Neurophylogeny: Architecture of the nervous system and a fresh view on arthropod phyologeny

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Synopsis The phylogenetic relationships within the Arthropoda have been controversial for more than a century. Today, comparative studies on the structure and development of the nervous system contribute important arguments to this discussion, so that the term "neurophylogeny" was coined for this discipline. The large number of recent studies on the nervous system in various nonmodel arthropods indicates that we are far advanced in the process of analyzing the cellular architecture of the arthropod nervous system in a depth that will ultimately provide characters at a level of resolution equal or even superior to that of characters traditionally used in morphological phylogenetic studies. This article sets out to summarize the current state of the discussion on arthropod phylogeny and briefly evaluates the morphological characters that have been used as arguments in favor of the traditional Tracheata hypothesis. Then, a thorough overview is given of characters derived from structure and development of the arthropod brain and the ventral nerve cord from the cellular level to the level of larger neuropil systems. These characters support the new Tetraconata hypothesis suggested by Dohle and provide evidence for a clade that unites malacostracan and remipede crustaceans with the Hexapoda.

Arthropod relationships: Morphology versus molecules

Within the Euarthropoda, the monophyletic taxa Crustacea (Malacostraca and Entomostraca) and Tracheata (Hexapoda and Myriapoda [Chilopoda and Progoneata]) traditionally have been perceived as sister groups (for example, Westheide and Rieger 1996; Kraus 1997, 2001; Ax 1999; Walossek 1999; Klass and Kristensen 2001; Waloszek 2003; Bitsch C and Bitsch J 2004). This view has been challenged in recent years by studies in the field of molecular phylogeny, most of which have not supported the monophyly of the Tracheata but instead have favored a close relationship of Hexapoda and Crustacea (for example, Shultz and Regier 2000; Cook and others 2001; Friedrich and Tautz 2001; Giribet and others 2001; Hwang and others 2001; Peterson and Eernisse 2001; Regier and Shultz 2001a, 2001b; Burmester 2002; Kusche and others 2002; Pisani and others 2004). Furthermore, some of these studies have also suggested a sister-group relationship of Myriapoda (Chilopoda plus Progoneata) and Chelicerata (for example, Hwang and others 2001; Kusche and Burmester 2001; "Paradoxopoda" in Mallatt and others 2004; "Myriochelata" in Pisani and others 2004), whereas other studies have not.

The morphological characters that support a monophyly of the Tracheata are currently being critically evaluated (for example, Dohle 1997, 2001; Paulus 2000; Harzsch 2001a; Nielsen 2001; Klass and Kristensen 2001; Richter 2002; Fanenbruck 2003; Bitsch C and Bitsch J 2004; Schram and Koenemann 2004) and an alternative hypothesis on euarthropod relationships has been suggested, the Tetraconata concept (Dohle 2001; Richter 2002). The Tetraconata embrace the hexapods as well as malacostracan and nonmalacostracan crustaceans, and their name refers to the tetrapartite crystalline cone in the ommatidia as a synapomorphy of these 3 groups. The most important characters discussed as possible synapomorphies uniting the Tracheata are briefly reviewed here.

An important synapomorphy of the Hexapoda and Myriapoda in the Tracheata hypothesis, the monophyletic origin of tracheae, has been extensively discussed by Dohle (1997), Klass and Kristensen (2001), and C Bitsch and J Bitsch (2004). Morphological (Hilken 1998) and palaeontological evidence (Haas F and others 2003; but see Willmann 2005) now sheds doubt on the homology of hexapodan and myriapodan

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tracheae and spiracles and instead suggests an independent conquest of land by Hexapoda, Chilopoda, and Progoneata. Dohle (1997) even suggests a 6-fold convergent evolution of tracheae in the Tracheata. In the ground pattern of Euarthropoda there exists a functional link between circulation and respiration (McMahon 2001). By contrast, in the Hexapoda and derived chilopod taxa (Pleurostigmorpha) oxygen transport is no longer accomplished by the circulatory system but by a sophisticated system of tracheae (Hertel and Pass 2002; Wirkner and Pass 2002). However, in the ground pattern of the Chilopoda, as represented by the Scutigeromorpha, the plesiomorphic euarthropod state of a circulatory system with respiratory function is still present (Wirkner and Pass 2002). This fact lends weight to the suggestion that resulting from the convergent innovation of the tracheal system in Scutigeromorpha and Pleurostigmorpha (Chilopoda) as well as Hexapoda (Hilken 1998), the circulatory system convergently lost its role in oxygen transport in Chilopoda and Hexapoda (Hertel and Pass 2002; Wirkner and Pass 2002). Furthermore, biochemical and molecular properties of arthropod hemocyanins recently excluded a close phylogenetic relationship of Diplopoda and Chilopoda with the Hexapoda (Jaenicke and others 1999; Kusche and Burmester 2001; Burmester 2002; Kusche and others 2002).

The malpighian tubules are another character that has traditionally been discussed as an apomorphy in the ground pattern of the Tracheata (Dohle 1997; Klass and Kristensen 2001; Nielsen 2001; Bitsch C and Bitsch J 2004). In Hexapoda and Myriapoda, these excretory organs are associated with the digestive system at the interface of the midgut and rectum. However, malpighian tubules with very similar functions and cytoarchitectonics are also present in Chelicerata and even Tardigrada (for example, Møbjerg and Dahl 1996). Therefore, and despite the open debate on their entodermal versus ectodermal developmental origin, Dohle (1997) and Klass and Kristensen (2001) consider the malpighian tubules to be only a weak argument for a monophyly of Tracheata; rather, they suspect a convergent evolution coinciding with the conquest of land.

Postantennal organs (also known as temporal organs or organs of Tömösváry) are sensory organs whose function has not yet been elucidated satisfactorily. Specifically, their relationship to possible crustacean homologs, the organs of Belonci, has not been explored in sufficient depth (Dohle 1997; Klass and Kristensen 2001; Bitsch C and Bitsch J 2004). Therefore, these authors take a rather cautious attitude and refrain from suggesting these structures are an apomorphy in the tracheatan ground pattern.

Myriapoda and Hexapoda lack the appendage (antenna 2 in Crustacea) of the tritocerebral segment (hence also the name "Atelocerata"). The absence of this appendage is regarded as a synapomorphy of Myriapoda and Hexapoda in the latest analysis of C Bitsch and J Bitsch (2004). However, several authors have repeatedly discouraged inclusion of the absence of characteristics in cladistic analyses. For example, Klass and Kristensen (2001) consider the absence of this appendage to be "not a strong argument," and Dohle (1997) calls it a "very weak argument."

The absence of an antagonistic muscle to the depressor of the last podomere of the walking limbs in Hexapoda, Chilopoda, and Diplopoda has been regarded as an autapomorphy of the Tracheata (Klass and Kristensen 2001; Bitsch C and Bitsch J 2004). However, Wolf and Harzsch (2002a) demonstrated that a similar arrangement is present in scorpions, too. What is more, they have summarized evidence that single muscles that lack an antagonistic counterpart but instead act against the passive bending of the joint by the animal's body weight, hemolymph pressure, or elastic properties of the cuticle are common within all arthropod taxa. Along the same lines of argument, the proximal location of the depressor of the last podomere (plus the long tendon) is an arrangement found in both Chelicerata and Tracheata. These points question the validity of the aforementioned argument for establishing the monophyly of Tracheata. Instead, they raise the possibility of a convergent evolution of these characteristics within Chelicerata, Hexapoda, Chilopoda, and Diplopoda. Rather than reflecting phylogenetic relationships, the absence of these muscles may have been promoted by mechanical constraints related to the marine versus terrestrial lifestyle (for example different Reynolds numbers; Wolf and Harzsch 2002a).

Neurophylogeny: The role of the nervous system

Hanström (1928) and his teacher Holmgren (1916) were among the first authors to explore the relevance of brain architecture in understanding arthropod phylogeny (Fig. 1). Since then, structure and development of the nervous system have played important roles in the debate on arthropod relationships ("neurophylogeny"; for reviews, see Arbas and others 1991; Breidbach 1995; Strausfeld and others 1995; Wegerhoff and Breidbach 1995; Whitington 1996; Nilsson and Osorio 1997; Whitington and Bacon 1997; Strausfeld 1998; Strausfeld and others 1998; Strausfeld and Hildebrand 1999; Paulus 2000; Dohle 2001; Harzsch 2001a, 2002c, 2004a; Richter 2002;

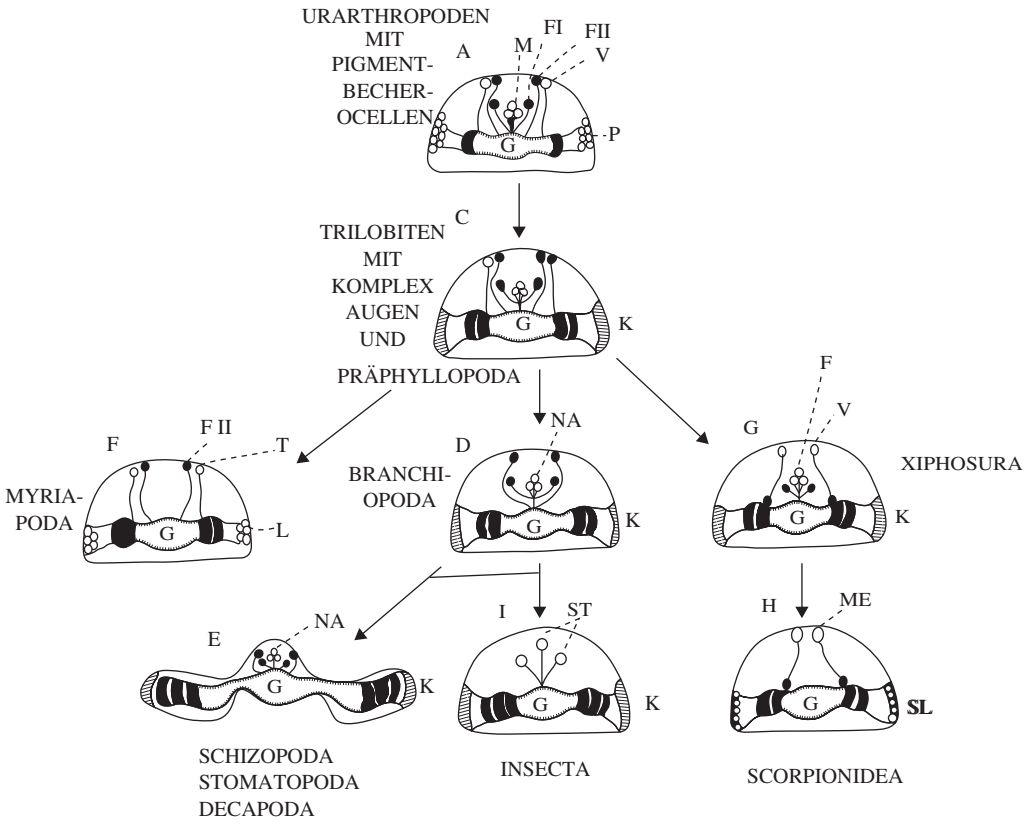


Fig. 1 Phylogeny of the Arthropoda based on neuronal characteristics. Modified from Hanström (1928).

Harzsch, Müller, and Wolf 2005; Strausfeld 2005). Recent examples of such phylogenetic studies have focused on brain design of Onychophora (Eriksson and Budd 2000; Eriksson and others 2003), Tardigrada (Dewel RA and Dewel WC 1996; Dewel and others 1999), Pycnogonida (Maxmen and others 2005), Chelicerata (Breidbach and Wegerhoff 1993; Strausfeld and Barth 1993; Strausfeld and others 1993; Breidbach and others 1995; Mittmann and Scholtz 2003; Harzsch, Wildt, and others 2005), remipede crustaceans (Fanenbruck and others 2004; Fanenbruck and Harzsch 2005), as well as the central complex (Utting and others 2000; Harzsch and Glötzner 2002; Loesel and others 2002; Loesel 2004) and the olfactory system of Mandibulata (Strausfeld and Hildebrand 1999; Schachtner and others 2005). Other features that are being explored are the structure (Melzer and others 1997; Richter 1999; Paulus 2000; Müller C and others 2003; Bitsch C and Bitsch J 2005) and development of the compound eyes (Melzer and others 2000; Hafner and Tokarski 2001) and optic ganglia (Harzsch, Benton, and others 1999; Harzsch and Walossek 2001; Harzsch 2002a; Wildt and Harzsch 2002; Sinakevitch and others 2003; Strausfeld 2005). Concerning the ventral nerve cord, the architecture of the thoracic ganglia (Wiens and Wolf 1993; Elsson 1996) and the morphology of individually identified neurons have been analyzed (Harzsch and Waloszek 2000; Harzsch 2003a, 2004b; reviewed in Harzsch, Müller, and Wolf 2005; Pflüger and Stevenson 2005). Furthermore, developmental aspects such as early axogenesis (Whitington 1996; Whitington and Bacon 1997; Gerberding and Scholtz 1999, 2001) and stem cell proliferation (Harzsch and others 1998; Harzsch 2001b; Stollewerk and others 2001; Dove and Stollewerk 2003; reviewed in Harzsch 2002b, 2003b; Stollewerk and others 2003; Stollewerk 2006) have been examined from an evolutionary point of view. This article sets out to summarize the current knowledge on nervous system evolution within the Euarthropoda and its impact on our understanding of arthropod phylogeny. Clearly, the large number of recent studies on the nervous system in various non-model arthropods (Fig. 2) indicates that we are far advanced in the process of analyzing the cellular architecture of the arthropod brain in a depth that will ultimately provide characters at a level of resolution equal to or even superior to that of the characters traditionally used in morphological phylogenetic studies.

