavily theory-laden, and any new account needs to consider a huge number of older theories and models (see Scholtz and Edgecombe 2005; 2006 for the most recent and detailed reviews). Although our understanding of and ideas about arthropod relationships have changed significantly over the last decade, the historical burden remains.

10.1   What is a Head?

In a recent debate, it has been suggested that morphological descriptions and terminology should be free of homology assumptions (Vogt 2008; Vogt et al. 2010). This approach is particularly challenging when it comes to a topic

like the 'arthropod head problem' where almost every statement implies something about homology and evolutionary transformation polarity. The idea that homology statements should be avoided is not intended to deny the existence of homology; however, it simply seeks to separate the various steps in (evolutionary) morphology. A purely descriptive first step is properly followed by an evolutionary approach which encompasses the conceptualization of evolutionary characters (Wirkner and Richter 2010). In this context, it is important to point out that not only should the terminology used for description be free of homology assumptions, but also the underlying concepts themselves should be based on 'pure' description. This does not necessarily imply that the situation in adults should be considered in isolation because developmental data are at least as important, and gene expression data also play an obvious role. Even more crucial, gene expression data are primarily descriptive (although they certainly have a functional role) and become evolutionarily interpretative only in the framework of evolutionary developmental biology, as part of the new extended evolutionary synthesis (Pigliucci and Müller 2010).

Following on from Johann Wolfgang von Goethe's description of an insect head,[1] let us start with a concept of the arthropod head: the *head* (or *cephalon*) is always an anterior structure which should include primarily sensorial appendages and a brain which processes the sensory input. We also consider it important that the head be somehow separated from the trunk (otherwise, any imposed boundary would be based on non-descriptive concepts) and note that it may include appendages for feeding.

In segmented organisms like arthropods, the most conspicuous boundaries are constituted by segment boundaries (for a discussion of the segment problem, see Scholtz (2002) and Chap. 9). In the anterior part of the body of arthropods, traces of segmental organization are often restricted to some internal anatomical systems and the appendages. The dorsal surface usually fails to reflect segmental organization and is formed by a continuous sclerotization which covers a number of anterior segments. The exact number of segments involved differs. If this *dorsal shield* spans the regions/segments of proto-, deuto-, trito-cerebrum and the three following segments, it is usually referred to as the head (for stem lineage arthropods see below). In myriapods and hexapods, the term *head capsule* is usually used and refers to the entire cuticular envelope of the head. The posterior part of the head is often referred to as the gnathocephalon and comprises the mandibular and two maxillary segments (i.e., the segments of the maxillula and maxilla). We find it difficult to draw a clear distinction between the concept of the head capsule and that of the dorsal shield. The pattern, in any case, is obscured by the high level of disparity in the number of segments subsumed under a common dorsal shield/head capsule in crustaceans. This phenomenon is well known, and carcinologists differentiate between the cephalon and cephalothorax to describe the different conditions (Gruner and Scholtz 2004). Nevertheless, following the same concept as that applicable in insects and myriapods, a head would be present, for example, in Cephalocarida, Branchiopoda and Mystacocarida, and within Malacostraca at least in Bathynellacea. In other taxa, developmental data show the anterior tagma, or cephalothorax, to additionally incorporate one or more thoracic segments (Casanova 1991). In some cases—the Amphipoda, for example—a purely descriptive concept of a head, however, might well be applicable to a cephalothorax including the first thoracic segment with its maxilliped, which is clearly separated from the remaining thorax (Gruner 1993). In the Cephalocarida, a particularly interesting case, a dorsal head shield covers the segments of the

---

[1] Man betrachte die vollendeten Insecten! … Das Haupt ist seinem Platze nach immer vorn, ist der Versammlungsort der abgesonderten Sinne und enthält die regierenden Sinneswerkzeuge, in einem oder mehreren Nervenknoten, die wir Gehirn zu nennen pflegen, verbunden. J.W. von Goethe—Erster Entwurf einer allgemeinen Einleitung in die vergleichende Anatomie ausgehend von der Osteologie. WA II, Bd 8, S. 13.

antennules, antennae, mandibles, maxillules and maxillae and clearly defines the border between the head and the trunk, although the maxillae and the first trunk limbs closely resemble each other (Fig. 10.1a). In the central nervous system, a well-demarcated brain can be distinguished from a subesophageal ganglion and the latter from the first thoracic ganglion (Stegner and Richter 2011; Fig. 10.1b). The sensorial appendages mentioned above as factors for inclusion in a concept of 'head' are the insect and myriapod antenna, and the crustacean antennules and antenna (Strausfeld 2012). Additional appendages are present (mandible, maxillule, maxilla/labium), though these are not primarily sense organs but rather are feeding organs.

Applying the concept of a head to chelicerates is most challenging. A prosomal shield covers eight regions/segments, including all the segments of the locomotory limbs (but note that in Xiphosura, the opisthosomal legs are used for locomotion as well), and no head capsule as such is present. To complicate matters further, the appendages of the prosoma, such as the chelicerae, pedipalps and walking legs, are not primarily sensorial (although this concept itself is weak because almost all arthropod appendages possess some kind of sensilla or sensory organs). Therefore, as most arachnologists would agree, the anterior tagma is not being considered as a head (but see below).

10.2   Endoskeleton

In addition to the exoskeleton, a number of endoskeletal structures in all arthropods both reinforce the head and serve as attachment sites for the cephalic musculature. Some of these structures are ingrowths from the cuticular invagination, whereas others are made up of connective tissue.
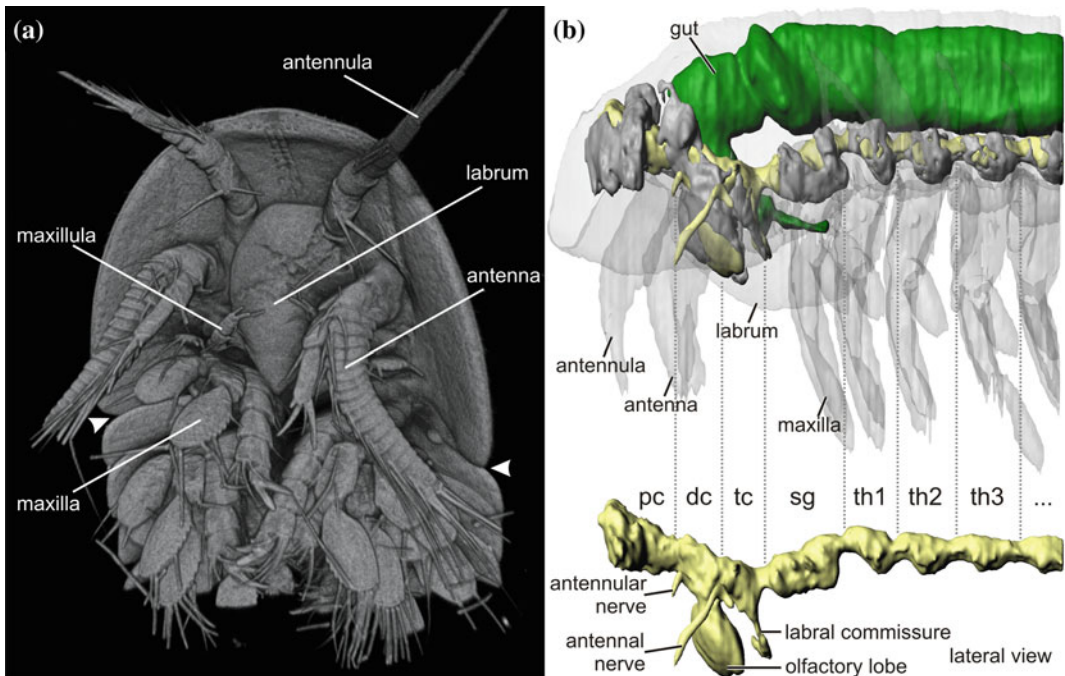

Fig. 10.1 a Head of *Lightiella incisa* (Cephalocarida). Note the distinct border between dorsal shield and thorax (*white arrow heads*), CLSM image. **b** Brain and ventral nerve cord of *Hutchinsoniella macracantha*. The brain clearly includes the tritocerebrum (tc); a subesophageal ganglion (sg) is present. Three-dimensional reconstructions of somata (*gray*) and neuropil (*yellow*) in relation to body contours (semitransparent) and the gut (*green*), based on semi-thin sections; modified after Stegner and Richter (2011)

In most chelicerates, the main endoskeletal structures are made up of connective tissue, and segmental organization is retained to a high degree. A horizontal tendinous plate known as the endosternum is stabilized by more or less segmentally arranged dorsal, lateral and ventral suspensors (Firstman 1973; Shultz 1999, 2000, 2007).

