

Architectural Principles and Evolution of the Arthropod Central Nervous System

13

Rudolf Loesel, Harald Wolf, Matthes Kenning,
Steffen Harzsch and Andy Sombke

Contents

13.1 The Ventral Nerve Cord	300
13.1.1 The Arthropod Ventral Nerve Cord is Segmentally Organized	300
13.1.2 The Segmental Ganglia are Highly Structured.....	301
13.1.3 Common Features in Arthropod Ventral Nerve Cord Structure are Based on Developmental and Genetic Similarities	306
13.1.4 Homologies Across the Arthropod Taxa....	307
13.2 The Brain	309
13.2.1 The Compound Eyes and Visual Neuropils	312
13.2.2 The Lamina	313
13.2.3 The Medulla	316
13.2.4 The Deeper Neuropils and Image Analysis	317
13.2.5 Evolution of Visual Neuropils.....	317
13.2.6 Olfactory Lobes.....	319
13.2.7 Mechanosensory Neuropils	324
13.2.8 The Mushroom Bodies.....	326
13.2.9 The Central Body.....	328
13.3 Phylogenetic Overview and Outlook	331
13.3.1 Ground pattern of the Arthropod Nervous System.....	331
References	332

R. Loesel
Institut für Biologie, RWTH Aachen, Lukasstr.
1, 52056, Aachen, Germany
e-mail: loesel@bio2.rwth-aachen.de

H. Wolf
Institute of Neurobiology, University of Ulm,
Albert-Einstein-Allee 11, 89081, Ulm/Donau,
Germany
e-mail: harald.wolf@uni-ulm.de

M. Kenning · S. Harzsch · A. Sombke (✉)
Zoological Institute and Museum, Department
of Cytology and Evolutionary Biology, Ernst Moritz
Arndt University of Greifswald, Soldmansstrasse
23, 17487, Greifswald, Germany
e-mail: andy.sombke@uni-greifswald.de

M. Kenning
e-mail: matthes.kenning@googlemail.com

S. Harzsch
e-mail: steffen.harzsch@uni-greifswald.de

This is an exciting time for arthropod neuro-anatomists! A wealth of reviews, special issues, book chapters, and entire book volumes published during the last 10 years shows the unbroken interest in and enthusiasm for the arthropod nervous system and for gaining insights into its architecture, physiology, and aspects of neuroethology (Barth and Schmid 2001; Wiese 2001, 2002; Barth 2002; North and Greenspan 2007; Breithaupt and Thiel 2011; Galizia et al. 2012; Land and Nilsson 2012; Strausfeld 2012). Numerous review articles and book chapters witness that neurobiology is one of the most active fields of arthropod research. Recently featured topics are, for example, the crustacean central nervous system (Schmidt and Mellon 2011; Harzsch et al. 2012; Sandeman et al. in press), structure and function of crustacean chemosensory sensilla (e.g. Hallberg and Skog 2011; Mellon and Reidenbach 2011),

chelicerate strain detection systems (Barth 2012), and insect olfaction (Galizia and Szyska 2008; Hansson and Stensmyr 2011; Hansson et al. 2011; Sachse and Krieger 2011). Moreover, the central nervous system and visual organs of neglected taxa such as Myriapoda (Sombke et al. 2011a, 2012), Onychophora (Mayer 2006; Strausfeld et al. 2006a, b; Eriksson and Stollewerk 2010; Whittington and Mayer 2011), Trilobita (Clarkson et al. 2006), and Xiphosura (Battelle 2006) have been analyzed with contemporary techniques. Furthermore, detailed reviews have been provided on specific substructures of the arthropod brain such as the central complex (Loesel et al. 2002; Homberg 2008), mushroom bodies (MBs) (e.g. Farris 2005, 2011; Strausfeld et al. 2009; Loesel and Heuer 2010; Heuer et al. 2012), and the peripheral and central olfactory pathways (e.g. Sandeman and Mellon 2002; Schachtner et al. 2005; Mellon 2007; Masse et al. 2009; Galizia and Rössler 2010; Hansson and Stensmyr 2011; Rössler and Zube 2011). Functional anatomy, physiology, and development of arthropod eyes and the optic neuropils seem to be endlessly appealing for arthropod neurobiologists (e.g. Egelhaaf et al. 2009; Borst et al. 2010; Borst and Euler 2011).

The past decade has also seen the emergence of the discipline of ‘neurophylogeny’ that is the synthesis of neurobiological questions and evolutionary aspects (e.g. Harzsch et al. 2005a, b; Harzsch 2006, 2007; Loesel 2006, 2011; Strausfeld 2009; Strausfeld and Andrews 2011). Methods such as immunohistochemistry combined with confocal laser scan microscopy have facilitated the analysis of neuroanatomy of non-model arthropods. These comparative data have yielded new insights into arthropod phylogeny. Within the limitations, a book chapter imposes the following: (i) we will focus on the central nervous system only and for all aspects of sensory systems refer the reader to some of the literature mentioned above; (ii) as a systematic overview touching all anatomical structures of the nervous system in all major taxa is impossible, we will try to extract some common architectural principles of the arthropod ventral

nerve cord and brain and will highlight evolutionary trends of these structures.

13.1 The Ventral Nerve Cord

13.1.1 The Arthropod Ventral Nerve Cord is Segmentally Organized

As a basic scheme, segmentation of the ventral nerve cord matches body segmentation, in the form of segmental ganglia connected by a pair of connectives. This holds for tagmata such as head and thorax, although the fusion of the segmental ganglia does not always follow the fusion pattern of the visible cuticle segments. Often, ganglia shift along the longitudinal body axis to join other ganglia, thus lengthening the nerves attached to them. This may be the result of actual morphogenetic movements in the embryonic nervous system. The segmental ganglia receive sensory input from the corresponding body segment, and the motoneurons in that ganglion supply the segmental muscles (Fig. 13.1a). There are, however, many exceptions, for instance, as far as intersegmental muscles are concerned. These muscles may be supplied from motoneurons in either of the adjacent segmental ganglia. Sensory neurons often do not branch just in the segmental ganglion but ascend further, sometimes up to the brain. Commissures connect the two sides of the body, in many Mandibulata via two sets of pathways: the anterior and posterior commissures. The commissures consist primarily of axons, whereas dendrites do not usually cross the ganglion midline (anatomical details, e.g., in Tyrer and Gregory 1982; Elson 1996) (Fig. 13.2).

In annelids, on each side of a body segment, separate ganglia which are connected by distinct axon bundles as commissures are formed by neuronal somata and neuropil center (Denes et al. 2007). The latter is defined as a network of dendrites and axons where synapses are present and in which somata do not occur (Richter et al. 2010). In Arthropoda, these two ganglia are usually fused across the body midline (exceptions include many Branchiopoda), thus forming

just a single segmental ganglion which consists of two hemiganglia, connected by the anterior and posterior commissures. The ganglia of adjacent body segments communicate via the connectives. Anastomoses of peripheral nerves are common and allow innervation across segment borders. The axons running in the connectives often do not terminate in the ganglia joined by the latter, but may extend along the ventral nerve cord for several neuromeres, or even the whole length. The latter is true for brain neurons descending all the way to the terminal ganglion and, vice versa, neurons from the terminal ganglion or from any of the more anteriorly located segmental ganglia that send axons into the brain. The axons in the connectives thus usually pass through the ganglia, giving off a few branches, and are joined by axons originating in the particular ganglion. The connectives do not pass the ganglion as a solid bundle but are arranged in separate longitudinal axon bundles that proceed through the ganglion's neuropil (Fig. 13.2).

In the arthropods, and actually in many invertebrates including molluscs and annelids, the somata of neurons are arranged around the periphery of the segmental ganglia. The soma layer may form a continuous rind, or cortex, coating the whole ganglion, particularly where the ganglion neuropil is relatively small and does not bulge and displace the soma cortex. A much larger number of somata and accordingly a thicker soma cortex invariably occur on the ventral side of the segmental ganglia, with a few soma groups extending towards the lateral and dorsal ganglion surfaces. Bundles of primary neurites extend from soma groups into the neuropil where they split up into dendritic and axonal fibers (Fig. 13.2b, d). Primary neurites of motoneurons perforate the ventral neuropil to reach the dorsal side of the ganglion where the motor neuropils are located.

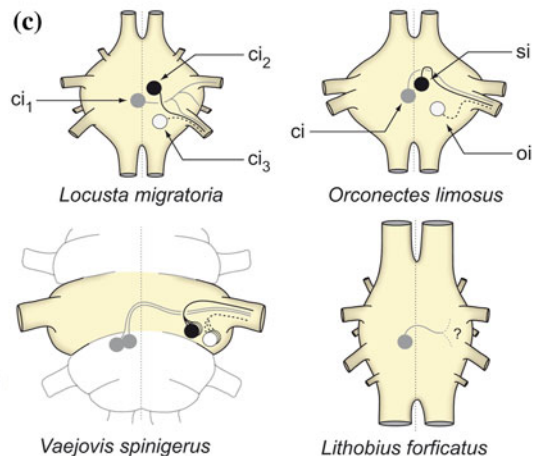
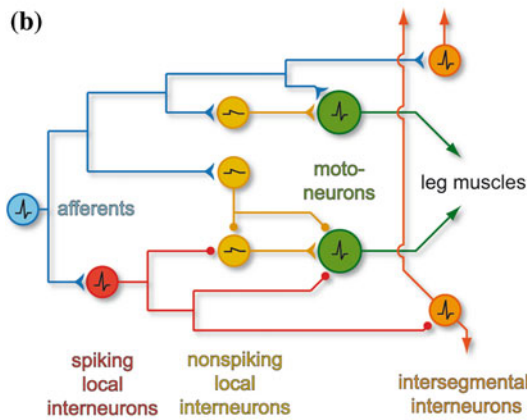
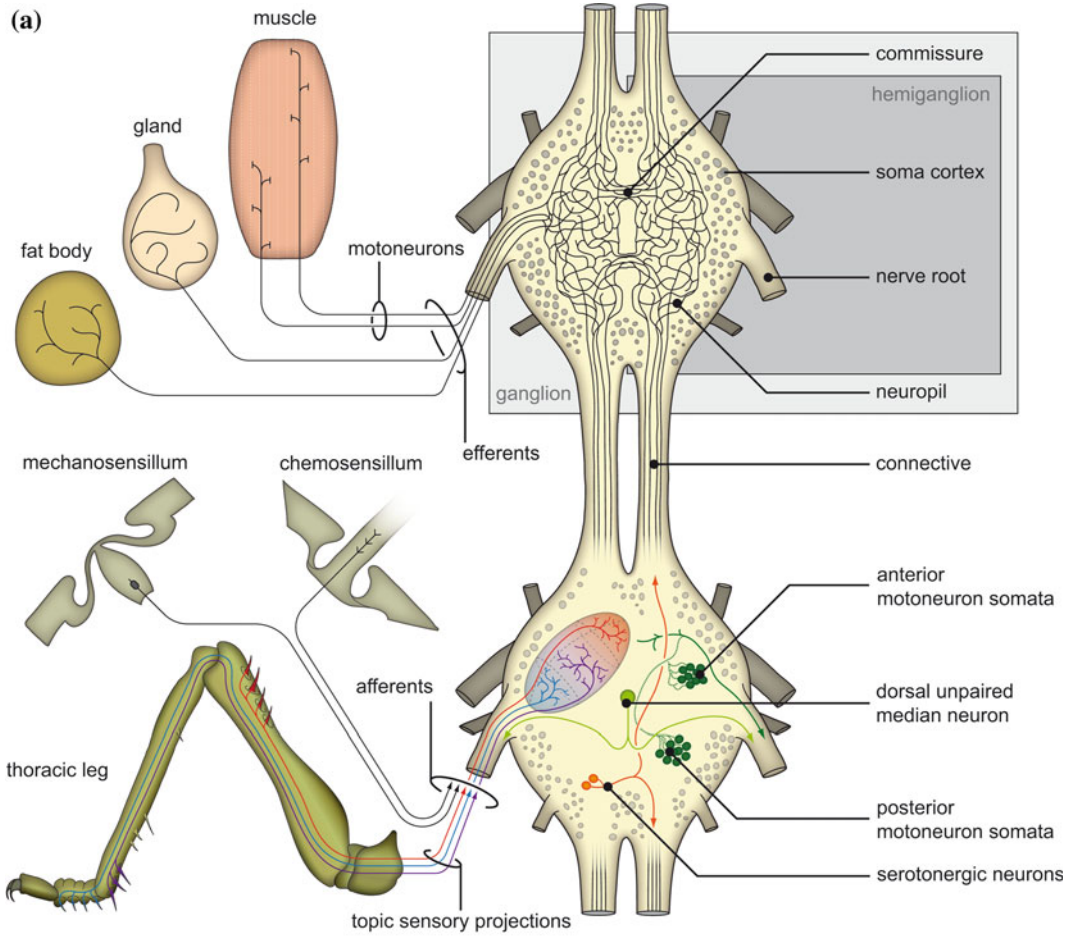
Examples for neurons that occur near the dorsal midline of the ganglion are the so-called dorsal unpaired median neurons, or DUMs (Fig. 13.1a, light green). In Hexapoda, this group of neurons originates in development from special unpaired neuroblasts and forms

important neurosecretory cells that release octopamine (review in Pflüger and Stevenson 2005). This neuron type or its precursors may represent an apomorphy of Mandibulata (Linne et al. 2012). It is also suggested that unpaired midline precursors evolved from the bilateral median domain of the ventral neuroectoderm.

13.1.2 The Segmental Ganglia are Highly Structured

The pattern of the connectives branching into the tracts is quite stereotypic, at least within a given arthropod subtaxon but probably beyond. It appears that corresponding tract patterns are present even across the different arthropod groups, such as hexapods, malacostracan crustaceans (Fig. 13.2a, c) (Skinner 1985a, b; Leise et al. 1986, 1987; Elson 1996), and chelicerates (Wolf and Harzsch 2002a). The conservation of fasciculation patterns in the development of axon pathways in the arthropods examined so far (reviews Whitington 1996; 2004, 2006; Whitington and Bacon 1997; Whitington and Mayer 2011) lends support to such an idea as far as hexapods and malacostracan crustaceans are concerned. Similarly, the presence of an anterior and a posterior commissure per segmental ganglion is consistent across the Tetraconata at least (compare Fig. 13.3). The segmental neuropils, too, exhibit structural properties that are common amongst the arthropods, and beyond. Motor neuropils are located in the dorsal half of the segmental ganglion, and sensory neuropils in the ventral half (Fig. 13.2). Besides this general pattern, sensory projections are also present in intermediate areas, between the dorsal and ventral neuropils proper, and some afferents even synapse in dorsal and medial neuropil areas. In the latter cases, there are usually monosynaptic connections from sensory afferents to motoneurons that support fast reflexes, for instance, in the context of locomotor control (Burrows 1996).

Within the neuropil, different sensory modalities often segregate to different regions (compare sensory projections in the brain, Sect.



◀ **Fig. 13.1** Architecture of the ventral nerve cord in an insect or malacostracan crustacean. **a** Two adjacent segmental ganglia are shown to illustrate major features and anatomical terms (*top ganglion*) and properties of selected neuron groups (*bottom ganglion*) of the ventral nerve cord; note color coding of topological sensory projections. Modified after Richter et al. (2010) and Burrows and Newland (1993). **b** Basic wiring diagram of the sensorimotor pathways in leg motor control. Modified after Burrows (1996). **c** Inhibitory motoneurons in

four sample arthropods: hexapod *top left*, malacostracan *top right*, scorpion *bottom left*, chilopod *bottom right*. The three different, and probably homologous, types of common inhibitors are marked by different shading (*grey*: hexapod ci_1 , *black*: hexapod ci_2 , *white*: hexapod ci_3). No homologization is possible yet for chilopods. Modified after Wiens and Wolf (1993), Harzsch et al. (2005a). *ci* common inhibitor, *si* stretcher-closer inhibitor, *oi* opener inhibitor

13.2 ff.), although exceptions exist. One such exception is the parallel projection of mechanosensory and gustatory input from the locust tarsus. In their target region within the central nervous system, the input from mechanosensory *versus* gustatory sensilla of the same region of the tarsus does not segregate into separate neuropil regions according to the two sensory modalities but rather project into largely overlapping areas in a topologically organized pattern (Newland et al. 2000). In the thoracic ganglia of hexapods, mechanoafferent neurites project mainly to three regions of the neuropil: the most ventral and dorsolateral regions, and the medioventral level of the neuropil. Mechanosensory receptors from the legs exhibit mostly local projections, while receptors from sternites and chordotonal organs form intersegmental projections in addition to local ones (Bräuning et al. 1983). Within a given sensory modality, an ordered structure of neuropil areas is usually observed, in the form of arrangement of sensory projections along gradient axes. For example, mechanosensory input from appendages is usually arranged in a topologically organized pattern (Fig. 13.1a, lower ganglion). That is, the neighboring relationships of sensory input from the body surface are preserved, thus producing a topographic representation of body surface within the ganglion (Burrows 1996). Input from more distal areas, for instance, on an appendage, typically projects to more distal areas in the segmental ganglion. Similarly, the anterior–posterior axis is preserved in the central nervous projections, although distortions occur as a result of differential growth in development.