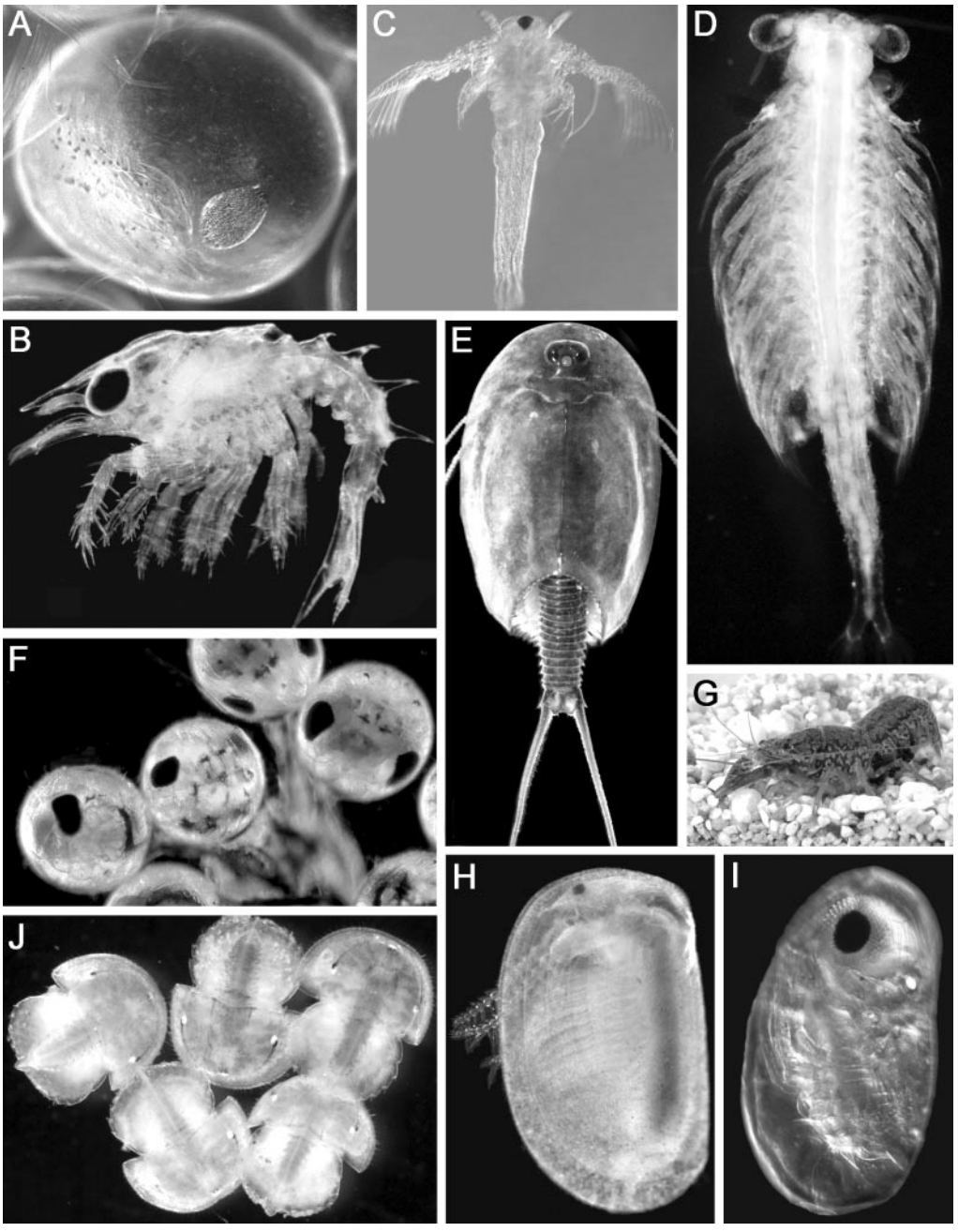


Fig. 2 Various nonmodel arthropods whose nervous systems are crucial for reconstructing arthropod phylogeny based on neuronal characteristics. (A) Embryo and (B) first larva of the American lobster *Homarus americanus* (Malacostraca, Decapoda, Homarida). (C) Metanauplius and (D) adult of the brine shrimp *Artemia salina* (Branchiopoda, Anostraca). (E) The dinosaur shrimp *Triops cancriformis* (Branchiopoda, Phyllopoda, Notostraca). (F) Embryos of the spider crab *Hyas araneus* (Malacostraca, Decapoda, Brachyura). (G) An adult marbled crayfish (Malacostraca, Decapoda, Astacida). (H) *Leptestheria dahalacensis* (Branchiopoda, Phyllopoda, Conchostraca). (I) Embryo of the shrimp *Palaemonetes argentinus* (Malacostraca, Decapoda, Caridea). (J) Trilobite larvae of the horseshoe "crab" *Limulus polyphemus* (Chelicerata, Xiphosura).

Structure of the lateral eyes

The visual system provides many important characteristics relevant to the debate on the phylogenetic relationships among arthropods. Discussion focuses on structure (Paulus 1979, 2000; Elofsson 1992a; Melzer and others 1997; Richter 1999; Müller C and others 2003; Bitsch C and Bitsch J 2005) and development of the lateral eyes (Melzer and others 2000; Hafner and Tokarski 2001) as well as the architecture of the optic ganglia (Harzsch, Benton, and others 1999, 2005a; Harzsch and Walossek 2001; Harzsch 2002a; Wildt and Harzsch 2002; Sinakevitch and others 2003;

Harzsch, Müller, and Wolf 2005; Strausfeld 2005). *Limulus polyphemus* is a representative of the Chelicerata in which lateral eyes, composed of several similar optical units, the ommatidia, are still present. Each ommatidium is composed of a variable number of more than 300 cells (Fahrenbach 1975), including approximately 100 distal infra-ommatidial pigment cells, approximately 100 cone cells, approximately 100 proximal pigment cells, and an average of 10–13 retinula cells and a single eccentric. Within the Chelicerata, the Scorpiones, Aranae, Pseudoscorpiones, Solifugae, and some Acari have a varying number of laterally dispersed eyes that by modification may have derived from lateral faceted eyes (Paulus 1979; Schliwa and Fleissner 1979, 1980; Spreitzer and Melzer 2003). Diplopoda and Chilopoda also have lateral eyes, which are composed of several similar subunits; however, in terms of the architecture of these subunits, Diplopoda and Chilopoda are in many aspects different from *L. polyphemus* (Paulus 1979, 2000) and have recently been shown to exhibit many similarities to Hexapoda and Crustacea (Müller C and others 2003). The eyes of Scutigeromorpha (Chilopoda: Notostigmophora) are composed of ommatidia, each consisting of a crystalline cone with 4 cone cell nuclei (except peripheral ommatidia, which are equipped with 5 cone cells), 9–12 distal and 4 proximal retinula cells, 8–10 primary pigment cells, and 14–16 interommatidial pigment cells (Müller C and others 2003). Hence, each ommatidium is composed of between 39 and 46 cells, with the number varying with eye region, although the number of cone cells and proximal retinula cells is relatively constant. The principal cell types in the eyes of Scutigeromorpha, in particular the crystalline cone cells, can be homologized with those of Hexapoda and Crustacea (Müller C and others 2003; see also Harzsch, Müller, and Wolf 2005).

Finally, the hexapods, as well as malacostracan and nonmalacostracan crustaceans, also possess compound eyes, which are composed of many similarly structured ommatidia. An increasing amount of evidence suggests that many aspects of retinal pattern formation, ommatidial differentiation, and optic stem cell proliferation are similar in representatives of these organisms (Fig. 3A; Harzsch and Dawirs 1995/96; Hafner and Tokarski 1998, 2001; Harzsch, Benton, and others 1999; Melzer and others 2000; Harzsch and Walossek 2001; Wildt and Harzsch 2002; Harzsch 2002b). Paulus (2000), Dohle (2001), and Richter (2002) suggested that in the ground pattern of these 3 groups, each ommatidium is composed of a constant number of cells that is very small in relation to the other arthropod groups discussed: 2 corneagenous cells, 4 crystalline cone cells, 8 retinula cells, and several pigment cells. They suggested this fixed architecture of the ommatidia to be a synapomorphy of these 3 groups, a taxon for which they suggested the name "Tetraconata," referring to the tetrapartite crystalline cone. The choice of name turns out to be rather unfortunate because, as mentioned, such a tetrapartite crystalline cone is also present in scutigeromorph Chilopoda (Müller C and others 2003). The crystalline cone therefore was suggested to be an important synapomorphy to characterize the ground pattern of Mandibulata (Harzsch, Müller, and Wolf 2005).

Paulus (1986, 2000) has suggested an evolutionary scenario to explain the relationships of these different eye types within the Arthropoda. According to his model, compound eyes with ommatidia similar to those of recent Crustacea and Hexapoda are the ancestral eye type of Mandibulata. From this plesiomorphic characteristic state, the compound eyes disintegrated into single ommatidia. Then, by fusion of several single ommatidia and/or increase of cell numbers in single ommatidia, multicellular ocelli (fusion stemmata) similar to those of Progoneata and Chilopoda emerged. However, Harzsch, Müller, and Wolf (2005), using cellular and developmental observations, have recently suggested an evolutionary scenario that took the opposite direction. They proposed that the multicellular eye subunits of Chelicerata/Xiphosura with their variable cell numbers are plesiomorphic for the Euarthropoda. In this scenario, basal genera of Progoneata and Chilopoda (*Scutigera*, *Polyxenus*) have reduced the number of cells of which each eye subunit is composed and some cell types now occur in constant numbers. They represent an intermediate point on the pathway toward the Hexapoda and Crustacea (Tetraconata) in which the eye subunits have a fixed architecture with a relatively low, constant cell number (Harzsch, Müller, and Wolf 2005). To test these competing scenarios, S. Harzsch, R. R. Melzer, and C. H. G. Müller (2006) recently analyzed eye growth in Myriapoda by mapping the arrangement of ocelli during postembryonic development and by localizing proliferating cells in the eyes by labeling with the mitosis marker bromodeoxyuridine. These experiments showed that during eye growth in Myriapoda new elements added to the side of the eye field elongate the rows of earlier generated optical units. This pattern closely resembles that in horseshoe crabs (Chelicerata) and Trilobita. In conclusion, it is proposed that the trilobite, xiphosuran, diplopod, and chilopod mechanism of eye growth represents the ancestral arthropod mode of visual system formation, which suggests that the eyes of Diplopoda and Chilopoda are not secondarily

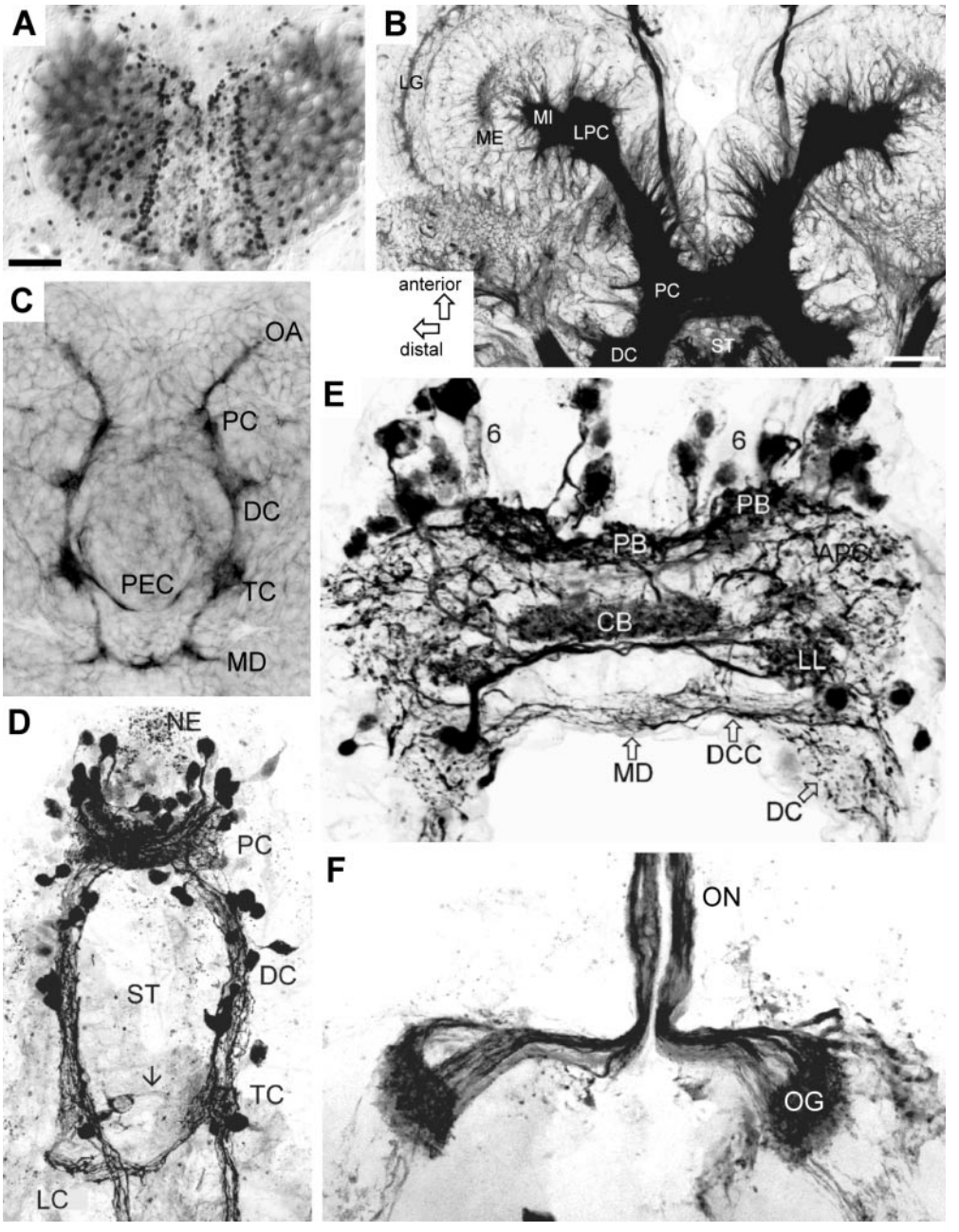


Fig. 3 (A) proliferating zone at the margin of the developing eyes in the metanauplius of the dinosaur shrimp *Triops cancriformis* (Branchiopoda). Whole-mount labeled with the mitosis marker bromodeoxyuridine. Modified from Harzsch and Walossek (2001). (B) Developing brain of the crayfish *Cherax destructor* (Malacostraca, Decapoda) as labeled by fluorescent conjugated phalloidin, confocal-laser scan image, inverted. Reprinted from Harzsch (2002a), with permission from Wiley. DC, deutocerebrum; LG, lamina ganglionaris; LPC, lateral protocerebrum; ME, medulla externa; MI, medulla interna/lobula; PC, medial part of the protocerebrum; ST, stomodaeum. (C) Embryonic brain of a crayfish, the Marmorkrebs, same technique as in (B). S. Harzsch and K. Vilpoux (unpublished data). DC, deutocerebrum; MD, mandibular neuromere; OA, optic anlagen; PC, medial part of the protocerebrum; PEC, postesophageal commissure; TC, tritocerebrum. (D) Antihistamine immunoreactivity in a stage 8 metanauplius of *Artemia salina* (Branchiopoda, Anostraca), ventral view. Reprinted from Harzsch and Glötzner (2002), with permission from Elsevier. Arrow denotes the tritocerebral commissure. (E) Antihistamine immunoreactivity in the brain of *Artemia salina*. Reprinted from Harzsch and Glötzner (2002), with permission from Elsevier. APC, anterior protocerebral neuropil; CB, central body; DC, deutocerebrum; DCC, deutocerebral commissure; LC, labral commissure; LL, lateral lobes; MD, median neuropil accompanying the deutocerebral commissure; NE, nauplius eye; PB, protocerebral bridge; PC, protocerebrum; ST, stomodaeum; TC, tritocerebrum 6 cell cluster 6. (F) Brain of the trilobite larva of *Limulus polyphemus* (Xiphosure, Chelicerata), histaminergic fibers in the ocellar nerve (ON) from the median ocelli target the bitareal ocellar ganglion (OG). Reprinted from Harzsch, Wildt, and others (2005), with permission from Elsevier.

reconstructed insect eyes (S. Harzsch, R. R. Melzer, and C. H. G. Müller, 2006).