The cephalic endoskeleton of myriapods is usually referred to as the *swinging tentorium* (Manton 1964; Koch 2003; Edgecombe 2004, 2010). As it is not fused to the head capsule, the tentorium has some degree of freedom of movement against it. Mandibular abduction is guided by the movements of the tentorium. In most Myriapoda, the tentorium is formed by a pair of internal cuticular processes (or tentorial arms) which are continuous with a number of exoskeletal bars integrated into membranous regions of the hypopharynx and the ventral head surface (Koch 2003; Szucsich et al. 2011). Most of the cuticular endoskeletal processes are associated with components made up of connective tissue. These tendinous structures either form bridges which link the cuticular processes or make up a horizontal framework suspended by muscles and tendons from the dorsal and lateral head capsule (Fig. 10.2).

In crustaceans, the cephalic endoskeleton is formed entirely of connective tissue. The segmental arrangement of components, which is easiest to follow in the trunk, is often still reflected in the cephalic endoskeleton (Fanenbruck 2003).

Although it displays some variation, the cephalic endoskeleton among groups of Hexapoda Ectognatha is always made up of a common set of components. This insect tentorium consists mainly of two pairs of cuticular invaginations. The anterior tentorial arms invaginate at the subgenal or epistomal ridges of the head exoskeleton and usually converge gradually in a caudal direction before merging to form the tentorial bridge. The tentorial bridge is formed by the fusion of the posterior tentorial arms, which invaginate at the ventral ends of the postoccipital ridge. In some groups, the central part of the resulting tentorium is enlarged, forming a plate-like structure known as the
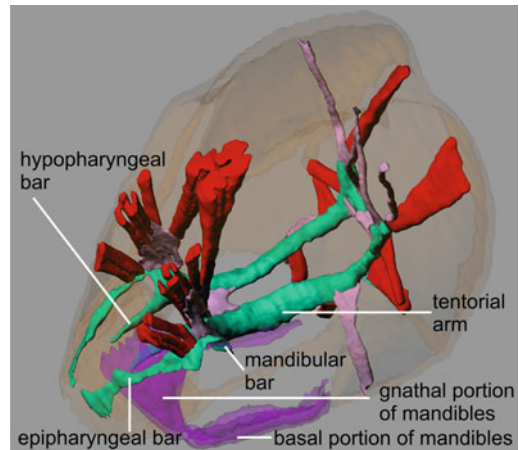

Fig. 10.2 Cephalic endoskeleton of *Scutigerella immaculata* (Symphyla) in dorsolateral view (3D reconstruction). The cephalic endoskeleton encompasses cuticular components (*green*), components made up of connective tissue (*pink*) and muscular components (*red*). A pair of cuticular tentorial arms has a continuous connection to three strongly sclerotized bars of the exoskeleton, all of them lying at the anterior end of the tentorium. All three exoskeletal bars (epipharyngeal, hypopharyngeal and mandibular bar) are surrounded by weakly sclerotized regions. Thus, the tentorium can be moved against the head capsule (*transparent brown*) and is usually referred to as "swinging tentorium." Mandibular abduction is guided by movements of the tentorium

corpotentorium. In many groups of insects, additional cuticular components are present. A pair of dorsal arms often extends from the anterior arms to the dorsal head capsule. Reconstructing the hexapod ground pattern remains problematic, since the basally branching lineages display great disparity with regard to the cephalic endoskeleton. While all structures in Diplura and Collembola are made entirely of connective tissue, Protura exhibit cuticularized components, though these can hardly be homologized with structures of the ectognathan tentorium (Denis and Bitsch 1973; Koch 2000; Bitsch and Bitsch 2002).

Scenarios which address the evolution of the endoskeleton in the head and the trunk of arthropods usually proceed on the assumption that structures in postoral segments are homonomous. Among extant arthropods, the prosomal endoskeleton of chelicerates is usually judged to most closely reflect the plesiomorphic state for

arthropods (Shultz 2007). Comparative investigations into extant and fossil groups indicate that a structure which Shultz (2001) termed the box-truss axial muscle system, which encompasses both muscular components and components made up of connective tissue, might be plesiomorphic for arthropods (Cisne 1974; Boudreaux 1979; Shultz 2001, 2007; Fanenbruck 2003). This structure is made up of a pair of longitudinal connectives situated dorsally of the nervous system. At the border of two segments, these longitudinal connectives are linked to each other by a transverse connective and connected to the dorsal and ventral cuticle by a pair of dorsal and ventral suspensors, respectively. The longitudinal connectives are additionally attached to the dorsal exoskeleton of the antecedent segment by a pair of anterior oblique suspensors and to the dorsal exoskeleton of the successive segment by a pair of posterior oblique suspensors. Objections to the scenario of a plesiomorphic box-truss axial muscle system mainly pertain to its underlying assumption that postoral structures are strictly homonomous, as mentioned above. In many arthropod groups in which the segmental organization of the endoskeleton is still clear, the anteriormost region of the postoral endoskeleton is far from being strictly homonomous, usually featuring an additional unpaired median component which is not present in more posterior segments (e.g., Hessler 1964; Fanenbruck 2003; Domínguez Camacho 2011). Most authors deem polarization to be unambiguous in only a few phylogenetic characters of the cephalic endoskeleton. An example is the presence of a 'swinging tentorium' in myriapods, frequently mentioned as one of the few synapomorphies supporting the monophyly of Myriapoda (Manton 1964; Koch 2003; Edgecombe 2004, 2010).

10.3   Brain

Arthropods possess a brain, known as the syncerebrum, which is generally interpreted to be the result of cephalization, that is, the structural and functional transformation of postoral neuromeres (usually considered to be ganglia) which are more or less fused to the pre-oral ancestral brain (Richter et al. 2010). A process of condensation can also be observed during development (e.g., Fritsch and Richter 2010), but the exact number of components involved is under dispute. A syncerebrum consisting of a protocerebrum, deutocerebrum and tritocerebrum can be identified in most adult mandibulate arthropods, though the borders between the three components are not always unambiguously recognizable. It could even be argued that a purely descriptive approach should omit the three terms. Generally, the three components are defined by the input of eyes, that is, compound eyes, median eyes, frontal eyes (protocerebrum), the input of the antennules (in crustaceans, but in the following, we include myriapod and insect antenna under the term antennule) (deutocerebrum) and the input of the (crustacean second) antenna (tritocerebrum).

Whether or not the tritocerebrum actually belongs to the arthropod brain is a matter of debate. Whereas Scholtz and Edgecombe (2006, p. 399) (see also Harzsch 2004) emphasize that 'its status as a brain neuromere' is evident, Mayer et al. (2010) suggest that the tritocerebrum (as a component of the syncerebrum) evolved in arthropod subgroups. Both views, obviously, are based on assumptions regarding the evolution of the syncerebrum and the arthropod ground pattern rather than simply describing an existing condition. Kirsch and Richter (2007), on the other hand, took a purely descriptive approach when considering the brain of the raptorial water flea *Leptodora kindtii* and concluded that it consists of a proto- and deutocerebrum only, because the tritocerebrum (or more precisely the ganglia which correspond to the tritocerebrum in taxa with a tripartite brain) is so far posterior in the head. Making the concept of the head independent from the concept of the syncerebrum affords a higher degree of freedom in discussions of possible evolutionary scenarios which involve both coupled and independent evolutionary events of cephalization and cerebralization. Whether or not the tritocerebrum is part of the brain varies among

arthropods, and descriptions should not be concerned with whether or not the composition of the brain is plesiomorphic or derived.

The separation of the protocerebrum into an archicerebrum (comprising the mushroom bodies and the optic lobes) and a prosocerebrum (comprising the central complex)—one belonging to the acron, the other to a pre-antennal segment—appears to be hypothetical (Siewing 1969); on the basis of segmental gene expression data at least, there is no indication of an additional segment between the eyes and the antennules/chelicerae (reviewed by Scholtz and Edgecombe 2006). However, recent *Six3+* and *Otx* gene expression data support the notion that the protocerebrum is made up of two different portions, though the authors explicitly avoid calling them the archi- and prosocerebrum (Steinmetz et al. 2010). Even if the presence of a bipartite protocerebrum were to find support as an evolutionary concept (e.g., Strausfeld 2012), there is no unambiguous evidence that the two portions of the protocerebrum can be separated in adult arthropods (see also the discussion by Scholtz and Edgecombe 2006). We suggest that only the term protocerebrum has a place in a purely descriptive approach (or even better, as outlined above, more functionally defined subunits such as central complex, optic lobes, etc., should be used).

In chelicerates, no syncerebrum is present following the standard definitions. The prosoma instead contains a 'prosomal ganglion' which is usually separated into a supra- and subesophageal ganglion, though this distinction is predominantly a conceptual one because the entire ganglion is surrounded by somata which are not separated into somata clusters (Klussmann-Fricke and Wirkner, in progress). As a whole, the prosomal ganglion fits in with the concept of a brain as the most anterior condensation of neurites (see Richter et al. 2010).