Further sensorimotor processing is brought about by different groups of interneurons with specific properties (Fig. 13.1b). A coarse outline is as follows: worked out primarily in hexapods (Burrows 1996) such as locust, stick insect or cockroach, and in crustaceans such as crayfish and lobster. The ordered projections of *sensory afferents* facilitate the generation of receptive fields in the first group of interneurons, the *local spiking interneurons* (LSIs). The receptive fields may have the shape of particular small regions of body surface and may possess an inhibitory surrounding area that supports contrast enhancement (e.g. von Békésy 1967). The sensory afferents may make contacts to all other neuron groups downstream of the LSIs, however, including the motoneurons as mentioned above. This downstream connectivity holds for all the other groups of interneurons, in principle, although it is dependent on a neurons' function in detail. One important function of the LSIs is transport of sensory information from the ventral primary projection areas to the dorsal motor areas. Consequently, LSIs typically have axons that extend from ventral dendrites to dorsal axonal processes. The LSIs make connections to *local non-spiking interneurons* (NSIs). A major function of this group of interneurons is the organization of a coordinated motor output. This is achieved by connections to the appropriate sets of motoneurons and by inhibitory connections amongst the NSIs that prevent co-contraction of antagonistic muscles, for example. This is illustrated by the fact that intracellular stimulation of a particular NSI will often result in the execution of a well coordinated movement, such as leg extension or leg flexion

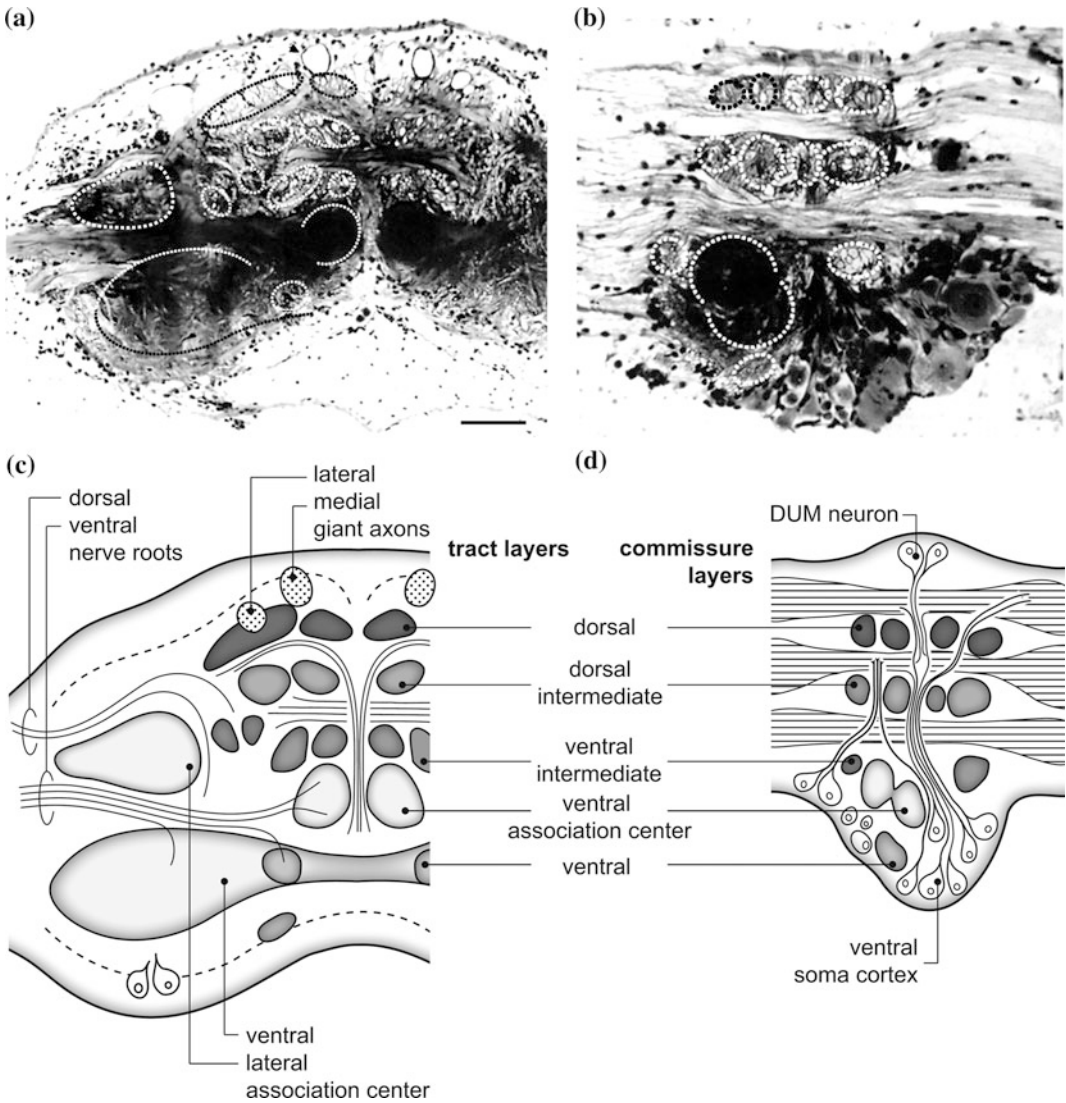


Fig. 13.2 Anatomical features of ventral ganglia, exemplified in a crayfish. Modified after Elson 1996. **a** Histological cross section and **b** parasagittal section illustrate the main features of the segmental ganglion, indicated by

dotted outlines. The drawings in **c** and **d** provide the corresponding labeling. Lateral and medial giant axons are particularities of crayfish used in reflex escape (review in Reichert 1988). Note dorsal DUM somata in **d**

involving all the appropriate joints and muscles (Burrows 1996). Signal propagation and transmitter release in the NSIs is via graded potentials, a mechanism that is possible due to the small length of the processes which are restricted to the particular ganglion or even hemiganglion (hence the term *local* interneurons). *Intersegmental interneurons* receive input from

all the upstream neurons and convey signals into neighboring ganglia, and sometimes up to the brain or down to the terminal ganglion. These are spiking neurons, of course, since they have to transfer signals across large distances to support the coordination of movement across the different body segments. The *motoneurons*, finally, convey excitation to the muscles to

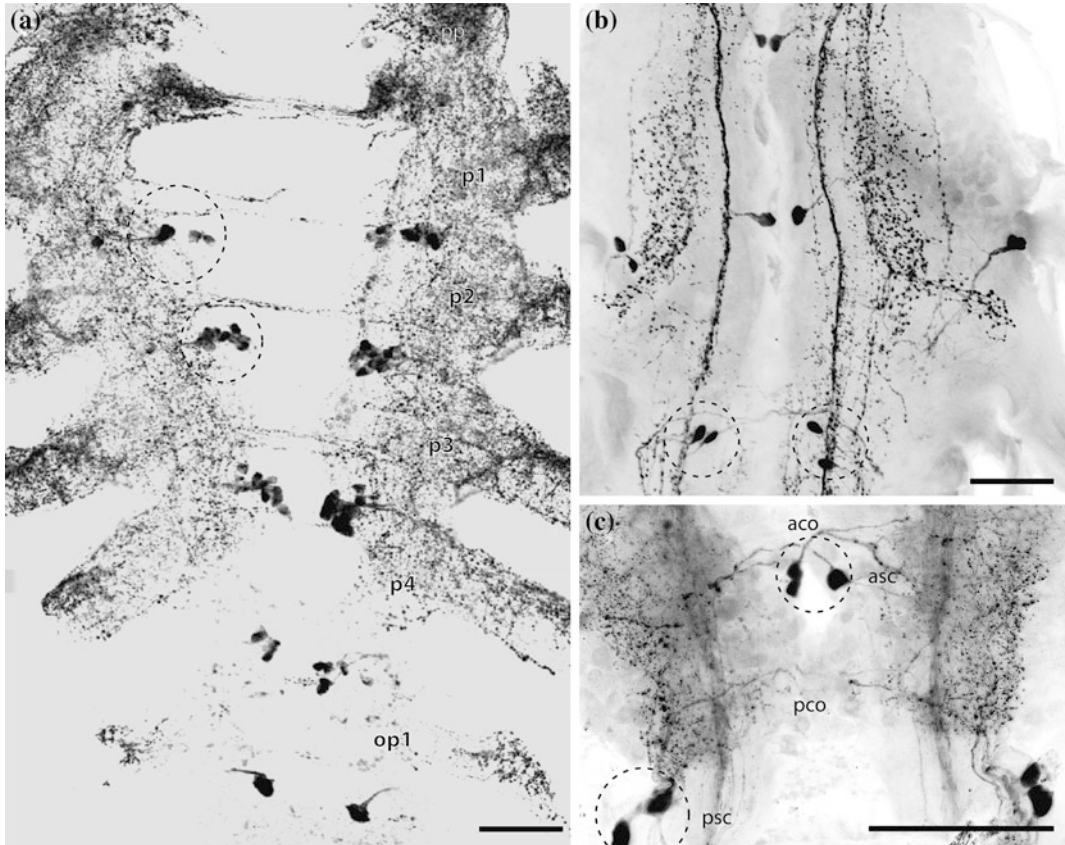


Fig. 13.3 Serotonin immunoreactivity in the ventral nerve cord. The situation in the fused ganglion complex of *Limulus polyphemus* (a), is compared to that in unfused segmental ganglia of *Lithobius forficatus* (b), and *Triops cancriformis* (c). Note posterior groups of serotonergic cell bodies with primary neurites extending contralaterally through the posterior commissures. A similar, anterior soma group with neurites extending contralaterally through the anterior commissure is present

in *Triops*. Selected soma groups are indicated by dotted circles. Further note larger number of somata per group in *Limulus*. Modified after Harzsch (2004a), Harzsch and Waloszek (2000). *aco* anterior commissure, *asc* anterior soma cluster, *op1* opisthosomal neuromere, *p1–p4* prosomal neuromeres, *pco* posterior commissure, *pp* pedipalp neuromere, *psc* posterior soma cluster. Anterior is to the top. Scale bars: 50 μm

produce muscle contraction and movement. In hexapods, motoneurons appear to be primarily output elements that do not usually make output connections within the central nervous system. In crustaceans, by contrast, motoneurons are often integral parts of motor control circuitry and thus make synapses to other motoneurons and interneurons. It should be noted, however, that the neural basis for sensorimotor processing in two other major arthropod groups—myriapods and chelicerates—has not been defined in

anywhere near the same detail as in hexapods and crustaceans.

Interesting examples with respect to the ordered arrangement of sensory projections are auditory receptor neurons that originate in tympanal organs. These have been studied in much detail in several hexapod groups (e.g. Oldfield 1988; Römer et al. 1988). Auditory input is usually represented in a tonotopic, or frequency-dependent manner. This tonotopic organization appears to be derived from the somatotopic

organization of mechanosensory input. Different sound frequencies are received by different though adjacent groups of sensory cells within the tympanal organs. In this way, map-like representations of mechanosensory input in the central nervous system translate into tonotopic representations in auditory neuropils (e.g. Kämper and Murphey 1987) (compare ordered mechanosensory projections indicated in Fig. 13.1a, lower half).

Chemosensory inputs, by contrast, are typically organized according to the molecular identity of the chemosensory neurons. That is, chemosensory cells responding to a particular group of chemicals—odorants or gustatory substances—project to particular small delineated areas of neuropil (details see Sect. 13.2.6). These neuropil areas are typically organized as circular glomeruli, ensheathed by glia and the axons of interneurons. The glomeruli formed by all the different groups of chemosensory receptor neurons form the chemosensory neuropil in the ganglion. The pectine neuropils of scorpions are segmental chemosensory and mechanosensory neuropils with glomerular organization (Wolf and Harzsch 2002b, 2012; Wolf 2008). Such organization appears to be a common feature in chelicerate arthropods, although their primary chemosensors are located on very different appendages (Strausfeld 2012). Again, exceptions exist and chemosensory inputs may project in parallel with the mechanosensory inputs from the respective body regions, for instance, in the bimodal chemo- and mechanosensory sensilla of the locust leg (Newland et al. 2000).

A similar segregation as outlined for the sensory neuropils may exist in the motor neuropils. For example, the arborizations of flight motoneurons in pterygote hexapods occupy the dorsalmost layer of the motor neuropil, while leg motoneurons occupy the ventrally adjacent neuropil areas with their dendritic arborizations (e.g. Robertson et al. 1982; Tyrer and Gregory 1982). Study of a possible segregation of motor neuropils is, unfortunately, more difficult than for sensory neuropils and has received much less attention.

13.1.3 Common Features in Arthropod Ventral Nerve Cord Structure are Based on Developmental and Genetic Similarities

The similarities of ventral nerve cord organization amongst the arthropod groups extend to individually identified neurons. This is true in particular for pioneer neurons that lay down the basic scaffold of axonal pathways in the developing peripheral and central nervous systems. There are apparent homologies of pioneer neurons and other individually identified nerve cells in hexapods and malacostracan crustaceans (Patel et al. 1989a, b; Whitington and Bacon 1997; Whitington 1996, 2004, 2006; Duman-Scheel and Patel 1999). It is not surprising, thus, that some individually identifiable neurons, especially motoneurons, can be homologized across a number of arthropod groups, with hexapods and malacostracan crustaceans having received particular attention in this respect (Wiens and Wolf 1993; Kutsch and Breidbach 1994).

The soma cortex consists of sometimes rather distinct groups of somata which in some cases may not immediately be obvious in histology (Fig. 13.2) but which have an ontogenetic basis. It is thought that during development of hexapods, neurons are generated by stereotyped patterns of cell divisions of neuronal stem cells that are the progeny of the neuroectoderm. Each of these stem cells—neuroblasts in hexapods and malacostracan crustaceans—generates a group of neurons, the somata of which are located in close proximity in the soma cortex, due to their common origin from a particular neuroblast (reviews Harzsch 2003; Whitington 2004, 2006; Stollewerk and Simpson 2005; Stollewerk and Chipman 2006; Stollewerk 2008). In Myriapoda, stem cells apparently of the hexapod/malacostracan neuroblast type do not exist (Whitington et al. 1991; Whitington 2004, 2006). The identity and location of neuronal progenitor cells in myriapods and chelicerates have been discussed by Whitington and Mayer (2011) who also reviewed the possible

homologies between neuron progenitor cells in the various arthropod groups.

For some insect neuroblasts, there is evidence that the progeny of one particular stem cell share physiological properties, for example, transmitter phenotype, and thus excitatory or inhibitory action on postsynaptic neurons. Or the progeny may be motoneurons or particular types of interneurons. However, in many cases, mixed lineages occur with the progeny even including glia cells (Bossing et al. 1996; Schmidt et al. 1997).

An obvious commonality across all arthropod groups is the arrangement of motoneuron somata which supply the leg muscles into two characteristic groups. These soma groups are located on the ventral side of the ganglion, one just anterior and the other just posterior to the entrance of the segmental leg nerve into the ganglion (Fig. 13.1a, dark green somata in lower ganglion). The respective motoneurons tend to innervate leg muscles that are located in the more anterior or the more posterior half of the appendage, respectively (Tyrer and Gregory 1982). By the same token, inhibitory interneurons occur in stereotyped groups that exhibit morphological and functional correspondences amongst the different arthropod groups (Watson 1986; Wolf and Harzsch 2002b) suggesting at least partial homology (Fig. 13.2c).

The structural properties outlined above for individual ganglia are maintained where several ganglia are fused. A typical example is the so-called subesophageal ganglia of scorpions—which comprises the neuromeres of the chelicerae, the pedipalp, and the four walking leg segments and two more posterior segments including that of the pectines (Wolf and Harzsch 2002a). Another example is the subesophageal ganglion of higher dipterans that represents the fusion product of all segmental ganglia posterior to the esophagus. These fused ganglia with their distinctly segmented structure exhibit almost all the characteristics outlined above for the individual ganglia within the respective neuromeres. The same is true for crustaceans, namely, the highly fused ventral nervous system of the crab, or the chelicerate *Limulus polyphemus* (shown in Fig. 13.3a, and compared to the

situation in *Triops cancriformis* and *Lithobius forficatus*).

13.1.4 Homologies Across the Arthropod Taxa

Considering the features outlined above, it is not surprising that several neurons, or groups of neurons, occur in more or less stereotyped fashion in most or all arthropods. Such neurons or neuron groups would appear to be homologous (Kutsch and Breidbach 1994). Correspondences occur not just between different arthropod groups but also in the ganglia along the ventral nerve cord of a given species. These so-called homonomies (serial homology) will vary, of course, depending on the segmental identity and the functional properties of that particular segment (e.g. Kutsch and Heckmann 1995a, b). For example, neurons relevant for the control of appendages, such as legs and wings, will be absent in neuromeres where the appendages have been reduced and are missing, or in species that lack the structures altogether. This is certainly true for the motoneurons supplying the appendage muscles, while the interneurons may be conserved and function in different contexts (e.g. Robertson et al. 1982).

Typical examples for homology across arthropods are the inhibitory motoneurons characteristic of arthropod motor control (Belanger 2005) (Fig. 13.1c). In hexapods and malacostracan crustaceans, the musculature of each walking leg is supplied by a set of three inhibitory motoneurons that adjust muscle performance in the time/velocity domain (Rathmayer 1990; Wolf 1990). It is not just the number of motoneurons but also soma location, anatomical characteristics, and muscle innervation patterns that support homology of the inhibitory leg motoneurons in the Tetraconata. Intriguingly, two of these inhibitory motoneurons serve different functions in hexapods and malacostracans. In hexapods, all three are common inhibitors, supplying partially different sets of muscles (the term common inhibitor alludes to the fact that it is common to several leg muscles). This function is fulfilled in

the malacostracans by just one of the inhibitors innervating all leg muscles. The other inhibitors are used to uncouple two distal leg muscles that are innervated by a single (common) excitatory motoneuron (Wiens 1989). Inhibitory motoneurons or groups of inhibitory motoneurons that possess intriguingly similar characteristics concerning soma location, certain anatomical features, and innervation patterns of leg muscles also occur in scorpions and centipedes (Harzsch et al. 2005a) (Fig. 13.1c). Apparent similarities are that, (i) these neurons use gamma-aminobutyric acid (GABA) as neurotransmitter, (ii) physiological activity of the inhibitors induces hyperpolarization in the muscles that they target, (iii) the number of inhibitory leg motoneurons within one hemiganglion is always three, (iv) the somata share corresponding positions within the ganglionic framework, and (v) their axons show a specific pattern of exiting the ganglia via the anterior or posterior nerve roots.