The optic neuropils of the lateral eyes

The structure and development of the optic neuropils associated with these compound eyes have been thoroughly studied in an evolutionary context down to the cellular level in many arthropod groups (Strausfeld and Nässel 1981; Chamberlain and Barlow 1982; Elofsson and Hagberg 1986; Fischbach and Dittrich 1989; Osorio and others 1995; Melzer and others 1996/97; Nilsson and Osorio 1997; Strausfeld 1998; Harzsch, Benton, and others 1999; Harzsch and Walossek 2001; Harzsch 2002b; Wildt and Harzsch 2002; Sinakevitch and others 2003; Harzsch, Wildt, and others 2005; Strausfeld 2005). The lateral eyes of *L. polyphemus* are associated with 2 retinotopic neuropils, called the lamina and medulla (Chamberlain and Barlow 1982). The fact that the fibers that link these 2 neuropils take a straight course without a chiasm in xiphosuran larvae (Harzsch, Wildt, and others 2005) may indicate that parallel fibers are plesiomorphic for the Euarthropoda. Before this issue can be settled, additional studies will be necessary to unravel how the developmental pathways that form the crossing of optic fibers, which seems to be present in adult Xiphosura (Chamberlain and Barlow 1982), compare with the optic chiasmata of Hexapoda and Malacostraca (Harzsch 2002b). Nevertheless, those representatives of the Chilopoda that have retained well-developed lateral eyes also have only 2 optic neuropils, which are linked by straight fibers (Melzer and others 1997; Sinakevitch and others 2003; Strausfeld 2005). It therefore seems likely that in the mandibulatan ground pattern the compound eyes were associated with 2 optic neuropils linked by straight fibers (compare Strausfeld 2005), much like the proposed xiphosuran ground pattern. Maxillopodan and branchiopodan crustaceans have retained this pattern as a plesiomorphic character, whereas it was largely modified in the ground pattern of Pterygota and Malacostraca (Fig. 5D; Strausfeld 2005).

Traditionally, it has been thought that in the Pterygota and Malacostraca, 3 and not just 2 layered optic neuropils, which primarily process visual information, underlie the compound eyes. Long visual fibers from photoreceptors in the retina and axons from lamina monopolar neurons travel from the first optic neuropil, the lamina, to the second optic neuropil, the medulla. These fibers form the outer optic chiasma. Other axons that link the medulla to the third optic neuropil, the lobula, form the inner optic chiasma (Strausfeld and Nässel 1981; Fischbach and Dittrich 1989; Meinertzhagen and Hanson 1993; Nilsson and Osorio 1997; Strausfeld 1998). As mentioned above, differences exist in the layout of the visual systems of Hexapoda and Malacostraca on one hand and Branchiopoda and Maxillopoda on the other in that the third optic neuropil as well as chiasmata are absent in the latter 2 groups, a long-known fact that has been termed the "nonmalacostracan enigma" (Elofsson and Dahl 1970; Nilsson and Osorio 1997). Recent reexamination of the mechanisms by which the fiber connections between the lamina and the medulla arise, and of the development and cellular composition of the lobula, has provided solid evidence for a homology of the chiasmata and the lobula (or protolobula) of Hexapoda and Malacostraca (Fig. 3B; Harzsch 2002b; Sinakevitch and others 2003) suggesting that the protolobula and the inner and outer optic chiasmata are synapomorphies that unite Hexapoda and Malacostraca. At the same time, developmental data confirmed that Branchiopoda lack a lobula and that their lamina and medulla are connected by optic fibers that take a straight course and develop differently from those of Hexapoda and Malacostraca (Wildt and Harzsch 2002; Harzsch 2002b).

Strausfeld (2005) pointed out the importance of another optic neuropil, the visual tectum, and proposed a radical new evolutionary scenario of mandibulation optic neuropils that I consider very convincing and will adopt for the phylogenetic analysis here (Fig. 5D). According to Strausfeld, in the ground pattern of Mandibulata, 2 optic neuropils were present: the outer plexiform layer (formerly called lamina, see above; pink in Fig. 5D) is linked by uncrossed axon projections to the visual tectum (lobula plate, sublobula; dark green in Fig. 5D). It is suggested that these 2 neuropils contain circuits for motion detection as an archaic attribute of visual systems (Strausfeld 2005). In this view, the medulla as the second optic neuropil of nonmalacostracan crustaceans is not equivalent to the medulla of Hexapoda and Malacostraca but to their lobula plate (visual tectum). It is proposed that the medulla in Hexapoda and Malacostraca arose by an ancestral duplication of the lamina proliferation zone of nonmalostracans that has resulted in a split of the ancestral lamina into an outer (pink) and an inner plexiform layer (dark gray in Fig. 5D). Strausfeld (2005) suggested that the separation of these 2 layers coincided with their developmental connection by the outer chiasm. Another duplication of a proliferation zone gave rise to a novel neuropil, the (proto)lobula (mid gray in Fig. 5D). In this new evolutionary scenario, separate outer and inner plexiform layers linked

by the outer optic chiasm and the lobula are synapomorphies of Malacostraca and Hexapoda. Strausfeld (2005) also discussed how the visual systems of wingless insects fit into this new model.

Was the brain of the arthropod ancestor a simple circumoral ring?

Eriksson and Budd (2000) suggested that the brain of a hypothetical onychophoran ancestor was shaped like a circumoral nerve ring bent dorsally out of the anterior-posterior neuraxis since the mouth is in a terminal rather than a ventral position in this taxon (see also Dewel and others 1999). In metanauplii of the branchiopod crustacean *Artemia salina*, the developing brain also has the shape of a neuropil ring that surrounds the stomodaeum (Fig. 3D; Harzsch and Glötzner 2002). A similar organization is present in embryos of malacostracan crustaceans (Fig. 3C; Elofsson 1969; Harzsch and others 1997; Vilpoux and others 2006) and has been reported during development of representatives of the Hexapoda (Boyan and others 1995; Wildeman and others 1997; Nassif and others 1998; Graf and others 2000; Ludwig and others 2001; Boyan, Reichert, and Hirth 2003) and Xiphosura (Chelicerata: Mittmann and Scholtz 2003). Regardless of the ancestral position of the mouth, an embryonic circumoral nerve ring most likely is part of the arthropod ground pattern. This is an important characteristic because the arthropod embryonic circumstomodeal nerve ring can now be compared with the developing nervous system in other taxa with regard to the new debate on the arthropod sister group (Eriksson and Budd 2000). What is more, Nielsen (2005) suggested that the protostome nervous system consists of a perioral nerve ring, paired nerve cords, and a perianal ring and that this nervous system evolved from a circumblastoporal nerve ring. Clearly, comparative data on the structure, development, and evolution of the arthropod nervous system may have a wider impact on our understanding of brain evolution in metazoans.

Brain segmentation in the ground pattern of the Euarthropoda

A widely accepted view holds that the 3 most anterior units of the mandibulate nervous system are the proto-, deuto-, and tritocerebrum (for example, Scholtz 1995; Boyan and others 2002; Boyan, Reichert, and Hirth 2003; Harzsch 2004a; Urbach and Technau 2003; Vilpoux and others 2006). The probability of older suggestions concerning the presence of another unit in front of the protocerebrum ("archicerebrum") has recently been discussed by Urbach and Technau (2003). Concerning brain segmentation, the traditional view has been that the Chelicerata and Mandibulata share a common protocerebral/ocular segment but that Chelicerata have reduced the segment, which in Mandibulata carries the first pair of antennae and corresponds to the deutocerebrum. This implies that the cheliceral neuromere of the Chelicerata should correspond to the tritocerebrum of the Mandibulata (second pair of antennae in Crustacea, intercalary segment in Hexapoda). This view has been challenged in recent years by molecular, developmental, and ontogenetic-morphological studies (Damen and others 1998; Telford and Thomas 1998; Damen and Tautz 1999; Hughes and Kaufman 2002; Vilpoux and Waloszek 2003) as well as paleontological data (Chen and others 2004). In particular, analyses of segmentation genes such as *engrailed* and of Hox genes such as *sex combs reduced*, *proboscipedia*, *orthodentical*, *labial*, *deformed*, *antennapedia*, *ultrabithorax*, and *abdominal-A* in the spider *Cupiennius salei* and the oribatid mite *Archegozetes longisetosus* have provided strong evidence for a direct correspondence of the cheliceral segment to the first antennal (deutocerebral) segment of Mandibulata and of the pedipalp segment to the second antennal (tritocerebral) segment of Mandibulata (Damen and others 1998; Telford and Thomas 1998; Damen and Tautz 1999; Hughes and Kaufman 2002). This new hypothesis was supported by Mittmann and Scholtz (2003), who in an analysis of the embryonic nervous system of the horseshoe crab *L. polyphemus* (Chelicerata, Xiphosura) also demonstrated that the cheliceral brain neuromere corresponds to the deutocerebrum of Mandibulata and that the subsequent (pedipalp) neuromere corresponds to the tritocerebrum. Hence, it is now understood that Chelicerata and Mandibulata share a corresponding pattern of brain segmentation into a proto-, deuto-, and tritocerebrum, which, consequently, also characterizes the euarthropodan ground pattern (Harzsch, Wildt and others 2005).

Furthermore, recent neuroembryological studies of representatives of the Chelicerata and Hexapoda (Boyan, Reichert, and Hirth 2003; Mittmann and Scholtz 2003) have shown that in both taxa the deutocerebral hemispheres are transversely connected by preoral commissures as well as by postoral fibers that join the tritocerebral components in the characteristic postoral commissure. In Crustacea, so far only preoral deutocerebral connections are known (Harzsch 2003b), but this issue has not yet been examined using methods that would allow the detection of postoral deutocerebral commissural fibers. Therefore, it has been suggested that in the euarthropodan ground pattern the esophagus did not pass between the

deutocerebrum and the tritocerebrum but was located *within* the deutocerebral segment (Boyan, Reichert, Hirth 2003; Harzsch 2004a). Likewise, the frontal commissure that gives rise to the hypostomal (the sternal plate of the antennal segment) and stomatogastric innervation has both deuto- and tritocerebral components in Chelicerata, Hexapoda, and Crustacea (Böhm and others 2001; Mittmann and Scholtz 2003).

Central projections of the median eyes in Euarthropoda

The structure of the median eyes of Euarthropoda and the implications for the phylogeny of this group have been discussed extensively in the past (for example, Hanström 1928; Elofsson 1963, 1965, 1966, 1992a, 1992b; Paulus 1972, 1979; Wägele 1993) and will be touched upon only briefly here. The fact that the photoreceptors in the median eyes of all Euarthropoda seem to utilize histamine as their neurotransmitter (Chelicerata: Battelle and others 1991, 1999; Bornhauser and Meyer 1997; Schmid and Becherer 1999; Crustacea: Callaway and Stuart 1999; Hexapoda: Homberg 1994, 2003; Nässel 1999) may indicate that in accordance with Paulus (1972, 1979) and Wägele (1993), they derive from a common ancestral eye.

In the xiphosuran chelicerate *L. polyphemus*, axons from the histaminergic photoreceptor cells and from secondary visual cells, the arhabdomeric cells, in the paired median ocelli target the paired ocellar ganglia (Fig. 3F; Battelle and others 1991, 1999; Calman and others 1991). The ocellar ganglia are also innervated by serotonergic neurons whose somata are located in the dorsal median group (Chamberlain and Wyse 1986; Harzsch, Wildt, and others 2005). On both sides of the brain the optic tract provides a bidirectional link of the ocellar ganglion to the medulla, the second optic neuropil of the lateral eyes.

The median eye of Malacostraca (strictly, the nauplius eye, that is, without the various so-called frontal organs some of which may also have a photoreceptive function) includes an unpaired median cup flanked by 2 lateral cups, as has been thoroughly explored by Elofsson (1963, 1965). The photoreceptor axons of the nauplius eye target 2 round, fine-fibered neuropils that are located close to the protocerebral bridge (Sandeman DC and others 1990) and are innervated by serotonin-immunoreactive neurons (Sandeman DC and others 1988). The somata that give rise to these fibers are located in the anterior medial cell cluster (cluster 6 according to Sandeman DC and others 1992), an anteriorly located cluster of neuronal somata that also houses the neurons that innervate the malacostracan central body (Utting and others 2000; see below). A distinct bundle of serotonin-immunoreactive fibers links the protocerebral bridge with the optic ganglia in the eyestalks (Sandeman DC and others 1988). In the anostracan *Artemia salina* the nauplius eye, which is composed of 3 subunits (Elofsson 1966; Rasmussen 1971; Anadón A and Anadón E 1980; Martin 1992), innervates an unpaired nauplius eye center, which Benesch (1969) described as being subdivided into a medial and 2 smaller lateral lobes with distinct fiber bundles intimately linking them to the protocerebral bridge. This innervation pattern is also present in the Maxillopoda (Elofsson 1966; Harrison PJH and Sandeman 1999). According to Paulus (1979), the nauplius eye in the ground pattern of the Entomostraca was composed of 4 units, but this holds true only for the phyllopodan Branchiopoda (autapomorphy of this taxon; Walossek 1993).