To conclude, while it is plausible to assume the presence of a syncerebrum in the last common ancestor of all arthropods, the exact composition of the ground pattern in terms of the number of neuromeres it included remains, in our view, uncertain.

10.4 Gene Expression Data

Gene expression data provide important support for theories regarding the composition of arthropod heads (e.g., Scholtz 1997; Telford and Thomas 1998). That the arthropod head is composed of several units, generally considered to be segments, is beyond doubt. This is clearly recognizable in development and supported by gene expression data. Segment polarity genes such as *engrailed* and *wingless* in particular reveal the presence of six units in the head of most mandibulates (e.g., Scholtz 1997). The three anterior units are the protocerebral region (leaving it open whether this region is composed of two units or not) plus the segments of the antennules and antennae in crustaceans, or the antennal and intercalary segments in myriapods and insects. Schaeper et al. (2010) and Janssen et al. (2011) have recently detected *collier* expression in the intercalary segment of insects and myriapods, which the latter authors interpret as potential support for the traditional Atelocerata concept. The mandible, maxillule and maxilla (or labium) segments are distinguished by the expression of segment polarity genes (Scholtz 1997). In addition, certain segments are identifiable by the expression of Hox genes, a good indicator of homology of segments and their appendages. The proposed homology of the segments of the chelicera and antennule is based on the expression of Hox genes (Telford and Thomas 1998) and on evidence from axogenesis (Mittmann and Scholtz 2003). Moreover, the exact match in the anterior expression boundaries of the Hox genes *labial*, *proboscipedia* and *Deformed* supports the notion that the chelifore segment in Pycnogonida and the chelicera segment in the remaining euchelicerates are homologous (Manuel et al. 2006), making the hypothesis that the chelifore is innervated by the protocerebrum (Maxmen et al. 2005) improbable (see also Brenneis et al. 2008 for additional contradictory evidence based on axogenesis).

A comparison of all the Hox genes expressed in the head of mandibulates with the expression pattern in a spider led Averof (1998) to conclude

that the spider prosoma indeed corresponds to the mandibulate head. On the basis of these data, the presence of a clear boundary between the prosoma and the opisthosoma coupled with the presence of a brain (i.e., the 'prosomal ganglion') might convince us to consider a head to be present in chelicerates too, despite the fact that this head is also used for walking and includes one more segment than the mandibulate head. This short summary shows that the gap between describing Hox gene expression and making assumptions about evolution is smaller than it may at first appear. Gene expression data certainly provide helpful arguments when it comes to establishing the homology of segments, but it must be borne in mind that the expression range of Hox genes might be subject to change, as in the case of crustacean maxillipeds (Averof and Patel 1997; Abzhanov and Kaufman 1999, 2000) to name but one example. Shared gene expression is not proof of segment homology. On the contrary, because Hox gene expression is responsible for certain aspects of, say, limb morphology, as in the case of the maxillipeds vs. non-specialized thoracopods (Liubicich et al. 2009; Pavlopoulos et al. 2009), Hox gene expression and the morphology of the limb cannot be used independently as support for homology hypotheses. We should also be aware that the developmental pathways of dorsal and ventral character systems may be decoupled (e.g., Janssen et al. 2006), an effect which might be especially pronounced in the anteriormost part of the body. This may account for at least some of the mismatches between the boundaries of different character systems.

10.5 Origin of the Arthropod Head

If a head is present in most arthropods and its components can reasonably be deemed to be homologous across all major taxa, the obvious question is how it evolved. Evolutionary scenarios need a starting point. The discussion of the origin of the arthropod head was once heavily influenced by the Articulata concept and the idea of an annelid-like ancestor developing from a trochophoran larva with epi- and hyposphera. The Ecdysozoa concept (Aguinaldo et al. 1997; Giribet 2003) initially appeared to make the discussion obsolete, but aspects such as the presence of potentially homologous mushroom bodies in arthropods, annelids and other lophotrochozoans (Heuer and Loesel 2009; Heuer et al. 2010) and the similarities in the development of the anteriormost brain region in all bilaterian animals (Steinmetz et al. 2010) show that the debate is by no means at an end (see also Strausfeld 2012). Whatever the case, we take a less inclusive approach and start at the evolutionary level (i.e., the ground pattern) of Panarthropoda: the arthropods, onychophorans and tardigrades. Onychophorans in particular are a good starting point for understanding the evolution of the arthropod head (bearing in mind that they too display heterobathmy, a mixture of plesiomorphic and apomorphic characters). Although we have no doubt that the Tardigrada belong to the Panarthropoda as well (Dunn et al. 2008; Campbell et al. 2011), the current lack of consensus regarding the tardigrade head and the composition of the tardigrade brain lead us to exclude them from this discussion (Dewel and Dewel 1996; Zantke et al. 2008; Persson et al. 2012).

Although there is no distinct border on the surface of the body in Onychophora which would support a division into head and trunk, the differentiated appendages of the anterior body may indicate just this. The anterior body bears a pair of antennae, a pair of eyes, a mouth with a pair of jaws, and a pair of slime papillae. A head, then, is apparently present. On the basis of the expression of the anterior Hox genes *labial*, *proboscipedia*, *Hox3* and *Deformed*, the onychophoran jaws can be aligned with the chelicerae and the antennules, and the slime papillae with the pedipalps and the crustacean antennae (Eriksson et al. 2010). The slime papilla segment, therefore, corresponds to the intercalary segment in myriapods and insects (Eriksson et al. 2010; Mayer et al. 2010). This supports previous suggestions based on neuroanatomical

data (Eriksson et al. 2003). Although the eyes might not correspond to the compound eyes but to the arthropod median eyes (Mayer 2006; but see Ma et al. 2012a supporting the idea that some fossil lobopodians possessed precursors of compound eyes), they belong to the corresponding region of the arthropod protocerebral region. However, it should be noted that Strausfeld (2012) suggests that the compound eyes are the structures which correspond to the segment associated with the onychophoran jaw, implying that the slime papilla corresponds in position to the chelicerae/antennules, which we do not hold to be very likely. Whatever the case, the onychophoran antenna is innervated by the anteriormost portion of the onychophoran brain (Eriksson et al. 2003). It has been suggested that the onychophoran brain is tripartite, as in arthropods, and that it features what Strausfeld et al. (2006) consider to be a protocerebrum, deutocerebrum and tritocerebrum. However, Mayer et al. (2010) performed backfills of cephalic segmental nerves in adult onychophorans and found that the somata of the neurons innervating the jaws and the slime papillae lie adjacent to the base of their nerves. While the neuron of the nerve innervating the jaws is situated in the posteriormost part of the brain (i.e., the deutocerebrum), the neurons innervating the slime papillae lie clearly separate from the brain in the ventral nerve cord. Following the definition of the brain in Richter et al. (2010), then, the onychophoran brain is clearly bipartite. Interestingly, while the onychophoran head consists of three units (protocerebral region and two segments), the brain encompasses two neuromeres only. However, we do not see any conceptual need for a strict correlation of these systems, that is, transformation of appendages and brain composition. Mayer and Harzsch (2008) considered the absence of ganglia in the ventral nerve cord of onychophorans to be the plesiomorphic condition, which could imply that the onychophoran brain is formed not by fused ganglia but by non-ganglionized neuromeres. In evolutionary terms, this assumption might imply that the cephalization of segmental units

preceded the formation of ganglia in the lineage leading to the arthropods. The syncerebrum could well represent a fusion of neuromeres but not of ganglia, potentially explaining why no clearly separated ganglia (corresponding to the proto-, deuto-, tritocerebrum) can be identified in the arthropod brain (see Richter et al. 2010 for more details, and Strausfeld (2012) for a different scenario). In an alternative scenario, the absence of distinct ganglia is interpreted as a secondary feature that is coupled with the probably secondary loss of the clear segmental organization of the body surface (something which in the main can now only be deduced from the distribution of the appendages).

Taking the onychophoran head as a starting point, the mandibulate head has three additional more posterior segments which are fused with the anterior part of the head. The question of when and how often the tritocerebrum became part of the brain remains open. The condition in the raptorial water flea *Leptodora* (Kirsch and Richter 2007) is certainly a secondary one. In Mystacocarida, for example, the tritocerebrum is only slightly separated from the proto–deutocerebral complex (Brenneis and Richter 2010). The presence of a brain featuring an incorporated tritocerebrum in myriapods seems to provide some support for the hypothesis that the mandibulate tripartite brain evolved only once (Sombke et al. 2012).

One remarkable transformation is that involving onychophoran jaws and mandibulate antennules. Taking into account the presence of the chelicerate chelicerae on the corresponding segment, a jaw-like structure might indeed represent the original condition. This would imply a major transformation in the stem lineage of Mandibulata from some kind of feeding structure to a 'secondary antenna' sensu Scholtz and Edgecombe (2005). On the basis of fossil lobopodians and arthropods, however, it seems more likely that the feeding structures evolved independently in onychophorans and chelicerates, with a non-specialized appendage as starting point (see Ou et al. 2012 and below).