Kutsch and Heckmann (1995a, b) analyzed the innervation of a group of body wall muscles, the dorsal longitudinal muscles (DLMs) in *Lithobius forficatus* (Chilopoda) and compared it with that in Hexapoda. Their study indicated that the set of motoneurons that innervate the DLMs of one segment is composed of two subgroups, the somata of which are arranged in two adjacent neuromeres. Kutsch and Heckmann (1995a, b) suggest that this situation is a plesiomorphic character state of Mandibulata. Considering morphological characteristics, several of the DLM motoneurons may be homologized across the hexapods. Further, the number of motoneurons that supply the DLMs in *L. forficatus* is close to that in the hexapods. However, the authors point out that the motoneurons' morphologies are dissimilar in hexapods and chilopods, a fact that argues against a homology of hexapodan and chilopodan longitudinal muscle motoneurons. The same appears to apply to the motoneurons supplying the intersegmental dorsoventral musculature (Kutsch and Heckmann 1995a, b). Not only the architecture of the motoneurons differs between hexapods and chilopods but also the pattern of axon exit through the ganglionic nerve roots. Once again,

these patterns share considerable similarities between malacostracan crustaceans and hexapods. Similar to the inhibitory leg motoneurons, more detailed analyzes of longitudinal muscle motoneuron architecture in a wider range of taxa will be necessary to fully appreciate and exploit the neurophylogenetic potential of these structures.

So far, similarities have been emphasized that unite the different arthropod taxa—suggesting homology—and similarities of the different segmental ganglia in any given species ('homonymy' sensu Kutsch and Heckmann 1995a, b). However, the partly different functions of inhibitory motoneurons in hexapods and malacostracans illustrate that idiosyncratic specializations may in fact be more interesting under physiological and evolutionary perspectives than the commonalities in basic structure. These differences are important since they may be used to delimit crown groups if they represent apomorphies. Moreover, such specializations may be of particular interest if they can be related to functional properties in physiology and ecology.

This holds true for serotonin-immunoreactive (5HT-ir) neuron groups in the different arthropod taxa. The segmental ganglia of virtually all arthropods investigated so far are characterized by the presence of a set of 5HT-ir cell bodies or small soma groups that possess a number of common features. This pattern is maintained if the segmental ganglia fuse into a larger complex (illustrated for *Limulus*, and compared with *Lithobius* and *Triops* in Fig. 13.3). A posterior group of 5HT-ir cell bodies with primary neurites that extend contralaterally through the posterior commissure is one such characteristic (indicated as orange neuron group in Fig. 13.1a). A similar, anterior soma group with neurites extending contralaterally through the anterior commissure is present in hexapods and malacostracan and other crustaceans, while it is absent in the chilopods. The situation in diplopods and chelicerates is less clear, although anterior and posterior 5HT-ir soma groups exist. The cell bodies are more numerous in the chelicerates, as appears to be typical of most or

even all neuron types investigated so far, including the inhibitory motoneurons mentioned above (Wolf and Harzsch 2002a, b). The features of 5HT-ir soma groups have actually been used to reconstruct arthropod phylogeny by exploiting both common features to be interpreted as plesiomorphies and consistent differences amongst the groups that have to be interpreted as apomorphies (Harzsch 2004a).

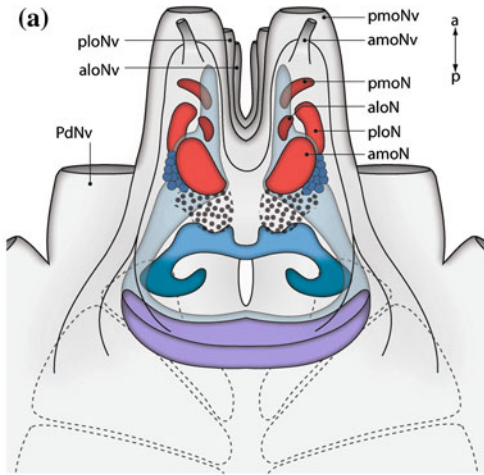
13.2 The Brain

The arthropod brain is a *syncerebrum* formed by the close association and structural and functional transformation of segmental cephalic ganglia (Richter et al. 2010). It is considered to be composed of three neuromeres, the protocerebrum, deutocerebrum, and tritocerebrum (Scholtz and Edgecombe 2006; Bitsch and Bitsch 2007, 2010; see Scholz and Richter in this book (arthropod head)) and hence has been termed a *tripartite brain* (Lichtneckert and Reichert 2005) although it needs to be critically evaluated where the posterior limit is of what we term ‘brain’ (Harzsch 2004b). Each neuromere is usually compartmentalized to some degree into definable clusters of neurons in the periphery that surround central neuropils (Strausfeld 1976; Sandeman et al. 1993; Doeffinger et al. 2010; Richter et al. 2010). A neuropil is defined as a network of dendrites and axons where synapses are present but neural somata do not occur. However, glial cell somata, tracts, hemolymph vessels, and tracheae may be embedded within a neuropil. A neuropil itself can also be compartmentalized into units which are also termed neuropils (Richter et al. 2010). However, these compartments usually are given specific names such as, for example, olfactory glomeruli (OG) (Fig. 13.4). In some Mandibulata, for example, *Scutigera coleoptrata* (Chilopoda) or *Apis mellifera* (Hexapoda), the axis of brain neuromeres (neuraxis) is bent out of the anterior–posterior body axis resulting in, for example, a dorsal or even posteriodorsal location of the protocerebrum with regard to body axis (Sandeman et al. 1993; Burrows 1996).

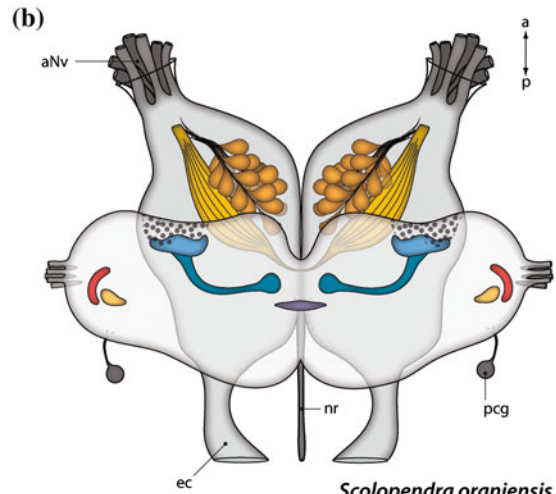
Therefore, the ventral surface of the brain can face forward in the head (compare Fig. 13.4d).

The chelicerate brain has been described in few species, most detailed in *Cupiennius salei* (Fig. 13.4a). Here, the nervous system is supraesophageal into two fused masses: the dorsal supraesophageal ganglion (brain) and the ventral subesophageal ganglion (VNC). The division of the three brain neuromeres in Chelicerata is, however, not easily identifiable. Traditionally, the neuromere associated with the chelicerae was considered to be homologous with the tritocerebrum of Mandibulata resulting in the absence of a deutocerebrum (Bitsch and Bitsch 2007). However, Mittmann and Scholtz (2003) and Harzsch et al. (2005b) showed similarities in the larval nervous system of *L. polyphemus* to that of Mandibulata which confirmed the assumption of a tripartite brain in Arthropoda. Recent comparisons of expression domains of the head *Hox* genes corroborate the assumption that a deutocerebrum is indeed present supporting the existence of a tripartite brain in the Chelicerata (Damen et al. 1998; Telford and Thomas 1998; Abzhanov and Kaufman 2004; Scholtz and Edgecombe 2006).

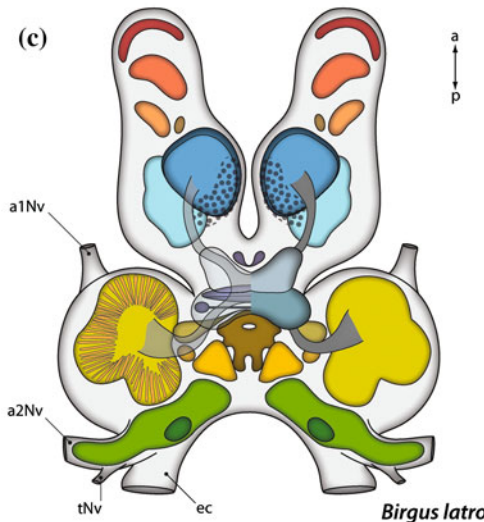
The *protocerebrum* is the anteriormost neuromere according to the neuraxis and receives input from the eyes (lateral compound eyes and/or median eyes) if present. Thus, the protocerebrum contains the optic neuropils and forms a prominent part of the brain (compare Fig. 13.4c, d, *Birgus latro* and *A. mellifera*). In *C. salei*, four pairs of optic nerves innervate the four first-order optic neuropils (anterior median, posterior median, posterior lateral, and anterior lateral; compare Fig. 13.4a). Besides the optic neuropils, the protocerebrum houses the mushroom bodies and the central body (see Sects. 13.2.8 and 13.2.9). In the Arthropoda, neurosecretory cells often form clusters whose axons leave the neuropil and project to neurohemal release sites and non-neuronal endocrine glands (Hartenstein 2006). The majority of neurosecretory cells are associated with the protocerebrum (pars intercerebralis and lateralis). Axons of neurosecretory cells project to neuroendocrine (or neurohemal) glands. In the brain of Arthropoda,



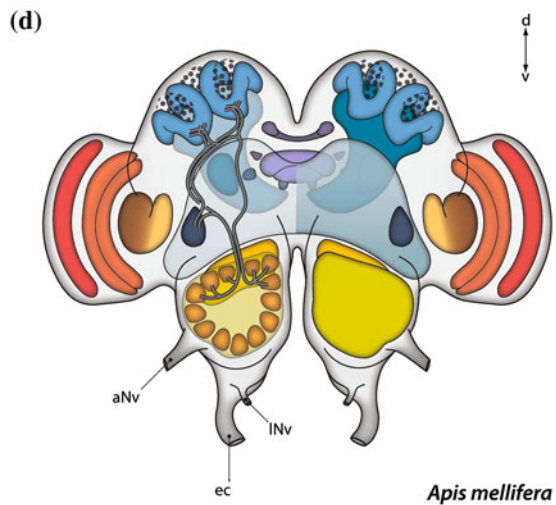
Cupiennius salei



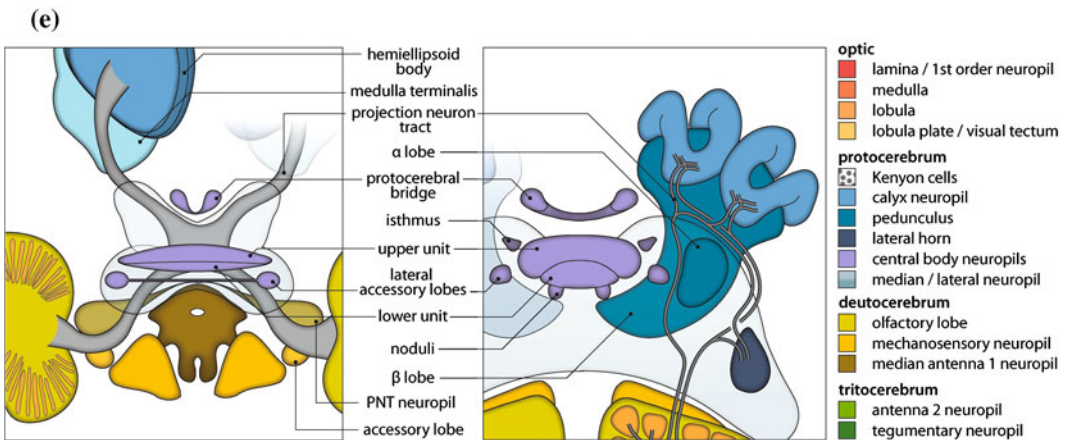
Scolopendra oraniensis



Birgus latro



Apis mellifera



◀ **Fig. 13.4** Schematic representation of selected arthropod brains (**a–c** dorsal, **d** frontal view). Compiled after Barth (2001), Galizia and Rössler (2010), Krieger et al. (2010), Sombke et al. (2012). **a** *Cupiennius salei* (Chelicerata). The first-order optic neuropils (red) are associated with a group of optic glomeruli (blue). The optic tracts (transparent blue) project to the central body. The nerves of the chelicerae are obscured by the optic nerves. **b** *Scolopendra oraniensis* (Myriapoda). The protocerebrum is bent dorsoposteriorly, thus resulting in a dorsal position with regard to body axis. The protocerebral glands (*pcg*) are located posteriorly. The antennal nerve (*aNv*) innervates the olfactory lobe and the mechanosensory neuropil. The nervus recurrens (*nr*) projects caudally on top of the esophagus. **c** *Birgus latro* (Crustacea). The optic neuropils as well as the hemiellipsoid body with the medulla terminalis are located in the anteriormost lateral protocerebrum. The central body is embedded in the median protocerebrum (**e, left**). The accessory neuropil as well as the projection neuron tract neuropil (*PNT neuropil*) are located in the median deutocerebrum (**e, left**). Besides the antenna 2

nerve (*a2Nv*), the tegumentary nerve (*tNv*) innervates the tritocerebrum. **d** *Apis mellifera* (Hexapoda). The pedunculus of the mushroom body houses the lateral horn and extends into the α and β lobes. The mechanosensory neuropil is located posteriorly of the olfactory lobe. The labral nerves (*lNv*) project ventrally (**e, right**). In all mandibulate taxa, the esophageal connectives (*ec*) link the tritocerebrum with the mandibular ganglion. **e** Detailed description of the proto- and deutocerebral neuropils of *Birgus latro* (left) and *Apis mellifera* (right) as well as the color code for all given structures. *a*↔*p* anterior↔posterior, *a1Nv* and *aNv* antenna 1 nerve, *a2Nv* antenna 2 nerve, *aloN* anterior lateral optic neuropil, *aloNv* anterior lateral optic nerve, *amoN* anterior median optic neuropil, *amoNv* anterior median optic nerve, *d*↔*v* dorsal↔ventral, *ec* esophageal connective, *lNv* labral nerve, *nr* nervus recurrens, *pcg* protocerebral gland, *PdNv* pedipalp nerve, *plon* posterior lateral optic neuropil, *plonv* posterior lateral optic nerve, *pmon* posterior median optic neuropil, *pmonv* posterior median optic nerve, *tNv* tegumentary nerve

they have different names like the Schneider's organ in Chelicerata, the protocerebral gland in Chilopoda (Fig. 13.4b), the corpora cardiaca and allata in Hexapoda, or the sinus gland in Crustacea (Tsuneki 1992; Hartenstein 2006; Sombke et al. 2011a).

In Chelicerata, the *deutocerebrum* is associated with the chelicerae while in the Mandibulata, it is associated with the first antennae. In the latter, it houses the olfactory lobes and the mechanosensory neuropils (see below). The antennal nerve contains axons of sensory receptor neurons (chemo- and/or mechanosensory) and motor neurons innervating the antennal muscles. In hexapods, a tegumentary nerve (innervating parts of the head capsule) is deutocerebral while in Crustacea, this nerve is tritocerebral and innervates an associated neuropil (Fig. 13.4c).

The *tritocerebrum*, flanking the esophagus, links the brain with the subesophageal ganglia. Both hemispheres are connected by tritocerebral commissures that are always located posteriorly. It is assumed that the possession of two tritocerebral commissures (like in the trunk ganglia) is a plesiomorphic feature of arthropods (Harzsch 2004b). In Chelicerata, the tritocerebrum is associated with the pedipalps, yet it is not clearly

demarcated in the adult brain. In Crustacea, the second antenna innervates the prominent antenna 2 neuropil which processes mostly mechanosensory information. The reduction of the second antenna in Myriapoda and Hexapoda (intercalary, postantennal, or premandibular segment) results in the absence of primary processing neuropils.

In addition, the tritocerebrum links the brain with the *stomatogastric nervous system* which consists of ganglia and nerves supplying the foregut and the clypeolabral region of the head (Bullock and Horridge 1965; Harzsch and Glötzner 2002; Bitsch and Bitsch 2010; Sombke et al. 2012). The frontal ganglion is connected via a pair of frontal connectives with the tritocerebrum (the stomatogastric bridge) and gives rise to the posteriorly projecting unpaired nervus recurrens (Fig. 13.4b: *nr*). In Chelicerata, a loop-shaped stomatogastric bridge innervates also a so-called labrum in Xiphosura and Scorpiones (Barth 2001; Harzsch et al. 2005b). However, it is assumed that in the ground pattern of Arthropoda, the stomatogastric bridge is formed by fibers of the deutocerebrum and tritocerebrum (Harzsch 2007).

In the Onychophora, the sister group to Arthropoda, the number of brain neuromeres is under debate (Mayer et al. 2010; Whitington and

Mayer 2011). Strausfeld et al. (2006b) proposed that the onychophoran brain is tripartite. However, what appears as a tritocerebrum could be part of the proto- or deutocerebrum or even the ventral nerve cord (Mayer et al. 2010; Whittington and Mayer 2011). The protocerebrum is innervated by the lateral eyes and antenna-like appendages that are regarded to be convergent to the mandibulate antennae (Mayer and Koch 2005; Scholtz and Edgecombe 2006). Within the protocerebrum, a distinct midline neuropil, antennal glomeruli, and MBs have been identified (Strausfeld et al. 2006a, b). The deutocerebrum is associated with the jaws. Backfills of the papillae suggest that the neural region supplying the appendages is part of the ventral nerve cord (Mayer et al. 2010). In conclusion, the brain architecture of Onychophora may represent plesiomorphic characters compared with arthropods, and the tritocerebrum represents an arthropod apomorphy (Whittington and Mayer 2011).