The organization of the central visual pathway associated with the insect dorsal ocellar system has been thoroughly investigated in representatives of the Collembola (Paulus 1972), the Blattariae (Mizunami 1995a, 1995b), the Caelifera (Goodman LG and others 1975; Goodman CS 1976; Goodman CS and Williams 1976; Guy and others 1977; Goodman LJ and others 1979), and the Diptera (Strausfeld 1976) (reviewed in Goodman LJ 1981; Mizunami 1995c; Simmons 2002). Nevertheless, for the present account, the organization of the ocellar system in primarily wingless insects is of particular importance in establishing the hexapodan ground pattern. Paulus (1972, 1979) suggested that 6 ocelli (plus 2 frontal organs) are present in the hexapodan ground pattern, whereas the number is reduced to 4 in the Pterygota; the medial 2 of these are frequently fused. In representatives of the Collembola, the axons of the receptor cells of all ocelli target the ocellar center in the protocerebrum (Paulus 1972), an innervation that quite closely resembles that present in entomostracan and malacostracan Crustacea. In adult animals of the Caelifera (Goodman LJ and others 1975; Goodman CS 1976; Guy and others 1977; Goodman LJ and others 1979), the Odonata (Chappell and others 1978), the Blattariae (Mizunami 1995a, 1995b), the Lepidoptera (Eaton and Pappas 1978), and the Diptera (Strausfeld 1976), 2 classes of ocellar second-order interneurons can be distinguished, the small and large interneurons, which target various protocerebral areas. Ontogenetic data obtained from Caelifera indicate that the primordial axons of the ocellar retinula cells terminate close to the protocerebral bridge (Mobbs 1976, 1979; Goodman LJ 1981; Toh and Yokahari 1988). Hence, also during early development of some Pterygota, a pattern of connectivity may be present that to some extent resembles the connectivity of the crustacean nauplius eyes. Later, however, the

neurites of second-order visual interneurons, the somata of which are located in an anteriorly located cell cluster (the pars intercerebralis), grow out along the established retinular axon pathway toward the ocelli (Mobbs 1976, 1979; Toh and Yokohari 1988). The axons of newly added retinula cells establish synaptic contacts with these visual interneurons, thereby forming a synaptic plexus immediately below the ocelli, the ocellar plexus. This peripheral ocellar plexus of the Pterygota is equivalent to the centrally located ocellar center of the Collembola (Paulus 1972).

Clearly, more information on the protocerebral connections of the insect ocelli and on the developmental of the ocellar pathway will be necessary before more detailed comparisons with crustaceans and xiphosurans can be made. Nevertheless, Harzsch, Wildt, and colleagues (2005) found it reasonable to suggest that in the ground pattern of Euarthropoda, the histaminergic axons of the medial eye photoreceptors project into a protocerebral neuropil located anteriorly to the central complex, the median eye center that is either bilaterally paired or medially fused ("ocellar ganglia" in Xiphosura; "nauplius eye center" in Entomostraca; 2 neuropils associated with the protocerebral bridge in some Malacostraca; "ocellar center" in Collembola; "ocellar plexus" in Pterygota). The median eye center is also innervated by interneurons with somata in an anteriorly located medial cell cluster, some of which are serotonergic ("dorsal median group" in Xiphosura; "anterior median cluster [cluster 6]" in Crustacea; "pars intercerebralis" in Hexapoda).

The central complex

The brains of many Euarthropoda bear a conspicuous spindle-shaped heterolateral neuropil, which is commonly referred to as the "central body." Whereas earlier neuroanatomists generously homologized the central body across arthropod phyla (Holmgren 1916; Hanström 1928), current authors are more cautious and legitimately have called for a sound substantiation of the homology based on a comparison of individually identifiable cells (Breidbach 1995; Strausfeld 1998). The term "central complex" in the brain of the Mandibulata describes the protocerebral bridge, the central body with the associated neuron clusters, and other accessory neuropils such as the lateral lobes/ventral bodies/isthmus (Fig. 3E; Branchiopoda: Harzsch and Glötzner 2002; Remipedia: Fanenbruck and others 2004; Fanenbruck and Harzsch 2005; Malacostraca: Utting and others 2000; Hexapoda: Williams 1975; Strausfeld 1976; Homberg 1994; Strausfeld 1998; Homberg 2003; Chilopoda: Loesel and others 2002; Loesel 2004; central complex absent in Diplopoda).

The most detailed description of the cellular structure and connections of the central complex in a malacostracan is that of Utting and colleagues (2000) in the crayfish *Cherax destructor*. In the crayfish, bundles of fibers from cell bodies in the anterior medial cell cluster (cluster 6) project into the central body similar to histaminergic cells in the branchiopod *Artemia salina* (Harzsch and Glötzner 2000). The location and axonal projection pattern of these histaminergic neurons in the brine shrimp closely correspond to the CBN1 and CBN2 classes of neurons in the crayfish central complex (Utting and others 2000). What is more, in *A. salina*, serotonin-immunoreactive neurons innervate the lateral lobes and then send their axons contralaterally in a commissure caudal to the central body. An identical type of serotonergic neuron as well as a serotonergic innervation of the central body is found in the spider crab larvae *Hyas araneus* as well as crayfish and lobster embryos (Sandeman RE and Sandeman DC 1990; Helluy and others 1993). Utting and colleagues (2000) described a similar class of serotonergic neurons (CBN4) with their somata in the laterally situated cell cluster (cluster 8) and a corresponding projection pattern.

Based on these similarities at the cellular level, Harzsch and Glötzner (2000) suggested that the central complexes in *A. salina* and *C. destructor* are homologous. Recent histological and immunohistochemical studies in representatives of the Dendrobranchiata, as well as Euphausiacea, Isopoda, and all major groups within the Pleocyemata (Sandeman DC and others 1992, 1993; Thompson and others 1994; Langworthy and others 1997; Dircksen and others 1999; Loesel and others 2002) demonstrate that central complexes with corresponding morphological characteristics are present in these taxa and support Hanström's (1928) suggestion that the central body as well as other components of the central complex is part of the malacostracan ground pattern. Although immunohistochemical studies at this level of resolution have not been carried out in other representatives of the Branchiopoda and Maxillopoda, a histochemical survey of the brains in representatives of the Copepoda, Ostracoda, Anostraca, and Phyllopoda nevertheless indicates that in these groups a central body is present that is innervated by monoaminergic fibers and has a shape and location that closely correspond to those in *A. salina* (Aramant and Elofsson 1976).

There is consensus now that the major components of the central complex are part of the ground pattern of the Tetraconata (Strausfeld 1998; Utting and others 2000; Harzsch and Glötzner 2002; Loesel and others 2002; Fanenbruck and others 2004; Loesel 2004; Fanenbruck and Harzsch 2005). In particular, although

the structure of the central complex is more complex in Hexapoda than in Crustacea, the arrangement of its main components is similar. In my view, the protocerebral bridges in insects and crustaceans correspond to each other (but see Strausfeld 1998) and the insect lateral accessory lobes/ventral bodies/isthmus are homologous to the crustacean lateral lobes, and the noduli seem to be apomorphic in Insecta. Loesel and colleagues (2002) suggested that the insect ellipsoid body corresponds to the central body in the euarthropod ground pattern and hence the crustacean central body, but this discussion is not yet finally settled (compare contributions by Strausfeld 1998; Utting and others 2000; Loesel and others 2002). Nevertheless, a central complex embracing the central body, protocerebral bridge, and lateral lobes/ventral bodies/isthmus characterize the ground pattern of Tetraconata.

In a thorough reinvestigation of the brain midline neuropils in several representatives of the Chilopoda, Loesel and colleagues (2002) and Loesel (2004) recently found that these animals do have a central body that is homologous to that of Crustacea and Hexapoda but that other components of the central complex such as protocerebral bridge and the lateral lobes are not yet developed. Also, the chilopod central body is not associated with the lateral cell clusters that characterize the crustacean subgroups and the Hexapoda. A comparison with Chelicerata as the outgroup (see below) suggests that concerning the central body, the Chilopoda represent the plesiomorphic characteristic status from the mandibulate ground pattern. Hence, the protocerebral bridge, lateral lobes, and the lateral cell clusters of Hexapoda and Crustacea are apomorphic characteristics in the ground pattern of the Tetraconata.

Although it has been thoroughly debated whether representatives of the Chelicerata share homologous components of the central complex with the Mandibulata (Breidbach and Wegerhoff 1993; Strausfeld and Barth 1993; Strausfeld and others 1993; Breidbach 1995; Breidbach and others 1995; Wegerhoff and Breidbach 1995), several recent systematic reinvestigations (Loesel and others 2002; Loesel and Strausfeld 2003; Loesel 2004; Harzsch, Wildt, and others 2005) now suggest that the "central body" (arcuate body) of the Chelicerata may in fact be homologous to the central body of the Mandibulata. A comparison with Onychophora even indicates that a central body may have been present already in the arthropod ground pattern so that it is plesiomorphic to Euarthropoda (Loesel and Strausfeld 2003; Loesel 2004).

The central body of all Euarthropoda is innervated by columnar ("small field") neurons with somata in the anteriorly located median cell cluster that also houses the neurons that innervate the visual interneurons associated with the median eyes, some of which are serotonergic ("dorsal median group" in Xiphosura; "anterior median cluster [cluster 6]" in Crustacea; "pars intercerebralis" in Hexapoda). The central body of Xiphosura (Fahrenbach and Chamberlain 1985; Chamberlain and Wyse 1986) and Arachnida (Strausfeld and others 1993) is dorsally, ventrally, and posteriorly enwrapped by several layers of neuronal cell bodies ("ganglion cells"). In Entomostraca, Malacostraca, and Hexapoda, similar layers are not present. Instead, there are bilaterally paired cell clusters situated laterally and posteriorly to the central body that mostly house the cell bodies of tangential ("wide-field") neurons of the central body ("lateral cells, cluster 8" in Entomostraca and Malacostraca: Utting and others 2000; Harzsch and Glötzner 2002; "inferior median and lateral protocerebrum" in Hexapoda: Homberg 1991; Vitzthum and others 1996; Müller M and others 1997; Vitzthum and Homberg 1998; Homberg and others 1999; Homberg 2003) and may correspond to the cell layers in the Xiphosura and Arachnida. An outgroup comparison with Onychophora (Loesel and Strausfeld 2003) revealed a single posterior layer of central body neurons reminiscent of that in Chelicerata. This may be interpreted in such a way that the association of the central bodies with layers of neuronal somata that surround it is a plesiomorphic feature in Chelicerata retained from the arthropod ground pattern, whereas the paired lateral clusters may be apomorphic to the Tetraconata.

The olfactory neuropil

The organization of arthropod olfactory brain centers was reviewed by Schachtner and colleagues (2005). The olfactory systems of Tetraconata provide a wealth of structures for evolutionary consideration. I briefly summarize the architecture of this system mainly in Crustacea and point out some features of phylogenetic importance.

The first antennae of malacostracan crustaceans typically bear several hundred olfactory aesthetascs, each of which is innervated by up to 300 sensory cells (reviewed in Hallberg and others 1992, 1997; Mellon and Alones 1993; Derby and Steullet 2001; Derby and others 2001; Schachtner and others 2005) as well as other bimodal chemomechanosensilla (Steullet, Cate, and Derby 2000; Steullet, Cate, Michel, and Derby 2000; Cate and Derby 2001, 2002a, 2002b; Steullet and others 2001, 2002; Derby and others 2003). The antennal afferents project into bilateral specialized

deutocerebral centers, the olfactory lobes, the neuropil of which is organized in conspicuous columnar glomeruli in all malacostracan species that have been studied so far (Fig. 4 A–E; Phyllocarida: Hanström 1928; Stomatopoda: Derby and others 2003; Caridea: Johansson 1991; Achelata: Schmidt A and Ache 1996; Schmidt M and Ache 1997; Wachowiak and Ache 1997; Beltz and others 2003; Astacida: Sandeman RE and Sandeman DC 1990; Sandeman RE and others 1990; Johansson 1991; Melon and Alones 1993; Sandeman DC and Sandeman RE 1994; Sandeman D and Mellon 2002; Beltz and others 2003; Sullivan and Beltz 2004, 2005; Homarida: Langworthy and others 1997; Harzsch, Miller, and others 1999; Beltz and others 2003; Brachyura and Anomala: Johansson 1991; Beltz and others 2003; Euphausicea and Mysidacea: Johansson and Hallberg 1992; reviewed in Schachtner and others 2005), so olfactory glomeruli are probably part of the malacostracan ground pattern. In Decapoda, Pleocyemata, the glomeruli are strongly innervated by serotonin- (Johansson 1991; Johansson and Hallberg 1992; Sandeman DC and Sandeman RE 1994; Langworthy and others 1997) and histamine-immunoreactive fibers (Langworthy and others 1997; Wachowiak and Ache 1997) as well as other neurotransmitters (Langworthy and others 1997; Schmidt M and Ache 1997; Wachowiak and Ache 1997). The architecture of the axonal terminations of the olfactory receptor neurons and of the neurites of local interneurons and projection neurons that branch in the olfactory glomeruli is known in great detail, as summarized by Schachtner and colleagues (2005).