10.6 The Fate of the Onychophoran Antenna

Another fascinating but problematic potential transformation is that from the onychophoran antenna (or any lobopodian antenniform appendage, see Ou et al. 2012) into the arthropod labrum. The homology of the labrum throughout arthropods appears to be strongly supported, particularly by the fact that its development is strikingly similar in chelicerates and mandibulates (Kimm and Prpic 2006). In many cases, the labrum anlage appears as a pair of structures at the front of the embryo, which later move backwards and fuse into a single organ (e.g., Ungerer and Wolff 2005; Mittmann and Wolff 2012). A comparable structure, however, is absent in Pycnogonida (Brenneis et al. 2011). There is some debate concerning the term 'labrum.' According to Maas et al. (2003) a 'fleshy labrum' evolved only in a taxon called Labrophora, which includes the extinct Phosphatocopina and a taxon which the authors call Eucrustacea, including all recent crustaceans and probably also all the hexapods (on the basis of molecular data; Regier et al. 2010; von Reumont et al. 2012). Non-Labrophora (particularly chelicerates and trilobites), then, are assumed to possess a structure called a hypostome, a sclerotized plate. Because of the detailed correspondences—as mentioned above—in the development of the 'upper lip' in chelicerates and crustaceans, a hypostome would also have to be present in crustaceans and the labrophoran labrum would have to be interpreted as a structure which evolved as part of the hypostome (Waloszek et al. 2007).

The segmental affinities of the labrum (or hypostome/labrum) have been debated intensively (see Scholtz and Edgecombe 2006 for a detailed discussion of labrum homology and segmental affinities). Recently, Posnien et al. (2009) showed that the labrum is formed by an appendage regulatory gene network and concluded as a result that the labrum is an appendage-like structure. Steinmetz et al. (2010) found *Six3* expression anterior to *Otx* expression in the anteriormost region of the developing brain in both arthropods (the area where the antenna originates) and onychophorans (the area which innervates the antenna). Interestingly, this comes close to the test suggested by Scholtz and Edgecombe (2006) for obtaining direct support for the homology of the onychophoran antenna and the arthropod labrum. On the basis of these findings and the alignment of the onychophoran jaw segment with the mandibulate antennule segment using *lab*, *pb*, *Hox3* and *Dfd* expression, Eriksson et al. (2010) suggested that the onychophoran antenna is indeed homologous to the labrum. This view is supported by Strausfeld (2012) who hypothesized a complex scenario for the evolutionary transformation from the location of the frontal appendage into the more posterior position of the labrum.

Although we might not be able to solve the labrum problem, we do have some evidence to support the alternative hypothesis for the fate of the (onychophoran) primary antenna discussed by Scholtz and Edgecombe (2006), according to which the frontal filaments on the anterior part of the head in Remipedia and cirripedian nauplius larvae represent remnants of the primary antenna. In branchiopods, Fritsch et al. (2013) distinguish between the filamentous external 'frontal filament' and an internal region beneath the frontal filaments which they term the 'frontal filament organ' (also known as organ of Belonci). Although the two structures undoubtedly form one functional unit, we support this distinction, which reflects the history of discovery of the two structures (see Fritsch et al. 2013). A pair of frontal filaments is present in Notostraca, and other Phyllopoda.

In addition frontal filaments are also be present in certain copepods (Elofsson 1971) and certain ostracodes (Andersson 1977). They are apparently absent in the chelicerates, but *Cambropycnogon* (probably a representative of the stem lineage of Pycnogonida) possesses structures very similar to those of Notostraca (see Waloszek and Dunlop 2002). Frase and Richter (2013) show that nerves of the frontal filament organs (also known as cavity receptor organ,

Elofsson and Lake 1971) in Anostraca appear at the same time as the anlagen of the protocerebrum in the embryonic stages, when no evidence of functionality exists so early on (i.e., serotonergic immunoreactivity starts later). These neurite bundles are still present in the larval stages, but as the protocerebrum, the compound eyes and their nerves grow, and they cover the frontal filament organs and cause them to lose their prominence. In adults, the external part of the frontal filament organs are recognizable only as small cavities (Møller et al. 2004 for *Eubranchipus*). The correspondences between the nerves of the frontal filament organs and those of the onychophoran antenna are remarkable. Both originate in the anterolateral region of the protocerebrum and appear at the same time as the protocerebrum early on in development (Eriksson and Budd 2000; Mayer et al. 2010). If our suggestion of homology of the onychophoran antenna and the crustacean frontal filaments (Fig. 10.3) is correct, the labrum problem would remain unsolved but the need for a complicated scenario of transformation of the primary antenna into the labrum in the ancestral lineage

of arthropods would be obsolete (see Frase and Richter, 2013).

10.7 A Fossil Perspective on the Evolution of the Arthropod Head

Our view of the evolution of the arthropod head has been dominated by neontological data, but the rich fossil record of (pan)arthropods cannot be left unconsidered. Over the last two decades, fossils have played an increasingly central role in hypotheses concerning the evolution of the arthropod head (e.g., Chen et al. 1995; Budd 2002; Scholtz and Edgecombe 2005; Waloszek et al. 2005). Data retrieved from the fossil record are mostly limited to external morphology though internal structures have been reported in rare instances. Relatively common are segmental mid-gut diverticula (Butterfield 2002; Vannier and Chen 2002), which have been used to infer head segment numbers (Zhang et al. 2007; Stein and Selden 2012). Rarely, and sometimes controversially, other internal anatomical features
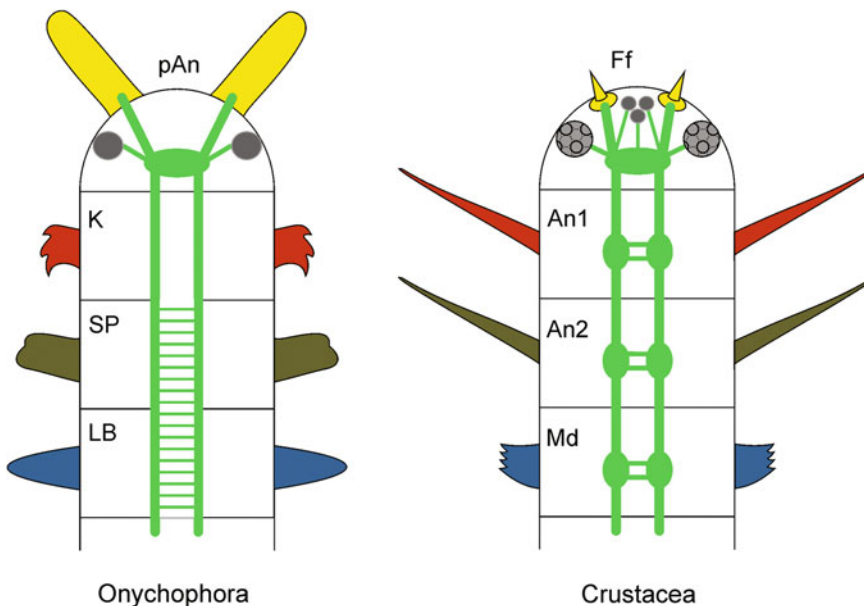

Fig. 10.3 Schematic comparison of the onychophoran and a crustacean head. The onychophoran antenna is suggested as being homologous to the crustacean frontal filaments

are preserved which could be informative about the evolution of the arthropod head. These include putative elements of the endoskeletal system (Cisne 1975; Whittington 1993; Stein 2010), the musculature (Eriksson et al. 2012) and the nervous system (Bergström et al. 2008; Ma et al. 2012b). Just as the interpretation of morphological structures, in particular internal, is problematic in fossils so is the phylogenetic position of the taxa in question. In fact, the two problems are often linked, as our interpretation of morphological features can be influenced by expectations derived from the assumed phylogenetic position of the taxon studied (see the debate about the presence of lobopodous limbs in *Opabinia regalis*; Budd 1996; Zhang and Briggs 2007; Budd and Daley 2011). This phenomenon arises even when every attempt is made—as is desirable—to describe morphological structures independently of phylogenetic position.