13.2.1 The Compound Eyes and Visual Neuropils

The faceted eyes of arthropods have fascinated arthropod neurobiologists for more than 100 years. Numerous book contributions were devoted to this topic and amongst the first and most important ones is probably Sigmund Exner's (1891) treatise on *Die Physiologie der facettierten Augen von Krebsen und Insekten* which was translated into English some 100 years later (Exner and Hardie 1989). Additional book volumes that are either exclusively devoted to arthropod eyes or contain significant chapters on arthropod visual systems are those by Wehner (1972), Horridge (1975), Autrum (1979), Eguchi and Tominaga (1999), as well as Stavenga and Hardie's (1989) *Facets of vision* and Warrant and Nilsson's (2006) *Invertebrate vision*. Evolutionary aspects of arthropod visual systems were dealt with in two special issues of *Arthropod Structure and Development* (Stavenga et al. 2006, 2007). The latest addition to this body of literature is the new edition of Land

and Nilsson's (2012) *Animal eyes*. Because the present chapter focuses on the central nervous system, sensory systems will not be treated here in any depth so that the reader who wants to newly engage in arthropod vision research is referred to the sources listed above.

It has long been known that the cellular architecture of the compound eye's ommatidia shows a strong correspondence between Crustacea and Insecta (Melzer et al. 1997, 2000; Paulus 2000; Dohle 2001; Richter 2002; Harzsch et al. 2005a) but the evolutionary relationships between the eyes of other Arthropoda is matter of debate (Nilsson and Osorio 1997; Paulus 2000; Müller et al. 2003; Spreitzer and Melzer 2003; Bitsch and Bitsch 2005; Harzsch et al. 2005a, b, 2007; Harzsch and Hafner 2006; Nilsson and Kelber 2007). Research on the architecture of the visual neuropils that process the retinal input has strongly focused on flies (Pterygota, Diptera; reviews Strausfeld et al. 2006c, Strausfeld 2012) and crayfish (Malacostraca, Decapoda; Nässel 1976, 1977; Nässel and Waterman 1977; Strausfeld and Nässel 1981) whereas the Chelicerata and Myriapoda have been unjustifiably neglected.

As for the ommatidial structure, a strong correspondence of the cellular components of the visual neuropils of crayfish and flies is obvious (Strausfeld and Nässel 1981; Nilsson and Osorio 1997; Strausfeld 2012). In most decapod crustaceans and pterygote insects, the visual input from the compound eyes is mapped onto four columnar optic neuropils, the lamina, medulla, and the lobula/lobula plate complex which are connected by two successive chiasmata (Figs. 13.5a, 13.7a). The hexapod medulla is divided into two distinct layers that are transversed by an axonal projection called the Cuccati bundle or serpentine layer (Strausfeld and Nässel 1981). In the visual neuropils, typically a columnar arrangement of neuronal elements interacts with the neurites of interneurons arranged in a stratified or tangential pattern. One ommatidium of both insects and malacostracan crustaceans contains a group of eight photoreceptors R1–R8 with the same optic axis. Developmental data indicate a homology of

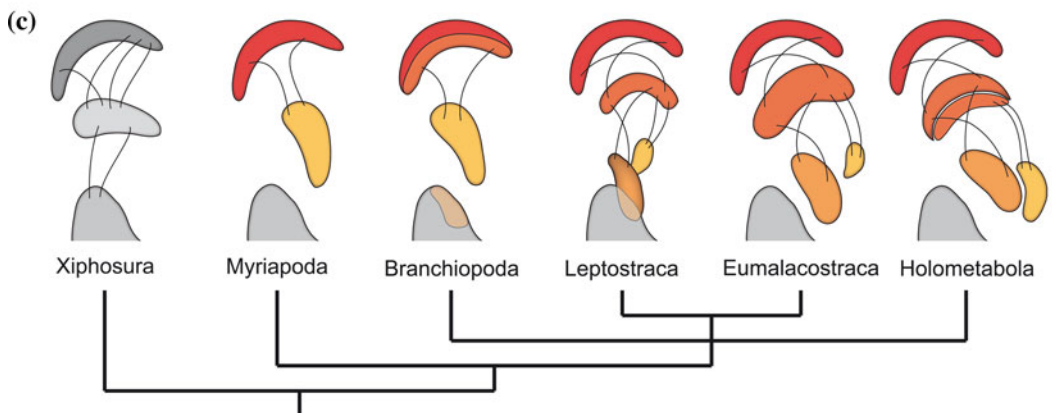
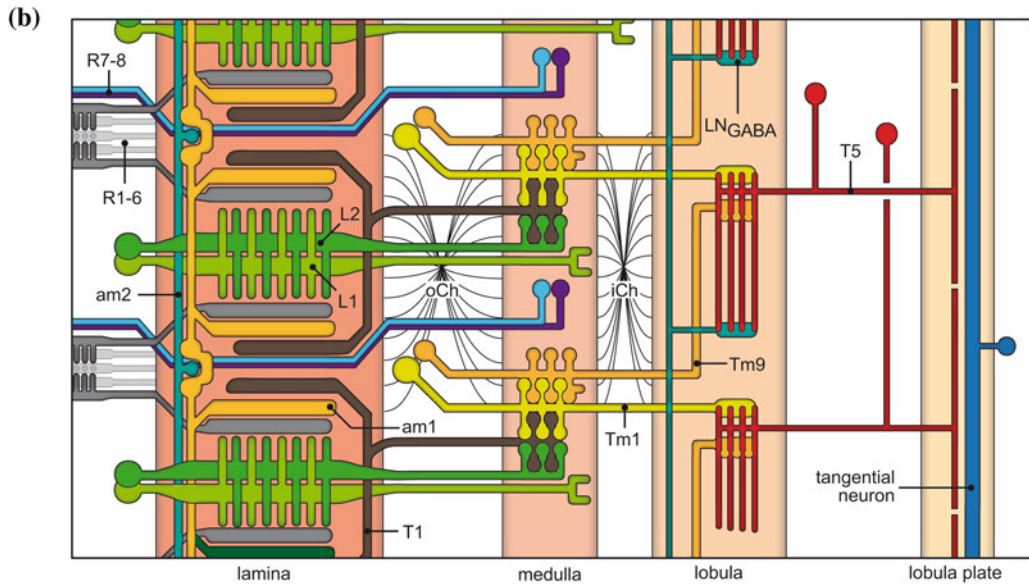
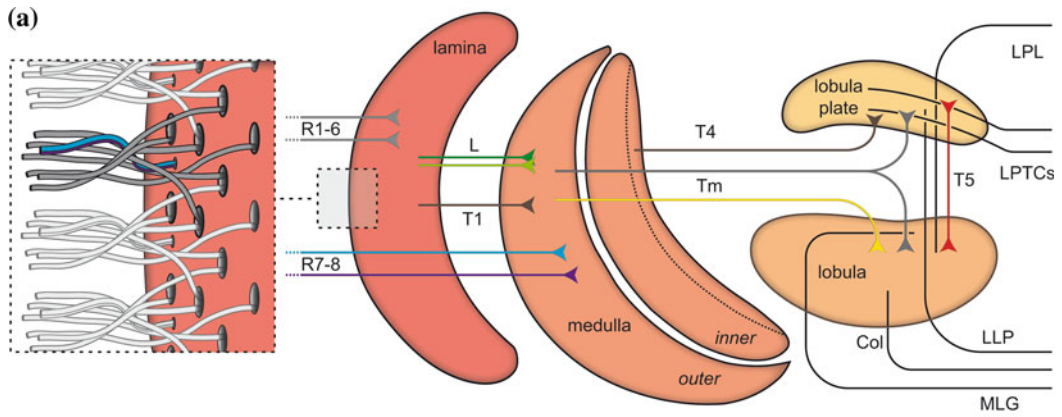
the insect and crustacean photoreceptor cells (Melzer et al. 1997, 2000; Hafner and Tokarski 2001; Harzsch and Waloszek 2001). These photoreceptors together constitute the rhabdom where light is absorbed by the visual pigments (reviews Paulus 2000; Osorio 2007; Friedrich et al. 2011). The photoreceptor axons project the retinal mosaic topically onto the first optic neuropil, the lamina (Fig. 13.5a, b), and histamine seems to be the neurotransmitter of these photoreceptors (review Hardie 1989; Callaway and Stuart 1999). Ontogenetically, the R1–R6 develop in three pairs, R1/R6, R2/R5, R3/R4, both in crustaceans and flies (Melzer et al. 1997; Friedrich et al. 2011), and the axons from R1 to R6 (‘short’ photoreceptor axons) innervate distinct underlying columnar modules in the lamina and retain their neighborhood relationship amongst themselves between the retina and lamina (Strausfeld and Nässel 1981; Sanes and Zipursky 2010; Strausfeld 2012). This architecture gives rise to retinotopic processing units in the lamina, the ‘optic cartridges’ with an almost crystalline regularity (Fig. 13.5b). The projection pattern of the dipteran photoreceptors is more complex; these animals have an open rhabdom and use the neural apposition mechanism (Nilsson 1989). In these animals, seven rhabdomeres of each ommatidium have divergent optical axes but single receptors (of the R1–R6 type) in six neighboring ommatidia project into one common cartridge in the lamina (Fig. 13.5a; Strausfeld and Nässel 1981 and references therein). Hence, in taxa with neural superposition, a complex sorting of the retina-lamina projections takes place which is not the case in the taxa with apposition and optic superposition designs (Nilsson 1989). In these, the photoreceptor axons project into the lamina cartridge directly beneath their parent ommatidium. In flies, R1–R6 are achromatic and most sensitive to green light whereas in crayfish, they are characterized as yellow–green sensitive. R7 and R8 develop as single units, and in flies, their axons project through the lamina (‘long’ photoreceptor axons) to terminate in the second optic neuropil, the medulla (Fig. 13.5a, b). They have a narrow

spectral sensitivity with R7 being a UV receptor and R8 being sensitive for blue light. In crayfish, however, only the axons of the blue/violet receptor R8 project through the lamina to terminate in the medulla (Nässel 1976, 1977) whereas R7 has a short axon to the lamina only. The evolutionary correspondence of insect and crustacean R7 and R8 cells needs further clarification.

13.2.2 The Lamina

Within the crayfish lamina, which is subdivided into two horizontal strata, the centripetal input provided from the photoreceptor axons diverges greatly and is relayed to visual interneurons. Of these, ten distinct classes have been identified according to their characteristic dendritic or axonal domains as well as their cell body locations, and more cell classes await discovery: five types of monopolar cells (M1–M5), two types of tangential T-neurons, one type of small-field T-neuron, one type of centrifugal cell, and one type of amacrine (anaxonal) cell (Strausfeld and Nässel 1981; Meinertzhagen 1991). All these neurons, except the anaxonal amacrine cells, connect the lamina with the medulla via the outer optic chiasm that also contains the ‘long’ photoreceptor axons. In the outer optic chiasm, the linear order of the columns is reversed but their spatial relationships are retained. The crayfish lamina monopolar cells as well as the transmedullary cells associated with the medulla constitute the retinotopic columnar pathway whereas amacrine (anaxonal) neurons, wide-field, and tangential elements possess neurites arranged in horizontal layers and modulate the excitability of the columnar projections (Strausfeld and Nässel 1981). The somata of the lamina monopolar neurons are located distally to the neuropil whereas the amacrine cells and the T-neurons have their cell bodies proximal to the lamina neuropil.

There is a strong correspondence between crayfish and fly laminae not only concerning the general arrangement of neuronal elements but also at the level of single classes of visual



◀ **Fig. 13.5 a** Schematic overview of the dipteran visual system with neural superposition showing some of the known classes of neuronal elements (compiled from Strausfeld and Nässel 1981; Strausfeld 1989; Douglas and Strausfeld 2003). The left box shows the complex sorting pattern of the R1–R6 photoreceptor axons (*grey*) from four rhabdoms of the retina that project to several neighboring lamina cartridges (*circles*). The axons of R7 and R8 (*blue* and *violet*) are not distributed to several cartridges but extend in tandem to pierce the lamina below their parent cartridge and to terminate in the medulla, which is divided into an inner and outer portion. Several types of lamina monopolar cells (L) are postsynaptic to the R1–R6 input and relay information to the medulla. Small-field T1-neurons also connect lamina and medulla. Transmedullary neurons (*Tm*) and T4 bushy T cells associated with the medulla relay information to the lobula and lobula plate, respectively. Wide-field lobula plate tangential cells (*LPTCs*) have dendrites in direction-specific layers of the lobula plate. Transmedullary neurons supply information about motion to directionally selective motion-sensitive neurons such as the male specific giant neurons (*MLG*) in the lobula. Small-field neurons associated with the lobula plate and lobula provide axonal outputs to the medial brain, and dendrites have their distalmost processes either in the lobula plate (*LPL*) or in the lobula. **b** Schematic representation of some identified neurons serving the achromatic photoreceptors in the fly visual system and successive levels of synaptic connections in the lamina, medulla, lobula, and lobula plate (figure and legend reproduced with modifications from Strausfeld et al. 2006a, b, c). Several known cell types are omitted for clarity. The axons of the color-sensitive R7 and R8 photoreceptors are also shown to pass through the lamina and terminate in the medulla. The inner and outer

interneurons (Strausfeld and Nässel 1981; Meinertzhagen 1991; Nilsson and Osorio 1997; Sinakevitch et al. 2003; Strausfeld et al. 2006c). Flies, like crayfish, possess five types of monopolar cells, termed L1–L5 (Fig. 13.5a, b). Three of these, the large monopolars (LMCs) L1–L3 are non-spiking neurons and directly postsynaptic to the R1–R6 afferents. L1 and L2 provide color-independent information by signaling changes of luminance. The L3 axons extend to the medulla alongside the long visual fibers of R7 and R8, together providing a trichromatic input to the medulla (Fig. 13.5a, b; Strausfeld 1989; Douglas and Strausfeld 2003; Strausfeld 2012). L4 and L5 are smaller cells that receive inputs from the LMCs. Based on physiological properties and architectural features, Strausfeld and Nässel (1981) and Nilsson and Osorio

(1997) suggested the fly LMCs to be equivalent to the crayfish monopolar neurons M1–M4 which are small-field elements, with their dendritic arbors restricted to the parent cartridge. The crayfish M5 represents a class of wide-field neurons the neurites of which spread through several (six or eight) cartridges and may correspond to the fly L4 or L5 monopolars. The lamina monopolar cells M1–M4 (crayfish) and L1–L3 (fly) in both cases are characteristically wired up to specific receptor terminal combinations by synapses arranged in triads (see Strausfeld and Nässel 1981). The small-field T-neuron (T1) with dendritic fields in the lamina and a cell body located close to the medulla is another columnar neuron that is part of the optic cartridges (Fig. 13.5a, b). Fly and crayfish small-field T-neurons were suggested to

chiasm (*iCh*, *oCh*) are indicated schematically. R1–R6 photoreceptors (*grey*) that use histamine as their transmitter provide inputs to type 1 amacrine (*am1*, *yellow*) and lamina monopolar cells L1 and L2 neurons (*green*; glutamatergic). The glutamate-immunoreactive type 1 amacrine are shown serially connected via NMDAR1-immunopositive type 2 amacrine (*am2*). The basket dendrites of T1 cells (*brown*) interact with type 1 amacrine. T1 cells, accompanied by L2 of the same optic cartridge, terminate at the dendrites of ChAT-positive paired transmedullary neurons (*Tm1*, *yellow*), the dendrites of which are coincident with those of the GABA-immunoreactive Tm9 neurons (*orange*). The Tm9 axon from the neighboring retinotopic medulla column converges with terminals of Tm1 neurons at the aspartate immunopositive T5 layer (*red*) in the lobula. A GABA-immunoreactive local interneuron (*LN GABA*, *blue*) provides arborizations within the T5 ensemble. T5 neurons terminate on glutamate-immunoreactive directionally selective tangential neurons in the lobula plate. **c** Evolution of optic neuropils associated with the lateral eyes of Euarthropoda. Modified from Strausfeld (2005). *Red*: outer plexiform layer (lamina), *yellow*: visual tectum (lobula plate), *dark orange*: outer medulla, *light orange*: lobula *Col* columnar neurons, *iCh* outer chiasm, *L* lamina monopolar cells, *L1*, *L2* lamina monopolar cells type one and two, *LLP* Lobula-lobula plate neurons, *LPL* Lobula plate-lobula neurons, *LN_{GABA}* GABA-immunoreactive local interneuron of the lobula, *LPTCs* wide-field lobula plate tangential cells, *MLG* male specific giant neurons, *oCh* outer chiasm, *R1–R8* axons of photoreceptors R1–R8, *T1* small-field T-neuron, *T4* bushy T cell, *T5* aspartate immunopositive bushy T cell, *Tm* transmedullary neurons, *Tm1* and *Tm9* transmedullary neurons types one and nine

be homologous (Nilsson and Osorio 1997). Tangential cells (Tan 1) of both crayfish and flies have dendritic fields whose arborizations invade both lamina strata and are not restricted to one optic cartridge but spread across several of these. The crayfish lamina has a second type of tangential neuron (Tan 2) with large vertically arranged branches beneath the lamina from which fibers ascend distally into the lamina's plexiform layer. Tan 2 lacks an obvious counterpart in the fly lamina. The axons of both types of tangential neurons project towards the medulla. The cell bodies of centrifugal neurons (C cells) are located between the medulla and lobula, and their axons project distally to invade the lamina and arborize diffusely over several cartridges. The architecture of these GABAergic centrifugal feedback neurons is very similar between insects and a malacostracan crustacean, an isopod in this case (Sinakevitch et al. 2003). Finally, anaxonal or amacrine neurons are associated with the lamina (Fig. 13.5a, b). Physiological and anatomical studies suggest a close correspondence of insect and crayfish amacrine cells (Nilsson and Osorio 1997). Their somata are located at the lamina's proximal surface and give rise to tangential branches from which numerous processes project through the plexiform layer, finally giving rise to lateral branchlets at the distal surface of the lamina. The amacrine neurons exert a presynaptic inhibitory action on the photoreceptor terminals and are thought to be part of the pathway that mediates lateral inhibition in the lamina (Glantz et al. 2000). All the aforementioned wide-field and tangential elements do not seem to be directly postsynaptic to receptor terminals but most probably interact with sets of other relay neurons in the lamina (Strausfeld and Nässel 1981).