The olfactory lobes of Cephalocarida and Remipedia clearly are also subdivided into functional subunits reminiscent of the malacostracan glomeruli (Elofsson and Hessler 1990; Fanenbruck and others 2004; Fanenbruck and Harzsch 2005). However, it is not known to what extent the cellular architecture in Cephalocarida and Remipedia is similar to that in Malacostraca. For the Remipedia, there is evidence of a similarity to the Malacostraca in the class of olfactory projection neurons that link the olfactory lobes to the hemiellipsoid bodies in the protocerebrum (Fanenbruck and others 2004; Fanenbruck and Harzsch 2005). The deutocerebrum in Branchiopoda and Maxillopoda receives a mixed mechanosensory and chemosensory input from the paired first antennae. There is a wealth of literature on malacostracan olfactory systems (Schachtner and others 2005), but the structure and distribution of sensilla on the first antennae of Branchiopoda and Maxillopoda have rarely been studied. Nevertheless, sensory structures with morphological characteristics of malacostracan chemosensory aesthetascs have been reported in Cladocera, Conchostraca, Notostraca (Hallberg and others 1992, 1997) and Copepoda (Boxshall and Huys 1998). On the other hand, the first antennae of *A. salina* are equipped with only 3 mechanosensory sensilla ("type 1") and 3 to 5 probably bimodal chemomechanosensilla ("type 2"; Tyson and Sullivan 1979). Benesch (1969) and Aramant and Elofsson (1976) provided no evidence for olfactory glomeruli in *A. salina.* Furthermore, using classical histology and immunohistochemistry against serotonin, histamine, and synapsins, Harzsch and Glötzner (2002) were unable to identify glomerular structures in the deutocerebral neuropil of adult *A. salina*, although these methods positively identify glomeruli in the olfactory system of Decapoda (histology: Helluy and others 1993; synapsin immunohistochemistry: Harzsch, Miller, and others 1999; Beltz and others 2003; serotonin and histamine immunohistochemistry: Johansson 1991; Sandeman DC and Sandeman RE 1994; Langworthy and others 1997; Wachowiak and Ache 1997). Also, in contrast to Benesch (1969), Harzsch and Glötzner (2002) were unable to trace any distinct deutocerebral neuropil (an olfactory lobe) as the termination site from the first antennae in this species; rather, the deutocerebrum was found to display a diffuse neuropil architecture. This result is perhaps not surprising considering the small number of afferent axons projecting into the deutocerebral neuropil. Likewise, olfactory glomeruli were not recognized in the deutocerebrum of barnacle cypris larvae (Maxillopoda; Harrison PJH and Sandeman 1999) and branchiopods of the genus *Triops* (Strausfeld and Hildebrand 1999), although Hanström (1928) reported antennal glomeruli to be present in these taxa. I conclude (in contrast to Schachtner and others 2005) that neither a distinct olfactory lobe nor olfactory glomeruli are part of the branchiopod ground pattern. As discussed below, the same is true for the Maxillopoda.

Many representatives of pterygotid insects also possess olfactory glomeruli in the deutocerebrum (Hanström 1928). Strausfeld (1998), Strausfeld and colleagues (1998), Strausfeld and Hildebrand (1999), and Schachtner and colleagues (2005) pointed out that pterygotid and malacostracan glomeruli are characterized by a number of fine structural similarities as well as differences. Nevertheless, olfactory glomeruli (that is, more or less spherical neuropil compartments devoted to chemosensory processing) are also present in various areas of the central nervous system other than the deutocerebrum that receive any kind of chemosensory input in, for example, Chelicerata, Onychophora, Chilopoda, Progoneata, and other Arthropoda (Strausfeld 1998; Strausfeld and others 1998; Strausfeld and Hildebrand 1999). The existence

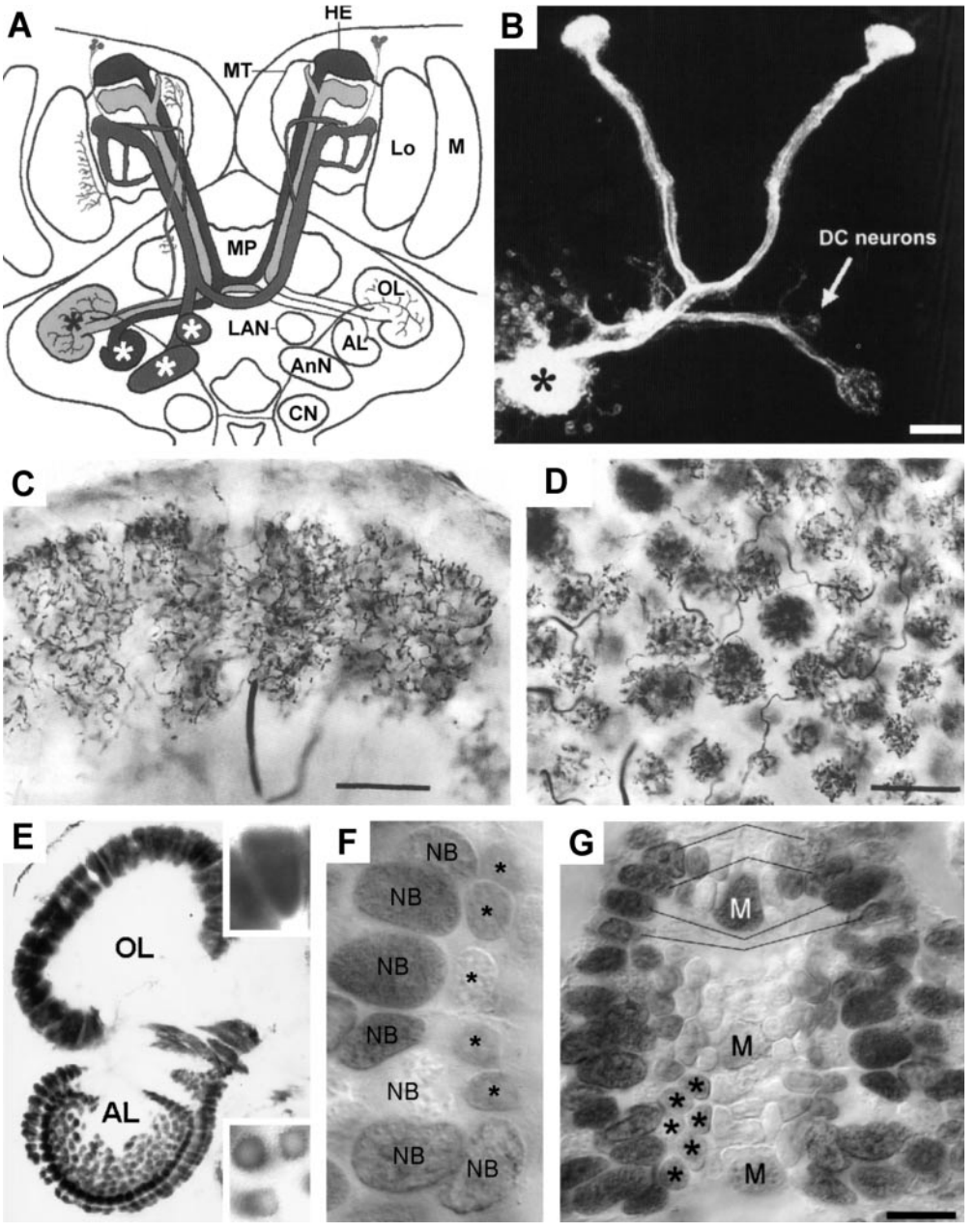


Fig. 4 (A) Schematic diagram summarizing the patterns of connectivity of the medulla terminalis in the embryonic brain of the American lobster *Homarus americanus*, as determined by dye injections into the olfactory lobe, the accessory lobe, and antenna 2 neuropil (asterisks indicate the sites of dye injection). Reprinted from Sullivan and Beltz (2001b), with permission from Wiley. AL, accessory lobe; AnN, antenna 2 neuropil; CN, commissural neuropil; HE, hemiellipsoid body; LAN, lateral antenna 1 neuropil; Lo, lobula; M, medulla; MP, medial protocerebrum; MT, medulla terminalis; OL, olfactory lobe. (B) Projection neuron pathway from the developing accessory lobe in a lobster embryo (*Homarus americanus*) at 75% of embryonic development stacked confocal image. This pathway projects bilaterally to the hemiellipsoid body. The asterisk indicates the site of the dye injection; axons of deutocerebral commissure neurons are also labeled (DC neurons). Reprinted from Sullivan and Beltz (2001b), with permission from Wiley. Scale bar 50 μm. (C and D) Serotonin immunoreactivity in the deutocerebrum of the crayfish *Cherax destructor* reveals the glomerular organization of the olfactory (C) and accessory lobes (D). Reprinted from Sandeman DC and Sandeman RE (1994), with permission from Wiley. Scale bars: 50 μm. (E) Glomeruli in the olfactory (OL) and accessory lobes (AL) of an embryonic lobster brain (*Homarus americanus*) as labeled by immunohistochemistry against synaptic proteins. Reprinted from Harzsch, Miller, and others (1999), with permission. (F and G) BrdU (bromodeoxyuridine) labeling of neuroblasts (NB in [F]) and their progeny, the ganglion mother cells (asterisks) in the neuromeres of the maxilla 1 to thorax 2 of an E35% embryo of the shrimp *Palaemonetes argentinus* (Malacostraca, Decapoda). Neuroblasts are arranged in several rows and columns (G). M identifies the median neuroblasts (G). Lines in (G) connect bilateral symmetrically arranged neuroblasts. Reprinted from Harzsch (2001b), with permission from Blackwell Publishers. Scale bar: (G) 15 μm.

of glomeruli alone is therefore not a good characteristic for phylogenetic considerations because they certainly evolved several times convergently at places in the central nervous system where chemosensory input needed to be processed. Nevertheless, the available data as summarized by Schachtner and colleagues (2005) allow the determination of a number of (most likely synapomorphic) characters related to the olfactory system that the members of the taxon N. N. (Fig. 6), the Pterygota, Malacostraca, Remipedia, and perhaps also the Cephalocarida have in common. In these taxa, the olfactory receptor neurons have acetycholine as their transmitter and the afferent axons of the receptors penetrate into the ipsilateral olfactory lobe in a radial manner. They have uniglomerular terminations. Local interneurons in the olfactory system of these taxa include serotonergic giant neurons. The olfactory lobes are linked to a lateral component of the protocerebrum: the multilobed complex in Cephalocarida, the lateral protocerebrum with hemiellipsoid body in Remipedia and Malacostraca, and the lateral horn in Hexapoda. This link is established by a characteristic fiber tract (olfactory globular tract) composed of the axons of olfactory projection neurons of olfactory interneurons.

The lateral/mechanosensory antenna 1 neuropil

In Malacostraca and Hexapoda as well as remipede Crustacea (unclear for Cephalocarida) the mechanosensory and chemosensory input from the first pair of antennae is processed in 2 distinct neuropil regions: the lateral/mechanosensory neuropil and the olfactory lobe, respectively (Strausfeld 1976; Sandeman DC and others 1992; Fanenbruck and others 2004; Fanenbruck and Harzsch 2005; Schachtner and others 2005). The presence of the lateral/mechanosensory antenna 1 neuropil that receives afferents from mechanoreceptors and nonaesthetasc chemoreceptors has not been described for any other arthropod and therefore may constitute another autapomorphy uniting Hexapoda, Malacostraca, and Remipedia.

Innervation of the labrum

The segmental origin and possible appendicular nature of the so-called labrum in the various euarthropod taxa has been the subject of an extensive debate (recent contributions: Rogers and Kaufman 1997; Popadic and others 1998; Scholtz and others 1998; Thomas and Telford 1999; Haas MS and others 2001a, 2001b; Boyan and others 2002; Boyan, Bräuning, Posser, Williams 2003; reviewed in Scholtz 1997; Dewel and others 1999). Furthermore, the paleontological evidence presented by Walossek and Müller (1998) and Walossek (1999, 2003) questions whether the structures called labrum in Eucrustacea, Insecta, Chilopoda, Progoneata, and Chelicerata are homologous at all. Snodgrass (1935, 1952) and more recently M. S. Haas and colleagues (2001b) discussed the innervation of the labrum with respect to its segmental status.

An innervation of the labrum in the branchiopod crustacean *A. salina* by the labral nerves that project from the frontal commissure (Fig. 3D) and originate in the tritocerebrum (and may also have deutocerebral components) has already been recognized by Claus (1886) and Benesch (1969). The frontal commissure is known from representatives of all major malacostracan and nonmalacostracan taxa (for example, Hanström 1928, 1932; Bullock and Horridge 1965; Aramant and Elofsson 1976; Robertson and Laverack 1979). A frontal commissure as the source of a labral innervation with a topology virtually identical to that in *A. salina* is present in the developing brain of *Drosophila melanogaster* ("frontal connective"; Nassif and others 1998; Boyan, Reichert, and Hirth 2003; Boyan, Bräuning, and others 2003) and is also found in other representatives of the Insecta (Holmgren 1916; Hanström 1928; Bullock and Horridge 1965). Furthermore, a similar structure that innervates the labrum is present in representatives of the Chilopoda and Progoneata, in which it is termed the "stomodeal bridge" (Holmgren 1916; Hanström 1928; Bullock and Horridge 1965). In Chelicerata, a loop-shaped external stomodeal bridge that gives rise to nerve branches that innervate the so-called labrum has been described in Xiphosura and Scorpiones but is internalized in the brain in Arachnida (Holmgren 1916; Hanström 1928; Henry 1950; Bullock and Horridge 1965; Weygoldt 1975; Barth 2001; Mittmann and Scholtz 2003).

The characteristic innervation, mostly of tritocerebral origin (but also with deutocerebral components; Boyan, Reichert, Hirth 2003), of the labrum in Crustacea, Insecta, Chilopoda, and Progoneata in my view strongly supports the suggestion of M. S. Haas and colleagues (2001b) that the labrum in these taxa is associated with the deuto- and tritocerebral segments but does not represent the appendage of a brain neuromere anterior to the protocerebrum. In addition, M. S. Haas and colleagues (2001a, 2001b) suggest that the insect labrum is the rudimentary endite of the reduced appendage of this segment. An appendicular origin of the labrum is also advocated by Popadic and colleagues (1998), Boyan and colleagues (2002), and Boyan, Bräuning, and colleagues (2003) but rejected by Scholtz and colleagues (1998) and Thomas and

Telford (1999). The fact that both the deuto- and tritocerebral segments in Crustacea are already equipped with full sets of appendages, the first and second pairs of antennae, in my view opposes the idea that the labrum in Crustacea may be the rudiment of medially fused appendages. Walossek and Müller (1998) and Walossek (1999) suggested that the eucrustacean labrum is a fleshy outgrowth of the posterior part of the hypostome and thus a structure associated with the stomodaeum. The fact that both the stomatogastric nervous system and the labral innervation in Eucrustacea and other Euarthropoda mostly originate in the tritocerebrum (Hanström 1928; Bullock and Horridge 1965) supports this notion. Regardless of the question of whether the labrum or the tissue from which it arises in representatives of the Crustacea, Insecta, and Chelicerata is an homologous structure (and thus part of the euarthropod ground pattern)—another problem that has been addressed in recent papers on the expression of molecular markers (Popadic and others 1998; Scholtz and others 1998; Thomas and Telford 1999; M. S. Haas and others 2001a)—I propose that the presence of the frontal commissure as the source of the labral innervation (when present) is part of the euarthropod ground pattern.