An important aspect of any discussion involving both fossil and recent arthropods is the distinction between crown group Arthropoda (the last common ancestor of Chelicerata and Mandibulata and all its descendants) and stem group arthropods, that is, all representatives of the pan-Arthropoda (see Lauterbach 1989, sensu Meier and Richter 1992) which do not belong to the crown group Arthropoda (see Edgecombe 2010). The exact composition of the stem group of arthropods depends on the position of the Onychophora and Tardigrada, which to date remains unresolved. There are a number of fossil taxa, collectively referred to as lobopodians, which have a tubular body and unjointed tubular appendages. These taxa include possible stem group representatives of Panarthropoda, Onychophora, Tardigrada and part of the stem group of Arthropoda. Lobopodia is sometimes considered a paraphyletic assemblage which also includes the crown group of Onychophora (e.g., Liu et al. 2011) or those of both Onychophora and Tardigrada (e.g., Ma et al. 2009) but not the crown group of Arthropoda. The more crown-ward representatives of the arthropod stem, the Arthropoda *sensu stricto* of Waloszek et al. (2005), have pivot-jointed appendages and sclerotized segmental tergites. There is

consensus on the placement of some prominent fossil taxa, such as Trilobita or the more inclusive Artiopoda (Trilobita and closely related, non-biomineralizing forms; Stein and Selden 2012) in the crown group Arthropoda, and some taxa, such as *Fuxianhuia protensa* and similar forms from the Early Cambrian of Chengjiang, in the arthropod stem group (e.g., Budd 2002; Waloszek et al. 2005; Edgecombe 2010). However, there are still taxa which are subject of debate with regard to their phylogenetic position, one being the 'great appendage arthropods,' or Megacheira, which are considered to be either stem group Arthropoda (e.g., Budd 2002, 2008; Legg et al. 2012) or stem group Chelicerata (e.g., Chen et al. 2004; Haug et al. 2012a) (Fig. 10.4). The first cephalic appendage in the megacheirans is a large, ostensibly raptorial appendage termed the great appendage or multi-chela (Haug et al. 2012b). Another controversial taxon is *Canadaspis*, which is considered to belong to either the stem group Arthropoda (e.g., Budd 2002; Waloszek et al. 2007) or Mandibulata (e.g., Briggs et al. 2008). This is an important problem since the advocates of a stem group position afford these taxa a pivotal role in hypotheses regarding the early evolution of the arthropod head (Budd 2002, 2008). Regardless of the phylogenetic position of these taxa, the fossils do permit some inferences to be made about cephalization in the stem species of Arthropoda.

In all unambiguous fossil members of the arthropod crown group, and in the megacheirans, a single dorsal shield is present which covers a number of segments which are fused into one unit (comparable to the condition in Cephalocarida; see Fig. 10.1a). The number of appendage-bearing segments incorporated into this unit in the arthropod ground pattern and the constancy of this number among the fossil taxa is still a matter of debate. In the Megacheira, three appendage-bearing segments have been suggested for a number of species and four for others (see e.g., Edgecombe et al. 2011). A key taxon for the presence of only three is *Leanchoilia superlata*, but a recent revision revealed a small, specialized appendage posterior to the
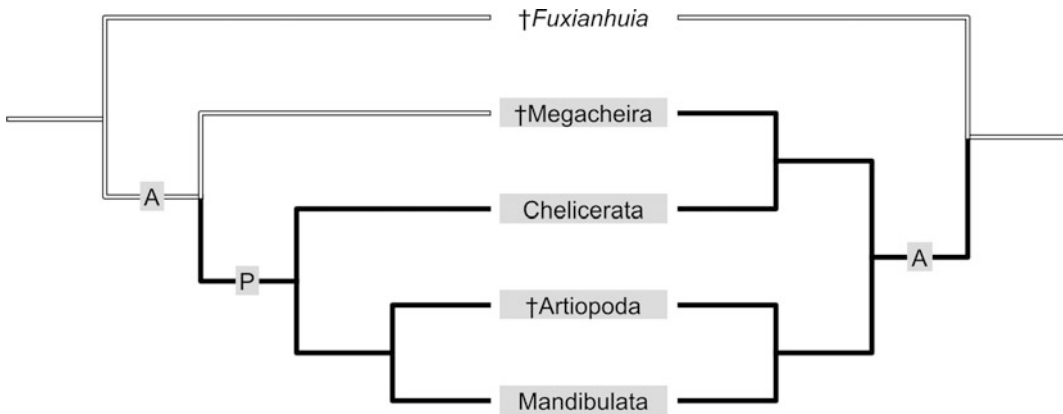
Fig. 10.4 Two alternative phylogenetic placements of the Megacheira and consequences for the occurrence of a head shield incorporating more than two appendage-bearing segments. *Left* Megacheira as stem group arthropods; the head shield, an autapomorphy (*A*) of crown group Arthropoda + Megacheira, is retained as a plesiomorphy (*P*) in the ground pattern of Arthropoda. *Right* Megacheira as stem group chelicerates; the head shield is an autapomorphy (*A*) of crown group Arthropoda. *Solid lines*: crown group Arthropoda; *halftone fill*: head shield incorporating more than two appendage-bearing segments

great appendage, increasing the segment count to four (Haug et al. 2012b). This is the number found in Trilobita as well as the early representatives of Cambrian Crustacea *sensu* Stein et al. (2005) (presumably stem lineage representatives of Tetraconata). The number of segments in the head of Artiopoda has been claimed to be highly unstable (e.g., Zhang et al. 2007), but a number other than four can only be substantiated for Naraoiidae, at least some of which have five (Zhang et al. 2007), and Xandarellida, which have five to seven (Ramsköld et al. 1997). Stein and Selden (2012), for instance, found that only four segments are present in *Emeraldella brocki*, one of the key taxa cited for deviating segment counts. Megacheirans and artiopodans display a lesser degree of cephalic limb specialization than the extant mandibulatan subtaxa, although recent restudies show evidence of a gradual differentiation across the head–trunk boundary in some representatives, with the appendages of the head and anterior trunk more adapted to feeding than the mid- to posterior trunk appendages (Stein and Selden 2012). Regardless of the degree of appendage differentiation in the head, the head would, with its cohesive shield, still act as a single unit distinct from the free tergite-bearing segments of the trunk and thus be separate from the trunk (see

above). It is also true that this head bears important sensory structures in the form of the eyes as well as sensory appendages (antennae in artiopodans, long flagella on the great appendages of some megacheirans) and appendages suited to nutrition (albeit often coupled with a locomotory function).

To which segments the appendages observed in the anterior and cephalic region of some fossil arthropods belong is another point of contention, in particular with regards to the great appendages of megacheirans and the so-called frontal appendages of some lobopodians and of taxa such as *Kerygmachela kierkegaardi* (Fig. 10.5) and possibly the anomalocaridids. The latter taxa are situated on either side of the lobopod-arthropod transition (a character-based distinction within the arthropod stem lineage). Because of its ostensible position as the most anterior appendage flanking the mouth, the frontal appendage of *Kerygmachela* is considered to be protocerebral and homologized with the onychophoran antenna (e.g., Budd 2002). Going even further, the frontal appendage of the putative anomalocaridid *Parapeytoia yunnanensis* has been homologized with the megacheiran great appendage, with the latter consequently also interpreted as being protocerebral (e.g., Budd 2002; Daley et al. 2009). The
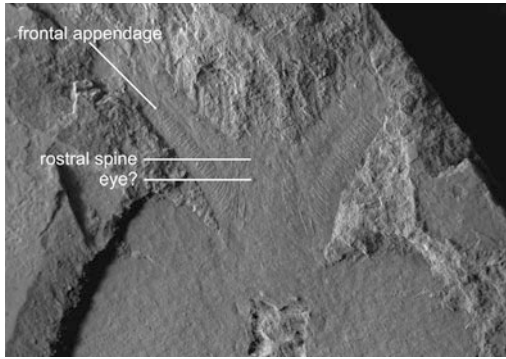
Fig. 10.5 *Kerygmachela kierkegaardi* with prominent frontal appendages, rostral spines and bulbous structures that could represent the eyes

anomalocaridid affinities of *Parapeytoia*, however, are questionable, and the taxon could represent a *bona fide* megacheiran (Stein 2010). The alternative interpretation of the megacheiran great appendage as deutocerebral has gained support and wider acceptance recently (Stein 2010; Haug et al. 2012a). An argument for the deutocerebral interpretation comes from the position of the great appendage; it inserts laterally to the hypostome/labrum (e.g., Haug et al. 2012b) and not directly anteriorly. If, however, we accept that the megacheiran great appendage is homologous with the frontal appendages of *Kerygmachela* and anomalocaridids (Stein 2010), the latter would need to be reinterpreted as deutocerebral appendages as well. In this regard, it is interesting that the onychophoran antenna and the crustacean frontal filaments are sensorial organs (see above). Among the species considered to be important in the lobopod-arthropod transition (Liu et al. 2006, 2007; Dzik 2011), only *Megadictyon* cf. *haikouensis*, *Jianshanopodia decora* and *Siberion lenaicus* have prominent frontal appendages comparable to those in *Kerygmachela*. The anterior appendages of most other lobopodians are commonly interpreted as sensory (e.g., Ramsköld and Chen 1998), while the frontal appendages of *Kerygmachela* and anomalocaridids are usually regarded as feeding appendages. On the other hand, structures comparable to the onychophoran antenna might be present in

Kerygmachela in the form of the 'rostral spines' dorsal to the mouth (Budd 1998). Like the onychophoran antenna, these spines are associated with structures which Budd (1998) interprets as eyes, and they are annulated or 'segmentally divided' (Budd 1998). They are in a similar position to the onychophoran antennae, while the frontal appendages flanking the mouth would be positionally homologous to the deutocerebral onychophoran jaws. Little information is available about the anterior regions of *Megadictyon*, *Jianshanopodia*, and *Siberion*. A new, alternative interpretation, therefore, could be that the frontal appendages of some lobopodians and anomalocaridids indeed represent the homologous appendage to the megacheiran great appendage but are deutocerebral rather than protocerebral.