13.2.3 The Medulla

As mentioned above, in crayfish and flies, the axons of M1–M5/L1–L5 and Tan1, Tan 2 travel towards the medulla via the first (outer) optic

chiasm in which the fibers cross but retain the retinotopic organization. The chiasm also comprises the axons of the R8 (crayfish) or R7 and R8 (fly), T1, and centrifugal neurons (Strausfeld and Nässel 1981). The fly medulla is divided into an outer and an inner neuropil by a layer of thick tangential axons, the serpentine layer or Cuccati bundle, but such a bundle does not seem to be present in malacostracan crustaceans (Sinakevitch et al. 2003). However, fly and crayfish show strong correspondence in their medullae in that the distal three-quarters (outer layer) contain the terminals of the M2–M4 lamina monopolar cells, the endings of the long visual fibers (R8) and the arborizations of the lamina tangentials, Tan 1 and 2 (Fig. 13.5a, b). In addition, the dendrites of medulla columnar neurons (the transmedullary neurons), as well as amacrine arbors, are arranged within the outer layers of this region (Strausfeld and Nässel 1981). In flies (but not necessarily other insects), this input to the medulla comprises at least four information channels: two color-insensitive channels, one polychromatic channel, and one channel relaying information about the E-vector of polarized light. In both taxa, small-field transmedullary neurons (Tm1–6) are arranged periodically in association with the long visual fibers (R7/8) and the incoming axons from the lamina monopolar cells. These transmedullary neurons relay the incoming retinotopic picture through the medulla and project to the lobula via the second (inner) optic chiasma. In addition, three classes of amacrine cells (Am) are present in the medulla, the neurites of which are either restricted to a single column or a specific domain of medulla columns and project to different depths of the neuropil (Strausfeld and Nässel 1981). Once again, the amacrine cells are involved in processes of lateral inhibition (Glantz and Miller 2002). The neurochemical architecture of both lamina and medulla is diverse and covered in the following reviews: Hardie 1989; Homberg 1994; Sinakevitch et al. 2003; Harzsch et al. 2012.

13.2.4 The Deeper Neuropils and Image Analysis

Whereas in the crayfish and fly, the lamina and medulla receive a direct photoreceptor input, visual interneurons relay information from the lamina and medulla to the deeper neuropils, lobula, and lobula plate (Fig. 13.5a, b). The structure of these two secondary neuropils cannot be described in any depth in this section which focusses on primary processing units. Nevertheless, structural properties of lobula and lobula plate are quite well understood (e.g. Strausfeld and Nässel 1981; Strausfeld 1989, 2012; Strausfeld et al. 2006c). The functions of lobula and lobula plate have been primarily discussed so far in the context of motion detection and these neuropils in Tetraconata are considered to play an integral part in processing optokinetic information (Sztarker et al. 2005). The entire field of how the visual input is processed to extract meaningful information about the image is a research field of its own that cannot be touched here (reviews, e.g., Wiersma et al. 1982; Franceschini et al. 1989; Glantz and Miller 2002; Zeil and Layne 2002; Douglas and Strausfeld 2003; Egelhaaf 2006; Egelhaaf et al. 2009; Borst et al. 2010; Borst and Euler 2011).

In general, it appears that the visual systems of insects and malacostracan crustaceans are organized into parallel processor channels that encode information about contrast and intensity separately from information about color and shape (Douglas and Strausfeld 2003; Strausfeld 2012). Most of the visual field is simultaneously analyzed in a sophisticated parallel-distributed information pathway by multiple classes of interneurons associated with the optic neuropils. Contrast, polarity, polarization angle, and local and global motion are assessed across the visual space at multiple loci defined by the visual receptive field (Glantz and Miller 2002). These aspects are best understood in the fly visual system (Douglas and Strausfeld 2003) and identified parallel retinotopic pathways through the dipteran nervous system include an achromatic pathway with information about the

orientation and direction of motion, three parallel channels that are achromatic and non-directional-sensitive, and a fifth channel that serves color vision.

13.2.5 Evolution of Visual Neuropils

There is little doubt about the homology of the ommatidia of insects and crustaceans (Melzer et al. 1997, 2000; Nilsson and Osorio 1997; Paulus 2000; Dohle 2001; Hafner and Tokarski 2001; Richter 2002; Bitsch and Bitsch 2005; Harzsch et al. 2005b, Harzsch and Hafner 2006; Nilsson and Kelber 2007), and the strong architectural correspondence of crayfish and fly laminae and medullae is unquestionable (Strausfeld and Nässel 1981; Meinertzhagen 1991; Nilsson and Osorio 1997; Harzsch 2002; Sinakevitch et al. 2003; Strausfeld et al. 2006c). However, it has long been noted that the visual neuropils of non-malacostracan crustaceans, especially studied in the branchiopod genera *Artemia*, *Triops*, *Branchinecta*, and *Daphnia* do not fit into this pattern because these taxa have only two visual neuropils, commonly termed lamina and medulla (reviewed in Strausfeld and Nässel 1981) that are linked by straight fibers without any chiasm. Whereas the neuroarchitecture of the branchiopod lamina resembles that of Malacostraca and Hexapoda even at the level of single cell types (Nässel et al. 1978; Elofsson and Hagberg 1986), the linking fibers take a different course in the two groups. More importantly, it is impossible to reconcile the neuroarchitecture of the branchiopod medulla with that of the other two taxa. Since the influential review by Elofsson and Dahl (1970) on this topic, several studies have readdressed this issue, either by collecting ontogenetic data on branchiopod taxa (Harzsch and Waloszek 2001; Harzsch 2002; Wildt and Harzsch 2002; reviewed in Harzsch and Hafner 2006) or by analysing the connectivity of the adult vision system of the taxa in question (Sinakevitch et al. 2003; Strausfeld 2005). This issue is far from settled and further complicated by the fact that

we do not have a robust scenario about the evolutionary position of Branchiopoda with regard to Hexapoda and Malacostraca. Currently, three hypotheses have been put forward to account for the fundamental differences of the malacostracan/hexapod lamina on one side and that of Branchiopoda on the other:

- (i) There has been convergent evolution of the visual pathways associated with the compound eyes in Branchiopoda versus Malacostraca/Hexapoda (Nilsson and Osorio 1997).
- (ii) Evolutionary changes concerning the proliferative activity of stem cells that give rise to the optic anlagen are responsible for an axonal rewiring of the fibers between lamina and medulla (Elofsson and Dahl 1970; Harzsch 2002).
- (iii) The branchiopod medulla does not correspond to the malacostracan/hexapod medulla but to a deeper optic neuropil (Strausfeld 2005).

In the light of the cellular similarities of the compound eyes and laminae in these three taxa, the first hypothesis seems unlikely. Strausfeld (2005) combined hypotheses (ii) and (iii) into a new scenario of optic neuropil evolution in Tetraconata with the fundamentally new idea that a mandibulate ancestor possessed only two visual neuropils, the plexiform layer and the visual tectum which correspond to the hexapod/malacostracan lamina and lobula plate, respectively (Fig. 13.5c). Both neuropils are connected by uncrossed fibers, an arrangement that characterizes Branchiopoda and Myriapoda (Melzer et al. 1996; Harzsch and Waloszek 2001; Harzsch 2002; Wildt and Harzsch 2002; Strausfeld 2005; Sombke et al. 2011a). The subsequent evolutionary scenario proposed by Strausfeld (2005) relies on the idea that Branchiopoda and Myriapoda represent a plesiomorphic character state from which the situation in Malacostraca and Hexapoda evolved. However, considering the unstable position of Branchiopoda in recent phylogenetic studies (Regier et al. 2010; Rota-Stabelli et al. 2011; Trautwein et al. 2012), we need to take into account that the architecture of the branchiopod visual system is derived and a

simplification from a more complex pattern. Furthermore, we know very little about the cellular architecture of the myriapod visual system beyond the simple facts that they have two visual neuropils and straight fibers, and therefore, we cannot claim that both share a similar neuroarchitecture representing an ancestral mandibulatan state.

Strausfeld (2005) proposed the following scenario for the evolution of the optic neuropils in the Tetraconata (Fig. 13.5c):

Step1: The malacostracan and hexapod medullae initially arose by a duplication of the outer optic anlagen, the proliferation zone of the lamina. This duplication led to a division of the ancestral plexiform layer into an outer and an inner stratum—the lamina and the nascent medulla, respectively. Due to the developmental organization of both layers, they are connected by means of a chiasm. The visual tectum now receives uncrossed projections from the inner layer.

Step2: The third optic neuropil, the lobula, is a protocerebral derivative and originated in a duplication event of the inner proliferation zone. It has been shown that this inner zone is separate from the outer one that generates the lamina (Nässel and Geiger 1983; Harzsch et al. 1999; Harzsch and Waloszek 2001). The lobula formed as an outgrowth of the lateral protocerebrum, as seen during development in some species. It is connected to the medulla via a chiasm, while the visual tectum is still linked by straight fibers. Based on structural similarities, the latter is regarded as the progenitor of the hexapodan and malacostracan lobula plate.

Step3: Within the hexapods, a reduplication of the inner optic anlagen gave rise to the proximal layer of the medulla.

In conclusion, Branchiopoda, Malacostraca, and Hexapoda are characterized by deep homologies of the cellular architecture of their compound eyes and laminae whereas strong differences of the deeper visual neuropils separate the Branchiopoda on the one side from

Malacostraca and Hexapoda on the other. It is very difficult to frame a simple evolutionary scenario that could transform the cellular architecture of the deeper branchiopod optic neuropil into that of Malacostraca/Hexapoda. This difficulty persists regardless of whether the branchiopod condition is plesiomorphic for Mandibulata or an apomorphy of Branchiopoda.

13.2.6 Olfactory Lobes

In the arthropod brain, the primary processing neuropils for chemosensory qualities are the olfactory lobes. In most bilaterians, olfactory receptor cells terminate in *glomerular neuropils* which are the subunits of the olfactory lobe (or olfactory bulb in Mammalia). In principle, a glomerulus is a spheroid synaptic complex that may be ensheathed by glia. Given their widespread phylogenetic distribution, glomeruli have either evolved once in a common ancestor or are a case of evolutionary convergence. The latter assumption points to a functional adaptation related to processing olfactory information or a space-efficient architecture bringing together axons of similarly tuned receptor neurons (reviewed in Eisthen 2002). Olfactory glomeruli (OG) are also known in Mollusca (Wertz et al. 2006), Annelida (Heuer and Loesel 2009), Onychophora (Strausfeld et al. 2006b), and several Chelicerata (Brownell 1989) as well as Mammalia (Strotmann 2001). In general, olfactory receptor neurons (ORNs) are bipolar and project into a fluid medium within olfactory sensilla. In detail, however, there are striking differences between arthropod and vertebrate olfactory systems: (1) odorant binding proteins (OBPs) that mediate the transfer of ligands to receptors on the ORNs do not show any structural similarity in Hexapoda vs. Mammalia (Bianchet et al. 1996) and (2) odorant receptors (ORs) known from Hexapoda show no homology to the OR families of Mammalia and Nematoda (Hansson and Stensmyr 2011). This clearly points to a *convergent evolution of olfactory systems* in bilaterians (Strausfeld and Hildebrand 1999). Ionotropic receptors (IRs),

which occur in ORNs proposed to be the ancestral chemosensory receptor, are found only in protostomes and are absent in vertebrates (Croset et al. 2010). IRs are specifically divided into antennal IRs and divergent IRs which are expressed in peripheral and internal gustatory neurons.

Not all chemosensory input from antennae, walking appendages, and even wings is processed in the olfactory lobes of the brain. As a consequence, in arthropods the processing of chemosensory input is achieved in any neuromere that innervates chemosensory appendages. However, usually only specialized appendages lead to distinct olfactory lobes. In Mandibulata, these specialized appendages are the antennae associated with the deutocerebrum. Within several taxa of Chelicerata, olfactory lobes composed of OG are known in parts of the nervous system other than the deutocerebrum (Brownell 1989; Szlendak and Oliver 1992; van Wijk et al. 2006a, b; Wolf 2008; Strausfeld and Reisenman 2009). Here, OG occur, for example, in association with chemosensory walking appendages, like the first leg pair in Acari (Szlendak and Oliver 1992) or Solifugae (Strausfeld and Reisenman 2009) or the pectines in scorpions (see Sect. 13.1.2). In Onychophora, the antenna-like appendages supply chemosensory centers in the protocerebrum which are also composed of glomerular neuropils (Strausfeld et al. 2006b). However, the onychophoran antennae are not homologous to the mandibulate antennae (Scholtz and Edgecombe 2006).

The sensory deutocerebral antenna is an apomorphic character of Mandibulata (Scholtz and Edgecombe 2006). Grounded in a consistent architecture, the olfactory lobes within the deutocerebrum of Mandibulata have been suggested to be homologous structures (e.g. Schachtner et al. 2005; Strausfeld 2009; Sombke et al. 2012). The paired olfactory lobes of Mandibulata are usually located in the anterior or ventral deutocerebrum (Fig. 13.4). The array of OG in Hexapoda is thought to represent a chemotopic map, which forms the basis of the olfactory code (Galizia and Menzel 2000; 2001; Ignell and Hansson 2005; Galizia and Szyska

2008). The olfactory lobes or rather the OG are innervated by axons of ORNs from antennal olfactory and/or gustatory sensilla (Keil and Steinbrecht 1984; Tichy and Barth 1992; Hallberg and Skog 2011; Schmidt and Mellon 2011; Sombke et al. 2011b; Keil 2012). The following architectural characteristics apply to both the olfactory system of insects and malacostracan crustaceans. Within the clearly demarcated dense OG, antennal ORNs terminate and form first synapses (Fig. 13.6). The input is integrated by local interneurons and then relayed to protocerebral neuropils via projection neurons (Schachtner et al. 2005). Local interneurons branch unilaterally within one, two, or even all OG resulting in connections of specific glomeruli. In addition, subclasses of interneurons can innervate certain regions of the OG (rim and core interneurons in Fig. 13.6a). Projection neurons connect single or several glomeruli with secondary processing centers such as the mushroom bodies via the projection neuron tract (PNT), also called antennocerebral tract in Hexapoda. In Malacostraca, the PNT (also called olfactory globular tract) targets the hemiellipsoid bodies (Galizia and Rössler 2010; Schmidt and Mellon 2011; Sandeman et al. in press; Strausfeld 2012; compare Fig. 13.6). In Tetraconata, the interconnection of primary and secondary processing centers is achieved by different pathways. While an ipsilateral connection is suggested to be plesiomorphic, in malacostracan Crustacea and Remipedia, a subset of neurons of the projection neuron tract projects to the contralateral hemiellipsoid body/medulla terminalis-complex (Fanenbruck and Harzsch 2005; Fig. 13.6a). In hexapods, several projection neuron tracts occur, the median, mediolateral, and lateral tracts (Galizia and Rössler 2010; compare Fig. 13.6b). In the honeybee, three different mediolateral tracts which target the lateral horn also branch in the lateral network (consisting of ring neuropil, triangle, and lateral bridge; compare Kirschner et al. 2006). The median and lateral tracts project either firstly into the MBs (lip- and basal ring region of the calyces) and secondly into the lateral horn, or vice versa (compare pathways in Fig. 13.6b).

Strausfeld (2012) listed a number of differences between hexapod and malacostracan OG. In most hexapods, each olfactory glomerulus gives rise to two or more uniglomerular projection neurons (with arborizations in only one glomerulus) whereas in malacostracan Crustacea, projection neurons are multiglomerular (with arborizations in several glomeruli). These multiglomerular projections might result in a higher discrimination capacity. Although in several tetraconate taxa (Crustacea + Hexapoda) olfactory lobes may be absent and structural differences occur, several shared characters are present that have been modified in many taxon-specific ways (Schachtner et al. 2005). The olfactory lobes of malacostracan Crustacea and neopteran Hexapoda share the following synapomorphies: (1) the OG are embedded in coarse neuropil, (2) ORNs are cholinergic, possess uniglomerular terminals, and penetrate the olfactory lobes in a radial manner from the periphery, (3) local interneurons are inhibitory, GABAergic or histaminergic, and contain neuropeptides as cotransmitters, (4) the olfactory lobe is innervated by at least one prominent serotonergic neuron (or dorsal giant neuron) with multiglomerular arborizations, (5) projection neurons (forming the projection neuron tract) pass the central body posteriorly and link the olfactory lobe with neuropils in the protocerebrum. Most of these characters are also present in representatives of the Myriapoda although projection neuron tracts linking the olfactory lobes with the MBs have not been demonstrated conclusively, most likely due to their diffuse arrangement of axons (Strausfeld et al. 1995). In this view, the absence of olfactory lobes in various Crustacea (for example in certain Branchipoda, Branchiura, and Thecostacra) and Hexapoda (Odonata, certain Hemiptera, and Coleoptera) can be interpreted as reductions (Sombke et al. 2012) within Tetraconata.