The brain of nonmalacostracan Crustacea

The central nervous system of nonmalacostracan crustaceans has not been examined in as much detail as the malacostracan nervous system (Sandeman DC and others 1992, 1993; Sandeman DC and Scholtz 1995; Harzsch and others 2006). Nevertheless, in most cases enough information is available on the central nervous system of these groups to allow a meaningful comparison with of the other arthropod taxa discussed in this article. In what follows I briefly summarize the current knowledge on brain structure of these less studied crustacean groups.

Mystacocarida

Detailed information on the nervous system of a representative of the Mystacocarida is available from the recent ultrastructural study by Elofsson and Hessler (2005), who report that the brain in the species they studied, *Derocheilocaris typica*, consists of a central neuropil surrounded by a cell body layer that is only 2 to 4 cells thick. Overall, the mystacocaridan brain is extremely small, as are these animals. The organ of Belonci is the only protocerebral sense organ, and no remnants of eyes are present. In general, these authors consider the protocerebrum to have undergone a process of strong reduction because the central body and protocerebral bridge as well as any equivalents of the malacostracan hemielipsoid body or the remipede multilobed complex are absent. The first antenna in this species is associated with the deutocerebrum, which, in contrast to many other crustaceans, has an unstructured neuropil without olfactory lobes. The well-elaborated tritocerebrum is associated with the labral innervation and is the origin of the stomatogastric innervation (Elofsson and Hessler 2005). Elofsson and Hessler suggest that, in contrast to other Crustacea, some parts of the central nervous system of mystacocarids, such as the deutocerebrum, provide examples of a conserved simple structure. This implies that the mystacocaridan brain (except the reduced protocerebrum) may represent the architecture of an ancestral crustacean brain.

Branchiopoda

The structure of the central nervous system of Branchiopoda is best understood in representatives of the genera *Artemia* (Anostraca), *Triops* (Notostraca), and *Daphnia* (Diplostraca) (summarized in Aramant and Elofsson 1976; Nässel and Elofsson 1987; Martin 1992; Harzsch and others 2006). The information available on the central and peripheral nervous system of less frequently examined groups of the Branchiopoda was reviewed by Martin (1992). Since the late 19th century, the structure of the nervous system in the brine shrimp *A. salina* and closely related anostracan crustaceans has been analyzed using classical histological methods (Claus 1886; Hanström 1924, 1928; Warren 1930; Henry 1948; Hentschel 1963; Benesch 1969; Elofsson and Lake 1971). Furthermore, data on the structure and development of the compound eyes and optic neuropils (Hentschel 1963; Elofsson and Dahl 1970; Elofsson and Odselius 1975; Nässel and others 1978; Elofsson and Hagberg 1986; Wildt and Harzsch 2002) and the median light sensitive organ, the nauplius eye (Elofsson 1966; Rasmussen 1971; Anadón A and Anadón E 1980), are available at the cellular level (summarized in Criel 1991; Martin 1992). The localization of neurotransmitters and neurohormones in the central nervous system has been studied histochemically (biogenic amines: Elofsson and Klemm 1971; Aramant and Elofsson 1976; acetylcholinesterase: Raineri and Falugi 1983) and immunohistochemically (crustacean hyperglycemic hormone: Zhang and others 1997; serotonin: Harzsch and Waloszek 2000; histamine: Harzsch and Glötzner 2002).

Early studies on the nervous system of representatives of the genus *Triops* include those by Claus (1873, 1886), Holmgren (1916), and Henry (1948)

and those by Dahl (1959) and Elofsson (1966) on the protocerebral sense organs (reviewed in Martin 1992). More recently, Diersch and colleagues (1999) and Melzer and colleagues (2000) reexamined the structure and development of the compound eyes and Harzsch and Walossek (2001) and Sinakevitch and colleagues (2003) reexamined the architecture and development of the optic ganglia. The morphology and arrangement of the optic ganglia and brain in this group are essentially the same as in *A. salina*, including the 2 optic neuropils, the lamina and medulla (linked by straight fibers), and the central complex. As in *A. salina*, a distinct deutocerebral olfactory lobe and glomeruli are absent (Strausfeld 1998; Strausfeld and others 1998; Strausfeld and Hildebrand 1999; S.H., unpublished data; contradicting Holmgren 1916 and Hanström 1924, 1928). The tritocerebral hemispheres are linked by 2 distinct postesophageal commissures (Henry 1948; reviewed in Martin 1992).

Studies on the nervous system of representatives of the genus *Daphnia* include those by Claus (1876), Cunnington (1903), Leder (1915), Sterba (1957), and Aramant and Elofsson (1976; reviewed in Martin 1992). The morphology of the visual system of *Daphnia magna* has been examined in great detail in a series of contributions by Lopresti and colleagues (1973, 1974) and Macagno and colleagues (1973). The localization of crustacean hyperglycemic hormone-immunoreactive neurons in the nervous system of 2 representatives of this group was analyzed by Zhang and colleagues (1997). A striking feature of their nervous system is the fusion of the originally paired compound eyes so that the paired laminae also fused to a single unit. Nevertheless, the 2 medullae are still recognizable as separate neuropils. Using the autofluorescent method to demonstrate monoaminergic structures, Aramant and Elofsson (1976) identified the central body and other protocerebral neuropils in the brain of *D. magna*. The protocerebrum also receives an input from the nauplius eye and frontal organ, which target a specific neuropil, the frontal area that also exhibits monoaminergic fluorescence (Aramant and Elofsson 1976). The deutocerebrum is weakly developed, and the tritocerebrum is mainly composed of the circumesophageal connectives giving rise to the labral commissure. The tritocerebral hemispheres are linked by distinct postesophageal commissures.

Maxillopoda

Among Maxillopoda, the nervous system of representatives of the Cirripedia has received considerable attention (reviewed in Gwilliam 1987; Walker 1992; Callaway and Stuart 1999). The morphology of the adult central nervous system in this group was examined by Gwilliam and Cole (1979), whereas Walley (1969) studied the development of the central nervous system from the nauplius to the adult and P. J. H. Harrison and Sandeman (1999) provided a thorough analysis of the nervous system of the cypris larva. The central nervous system of barnacles is most elaborate in the cypris larva but partly degenerates after settlement (Walker 1992). Compound eyes are present in the cypris (Hallberg and Elofsson 1983) but also degenerate after settlement. The nauplius eyes are remodeled during metamorphosis into the adult ocelli (Clare and Walker 1989; Takenaka and others 1993). The adult ocelli, which most likely are histaminergic, have lent themselves to the study of visual transduction, photoreceptor membrane properties, and mechanisms of synaptic transmission (reviewed in Callaway and Stuart 1999). Immunohistochemical studies have localized neurons with a number of different transmitters including FMRFamide-like peptides (Gallus 1997), pigment-dispersing hormone, and crustacean cardioactive peptide (Webster 1998) as well as serotonin and histamine (Callaway and Stuart 1999).

The central nervous system of barnacles gradually develops throughout the metanauplius stages and is most elaborate in the cypris larva (Walley 1969; Harrison PJH and Sandeman 1999). At this stage, compound eyes are present (Hallberg and Elofsson 1983) that send their axons via the optic nerve toward an optic neuropil (Harrison PJH and Sandeman 1999). This optic neuropil does not seem to be subdivided into a lamina or medulla (as for example in Branchiopoda), perhaps reflecting the rather rudimentary and transitional status of the compound eyes, which degenerate after metamorphosis. The optic tract links this neuropil to the protocerebrum. Axons from the nauplius eye target a distinct medial eye neuropil (Aramant and Elofsson 1978; Harrison PJH and Sandeman 1999). Aramant and Elofsson (1978) also traced the central body in the protocerebrum of a barnacle cypris larva. The deutocerebrum of cypris larvae is subdivided into 2 distinct parts, the circular deutocerebral neuropils and the median deutocerebral neuropils (Harrison PJH and Sandeman 1999), which are innervated by the antenna 1 nerve. This nerve is associated with the antennular soma cluster, which is composed of the cell bodies of bipolar neurons, possibly chemoreceptors or mechanoreceptors. The tritocerebrum gives rise to the labral commissure but is otherwise feebly developed in cypris larvae (Aramant and Elofsson 1978). The central neuropil of the cypris brain is surrounded by an outer soma layer between 1 and 5 cells thick. The total number of neurons associated with the brain is estimated to

be approximately 750 (Harrison PJH and Sandeman 1999).

Among the few studies of the central nervous system of representatives of the Copepoda, the papers by Hanström (1924), Lowe (1935), Fahrenbach (1962), Park (1966), and Aramant and Elofsson (1978) are probably the most important (reviewed in Boxshall 1992). The lack of compound eyes in the Copepoda has led to a much reduced protocerebral part of the brain. Using the autofluorescent method to demonstrate monoaminergic structures, Aramant and Elofsson (1978) identified the central body and another protocerebral neuropil in the brain of *Cyclops strenuous*, which they termed the 3-lobed area and which may be the target of the frontal eye complex or correspond to the protocerebral bridge. The protocerebrum also contains a distinct central body. The well-developed deutocerebrum occupies the lateral lobes of the brain, whereas the tritocerebrum lies on the esophageal connectives (summarized in Aramant and Elofsson 1978).

Reports on the central nervous system of other representatives of the Maxillopoda are scarce. Maddocks (1992) summarized the information available on the nervous system of ostracods. Weygoldt (1960) provided a thorough study of the structure and development of the nervous system in *Cyprideis litoralis* (Ostracoda). In the brain of this organism, he identified the central complex including protocerebral bridge, central body, and lateral lobes as well as a deutocerebral and a tritocerebral compartment from which the labral commissure arises. Information on other maxillopodan groups is reviewed in Bullock and Horridge (1965) and F. W. Harrison and Humes (1992).

Cephalocarida

Among the Cephalocarida, the nervous system is best understood in *Hutchinsoniella macracantha* (Elofsson and Hessler 1990; Elofsson 1992b). Among the most remarkable features of the brain of this species is the complete lack of compound eyes (contradicting Burnett 1981) and nauplius eye, and with this the lack of the optic ganglia and important protocerebral structures such as the central complex. This absence of visual input is probably the primary factor explaining the unique structure of this brain. Yet, the olfactory lobes in the deutocerebrum are well elaborated, so Elofsson and Hessler (1990) suggested that this might be the product of an extremely long period of evolutionary adaptation for existence without eyes.

Elofsson and Hessler (1990) subdivided the anterior part of the brain in *Hutchinsoniella macracantha* into 3 distinct regions: the central cephalic region, the head shield region, and the ventrally situated "clypeal" region. A clear subdivision of this anterior part into protocerebral or deutocerebral regions is not possible. The central cephalic region is concentrated around the midline and consists of a large neuropil, which along its dorsal and anterior margins contains a number of paired and unpaired structures connected to each other by distinct tracts. Elofsson and Hessler (1990) refer to this structure as the "mushroom body complex," although they state that it does not bear any resemblance to the mushroom bodies found in Hexapoda. Therefore, and in order to avoid any confusion with the hexapod nomenclature, I reject the term "mushroom body complex" and instead suggest the more neutral term "multilobed complex" while its function and relation to the brain structures of other Euarthropoda is unknown. The multilobed complex is composed of 9 interconnected lobes, and a remarkable feature is that it is linked with the deutocerebral olfactory lobes by paired tracts that enter lobe number 8 of the multilobed complex. Elofsson and Dahl (1970) suggest that this pair of tracts is equivalent to the olfactory globular tracts of the malacostracan brain, although they do not cross in *H. macracantha* but remain ipsilateral. In this view, the multilobed complex is formally equivalent to the medulla terminalis of Malacostraca and Remipedia and the lateral horn of Hexapoda and hence probably a protocerebral structure. The head shield region is mostly composed of the cell somata innervating the multilobed complex but also contains an unstructured neuropil.

The paired olfactory lobes are located in the "clypeal" region of the brain and are by definition a deutocerebral structure. As in Remipedia, they are extremely large in comparison with the other brain components. The organization of the neuropil of the olfactory lobes displays a conspicuous pattern in that each discoid lobe consists of 6 to 8 vertical sublobes or columns in which profuse branching of axons and dendrites gives rise to horizontal layers of ordered microvilli-like split terminals. The direction of these layers alternates. This layered appearance is enhanced by a compartmentalization by glial cells. In Elofsson and Hessler's (1990) view, the micro-architecture of these sublobes is markedly different from that of the spherical glomeruli in the olfactory lobes of Malacostraca.

The central cephalic region is linked to the ventral nerve cord by the pair of thick circumesophageal connectives that constitutes the tritocerebrum. The tritocerebrum is targeted by the nerves of the second antennae and also gives rise to the tegumentary nerves as well as the frontal commissure, a nerve loop running

anteriorly around the esophagus that gives rise to the innervation of the labrum. A distinct pair of commissures behind the esophagus also links the 2 halves of the tritocerebrum.

Elofsson and Hessler (1990) conclude that the cephalocaridan nervous system possesses a high degree of organization unseen in representatives of the Branchiopoda and Maxillopoda and more reminiscent of the malacostracan brain. The Cephalocarida and also the Remipedia are regarded as a basal crustacean taxon that has retained many plesiomorphic features; yet the complex architecture of their brain is not compatible with this view.