Recently, a specimen of the stem group arthropod *F. protensa* has been reported in which the nervous system is said to be preserved (Ma et al. 2012b), and it has been suggested that the syncerebrum already present in the ground pattern of (crown group) Arthropoda was tripartite, that is, that the tritocerebral part was fused to the proto- and deutocerebrum. There has been a contentious debate whether the first, antenna-like appendage of *Fuxianhuia,* was a sensory protocerebral 'primary' antenna (e.g., Scholtz and Edgecombe 2005) or a deutocerebral appendage that was largely unspecialized and served both in nutrition and as a sensory organ (e.g., Waloszek et al. 2005; Bergström et al. 2008). The new material seems to lend further support for the appendage being deutocerebral. The primary function (if any) remains unclear, but it is possible that a sensory 'secondary' antenna was already present in the arthropod ground pattern and not only in the mandibulate lineage. We hold the interpretation of this single specimen to be somewhat problematic, however, and would hesitate for the moment to reach such general conclusions on the basis of this specimen alone.

In summary, there is fossil evidence that the last common ancestor of Chelicerata and Mandibulata (i.e., crown group Arthropoda) had a head comprising the ocular region and at least

three, but more likely four appendage-bearing segments. The anterior appendage inserts laterally to the hypostome/labrum and probably represents the deutocerebral appendage, but a smaller appendage-like structure might have been present anteriorly of this appendage. The postantennular appendages display little differentiation other than a gradual shift anteriorly toward limbs more adapted to feeding.

References

Abzhanov A, Kaufman TC (1999) Novel regulation of the homeotic gene *Scr* associated with a crustacean leg-to-maxilliped appendage transformation. Development 126:1121–1128

Abzhanov A, Kaufman TC (2000) Embryonic expression patterns of the Hox genes of the crayfish *Procambarus clarkii* (Crustacea, Decapoda). Evol Dev 2:271–283

Aguinaldo AMA, Turbeville JM, Linford LS, Rivera MC, Garey JR, Raff RA, Lake JA (1997) Evidence for a clade of nematodes, arthropods and other moulting animals. Nature 387:489–493

Andersson A (1977) The organ of Bellonci in ostracodes: an ultrastructural study of the rod-shaped, or frontal, organ. Acta Zool (Stockh) 58:197–204

Averof M (1998) Origin of the spider's head. Nature 395:436–437

Averof M, Patel NH (1997) Crustacean appendage evolution associated with changes in Hox gene expression. Nature 388:682–686

Bergström J, Hou X, Zhang X, Clausen S (2008) A new view of the Cambrian arthropod *Fuxianhuia*. GFF 130:189–201

Bitsch C, Bitsch J (2002) The endoskeletal structures in arthropods: cytology, morphology and evolution. Arthropod Struct Dev 30:159–177

Boudreaux HB (1979) Significance of intersegmental tendon system in arthropod phylogeny and monophyletic classification of Arthropoda. In: Gupta AP (ed) Arthropod phylogeny. Van Nostrand Reinhold, New York, pp 551–586

Brenneis G, Arango CP, Scholtz G (2011) Morphogenesis of *Pseudopallene* sp. (Pycnogonida, Callipallenidae) I: embryonic development. Dev Genes Evol 221:309–328

Brenneis G, Richter S (2010) Architecture of the nervous system in Mystacocarida (Arthropoda, Crustacea)—an immunohistochemical study and 3D reconstruction. J Morphol 271:169–189

Brenneis G, Ungerer P, Scholtz G (2008) The chelifores of sea spiders (Arthropoda, Pycnogonida) are the appendages of the deutocerebral segment. Evol Dev 10:717–724

Briggs DEG, Lieberman BS, Hendricks JR, Halgedahl SL, Jarrard RD (2008) Middle Cambrian arthropods from Utah. J Paleontol 82:238–254

Budd GE (1996) The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. Lethaia 29:1–14

Budd GE (1998) The morphology and phylogenetic significance of *Kerygmachela kierkegaardi* Budd (Buen Formation, Lower Cambrian, N Greenland). Trans R Soc Edinb Earth Sci 89:249–290

Budd GE (2002) A palaeontological solution of the arthropod head problem. Nature 417:271–275

Budd GE (2008) Head structure in upper stem-group euarthropods. Palaeontology 51:561–573

Budd GE, Daley AC (2011) The lobes and lobopods of *Opabinia regalis* from the middle Cambrian Burgess Shale. Lethaia 45:83–95

Butterfield NJ (2002) *Leanchoilia* guts and the interpretation of three-dimensional structures in Burgess Shale-type fossils. Paleobiology 28:155–171

Campbell LI, Rota-Stabelli O, Edgecombe GD, Marchioro T, Longhorn SJ, Telford MJ, Philippe H, Rebecchi L, Peterson KJ, Pisani D (2011) MicroRNAs and phylogenomics resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of Arthropoda. Proc Natl Acad Sci USA 108:15920–15924

Casanova B (1991) Origine protocéphalique antennaire de la carapace chez les Leptostracés, Mysidacés et Eucarides (Crustacés). Cr hebd Acad Sci 312(III):461–468

Chen J, Edgecombe GD, Ramsköld L, Zhou G (1995) Head segmentation in Early Cambrian *Fuxianhuia*: Implications for arthropod evolution. Science 268:1339–1343

Chen J, Waloszek D, Maas A (2004) A new 'great-appendage' arthropod from the Lower Cambrian of China and homology of chelicerate chelicerae and raptorial antero-ventral appendages. Lethaia 37:3–20

Cisne JL (1974) Trilobites and the origin of arthropods. Science 186:13–18

Cisne JL (1975) Anatomy of *Triarthrus* and the relationships of the Trilobita. Fossils Strata 4:45–63

Daley AC, Budd GE, Caron J, Edgecombe GD, Collins D (2009) The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. Science 323:1597–1600

Denis JR, Bitsch J (1973) Structure céphalique dans les ordres des insectes. In: Grassé PP (ed) Traité de zoologie: Anatomie, systématiques, biologie, tome VIII Insectes: tête, aile, vol. Masson, Paris, pp 101–593

Dewel RA, Dewel WC (1996) The brain of *Echiniscus viridissimus* Peterfi, 1956 (Heterotardigrada): A key to understanding the phylogenetic position of tardigrades and the evolution of the arthropod head. Zool J Linn Soc 116:35–49

Domínguez Camacho M (2011) Cephalic musculature in five genera of Symphyla (Myriapoda). Arthropod Struct Dev 40:159–185

Dunn CW, Hejnol A, Matus DQ, Pang K, Browne WE, Smith SA, Seaver E, Rouse GW, Obst M, Edgecombe GD, Sorensen MV, Haddock SHD, Schmidt-Rhaesa A, Okusu A, Kristensen RM, Wheeler WC, Martindale MQ, Giribet G (2008) Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452:745–749

Dzik J (2011) The xenusian-to-anomalocaridid transition within the lobopodians. Boll Soc Paleontol Ital 50:65–74

Edgecombe GD (2004) Morphological data, extant Myriapoda, and the myriapod stem-group. Contrib Zool 73(3):207–252

Edgecombe GD (2010) Arthropod phylogeny: an overview from the perspectives of morphology, molecular data and the fossil record. Arthropod Struct Dev 39:74–87

Edgecombe GD, García-Bellido DC, Paterson JR (2011) A new leanchoiliid megacheiran arthropod from the Lower Cambrian Emu Bay Shale, South Australia. Acta Palaeontol Polon 56:385–400

Elofsson R (1971) The ultrastructure of a chemoreceptor organ in the head of copepod crustaceans. Acta Zool 52:299–315

Elofsson R, Lake PS (1971) On the cavity receptor organ (X-organ or organ of Bellonci) of *Artemia salina* (Crustacea: Anostraca). Ztschr Zellforsch mikr Anat 326:319–326

Eriksson BJ, Budd GE (2000) Onychophoran cephalic nerves and their bearing on our understanding of head segmentation and stem-group evolution of Arthropoda. Arthropod Struct Dev 29:197–209

Eriksson BJ, Tait NN, Budd GE (2003) Head development in the onychophoran *Euperipatoides kanangrensis* with particular reference to the central nervous system. J Morphol 255:1–23

Eriksson BJ, Tait NN, Budd GE, Janssen R, Akam M (2010) Head patterning and Hox gene expression in an onychophoran and its implications for the arthropod head problem. Dev Genes Evol 220:117–122