The shape and arrangement of OG are probably rather subjected to functional and/or physiological aspects than to phylogenetic constraints (Schachtner et al. 2005). Structural and physiological changes that lead to improved

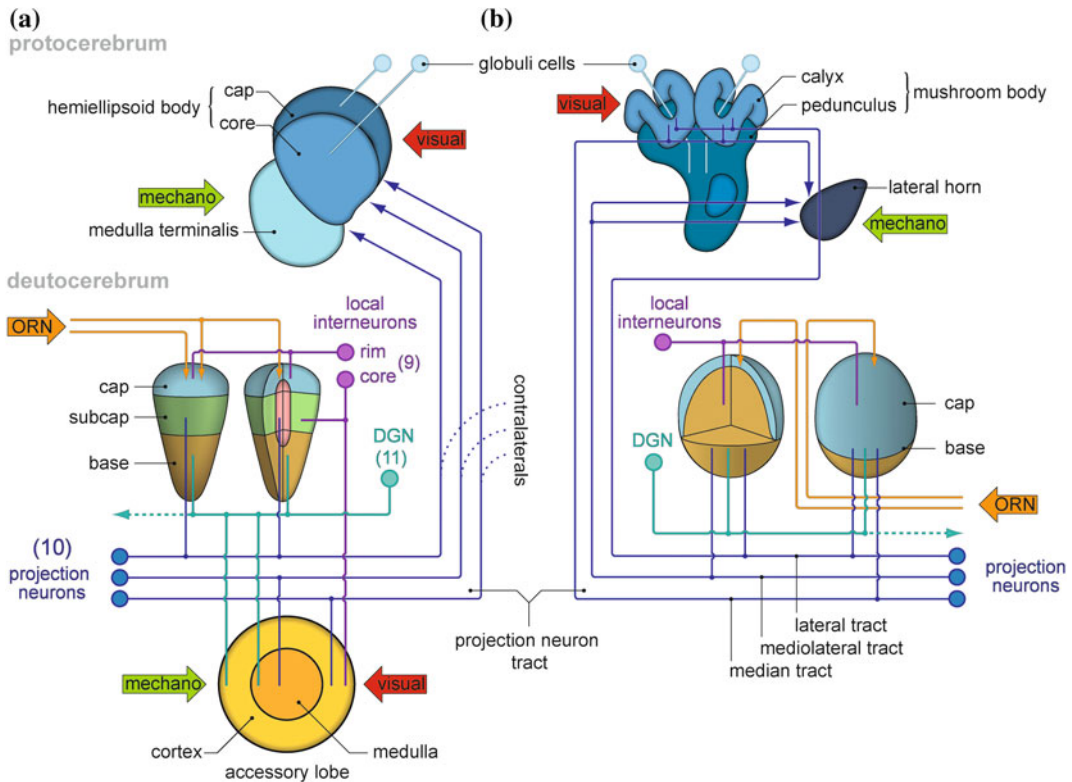


Fig. 13.6 Overview of the central olfactory pathway in a malacostracan crustacean and a hexapod. The ORNs (orange) are the primary sensory input and innervate the cap of the olfactory glomeruli. Local interneurons (purple) and dorsal giant neurons (serotonergic, turquoise) are associated with the olfactory and the accessory lobe (in malacostracan crustaceans). Processed information is relayed from the olfactory lobe to the secondary computational centers via projection neuron tracts (blue). **a** *Cherax destructor* (Crustacea). Modified after Sandeman et al. in press. The olfactory glomeruli are compartmentalized into the cap, subcap, and base as well as the central rod (red). Local interneurons innervate specific compartments of the olfactory glomeruli, for example, the rim local interneurons. Core local interneurons relay information from the subcap to the cortex of the accessory lobe. The dorsal giant neuron (DGN) innervates the olfactory glomeruli as well as the accessory lobe. Olfactory information from the olfactory and accessory lobe is then relayed to the protocerebral medulla terminalis and the cap region of the hemiellipsoid body. In addition, the accessory lobe and the

hemiellipsoid body's core region receive mechanosensory and visual input via interneurons. Furthermore, information from the accessory lobe and the core region of the hemiellipsoid body converges in the medulla terminalis. **b** *Apis mellifera* (Hexapoda). Compiled after Kirschner et al. (2006), Galizia and Szyska (2008). ORNs (orange) innervate the cap of the olfactory glomeruli from the periphery though they enter the core of the olfactory lobe and resurface between the glomeruli (as indicated). Local interneurons (purple) innervate the cap and base of the olfactory glomeruli. The dorsal giant neuron (serotonergic, turquoise) innervates multiple olfactory glomeruli. Different projection neuron populations (blue) relay information from the olfactory lobe to the mushroom body and the lateral horn. The lateral tract (multiglomerular) projects through the lateral horn into the calyces (with arborizations in the lip and basal ring). The median tract (uniglomerular) projects through the calyces (with arborizations in the lip and basal ring) into the lateral horn. The mediolateral tracts project into the lateral horn either through the lateral protocerebrum or with arborizations in the lateral network (not shown)

function drive phylogenetic change. This means that the shape of olfactory neuropils does not provide a stable phylogenetic signal as far as large-scale phylogeny of arthropods is concerned. However, a trend in transforming the

shape of OG can be observed in interordinal relationships and thus could provide phylogenetically informative characters. This is for example the case when looking at decapod crustaceans. While a spheroid shape is present in

Onychophora and Chelicerata, tremendous diversity in shape and arrangements occurs within the Mandibulata. In Myriapoda, for example, the shape of OG ranges from elongated cylindrical in the Scutigermorpha through drop-shaped to spheroid in the Geophilomorpha (Sombke et al. 2012). In centipedes, the glomeruli are arranged in a parallel or grape-like pattern (Fig. 13.4b). As in scutigermorph Chilopoda, the olfactory lobe in Archaeognatha (Hexapoda) and Cephalocarida (Crustacea) is composed of elongated cylindrical glomeruli (Mißbach et al. 2011; Stegner and Richter 2011). In many pterygote hexapod species, the OG are spheroid and surround a coarse neuropil, for example, in Dictyoptera (Boeckh and Tolbert 1993), Hymenoptera (Galizia et al. 1999), Lepidoptera, and Diptera (reviewed in Schachtner et al. 2005) (Fig. 13.4d). In malacostracan Crustacea, the OG are arranged radially around the periphery of a loose core of neuronal processes. Interestingly, the trend of transforming OG seen in Chilopoda (elongated to spheroid) is found in the malacostracans as well, but according to the phylogenetic relationships in this taxon, it is reversed (spheroid to elongated). The shape ranges from spheroid in the Leptostacra (Strausfeld 2012), marine Isopoda, and Euphausiacea (Johansson and Hallberg 1992; Harzsch et al. 2011) across wedge-shaped in several reptantian Decapoda (Sandeman et al. 1992, 1993; Schmidt and Ache 1996a; Schachtner et al. 2005; Krieger et al. 2012) to markedly elongated columns which are aligned in parallel in eurentant Anomura (Harzsch and Hansson 2008; Krieger et al. 2010) (Fig. 13.4c). Moreover, in hermit crabs, the olfactory lobes can be enlarged by the presence of sublobes (Krieger et al. 2010). In Remipedia, the olfactory lobes are also divided into several sublobes, however, the shape of OG is roughly spheroid (Fanenbruck and Harzsch 2005).

Sexual dimorphism of olfactory lobes and OG is known in several neopteran Hexapoda, for example, cockroaches (Rospars 1988), moths (Rospars and Hildebrand 2000), or honeybees (Galizia et al. 1999) and have most likely occurred convergently (Schachtner et al. 2005).

Macroglomeruli (or macroglomerular complexes) are present in males and are innervated by specific sex-pheromone receptors on the antennae. The OG themselves can be compartmentalized. In honeybees (Hexapoda), OG have a layered organization (Pareto 1972; Arnold et al. 1985; Fonta et al. 1993; Sun et al. 1993; Galizia et al. 1999) where only the periphery (or cap) is innervated by sensory afferents (Fig. 13.6). Different populations of projection neurons and local interneurons innervate the central and peripheral areas (Fig. 13.6b). A longitudinal subdivision of the OG into cap, subcap, and base has been well documented in malacostracan crustaceans such as crayfish, clawed and clawless lobsters, hermit crabs, and brachyuran crabs (Sandeman and Luff 1973; Sandeman and Sandeman 1994; Langworthy et al. 1997; Schmidt and Ache 1997; Wachowiak et al. 1997; Harzsch and Hansson 2008; Krieger et al. 2010; 2012; compare Fig. 13.6a). In Archaeognatha and Chilopoda, the OG are not compartmentalized (Mißbach et al. 2011; Sombke et al. 2011c). The number of OG is thought to be species specific. In Chilopoda, the number per olfactory lobe ranges from 34 to 97 (Sombke et al. 2012), in Hexapoda from about 20 in Collembola to approx. 250 in ants (reviewed in Schachtner et al. 2005; Kollmann et al. 2011) and seems to be invariant within species (Chambille and Rospars 1981; Rospars 1983; Rospars and Hildebrand 1992; Galizia et al. 1999; Laissue et al. 1999; Berg et al. 2002; Huetteroth and Schachter 2005; Kirschner et al. 2006; Ghaninia et al. 2007; Zube et al. 2008; Dreyer et al. 2010). In Crustacea, the number of OG varies from approx. 150 to 1,300 (reviewed in Beltz et al. 2003; Schachtner et al. 2005; Krieger et al. 2010). It should be noted that crustaceans probably do not feature a species-specific constant number of OG (compare Blaustein et al. 1988; Beltz et al. 2003).

In addition to the olfactory lobes, several deutocerebral *accessory neuropils* occur in some tetraconate taxa. In eurentant Crustacea (e.g. Homarida, Brachyura and Achelata), large and complex accessory lobes occur (Figs. 13.4, 13.6a). In spiny lobsters, the accessory lobe

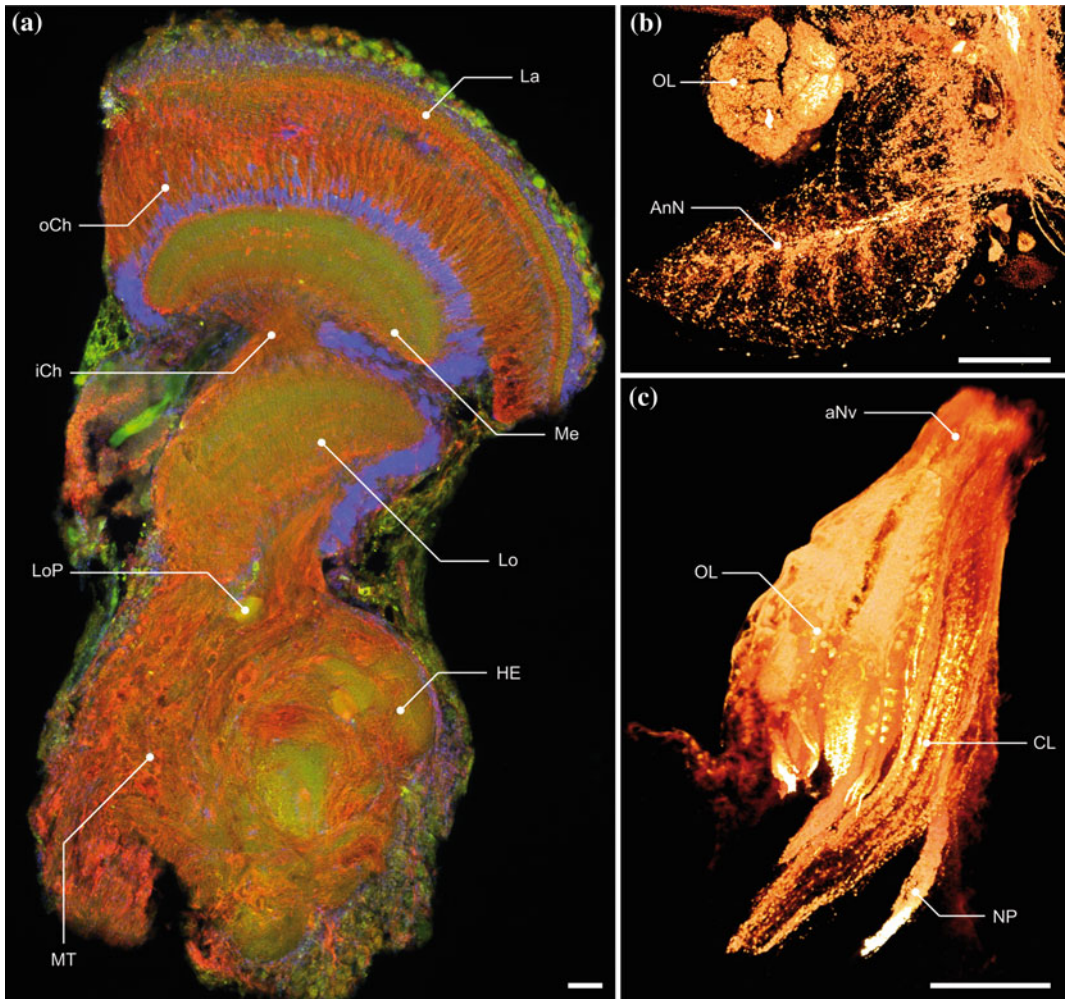


Fig. 13.7 **a** Lateral protocerebrum of *Carcinus maenas* (Crustacea: Decapoda) and optic neuropils (red: synapsin-like immunoreactivity, green: serotonin-like immunoreactivity, blue: nuclear stain). **b** Structural composition of the tritocerebral antenna 2 neuropil of *Idotea baltica* (Crustacea: Isopoda). The AnN is transversely divided into segment-like synaptic fields. The olfactory lobe is composed of spheroid olfactory glomeruli (3D reconstruction, RFamid-like immunoreactivity). **c** Antennal neurobiotin backfill of *Lithobius forficatus*

(Myriapoda: Chilopoda) showing the structural composition in distinct lamellae of the deutocerebral *c. lamellosum*. Antennal afferents innervate the olfactory lobe as well as the subesophageal ganglia via antennal neurite projections (3D reconstruction). AnN antenna 2 neuropil, aNv antennal nerve, CL *c. lamellosum*, HE hemiellipsoid body, iCh inner optic chiasm, La lamina, Lo lobula, LoP lobula plate, Me medulla, MT medulla terminalis, NP neurite projections, OL olfactory lobe. Scale bars: 100 μ m

(AcL) is composed of three neuropilar layers (Blaustein et al. 1988). The AcL receives input from the olfactory lobe via local interneurons (Sullivan and Beltz 2005). In *Cherax destructor* (Decapoda), it has been shown that the accessory lobe receives unilateral input from the proto- and deutocerebrum and bilateral input from the tritocerebrum. In addition, bilateral output to the

contralateral olfactory and accessory lobe via the deutocerebral commissure occurs (Sandeman et al. 1995). Therefore, it is suggested that the AcL integrates mechano- and chemosensory information. In certain hemimetabolous Hexapoda, gustatory and probably olfactory input from the mouthparts is processed in the lobus glomerulatus (LG). The output is transferred via

the tritocerebral tract to the mushroom bodies. In holometabolous hexapods, the LG is not present as a distinct neuropil but instead appears to be fused with the olfactory lobe (Farris 2008).

13.2.7 Mechanosensory Neuropils

Apart from their presence in the ventral nerve cord of Arthropoda (see above), mechanosensory neuropils are known from the brains of Mandibulata. The deutocerebrum is characterized by (at least) one bilaterally paired neuropil processing mechanosensory input from the first antennae (Fig. 13.4a–c). The deutocerebral mechanosensory neuropils have been called *dorsal lobe* in Hexapoda, *lateral antennular neuropil* in malacostracan Crustacea, and *corpus lamellosum* in Myriapoda. The general organization of the lateral antennular neuropil and the *c. lamellosum* in many respects matches the innervation and connections of the hexapod dorsal lobe. Therefore, these paired neuropils have been unified under the term deutocerebral mechanosensory neuropil (Sombke et al. 2012). In some mandibulate taxa, mechanosensory neuropils with a general striate or palisade shape are known, for example, in *Zygentoma* and Chilopoda (Tautz and Müller-Tautz 1983; Strausfeld 1998; Sombke et al. 2011a, 2012). In contrast to ORNs, mechanosensory neurons appear much thicker and possess several side branches.