Remipedia

Remipedes lack any kind of eyes since their habitat is absolutely aphotic, and chemical (and tactile) clues most likely play a major role in orientation. Fanenbruck and colleagues (2004) and Fanenbruck and Harzsch (2005) presented a detailed histological study and reconstruction of the brain anatomy of *Godzilliognomus frondosus* Yager, 1989 (Remipedia, Godzilliidae; Fig. 5), from Grand Bahama Island (Yager 1989), including a discussion of ecological and phylogenetic implications. An outstanding feature of the anterior brain of *G. frondosus* is the inverted neuraxis, caused by the striking elevation of the proto- and deutocerebrum, which are additionally bent almost 180° backward so that the neuraxis is inverted with respect to the body axis. In consequence, the protocerebrum is oriented upside down and located posteriorly to the deutocerebrum, which points upward and backward with the olfactory neuropils sticking out anteriorly.

Major components of the protocerebrum are the paired hemiellipsoid bodies, the olfactory-globular tracts, and the central complex (Fig. 5D). The hemiellipsoid bodies are neuropils with a fine, dense texture that are linked to the olfactory neuropils by the olfactory-globular tracts, as is the case in the ground pattern of taxon N. N. (Fig. 6). The 2 arms of this tract touch each other medially, forming a characteristic chiasm located next to the central body. The protocerebrum is subdivided into at least 4 sublobes (lobes a through d) in addition to the hemiellipsoid bodies. Within both hemispheres, lobe a is located next to the hemiellipsoid bodies. Therefore, these structures together may constitute the medulla terminalis (lateral protocerebrum). All components of the central complex as described in the ground pattern of taxon N. N. are present in the brain of Remipedia (Fanenbruck and others 2004; Fanenbruck and Harzsch 2005).

The deutocerebrum adjoins the protocerebrum rostrally. It consists of the median antenna 1 neuropil and the paired lateral antenna 1 neuropils that receive a distinct input from the nerves of the first antenna (Fig. 5D). On both sides, the lateral antenna one neuropil (LAN) is subdivided into 2 distinct compartments (LAN1 and LAN2). The antenna 1 nerves are mixed sensory and motor nerves and innervate both rami of the first antennae, which are equipped with numerous setae (Yager 1989). Approaching the brain the antenna 1 nerves split up into a smaller and a larger portion, which target LAN1 and LAN2, respectively. This separation may coincide with a separation of motor and sensory qualities within the nerves.

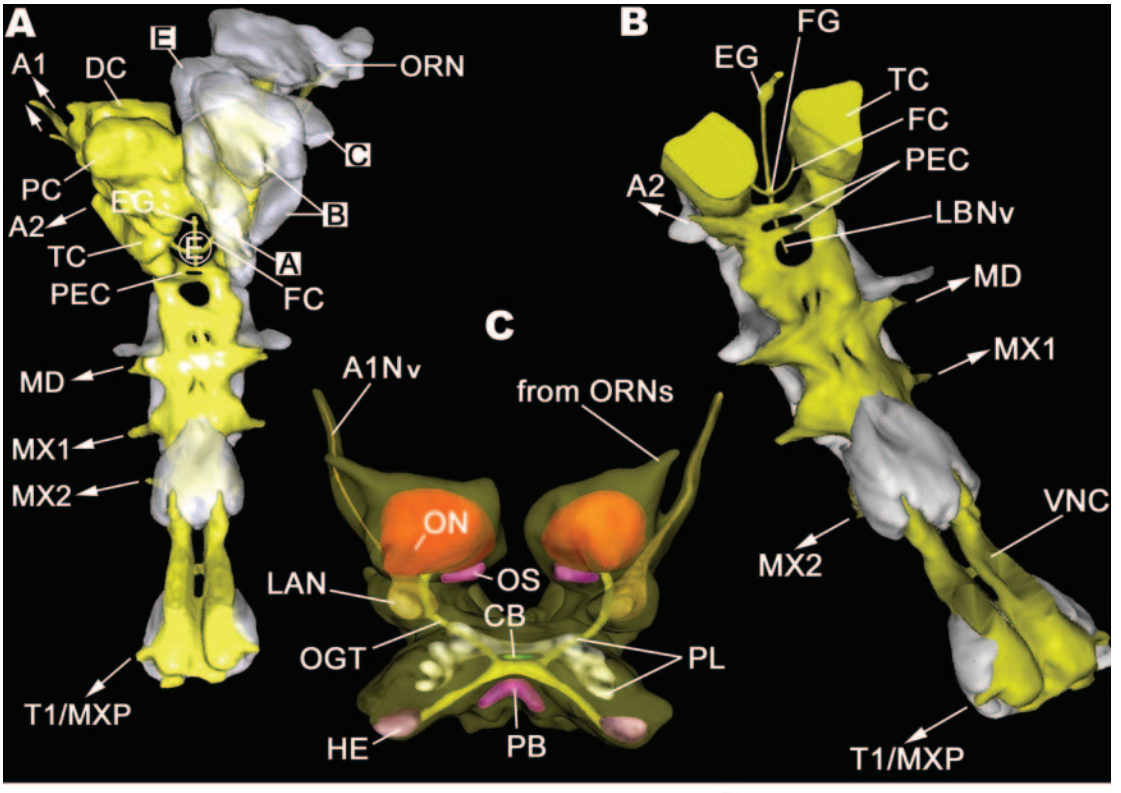
The basal segments of antennae 1 in remipedes are equipped with dense tufts of olfactory receptors, the aesthetascs. These are arranged in several rows and in *G. frondosus* amount to approximately 40 on each side. The somata of the olfactory receptor neurons (ORNs) are arranged in conspicuous clusters within the basal portion of the first antennae immediately adjacent to the brain. These clusters comprise thousands of somata and provide a massive input to the dominating olfactory neuropils. The neuropil of the olfactory lobes is differentiated into characteristic olfactory glomeruli, which give it the shape of a cauliflower. In Malacostraca, these glomeruli serve as functional units for olfactory processing and are the sites where the primary chemosensory afferents contact the dendrites of second-order neurons (see above; Schmidt A and Ache 1996; Schmidt M and Ache 1997; Sandeman D and Mellon 2002; Beltz and others 2003; Schachtner and others 2005). Two paired cell clusters, named D and E, both of which comprise several hundred neuronal somata, are associated with each olfactory neuropil. Fibers emerging from these clusters target the core of the neuropil, suggesting that these neurons are olfactory interneurons, an arrangement that closely resembles that in Malacostraca (Schmidt A and Ache 1996; Schmidt M and Ache 1997; Sandeman D and Mellon 2002; Beltz and others 2003). The olfactory globular tracts in the remipede brain appear as thick fiber tracts that emerge from the olfactory neuropils to veer anteriorly and are composed of the axons of olfactory projection neurons that target the hemiellipsoid bodies, as in Malacostraca (Sullivan and Beltz 2001a, 2001b, 2004, 2005).

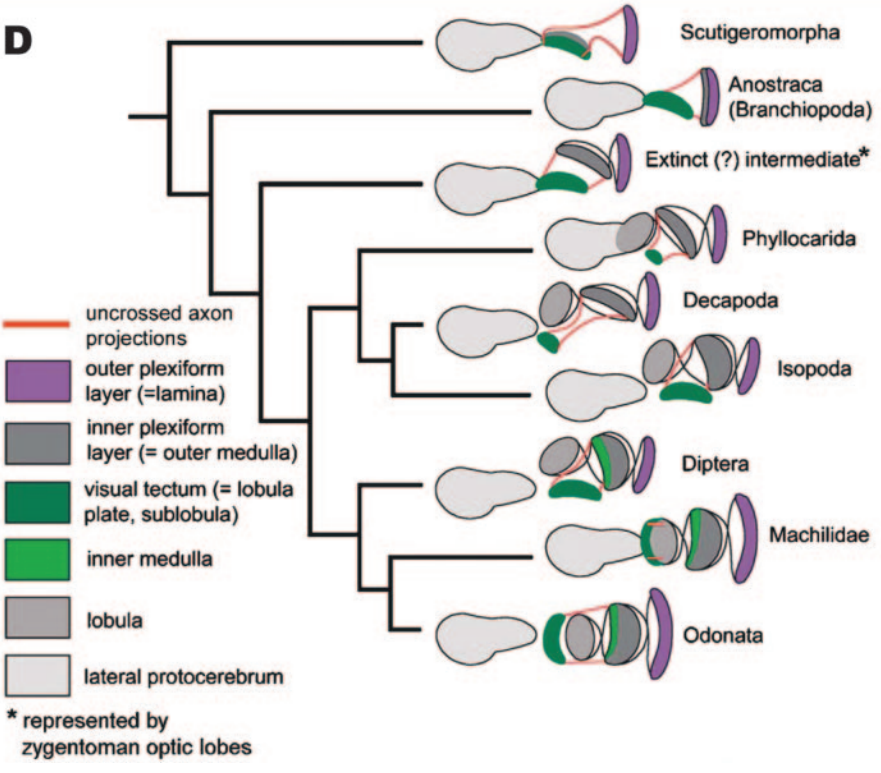
The tritocerebrum adjoins the deutocerebrum ventrally. It is associated with the antenna 2 nerves and the tegumentary nerves innervating the integument of the cephalic shield. The paired tritocerebral lobes are transversely joined by a double postesophageal commissure. They also give rise to a frontal connective that innervates a first unpaired frontal ganglion rostral to

the esophagus, from which a nerve projects ventrally to innervate the labrum. In summary, the layout of the remipede brain is virtually identical to that of Malacostraca but the 3 optic neuropils associated with the lateral eyes as well the input from the median eyes are absent.

Neurogenesis

Several recent reports on neurogenesis in less well-studied arthropod taxa now make it possible to compare aspects of neurogenesis across the Euarthropoda in order to get an idea of neurogenic mechanisms in the





ground pattern of this group (reviewed in Harzsch, Müller, and Wolf 2005; Stollewerk 2006). Eriksson and colleagues (2003) explored aspects of nervous system formation in an onychophoran. In this taxon, neurons arise through the mitotic activity of cells within the neuroectoderm that generate neuron precursor cells. All of the neuroectoderm seems to be involved in this generalized and unordered proliferation (Eriksson and others 2003). In a representative of the Arachnida, Stollewerk and colleagues found that neuronal precursors are also generated by the generalized mitotic activity of the neuroectoderm (Stollewerk and others 2001, 2003; Stollewerk 2002, 2006). In Chelicerata, clusters of these precursor cells are then singled out from the neuroectoderm by lateral inhibition as mediated by the activity of proneural genes and invaginate at specific sites arranged in a stereotypical pattern. In Onychophora, these processes have not yet been explored with techniques that would allow a meaningful comparison with Chelicerata (Eriksson and others 2003). *L. polyphemus*, as another representative of the Chelicerata, seems to share many features of neurogenesis with the Arachnida as laid out above (Mittmann 2002). Similar to the Arachnida, in a diplopod clusters of neural precursors invaginate. These precursors, however, are generated by neurogenic activity restricted to these invagination sites (Dove and Stollewerk 2003). Mitotic activity in a scolopendromorph chilopod is distributed across the whole extent of the neuroectoderm, but a clustering of neural precursors into proliferative units has also been observed (Whitington 1991). Recently, it was shown that in the chilopod *Lithobius forficatus* the arrangement of the invaginating clusters in the neuroectoderm is strikingly similar to that in Diplopoda and Chelicerata (Kadner and Stollewerk 2004). A generalized mitotic activity of the neuroectoderm, perhaps with concentrations at invagination sites, therefore seems to characterize the ground pattern of Euarthropoda (Dove and Stollewerk 2003; Kadner and Stollewerk 2004). In none of the groups discussed so far is the generation of neurons restricted to asymmetrically dividing stem cells, as now described for Hexapoda and Crustacea.

In Hexapoda, neuronal precursor cells (the ganglion mother cells) are generated by the mitotic activity of neuronal stem cells, the neuroblasts. These neuroblasts repeatedly undergo unequal divisions to produce ganglion mother cells, which later divide again to produce ganglion cells (neurons; reviewed in Goodman and Doe 1993; Doe and Skeath 1996; Campos-Ortega and Hartenstein 1997; Doe and others 1998; Skeath 1999; Matsuzaki 2000). Neuroblasts are also present in the silverfish, a primarily wingless insect, and the array of neuroblasts in this species is evolutionarily conserved in the winged insects (Truman and Ball 1998). Neuroblasts emerge in the early germ band and are singled out by cell-to-cell interactions within the neuroectoderm. There are only a small number of neuroblasts in each hemineuromere of the ventral nerve cord (approximately 25). Neuroblasts with similar proliferative characteristics are also present in malacostracan Crustacea (Fig. 4F and G; reviewed in Scholtz and Dohle 1996; Harzsch 2002a, 2003a; Dohle and others 2004; Whitington 2004) and most likely also in entomostracan crustaceans (Gerberding 1997; Harzsch 2001b). However, in contrast to Hexapoda, malacostracan neuroblasts originate from ectoteloblasts by an invariant lineage. The question of whether hexapodan and crustacean neuroblasts represent a homologous class of neuronal stem cells is still unsettled (reviewed in Whitington 1996; Dohle and Scholtz 1997; Dohle 1997; Whitington and Bacon 1997; Harzsch 2003b; Dohle and others 2004; Whitington 2004).

In summary, Harzsch, Müller, and Wolf (2005) suggested that a generalized mitotic activity of the neuroectoderm that may be concentrated at invagination sites is the plesiomorphic mechanism of neurogenesis in the Euarthropoda as it is still represented in

Fig. 5 (A–C) 3D renderings of the anterior nervous system of the remipede crustacean *Godzilliognomus frondosus*. (A) Anterior nervous system seen from posteriodorsal with neuropil (yellow) and clusters of neuronal somata (gray; *A*, *B*, *C*, *E*, ORN); anterior is toward the top. Modified from Fanenbruck and others (2004), with permission of the publishers. (B) Rendering of the tritocerebrum (TC) and the subsequent ventral nerve cord (VNC) as well as the labral innervation and the esophageal ganglion. Modified from Fanenbruck and others (2004), with permission of the publishers. (C) 3D rendering of proto- and deutocerebrum. Orientation is according to the body axis not neuraxis, with anterior to the top. Modified from Fanenbruck and others (2004), with permission of the publishers. *A*, *B*, *C*, *E*, clusters of neuronal cell somata; A1, first antenna; A1NV, nerve of the first antenna; A2, second antenna; CB, central body; DC, deutocerebrum; E, esophagus; EG, esophageal ganglion; FC, frontal commissure; FG, frontal ganglion; HE, hemiellipsoid body; LAN, lateral antennal neuropils; LBNv, labral innervation by labral nerve; MD, mandible; MX1, first maxilla; MX2, second maxilla; OGT, olfactory globular tract; ON, olfactory neuropil; ORN, somata of olfactory receptor neurons; OS, olfactory satellite neuropil; PB, protocerebral bridge; PC, protocerebrum; PEC, postesophageal commissure; PL, protocerebral lobes; T1/MXP, first thoracopod or maxilliped; TC, tritocerebrum; VNC, ventral nerve cord. (D) Evolution of the optic neuropils in Mandibulata. For details, see text. Reprinted from Strausfeld (2005), with kind permission of Elsevier.