Eriksson ME, Terfelt F, Elofsson R, Marone F (2012) Internal soft-tissue anatomy of Cambrian 'Orsten' arthropods as revealed by synchrotron x-ray tomographic microscopy. PLOSone 7(8):e42582. doi: 10.1371/journal.pone.0042582

Fanenbruck M (2003) Die Anatomie des Kopfes und des cephalen Skelett-Muskelsystems der Crustacea, Myriapoda und Hexapoda: Ein Beitrag zum phylogenetischen System der Mandibulata und zur Kenntnis der Herkunft der Remipedia und Tracheata. Doctoral Thesis, Fakultät für Biologie, Ruhr-Universität Bochum, Bochum

Firstman B (1973) The relationship of the chelicerate arterial system to the evolution of the endosternite. J Arachnol 1:1–54

Frase T, Richter S (2013) The fate of the onychophoran antenna. Dev Genes Evol. doi:10.1007/s00427-013-0435-x

Fritsch M, Kaji T, Olesen J, Richter S (2013) The development of the nervous system in Laevicaudata (Crustacea, Branchiopoda): Insights into the evolution and homologies of branchiopod limbs and 'frontal organs'. Zoomorphology. doi:10.1007/s00435-012-0173-0

Fritsch M, Richter S (2010) The formation of the nervous system during larval development in *Triops cancriformis* (Bosc) (Crustacea, Branchiopoda): An immunohistochemical survey. J Morphol 271:1457–1481

Giribet G (2003) Molecules, development and fossils in the study of metazoan evolution; articulata versus Ecdysozoa revisited. Zoology 106:303–326

Gruner HE (1993) Arthropoda (ohne Insecta). In: Gruner HE (ed) Lehrbuch der speziellen Zoologie. Gustav Fischer Verlag, Jena. I(4):1–1279

Gruner HE, Scholtz G (2004) Segmentation, tagmata, and appendages. In: Forest J, von Vaupel Klein JC, Schram FR (eds) Treatise on Zoology—anatomy, taxonomy, biology. The Crustacea revised and updated from the Traité de Zoologie, vol 1. Brill, Leiden, pp13–57

Harzsch S (2004) Phylogenetic comparison of serotonin-immunoreactive neurons in representatives of the Chilopoda, Diplopoda and Chelicerata: implications for arthropod relationships. J Morphol 259:198–213

Haug JT, Briggs DE, Haug C (2012a) Morphology and function in the Cambrian Burgess Shale megacheiran arthropod *Leanchoilia superlata* and the application of a descriptive matrix. BMC Evol Biol 12:162. doi:10.1186/1471-2148-12-162

Haug JT, Waloszek D, Maas A, Liu Y, Haug C (2012b) Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. Palaeontology 55:369–399

Hessler RR (1964) The Cephalocarida: comparative skeletomusculature. Mem Connect Acad Arts Sci 16:1–97

Heuer CM, Loesel R (2009) Three-dimensional reconstruction of mushroom body neuropils in the polychaete species *Nereis diversicolor* and *Harmothoe areolata* (Phyllodocida, Annelida). Zoomorphology 128:219–226

Heuer CM, Müller CHG, Todt C, Loesel R (2010) Comparative neuroanatomy suggests repeated reduction of neuroarchitectural complexity in Annelida. Front Zool 7:13. doi:10.1186/1742-9994-7-13

Janssen R, Damen WGM, Budd GE. (2011) Expression of *collier* in the premandibular segment of myriapods: support for the traditional Atelocerata concept or a case of convergence? BMC Evol Biol 11:50. doi:10.1186/1471-2148-11-50

Janssen R, Prpic N-M, Damen WGM (2006) A review of the correlation of tergites, sternites, and leg pairs in diplopods. Front Zool 3:2

Kimm MA, Prpic NM (2006) Formation of the arthropod labrum by fusion of paired and rotated limb-bud-like primordia. Zoomorphology 125:147–155

Kirsch R, Richter S (2007) The nervous system of *Leptodora kindtii* (Branchiopoda, Cladocera) surveyed with Confocal Scanning Microscopy (CLSM), including general remarks on the branchiopod neuromorphological ground pattern. Arthropod Struct Dev 36:143–156

Koch M (2000) The cuticular cephalic endoskeleton of primarily wingless hexapods: Ancestral state and evolutionary changes. Pedobiologia 44:374–385

Koch M (2003) Monophyly of the Myriapoda? Reliability of current arguments. Afr Invertebr 44:137–153

Lauterbach KE (1989) Das Pan-Monophylum—Ein Hilfsmittel für die Praxis der phylogenetischen Systematik. Zool Anz 223:139–156

Legg DA, Sutton MD, EdgecombeGD, Caron J-B (2012) Cambrian bivalved arthropod reveals origin of arthrodization. Proc R Soc B doi:10.1098/rspb.2012.1958

Liu J, Shu D, Han J, Zhang Z, Zhang X (2006) A large xenusiid lobopod with complex appendages from the Lower Cambrian Chengjiang Lagerstätte. Acta Pal Pol 51:215–222

Liu J, Shu D, Han J, Zhang Z, Zhang X (2007) Morphoanatomy of the lobopod *Magadictyon* cf. *haikouensis* from the Early Cambrian Chengjiang Lagerstätte, South China. Acta Zool 88:279–288

Liu J, Steiner M, Dunlop JA, Keupp H, Shu D, Ou Q, Han J, Zhang Z, Zhang X (2011) An armoured Cambrian lobopodian from China with arthropod-like appendages. Nature 470:526–530

Liubicich DM, Serano JM, Pavlopoulos A, Kontarakis Z, Protas ME, Kwan E, Chatterjee S, Tran KD, Averof M, Patel NH (2009) Knockdown of *Parhyale* Ultrabithorax recapitulates evolutionary changes in crustacean appendage morphology. Proc Natl Acd Sci USA 106:13892–13896

Ma X, Hou X, Aldridge RJ, Siveter DJ, Siveter DJ, Gabbott SE, Purnell MA, Parker AR, Edgecombe GD (2012a) Morphology of Cambrian lobopodian eyes from the Chengjiang Lagerstätte and their evolutionary significance. Arthropod Struct Dev 41:495–504

Ma X, Hou X, Bergström J (2009) Morphology of *Luolishania longicruris* (Lower Cambrian, Chengjiang Lagerstätte, SW China) and the phylogenetic relationships within lobopodians. Arthropod Struct Dev 38:271–291

Ma X, Hou X, Edgecombe GD, Strausfeld NJ (2012b) Complex brain and optic lobes in an early Cambrian arthropod. Nature 490:258–262

Maas A, Waloszek D, Müller KJ (2003) Morphology, ontogeny and phylogeny of the Phosphatocopina (Crustacea) from the Upper Cambrian 'Orsten' of Sweden. Fossils Strata 49:1–238

Manton SM (1964) Mandibular mechanisms and the evolution of arthropods. Phil Trans R Soc B 247:1–183

Manuel M, Jager M, Murienne J, Clabaut C, Le Guyade H (2006) Hox genes in sea spiders (Pycnogonida) and the homology of arthropod head segments. Dev Genes Evol 216:481–491

Maxmen A, Browne WE, Martindale MQ, Giribet G (2005) Neuroanatomy of sea spiders implies an appendicular origin of the protocerebral segment. Nature 437:1144–1148

Mayer G (2006) Structure and development of onychophoran eyes: what is the ancestral visual organ in arthropods? Arthr Struct Dev 35:231–245

Mayer G, Harzsch S (2008) Distribution of 5-HT-like immunoreactivity in the trunk of *Metaperipatus blainvillei* (Onychophora, Peripatopsidae): Implications for nervous system evolution in Arthropoda. J Comp Neurol 507:1196–1208

Mayer G, Whitington PM, Sunnucks P, Pflüger H-J (2010) A revision of brain composition in Onychophora (velvet worms) suggests that the tritocerebrum evolved in arthropods. BMC Evol Biol 10:255. doi:10.1186/1471-2148-10-255

Meier R, Richter S (1992) Suggestions for a more precise usage of proper names of taxa. Ambiguities related to the stem lineage concept. Ztschr Zool Syst Evolforsch 30:81–88

Mittmann B, Scholtz G (2003) Development of the nervous system in the "head" of *Limulus polyphemus* (Chelicerata: Xiphosura): Morphological evidence for a correspondence between the segments of the chelicerae and of the (first) antennae of Mandibulata. Dev Genes Evol 213:9–17

Mittmann B, Wolff C (2012) Embryonic development and staging of the cobweb spider *Parasteatoda tepidariorum* C. L. Koch, 1841 (syn.: *Achaearanea tepidariorum*; Araneomorphae; Theridiidae). Dev Genes Evol 222:189–216