In Chilopoda, the *c. lamellosum* is innervated by the posterior partition of the antennal nerve. The neuropil is composed of parallel neuropilar lamellae (Sombke et al. 2011a, b, 2012) including a contralateral connection. In malacostracan Crustacea, mechanosensory and non-olfactory input from the first antennae is processed in the lateral antennular neuropil (LAN) (Schmidt and Ache 1993, 1996b; Harzsch and Hansson 2008) which contains synaptic fields of the motor neurons that control the movements of the ipsilateral antennule (Sandeman et al. 1992; Schmidt et al. 1992). In Decapoda, contralateral connections between the LANs occur. In malacostracan Crustacea and Remipedia, an additional *median antennular*

neuropil (MAN) processes mechanosensory input (Sandeman et al. 1992, 1993; Schmidt and Ache 1996b, Fanenbruck and Harzsch 2005; Harzsch and Hansson 2008). In crabs and crayfish, it receives branches of interneurons related to input from the statocysts and mechanoreceptive input from the base of the antennae (Schmidt and Ache 1993; Schmidt et al. 1992). Whether the MAN of Malacostraca and Remipedia are homologous neuropils, is still debated. In pterygote Hexapoda, mechanosensory afferents from the scapus and pedicellus of the antennae project into the dorsal lobe (or AMMC = antennal mechanosensory and motor center). The dorsal lobe is also innervated by neurites of antennomuscular motoneurons. The flagellar sensilla whose neurons project into the olfactory lobe are mostly specialized for chemoreception (Rospars 1988; Homberg et al. 1989). Usually, the mechanosensory neuropil is located in the posterior region of the deutocerebrum, for example, in *Periplaneta americana* (Burdohan and Comer 1996; Nishino et al. 2005), *A. mellifera* (Kloppenborg 1995), *Gryllus bimaculatus* (Staudacher 1998; Staudacher and Schildberger 1999), and *Aedes aegypti* (Ignell and Hansson 2005; Ignell et al. 2005). In these organisms, presumptive tactile antennal afferents provide two pairs of long and several short branches which are orientated laterally and form a multilayered arrangement medially in the dorsal lobe.

In malacostracan Crustacea, the tritocerebral neuromere is characterized by the bilaterally paired *antenna 2 neuropil* (AnN), stretching posterolaterally to either side of the esophageal foramen (Fig 13.4c). Afferents ascending from the second antenna project into this neuropil which may have a specialized chemosensory function (reviewed in Schmalfuss 1998) in addition to its role in processing mechanosensory information (Sandeman and Luff 1973; Hoese 1989; Sandeman et al. 1992; Schmidt and Ache 1992; Schachtner et al. 2005). Moreover the tritocerebrum of Malacostraca and Remipedia is innervated by the tegumentary nerve which carries mechanosensory information from the carapace, and projects into the *tegumentary*

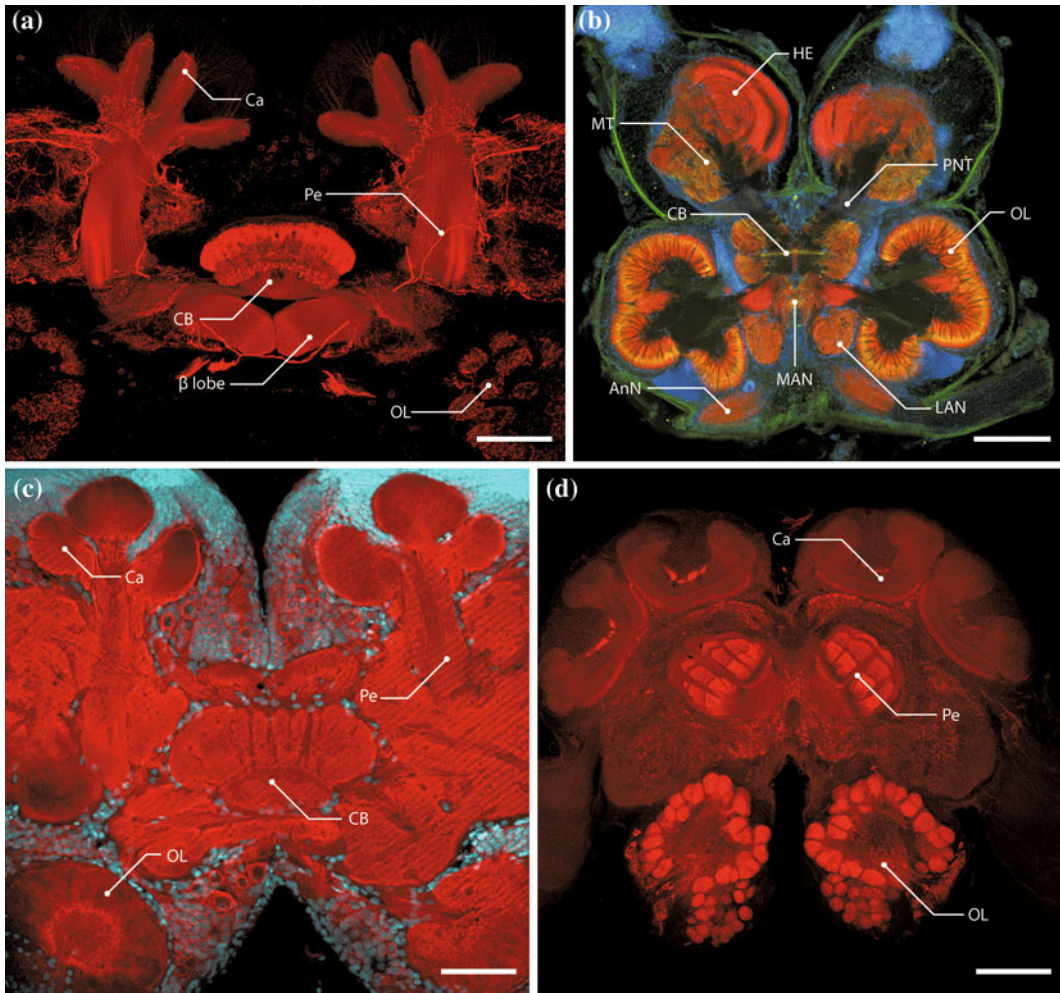


Fig. 13.8 Sections through the brains of **a** the cockroach *Rhyarobia maderae* (allatostatin-like immunoreactivity) from Loesel and Heuer (2010), **b** *Birgus latro* modified from Krieger et al. (2010) (red: synapsin immunoreactivity, green: allatostatin-like immunoreactivity, blue: nuclear stain), **c** the desert locust *Locusta*

migratoria (red: HRP-like immunoreactivity, blue: nuclear stain), and **d** the ant *Camponotus floridanus* (allatostatin-like immunoreactivity). Ca calyx of mushroom body, CB central body, OL olfactory lobe, Pe peduncle of mushroom body. Scale bars: **a**, **c** 200 μm , **d** 100 μm , **b** 500 μm

neuropil, located within the complex of the AnN (Sandeman et al. 1992). In some representatives of Decapoda and Isopoda, the AnN is transversely divided into repetitive synaptic fields (Tautz and Müller-Tautz 1983; Harzsch et al. 2011; Sandeman et al. in press; see Fig. 13.7). It has been suggested that this organization might be a somato- or spatiotopic representation of the mechanoreceptors along the length of the second antenna. Evidence for this comes from behavioral studies on blinded crayfish, which precisely

touch the point of the antenna where they have been stimulated (Zeil et al. 1985; Sandeman and Varju 1988). For Remipedia, not much is known about the tritocerebral morphology, although in two species two pairs of tritocerebral nerves have been identified (i.e. tegumentary nerves and antenna 2 nerves; Fanenbruck and Harzsch 2005) suggesting the presence of associated neuropils (antenna 2 neuropil and tegumentary neuropil). Tritocerebral neuropils that are associated with the antenna 2 and tegumentary

nerves, suggestive of a tegumentary neuropil, have also been reported for Branchiopoda (Fritsch and Richter 2010) and Cephalocarida (Stegner and Richter 2011).

In Hexapoda and Myriapoda, the tritocerebrum lacks tritocerebral appendages and consequently associated neuropils. In Onychophora and Chelicerata, distinct mechanosensory neuropils associated with antennae (Onychophora) and cheliceres/pedipalps (Chelicerata) have not been described satisfactorily. Whereas the pedipalp provides mechanosensory input into what can be regarded as the chelicerate tritocerebrum, nothing is known about the corresponding brain regions in Onychophora that are connected to the jaws (see Sect. 13.2).

13.2.8 The Mushroom Bodies

The mushroom bodies (MB) are the most prominent and conspicuous neuropils in the central brain of arthropods, onychophorans, and vagile polychaete annelids but have not been described in any other animal group with complex brain architecture. Due to a number of unique neuroanatomical characters, MBs can easily be identified and distinguished from other brain centers.

A good starting point for a morphological comparison of MB structures is the insects, where the literature on brain architecture and function is vast. In this group, the MBs are located in the protocerebrum (Figs. 13.4d, e, 13.6b, 13.8a, c, d). They act as centers for sensory integration (Gronenberg 2001), memory formation (Heisenberg 2003), and represent the neuronal basis for associative and flexible behaviors (Farris and Roberts 2005). With the exception of the archaeognathans (see below), the remaining insect taxa share a common ground plan in terms of mushroom body cellular architecture and connectivity. MBs consist of several thousand parallel fibers of intrinsic neurons, called Kenyon cells. Their perikarya are densely packed and surround the calyces which contain the dendritic arborizations of the Kenyon cells. The calyces represent the major synaptic input region to the MBs. The most

prominent inputs to the calyces originate in the antennal lobes through collaterals of olfactory interneurons that connect the antennal lobe with the protocerebrum via an projection neuron tract. MBs, however, are not merely higher order olfactory neuropils, but are present even in anosmic insects (Strausfeld et al. 1998). In a variety of social hymenopterans and in the cockroach *Periplaneta americana*, additional inputs originate in the optic lobes.

The axons of Kenyon cells project from the calyx into the peduncle. They then bifurcate and form the lobes (usually an α - and a β -lobe), the major output regions of the MBs (Laurent and Naraghi 1994). This basic neuroanatomical motif is highly conserved and has been described in all insect representatives investigated so far (Strausfeld 1998; Farris and Sinakevitch 2003; Strausfeld 2012).

Brain centers that adhere to the architectural designs of insect MBs are found in other arthropod groups (albeit not analyzed in as much detail) including myriapods (Holmgren 1916; Hanström 1928; Strausfeld et al. 1995; Loesel et al. 2002) and chelicerates (in the older literature referred to as ‘*corpora pedunculata*’; Holmgren 1916; Hanström 1928; Strausfeld and Barth 1993; Wegerhoff and Breidbach 1995; Strausfeld et al. 2006a, b). In crustaceans, on the other hand, second-order olfactory neuropils connected to the antennal lobes differ in morphology from the insect MBs. Since crustaceans are the sister taxon to the hexapods, or even the group containing the hexapods (Dohle 2001; Giribet et al. 2001; Loesel et al. 2002; Regier et al. 2005; Ungerer and Scholtz 2008), these apparent differences have resulted in conflicting views on the evolutionary origin of insect MBs and their possible homology to their namesakes in myriapods and chelicerates.

In the Malacostraca (higher crustaceans) and in the homonomously segmented Remipedia, interneurons originating in the olfactory lobes innervate the so-called hemiellipsoid bodies (Figs. 13.4c, e, 13.6a, 13.8b) that either reside in the eyestalks or in the protocerebrum as demonstrated for several crab species. The hemiellipsoid bodies are associated with thousands of

densely packed perikarya of globuli cells (the equivalent of Kenyon cells in insects), the ramifications of which contribute to the internal matrix of the hemiellipsoid bodies. This neuropil, however, does not comprise a peduncle and elongated lobes, thus being dissimilar to the external shape of the hexapod MB (Hanström 1928; Sandeman and Scholtz 1995; Strausfeld et al. 1995; Fanenbruck and Harzsch 2005). Since the neuronal organization of the hemiellipsoid body, however, is similar to the cellular architecture of the hexapod MB, hemiellipsoid bodies are today being interpreted by most specialists as modified MBs (Wolff et al. 2012). This view is supported by the fact that the brain of a basal hexapod taxon, the Archaeognatha, contains second-order olfactory neuropils which resemble hemiellipsoid bodies rather than MBs (Strausfeld 2012).

Investigations into myriapod brain anatomy (Fig. 13.4b) are scarce, and descriptions of MB neuropils are available only for a limited number of species. Diplopods (*Orthoporus ornatus*, *Julus scandinavicus*) and chilopods (*Lithobius variegatus*) exhibit clusters of small-diameter globuli cells that supply ramifications to MBs which comprise a pedunculus and lobes and which are connected to the antennal lobes via a tract of interneurons (Hanström 1928; Strausfeld et al. 1995). These commonalities suggest close affinities with the insect MB. In *Lithobius variegatus*, the lobes have been described to represent spherical outswellings, a motif similar to the MB organization of the apterygote hexapod *Lepisma saccharina*, where the pedunculus provides several outswellings as well (Böttger 1910; Strausfeld et al. 1995).

Amongst the chelicerate taxa, the neuronal architecture of the MBs has probably been most thoroughly investigated in the xiphosuran *L. polyphemus* (Hanström 1926; Fahrenbach 1977, 1979; Chamberlain and Wyse 1986; Fahrenbach and Chamberlain 1987). Dwarfing the MBs of other arthropod and non-arthropod species alike, the MBs in adult horseshoe crabs are composed of an estimated 100 Mio globuli (=Kenyon) cells (Fahrenbach 1979) and account for approximately 80 % of the total brain

volume (Hanström 1926). The aggregated somata of the globuli cells form a ventral hemisphere which enfolds the elaborately lobed neuropil in a fashion that has been likened to a cauliflower. The orientation of the MBs in *L. polyphemus* is clearly ventral—a unique condition that has not been observed in any other MBs investigated so far. Despite their highly deviant morphology, the xiphosuran MBs seem to be involved in the same tasks as their hexapod counterparts. Lacking antennae, the input to the MBs is provided by glomeruli that receive terminals from chemoreceptors located in the legs and gills (Fahrenbach 1979). In other chelicerates, chemoreceptors are located in specialized organs (pectines in scorpions, malleoli in solpugids) or modified walking limbs (uropygid and amblypygid). Similar to the condition observed in *L. polyphemus*, the OG in these taxa are not situated within the brain but in the segmental neuromeres associated with the olfactory appendages (Strausfeld et al. 1998; Wolf 2008; and Sect. 13.1.2). Ascending axons of projection neurons relay the information to the protocerebral MBs. In derived araneans such as the wandering spider *C. salei* (Fig. 13.4a), evidence for an association of the MBs with chemosensory pathways is lacking. The neuropils receive, however, direct input from a second-order visual neuropil (Strausfeld and Barth 1993). The changed connectivity suggests that the MBs in this group might have undergone major evolutionary changes with regard to their function.

Direct connections to a second-order visual neuropil are also evident in onychophoran MBs (Strausfeld et al. 2006a, b). As in arthropod taxa, onychophoran MBs are composed of a peduncle and several output lobes formed through parallel axons of a dense cluster of small-diameter perikarya of intrinsic neurons (globuli cells). One characteristic the MBs of onychophorans share with those of chelicerates but with no other arthropod group is the presence of a commissure that renders the MBs into one confluent structure.

Although architectural differences in the MBs of hexapods, myriapods, chelicerates, onychophorans, and the hemiellipsoid bodies of

crustaceans still stimulate discussions about the homology of these brain centers, the assumption of a common phylogenetic origin nevertheless seems a plausible working hypothesis due to the many commonalities that have been described. Hence, we suggest that in the ground pattern of the common ancestor of arthropods, a basal computational circuit was present that included olfactory afferents, local olfactory interneurons, second-order olfactory projection neurons, and intrinsic MB cells (Kenyon- or globuli cells). This ancestral circuitry has been retained in all osmic panarthropods and was elaborated in different functional directions at least within Tetraconata, as the difference in the structure between the olfactory system in hexapods and crustaceans suggest.

This implies the possibility that arthropod MBs are symplesiomorphic and may be of a more ancient evolutionary origin than the arthropods themselves. This idea has recently been supported by the finding that the neuronal architecture of MB-like neuropils described in vagile polychaetes is almost identical to that of insects (Heuer and Loesel 2008) and that insect and annelid MBs express the same specific set of genes that orchestrate MB development (Tomer et al. 2010). Taken together these findings suggest a deep-time origin of MBs possibly dating back to the last common ancestor of protostomes, or beyond.

13.2.9 The Central Body

All major arthropod groups possess a brain midline neuropil called the central body. Several lines of evidence from behavioral and comparative studies suggest that the central body serves as a motor control centers that is involved in orchestrating limb actions. Based on its neuronal architecture, the central body of various arthropod groups is characterized by several distinct features that will be summarized below.

Again, the most thoroughly investigated taxa are insects and crustaceans. Here, the so-called 'central complex' is an assemblage of unpaired midline neuropils that comprises the central body and the protocerebral bridge (Figs. 13.4d, e,

13.8a–c). The central body itself is subdivided into several layers and columns. Connections of the central body to the protocerebral bridge are provided via columnar neurons that form a complicated but highly conserved pattern of chiasmata. The entire complex receives and provides axons from and to other protocerebral neuropils. The most prominent of these satellite neuropils are the paired noduli and the lateral accessory lobes. Presumably, the lateral accessory lobes are the sites where the central body connects to ascending and descending fibers from and to the thoracic ganglia. These features are common in all investigated neopteran insects and have been demonstrated in several decapod crustaceans. (For a synopsis of literature on central complex neuroarchitecture of individual species see Loesel et al. 2002). Especially in flies and locusts, the neuroarchitecture of the central complex has been analyzed to an extent that made it possible to construct a wiring diagram of this brain region. While the number and arrangement of columns is identical in insects and decapods (Utting et al. 2000), there are differences in the number and shape of layers of the central body which, especially in decapods, differs even between closely related species (Loesel et al. 2002). It will be an interesting challenge for future research to homologize individual layers between different species and correlate the findings with the behavioral repertoire of the animals.

Immunohistochemical studies demonstrated the presence of a wide variety of neuroactive substances in different parts of the central complex (Homberg 1994). In addition to biogenic amines such as octopamine, serotonin, dopamine, and allatostatin, to name just a few, neurotransmitters like histamine (Loesel and Homberg 1999) and GABA (Homberg et al. 1999) have been found. Immunocytochemistry proved to be a powerful phylogenetic tool that has helped to establish homologies between subcompartments of the central complex in different species. GABA, for example, has been shown to be present only in one central body layer, the so-called ellipsoid body (also termed lower division) in all investigated insect species (Homberg et al. 1999).