Chelicerata, Chilopoda, and Progoneata. The restriction of neuronal production to a small number of specialized asymmetrically dividing and individually identifiable stem cells is a synapomorphic characteristic of Tetraconata.

Serotonin-immunoreactive neurons

In a series of reports, Harzsch and Waloszek have recently examined serotonin-immunoreactive neurons in the ventral nerve cord of Euarthropoda against a phylogenetic background (Harzsch and Waloszek 2000; Harzsch 2003a, 2004b). In *L. polyphemus* (Xiphosura) and *Pandinus imperator* (Scorpiones), as representatives of the Chelicerata, clusters of segmentally iterated serotonergic neurons comprising a variable number of 6 to 12 or even more somata were present in each hemineuromere of the ventral nerve cord (Harzsch 2004b). Similar clusters (comprising only 4 cells, though with ipsilateral neurites) are also present in the opisthosomal ganglia of the harvestman *Rilaena triangularis* (Arachnida, Opiliones; Breidbach and Wegerhoff 1993). In most recent studies the Xiphosura emerge as being more basal chelicerates than spiders (the question of the Pycnogonida will not be touched upon here). For this reason and because Xiphosura and Scorpiones share a similar number of serotonergic neurons, I assume that these 2 groups are more likely to represent the chelicerate ground pattern than are spiders. Hence, the arrangement of serotonergic neurons in the ground pattern of the Chelicerata was tentatively reconstructed as comprising an anterior and a posterior cluster with a variable number of serotonergic neurons linked by commissural fibers (Harzsch 2004b), and I suggest that the presence of clusters with about a dozen of these neurons also characterizes the euarthropodan ground pattern.

Chilopoda and Diplopoda have derived from this plesiomorphic condition in that there are typically groups that comprise single cells or pairs of serotonergic neurons, the maximum number observed in 1 group being 4 neurons (Harzsch 2004b). These cells are individually identifiable in successive ganglia and from animal to animal. The pattern of serotonergic neurons in the ventral nerve cord of Hexapoda and Crustacea is even more invariant and restricted. Harzsch and Waloszek (2000) and Harzsch (2003b) suggested that the ground pattern of Hexapoda as well as malacostracan and entomostracan crustaceans comprises an anterior and a posterior pair of individually identifiable serotonergic neurons per hemiganglion (some of these were convergently reduced in several of the hexapod and crustacean subgroups). These observations suggest that in Xiphosura and Scorpiones clusters of neurons fulfill the functions that in Entomostraca, Malacostraca, and Hexapoda are accomplished by a much smaller set of neurons and that these differences in cell numbers are related to the differences in neurogenesis (Harzsch, Müller, and Wolf 2005).

Other neuronal features

A number of other neuronal features have been discussed with regard to arthropod phylogeny (reviewed in Dohle 2001; Richter 2002; Harzsch, Müller, and Wolf 2005; Pflüger and Stevenson 2005). Additional support for the Tetraconata concept stems, for example, from the general structure of the ventral nerve cord (Wiens and Wolf 1993; Elsson 1996) and from phylogenetic analyses of the morphology of individually identified neurons in the ventral nerve cord such as peptidergic interneurons (Agricola and Bräunig 1995; Dircksen 1998), motoneurons (Wiens and Wolf 1993; Kutsch and Breidbach 1994; Kutsch and Heckmann 1995; Wolf and Harzsch 2002a, 2002b), unpaired median neurons (Bräunig and Pflüger 2001; Pflüger and Stevenson 2005), and *engrailed* and *even-skipped* expressing cells (Duman-Scheel and Patel 1999). Furthermore, developmental aspects such as early axogenesis (Whitington 1996; Whitington and Bacon 1997; Gerberding and Scholtz 1999, 2001) lend support to the Tetraconata hypothesis. However, contrary to the characters discussed at length above, most of these other characters have been explored only in a subset of the relevant taxa, so it is difficult at this point to draw sound phylogenetic conclusions from this set of characters.

Reconstructing ground patterns

The large number of characters discussed in this article, including numerous nonmodel arthropods, shows that the nervous system provides a wealth of structures that are extremely useful for discussing aspects of arthropod phylogenetic relationships. However, it is beyond the scope of this article to analyze these features in a cladistic way using a data matrix. Rather, I try to reconstruct the ground patterns of the various arthropod groups and from these ground patterns tentatively suggest a hypothesis on arthropod relationships as derived from neuronal characteristics (Fig. 6; deliberately ignoring other morphological characteristics as well as fossil arthropods).

The ground pattern of Euarthropoda (node A in Fig. 6)

Here, I summarize those neuronal features that are good candidates for being part of the ground pattern of Euarthropoda (Fig. 6, node A). The character status

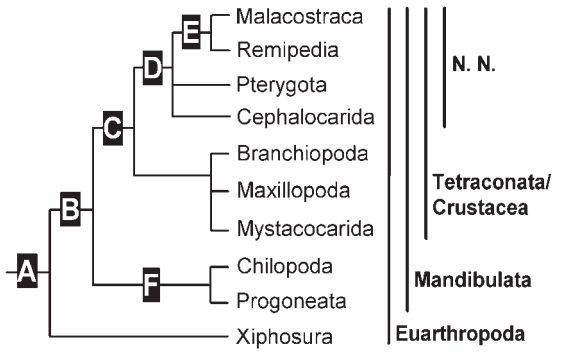


Fig. 6 Arthropod relationships as determined by the analysis of brain morphology (other morphological characters and fossil taxa are deliberately ignored). The reconstructed ground patterns of the various groups are indicated by the letters A to F on the various nodes. This new analysis, similar to that of Hanström (1926; Fig. 1), provides morphological evidence for a paraphyly of both Tracheata and Crustacea (as we traditionally perceive these groups) but instead advocates the Tetraconata concept as laid out by Dohle (2001). For further explanations, see text.

of these features as plesiomorphic or apomorphic remains unclear. It is to be hoped that more characters will emerge in the near future. Although recently new interest has arisen in the brain design of Onychophora (Schürmann 1995; Eriksson and Budd 2000; Eriksson and others 2003), Pycnogonida (Maxmen and others 2005), and Tardigrada (Dewel and others 1999), our knowledge on these groups is still too limited to allow a meaningful comparison with brain structure in Chelicerata and Mandibulata. Therefore, in the summary of the euarthropod ground pattern, the status of the various characters as plesiomorphic or apomorphic cannot be determined.‘

- The 3 anterior neuromeres of the euarthropod nervous system are the protocerebrum (ocular segment), deutocerebrum (cheliceral segment in Chelicerata, first antennal segment in Mandibulata), and tritocerebrum (pedipalp segment in Chelicerata, second antennal segment in Crustacea, intercalary segment in Hexapoda). Most likely the esophagus did not pass *between* the deutocerebrum and the tritocerebrum but *through* the deutocerebral segment.
- Bilateral symmetrically arranged median eyes with histaminergic photoreceptors are present in the ground pattern, but the exact ultrastructure of these has not been reconstructed. The axons of these photoreceptors project into a protocerebral neuropil, the median eye center, that is either bilaterally paired or medially fused (“ocellar ganglia” in Xiphosura; “nauplius-eye center” in Entomostraca; 2 small spherical neuropils associated with the protocerebral bridge in Malacostraca; “ocellar center” in Collembola; “ocellar plexus” in Pterygota). The median eye center is innervated by interneurons with somata in an anteriorly located medial cell cluster, some of which are serotonergic (“dorsal median group” in Xiphosura; “anterior median cluster [cluster 6]” in Crustacea; “pars intercerebralis” in Hexapoda).
- The ground pattern of the Euarthropoda also includes a transverse median unpaired neuropil, the central body, enwrapped in layers of neuronal somata. The central body is also innervated by columnar neurons with somata in the anteriorly located median cell cluster, which also houses the interneurons associated with the median eyes.
- Lateral eyes, which are composed of subunits comprising several hundred cells (most likely a variable cell number), are part of the euarthropodan ground pattern. The photoreceptors in these lateral eyes are histaminergic. The eyes are associated with 2 optic neuropils, which are most likely linked by straight fibers.
- The lateral eyes are associated with 2 optic neuropils that provide an input into the protocerebrum.
- During growth of the lateral eyes new elements are added to the side of the eye field from a growth zone and elongate the rows of earlier generated optical units.
- A preoral frontal commissure is present that is composed of deuto- and tritocerebral fibers. It gives rise to nerves innervating the hypostome, esophagus, and anterior part of the gut.
- Neurogenesis involves a generalized mitotic activity of the neuroectoderm that may be concentrated at invagination sites.
- In the ventral nerve cord, an anterior and a posterior cluster with a variable number (approximately a dozen) of serotonergic neurons are present in each hemineuromere, which are transversely linked by commissural fibers.

The ground pattern of Mandibulata (node B in Fig. 6)

- Compared with the euarthropod ground pattern, the number of cells of which each eye subunit is composed is reduced, some cell types now occur in constant numbers, and a crystalline cone is present in each eye unit (apomorphic).
- The visual input from the lateral eyes is processed in 2 motion detection neuropils, the outer plexiform layer (lamina) and the visual tectum (lobula plate,

sublobula) linked by straight visual fibres (unclear character status, most likely plesiomoprhic).
- The appendage associated with the deutocerebrum provides a sensory input that is mostly mechanosensory and to a lesser extent chemosensory (unclear character status).
- The appendage associated with the tritocerebrum provides a mostly mechanosensory input (unclear character status).
- In each hemineuromere of the ventral nerve cord, single cells or pairs of serotonergic neurons occur, the maximum number observed in a group being 4 neurons (apomorphic). These cells are individually identifiable in successive ganglia and from animal to animal.
- All other characters from the euarthropod ground pattern as plesiomorphic characters.

The ground pattern of the Tetraconata (node C in Fig. 6)

- Each ommatidium of the lateral eyes has a fixed architecture and is composed of a constant number of individually identifiable cells: 2 corneagenous cells, 4 crystalline cone cells, 8 retinula cells, and pigment cells.
- A central complex is present that includes the anterior medial cell cluster (plesiomorphic); the protocerebral bridge (apomorphic); the central body (plesiomorphic); the paired lateral lobes linked by commissural fibers (apomorphic); and the paired lateral cell clusters slightly posterior to the central body (apomorphic).
- In terms of neurogenesis, the restriction of neuronal production to a small number of specialized asymmetrically dividing and individually identifiable stem cells is an apomorphic character of Tetraconata.
- There is an anterior and a posterior pair of individually identifiable serotonergic neurons per hemiganglion (apomorphic).
- All other characters from the mandibulatan ground pattern as plesiomorphic characters.

Summary of the ground pattern of taxon N. N. (node D in Fig. 6)

- An outer plexiform layer (lamina) is present as the most distal optic neuropil, which is linked to the clearly separated inner plexiform layer (outer medulla, apomorphic) by the outer optic chiasm (apomorphic).
- A third optic neuropil, the protolobula (apomorphic), is present that is linked to the inner plexiform layer by the inner optic chiasma (apomorphic).
- The first pair of antennae provides a primarily chemosensory input to the deutocerebrum (apomorphic).
- The olfactory receptor neurons have acetycholine as their transmitter and the afferent axons of the receptors penetrate into the ipsilateral olfactory lobe in a radial manner. They have uniglomerular terminations (apomorphic).
- Local interneurons in the olfactory system of these taxa include serotonergic giant neurons (apomorphic).
- The olfactory lobes are linked to a lateral component of the protocerebrum, the multilobed complex in Cephalocarida, the lateral protocerebrum with hemiellipsoid body in Remipedia and Malacostraca, and the lateral horn in Hexapoda. This link is established by a characteristic fiber tract (olfactory globular tract), which is composed of the axons of olfactory projection neurons of olfactory interneurons (all characters apomorphic).
- The lateral/mechanosensory antenna 1 neuropil is present in the deutocerebrum (apomorphic).
- All other characteristics from the ground pattern of the Tetraconata as plesiomorphic characters.

The ground pattern of Remipedia and Malacostraca (node E in Fig. 6)

- The olfactory-globular tract has a characteristic crossover (chiasm) located dorsally close to the central body (apomorphic).
- All other characters from the ground pattern of the taxon N. N. as plesiomorphic characters.

The ground pattern of the Myriapoda (node F in Fig. 6)

- Chilopoda and Diplopoda share a corresponding pattern of serotonergic neurons (apomorphic; cell groups b–e), the maximum number observed in a group being 4 neurons (Harzsch 2004b). These cells are individually identifiable in successive ganglia and from animal to animal.
- The median eye is reduced (apomorphic).
- The appendage associated with the deutocerebrum is reduced (apomorphic).
- All other characters from the ground pattern of Mandibulata as plesiomorphic characters.

Concluding remarks

In summary, the characters derived from brain morphology discussed here conflict with the traditional

phylogenetic relationships within the Arthropoda. They support those molecular (for example, Shultz and Regier 2000; Cook and others 2001; Friedrich and Tautz 2001; Hwang and others 2001; Peterson and Eernisse 2001; Regier and Shultz 2001a, 2001b; Burmester 2002; Kusche and others 2002) and morphological studies (for example, Dohle 1997, 2001; Paulus 2000; Harzsch 2001a; Nielsen 2001; Richter 2002) that argue in favor of the Tetraconata concept and suggest a paraphyly of the Tracheata and Crustacea as we traditionally perceive these taxa. This article indicates that it is essential at this point to reexamine the traditional morphological characteristics (see, for example, Dohle 2001; Richter 2002) with regard to the new phylogenetic relationships suggested by the molecular data and brain architecture in order to explore why the traditional morphological and molecular hypotheses on arthropod relationships conflict so significantly.

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