Møller OS, Olesen J, Høeg JT (2004) On the larval development of *Eubranchipus grubii* (Crustacea, Branchiopoda, Anostraca), with notes on the basal phylogeny of the Branchiopoda. Zoomorphology 123:107–123

Ou Q, Shu D, Mayer G (2012) Cambrian lobopodians and extant onychophorans provide new insights into early cephalization in Panarthropoda. Nat Commun 3:1261. doi:10.1038/ncomms2272

Pavlopoulos A, Kontarakis Z, Liubicich DM, Serano JM, Akam M, Patel NH, Averof M (2009) Probing the evolution of appendage specialization by Hox gene misexpression in an emerging model crustacean. Proc Natl Acad Sci USA 106:13897–13902

Persson DK, Halberg KA, Jørgensen A, Møbjerg N, Kristensen RM (2012) Neuroanatomy of *Halobiotus crispae* (Eutardigrada: Hypsibiidae): Tardigrade brain structure supports the clade Panarthropoda. J Morphol 273:1227–1245

Pigliucci M, Müller GB (2010) Elements of an extended evolutionary synthesis. In: Pigliucci M, Müller GB (eds) Evolution: the extended synthesis. MIT Press, Cambridge, pp 3–18

Posnien NF, Bashasab F, Bucher G (2009) The insect upper lip (labrum) is a nonsegmental appendage-like structure. Evol Dev 11:479–487

Ramsköld L, Chen J (1998) Cambrian lobopodians: morphology and phylogeny. In: Edgecombe GD (ed) Arthropod fossils and phylogeny. Columbia University Press, New York, pp 107–150

Ramsköld L, Chen J, Edgecombe GD, Zhou G (1997) *Cindarella* and the arachnate clade Xandarellida (Arthropoda, Early Cambrian) from China. Trans R Soc Edinb Earth Sci 88:19–38

Regier JC, Shultz JW, Zwick A, Hussey A, Ball B, Wetzer R, Martin JW, Cunningham CW (2010) Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. Nature 463:1079–1083

Richter S, Loesel R, Purschke G, Schmidt-Rhaesa A, Scholtz G, Stach T, Vogt L, Wanninger A, Brenneis G, Döring C, Faller S, Fritsch M, Grobe P, Heuer CM, Kaul S, Møller OS, Müller CHG, Rieger V, Rothe BH, Stegner MEJ, Harzsch S (2010) Invertebrate neurophylogeny—suggested terms and definitions for a neuroanatomical glossary. Front Zool 7:29. doi: 10.1186/1742-9994-7-29

Schaeper ND, Pechmann M, Damen WG, Prpic NM, Wimmer EA (2010) Evolutionary plasticity of collier function in head development of diverse arthropods. Dev Biol 344:363–376

Scholtz G (1997) Cleavage, germ band formation and head segmentation: the ground pattern of the Euarthropoda. In: Fortey RA, Thomas RH (eds) Arthropod relationships. Chapman & Hall, London, pp 317–332

Scholtz G (2002) The Articulata hypothesis—or what is a segment? Org Divers Evol 2:197–215

Scholtz G, Edgecombe GD (2005) Heads, Hox and the phylogenetic position of trilobites. In: Koenemann S, Jenner R (eds) Crustacea and arthropod relationships (Crustacean Issues 16). CRC Press, Boca Raton, pp 139–165

Scholtz G, Edgecombe GD (2006) The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. Dev Genes Evol 216:395–415

Shultz JW (1999) Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock) (Arachnida: Amblypygi), and its evolutionary significance. Zool J Linn Soc 126:81–116

Shultz JW (2000) Skeletomuscular anatomy of the harvestman *Leiobunum aldrichi* (Weed, 1893) (Arachnida: Opiliones) and its evolutionary significance. Zool J Linn Soc 128:401–438

Shultz JW (2001) Gross muscular anatomy of *Limulus polyphemus* (Xiphosura, Chelicerata) and its bearing on evolution in the Arachnida. J Arachnol 29:283–303

Shultz JW (2007) Morphology of the prosomal endoskeleton of Scorpiones (Arachnida) and a new hypothesis for the evolution of cuticular cephalic endoskeletons in arthropods. Arthropod Struct Dev 36:77–102

Siewing R (1969) Lehrbuch der vergleichenden Entwicklungsgeschichte der Tiere. Parey, Hamburg

Sombke A, Lipke E, Kenning M, Müller C, Hansson BS, Harzsch S (2012) Comparative analysis of deutocerebral neuropils in Chilopoda (Myriapoda): Implications for the evolution of the arthropod olfactory system and support for the Mandibulata concept. BMC Neurosci 13:1. doi:10.1186/1471-2202-13-1

Stegner MEJ, Richter S (2011) Morphology of the brain in Hutchinsoniella macracantha (Cephalocarida, Crustacea). Arthr Struct Dev 40:221–243

Stein M (2010) A new arthropod from the Early Cambrian of North Greenland with a 'great appendage' like antennula. Zool J Linn Soc 158:477–500

Stein M, Selden PA (2012) A restudy of the Burgess Shale (Cambrian) arthropod *Emeraldella brocki* and reassessment of its affinities. J Syst Palaeontol 10:361–383

Stein M, Waloszek D, Maas A (2005) *Oelandocaris oelandica* and the stem lineage of Crustacea. In: Koenemann S, Jenner RA (eds) Crustacea and arthropod relationships (Crustacean Issues 16). CRC/Taylor and Francis, Boca Raton, pp 55–72

Steinmetz PR, Urbach R, Posnien N, Eriksson J, Kostyuchenko RP, Brena C, Guy K, Akam M, Bucher G, Arendt D (2010) Six3 demarcates the anterior-most developing brain region in bilaterian animals. EvoDevo 1:14. doi:10.1186/2041-9139-1-14

Strausfeld NJ (2012) Arthropod brains: evolution, functional elegance and historical significance. Belknap Press, Cambridge

Strausfeld NJ, Strausfeld MC, Stowe S, Rowell D, Loesel R (2006) The organization and evolutionary implications of neuropils and their neurons in the brain of the onychophorans *Euperipatoides rowelli*. Arthropod Struct Dev 135:169–196

Szucsich NU, Pennerstorfer M, Wirkner CS (2011) The mouthparts of *Scutigerella immaculata*: correspondences and variation among serially homologous head appendages. Arthropod Struct Dev 40:105–121

Telford MJ, Thomas RH (1998) Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. Proc Natl Acad Sci USA 95:10671–10675

Ungerer P, Wolff C (2005) External morphology of limb development in the amphipod *Orchestia cavimana* (Crustacea, Malacostraca, Peracarida). Zoomorphology 124:89–99

Vannier J, Chen J (2002) Digestive system and feeding mode in Cambrian naraoiid arthropods. Lethaia 35:107–120

Vogt L (2008) Learning from Linnaeus: towards developing the foundations for a general structure concept for morphology. Zootaxa 1950:123–152

Vogt L, Bartolomaeus T, Giribet G (2010) The linguistic problem of morphology: structure versus homology and the standardization of morphological data. Cladistics 26:301–325

von Reumont BM, Jenner RA, Wills MA, Dell'Ampio E, Pass G, Ebersberger I, Meyer B, Koenemann S, Iliffe TM, Stamatakis A, Niehuis O, Meusemann K, Misof B (2012) Pancrustacean phylogeny in the light of new

phylogenomic data: support for Remipedia as the possible sister group of Hexapoda. Mol Biol Evol 29(3):1031–1045

Waloszek D, Chen J, Maas A, Wang X (2005) Early Cambrian arthropods—new insights into arthropod head and structural evolution. Arthropod Struct Dev 34:189–205

Waloszek D, Dunlop J (2002) A larval sea spider (Arthropoda: Pycnogonida) from the Upper Cambrian "Orsten" of Sweden, and the phylogenetic position of pycnogonids. Palaeontology 45:421–446

Waloszek D, Maas A, Chen J, Stein M (2007) Evolution of cephalic feeding structures and the phylogeny of Arthropoda. Palaeogeogr Palaeocl 254:273–287

Whittington HB (1993) Anatomy of the Ordovician trilobite Placoparia. Phil Trans R Soc B 339:109–118

Wirkner CS, Richter S (2010) Evolutionary morphology of the circulatory system in Peracarida (Malacostraca; Crustacea). Cladistics 26:143–167

Zantke J, Wolff C, Scholtz G (2008) Three-dimensional reconstruction of the central nervous system of *Macrobiotus hufelandi* (Eutardigrada, Parachela): Implications for the phylogenetic position of Tardigrada. Zoomorphology 127:21–36

Zhang X, Briggs DEG (2007) The nature and significance of the appendages of *Opabinia* from the Middle Cambrian Burgess Shale. Lethaia 40:161–173

Zhang X, Shu D, Erwin DH (2007) Cambrian naraoiids (Arthropoda): morphology, ontogeny, systematics, and evolutionary relationships. J Paleontol 81(68): 1–52