Despite our detailed knowledge about the central complex neuroarchitecture, its role in controlling the animal's behavior is only partially understood, especially when it comes to assigning certain functions to individual subunits of the central complex. In intracellular recordings from locusts and bees, a subset of neurons of the central body respond to multimodal stimuli and the e-vector of polarized light (Homberg 1985; Milde 1988; Vitzthum et al. 2002; Heinze and Homberg 2007). The central body of flies incorporated radioactive-labeled deoxyglucose during visual stimulation, indicating that the metabolic rate of central body neurons was elevated at this time (Bausenwein et al. 1994). Such studies suggest that the central complex receives visual input. It is, however, unlikely that its main function is visual information processing since eyeless workers of the ant *Myrmica* sp. (Gronenberg, personal communication) and the blind cave beetle *Neophaenops tellkampfi* (Ghaffar et al. 1984) possess a well-developed central complex.

Functions ascribed to the central complex come mainly from studies of behavioral mutants of *Drosophila*, where specific deficits in limb coordination relate to structural defects in the central complex. Especially, the fly's ability to execute asymmetrical limb movements (e.g. in turning) is severely impaired in animals with a damaged central complex (Strauss and Heisenberg 1990, 1993; Strauss et al. 1992; reviewed by Strauss 2002). In these mutants, the overall locomotor activity and the ability to retain direction towards a landmark, which becomes invisible during approach, are also diminished (Strauss 2003). Comparative studies further support the notion that the central complex relates to leg coordination. In cell-building social insects that can perform complicated and heterolaterally independent limb movements, the cellular organization of the individual subunits of the central complex is elaborate. In nocturnal Lepidoptera, which mainly use their legs for grasping but not for walking, central body layers and the protocerebral bridge are reduced (Strausfeld 1999). In aquatic Hemiptera, which primarily perform bilaterally coupled

swimming strokes, central complex elaboration is significantly impoverished (Strausfeld 1999).

Similar studies have been carried out in decapod crustaceans. Fiddler crabs of the genus *Uca* exhibit strong sexual dimorphism in the size of their claws. Male fiddler crabs have one large front claw and one small one, while females have two small claws. The male fiddler crab waves this claw and wrestles other males to mark his territory and attract mates. The small claw is needed for gathering food. Since males use their front claws for two different tasks, they have a higher ability to uncouple the movements of right and left front claws as compared to females. This difference in locomotor abilities possibly correlates with a pronounced dimorphism in the relative size and shape of the central body (Loesel 2004). Such a dimorphism has not been observed in any of the other investigated crustacean genera. Together, the available data suggest that the central complex is a higher brain center of insects and malacostracan crustaceans for navigational control and limb coordination that is especially involved in locomotor patterns that require heterolaterally independent leg movements.

In all investigated species of the Chelicerata (spiders, scorpions, horseshoe crabs), the central body (for historical reasons often referred to as 'arcuate body') is a crescent-shaped, unpaired neuropil extending across the entire width of the brain (Fig. 13.4a). In each representative, the central body was found to be the posterior-most cerebral neuropil. A protocerebral bridge and satellite neuropils such as noduli or ventral bodies have not been found. A variety of staining techniques reveal that the neuroarchitecture of the central body of chelicerates is characterized by a palisade-like arrangement of a large number of columnar fibers that project through consecutive layers. These layers are demarcated by successive strata of tangential neurons and by the density of presynaptic terminals. Unlike in insects and decapods, columnar neurons of chelicerates are not bundled into discrete columns but innervate the central body uniformly across its entire lateral extension. Immunocytochemical studies revealed that a large number of

neuroactive substances such as allatostatin, proctolin, crustacean-cardioactive peptide, and GABA that have been detected in the insect central body are likewise present in the central body of spiders (Loesel et al. 2002, 2011). While the spider's central body receives direct visual input from second-order optic neuropils (Strausfeld et al. 1993), its main function seems to be locomotor control, too. The evidence is somewhat anecdotal, but comparative studies have demonstrated that chelicerate central body elaboration and relative size correlate to the animal's motoric repertoire (Strausfeld 2012). Besides striking similarities in neuroarchitecture and transmitter content, a further argument for a common origin of the central bodies in chelicerates and in the hexapod–crustacean clade is the presence of a central body in even the most basal chelicerate representatives such as the horseshoe crab *L. polyphemus* and the segmented spider *Heptathela kimurai*.

Onychophorans which are the sister group to arthropods have a well-developed central body, as well. A thorough analysis of the brain of *Euperipatoides rowellii* revealed that the basic neuroarchitecture of the central body of this velvet worm is practically indistinguishable from that of chelicerates. As is the case in spiders, allatostatin is a major neurotransmitter in certain layers of the central body in this onychophoran species, too (Strausfeld et al. 2006a, b, c).

From the morphological point of view, the central body of chilopods (Fig. 13.4b) is an intermediate between the central bodies of the Tetraconata and the Chelicerata/Onychophora. In several representatives of the Chilopoda the central body is a roughly hemiellipsoid midline neuropil that is situated between the proximal tips of the mushroom body's medial lobe. It consists of several horizontal layers and is innervated by columnar fibers. Two classes of columnar neurons can be distinguished. One (allatostatin-immunoreactive) class innervates the central body without crossing the trajectory of another allatostatin-ir fiber. The second subset of columnar neurons forms a system of interweaving fibers across the entire lateral extension

of the central body. A protocerebral bridge or any other satellite neuropils have not been identified. Columnar neurons of the chilopod central body, however, are in close spatial contact to commissures that connect both hemispheres of the brain and might retrieve information from there (Loesel et al. 2002). The anatomy of the central body of centipedes bears resemblance to the central bodies of chelicerates as well as of that of insects. The position, external shape, and relative size of the centipede central body are comparable to the conditions found in insects. On the other hand, the way the columnar neurons innervate consecutive layers of the central body is reminiscent of the situation found in chelicerates. A shared feature in all these taxa is the presence of allatostatin-immunoreactive columnar fibers.

Several staining techniques failed to identify a midline neuropil in the brain of the second major myriapod clade, the Diplopoda (Loesel et al. 2002). Here, the entire midbrain consists of numerous commissural tracts that connect both hemispheres. This would require a secondary loss of the central body in the diplopod brain. The hypothesis is at least plausible since diplopods do not change the locomotor pattern of their many legs when turning, as is the case in chilopods. Diplopods rather bend their body, presumably by contracting their lateral body muscles, and their legs just follow this curve. Hence, necessity for a brain control center that uncouples bilateral limb movements would not be there.

Taking all the available data together, it seems highly unlikely that the central body has evolved several times during arthropod evolution. Beside striking similarities in its neuroanatomical Leitmotif, the shared neurotransmitter equipment (e.g. allatostatin is always found in columnar fibers) argues for a one-time evolutionary event that brought about the progenitor of the central body. Another strong argument is the fact that a central body has been found even in the most basal representatives of crustaceans, hexapods, and chelicerates. In crustaceans, the central body neuroarchitecture of basal groups is not well investigated. However, in the branchiopod *Triops longicaudatus*, a central body is certainly present

(Loesel 2004) and it contains allatostatin and tachykinin-related peptide as is also the case in decapods and hexapods.

What did the ancestral central body look like? Many basal features may have been retained in the central body of chilopods. Its palisade-like arrangement of columnar neurons that possibly retrieve information from commissural fibers and subsequently innervate a small and layered midline neuropil may initially have served to compare neuronal information from both sides of the brain. To enable this, a subset of columnar neurons evolved into a chiasmatic pattern of interweaving fibers that has finally been organized into discrete columns. In the Tetraconata, the protocerebral bridge and satellite neuropils have been added. In chelicerates and onychophorans, the ground pattern that has been retained in the chilopod central body may have been conserved but elaborated with respect to the neuropil's relative size, width, and stratification.

The available data suggest that the neuro-anatomical Leitmotif of the central body has been highly conserved during arthropod evolution and originated at least 600 million years ago, well before the first terrestrial arthropods emerged. Small central midline neuropils that are in some respects reminiscent of the arthropod central body have recently been described in predatory polychaetes that use their parapodia for rapid locomotion during hunting (Heuer et al. 2010). This might be another piece of evidence that the central body evolved together with the ability to coordinate limb movements.

13.3 Phylogenetic Overview and Outlook

Despite three decades of molecular phylogenetic analyzes of arthropod relationships using constantly increasing data sets and analysis methods (recent examples are Koenemann et al. 2010; Regier et al. 2010; Rota-Stabelli et al. 2011; Trautwein et al. 2012; von Reumont et al. 2012), we are still far from a reliable and robust hypothesis on arthropod main clade phylogeny (see Chap. 2). Arthropod neuroanatomists

realized early that the arthropod nervous system includes a wealth of structures that can be used both for analysing the phylogeny of arthropods and for describing evolutionary transformations within the arthropod brain (Holmgren 1916; Hanström 1928). In the past 25 years, structure and development of the arthropod nervous system have made a major contribution to the raging debate on arthropod phylogeny and the discipline of 'neurophylogeny' attempts to synthesize neurobiological questions and evolutionary aspects (e.g. Arbas et al. 1991; Breidbach and Kutsch 1995; Whittington 1996; Nilsson and Osorio 1997; Strausfeld 1998; Loesel 2004; Harzsch and Hafner 2006; Harzsch 2006, 2007; Loesel 2006, 2011; Strausfeld 2009; Strausfeld and Andrews 2011; Strausfeld 2012). In the following, we summarize architectural features of the nervous system that we consider to be part of the ground pattern of Arthropoda.

13.3.1 Ground pattern of the Arthropod Nervous System

- (i) The three preoral neuromeres of the arthropod brain are the protocerebrum (ocular segment), deutocerebrum (chelicera segment in Chelicerata, first antennal segment in Mandibulata), and tritocerebrum (pedipalp segment in Chelicerata, second antennal segment in Crustacea, intercalary segment in Hexapoda and Myriapoda)
- (ii) The axons of bilaterally symmetric median eyes project into a protocerebral neuropil (the median eye center). The median eyes can be paired or unpaired (ocellar ganglia in Xiphosura, nauplius eye center in Branchiopoda, ocellar plexus in Pterygota). The median eye center is innervated by interneurons with somata located anteriorly (dorsal median group in Xiphosura, cluster 6 in Crustacea, pars intercerebralis in Hexapoda)
- (iii) The lateral eyes are associated with two optic neuropils which are linked by

- straight fibers and provide input to the protocerebrum
- (iv) During growth of the lateral eye, new elements are added to the side of the existing eye field and elongate the rows of earlier generated units
 - (v) Photoreceptors of both median and lateral eyes use histamine as neurotransmitter
 - (vi) The central body is enwrapped by layers of neuronal somata and is also innervated by columnar neurons with somata located in the anterior soma cluster (see median eye center somata)
 - (vii) A preoral frontal commissure (e.g. stomatogastric bridge) is present which is composed of deuto- and tritocerebral fibers and gives rise to nerves innervating the hypostome, esophagus, and the anterior part of the gut
 - (viii) In the ventral nerve cord, an anterior and posterior group of serotonergic neurons with variable number is present in each hemiganglion, which is connected by transversely linked fibers to its contralateral unit
 - (ix) Excitatory motoneurons supplying appendages are arranged in an anterior and a posterior soma cluster (according to the muscles they innervate)
 - (x) In addition to excitatory motoneurons, single or small groups of inhibitory motoneurons are present that also innervate the appendage muscles.

A number of character complexes related to the nervous system promise to contribute meaningful data for future in-depth phylogenetic analyzes. Studying mechanisms of neurogenesis such as stem cell proliferation and growth of pioneer neurons has already provided important insights into arthropod relationships. At the cellular level, individually identifiable neurons in the ventral nerve cord and the brain which can be identified by their transmitter expression and the morphology of which can be mapped by confocal laser scan analysis have a high potential to unravel homologies between arthropod

taxa. At the level of brain neuropils and associated sensory systems, structures that are in the focus of comparative analyzes are the optic neuropils and optic chiasmata, the architecture and connectivity of the central complex, olfactory, and mechanosensory systems as well as the mushroom and hemiellipsoid bodies. It will be vital in the future to analyze these structures in more and more non-model organisms.

References

- Abzhanov A, Kaufman TC (2004) *Hox* genes and tagmatization of the higher Crustacea (Malacostraca). In: Scholtz G (ed) Evolutionary developmental biology of Crustacea (Crustacen issues 15). Balkema, Lisse, pp 41–74
- Arbas EA, Meinertzhagen IA, Shaw SR (1991) Evolution in nervous systems. *Annu Rev Neurosci* 14:9–38
- Arnold G, Masson C, Budharugsa S (1985) Comparative study of the antennal lobes and their afferent pathway in the worker bee and the drone (*Apis mellifera*). *Cell Tiss Res* 242:593–605
- Autrum H (1979) Comparative physiology and evolution of vision in invertebrates. A: Invertebrate photoreceptors. Springer, Berlin
- Barth FG (2001) Sinne und Verhalten—Aus dem Leben einer Spinne. Springer, Berlin
- Barth FG (2002) A spider's world: senses and behavior. Springer, Berlin
- Barth FG (2012) Spider strain detection. In: Barth FG, Humphrey JAC (eds) Frontiers in sensing. Springer, Wien, pp 251–273
- Barth FG, Schmid A (2001) Ecology of sensing. Springer, Berlin
- Battelle B-A (2006) The eyes of *Limulus polyphemus* (Xiphosura, Chelicerata) and their afferent and efferent projections. *Arthropod Struct Dev* 35:261–274
- Bausenwein B, Müller NR, Heisenberg M (1994) Behavior-dependent activity labeling in the central complex of *Drosophila* during controlled visual stimulation. *J Comp Neurol* 340:255–268
- Belanger JH (2005) Contrasting tactics in motor control by vertebrates and arthropods. *Integr Comp Biol* 45:672–678
- Beltz BS, Kordas K, Lee MM, Long JB, Benton JL, Sandeman DC (2003) Ecological, evolutionary, and functional correlates of sensilla number and glomerular density in the olfactory system of decapod crustaceans. *J Comp Neurol* 455:260–269
- Berg BG, Galizia CG, Brandt R, Mustaparta H (2002) Digital atlases of the antennal lobe in two species of tobacco budworm moths, the oriental *Helicoverpa*

- assulta* (male) and the American *Heliothis virescens* (male and female). *J Comp Neurol* 446:123–134
- Bianchet MA, Bains G, Pelosi P, Pevsner J, Snyder SH, Monaco HL, Amzel LM (1996) The three-dimensional structure of bovine odorant binding protein and its mechanism of odor recognition. *Nature Struct Mol Biol* 3:934–939
- Bitsch C, Bitsch J (2005) Evolution of eye structure and arthropod phylogeny. In: Koenemann S, Jenner RA (eds) *Crustacea and arthropod relationships*. Taylor & Francis, New York, pp 81–111
- Bitsch J, Bitsch C (2007) The segmental organization of the head region in Chelicerata: a critical review of recent studies and hypotheses. *Acta Zool* 88:317–335
- Bitsch J, Bitsch C (2010) The tritocerebrum and the clypeolabrum in mandibulate arthropods: segmental interpretations. *Acta Zool* 91:249–266
- Blaustein DN, Derby CD, Simmons RB, Beall AC (1988) Structure of the brain and medulla terminals of the spiny lobster *Panulirus argus* and the crayfish *Procambarus clarkii* with an emphasis on olfactory centers. *J Crustac Biol* 8:493–519
- Boeckh J, Tolbert LP (1993) Synaptic organization and development of the antennal lobe in insects. *Microsc Res Tech* 24:260–280
- Borst A, Euler T (2011) Seeing things in motion: models circuits, and mechanisms. *Neuron* 71:974–994
- Borst A, Haag J, Reiff DF (2010) Fly motion vision. *Annu Rev Neurosci* 33:49–70
- Bossing T, Udolph G, Doe CQ, Technau GM (1996) The embryonic central nervous system lineages of *Drosophila melanogaster*. I. Neuroblast lineages derived from the ventral half of the neuroectoderm. *Dev Biol* 179:41–64
- Böttger O (1910) Das Gehirn eines niederen Insektes (*Lepisma saccharina* L.). *Jenaer Ztschr Naturwiss* 46:801–844
- Bräuning P, Pflüger H-J, Hustert R (1983) The specificity of central nervous projections of locust mechanoreceptors. *J Comp Neurol* 218:197–207
- Breidbach O, Kutsch W (1995) The nervous systems of invertebrates: an evolutionary and comparative approach. Birkhäuser Verlag, Basel
- Breithaupt T, Thiel M (2011) Chemical communication in crustaceans. Springer, New York
- Brownell PH (1989) Glomerular cytoarchitectures in chemosensory systems of Archnids. *Ann N Y Acad Sci* 855:502–507
- Bullock TH, Horridge GA (1965) Structure and function in the nervous system of invertebrates, vol II. Freeman, San Francisco
- Burdohan JA, Comer CM (1996) Cellular organization of an antennal mechanosensory pathway in the cockroach *Periplaneta americana*. *J Neurosci* 16:5830–5843
- Burrows M (1996) Neurobiology of an insect brain. Oxford University Press, Oxford
- Burrows M, Newland PL (1993) Correlation between the receptive fields of locust interneurons, their dendritic morphology, and the central projections of mechanosensory neurons. *J Comp Neurol* 329:412–426
- Callaway JC, Stuart AE (1999) The distribution of histamine and serotonin in the barnacle's nervous system. *Microsc Res Tech* 44:94–104
- Chamberlain SC, Wyse GA (1986) An atlas of the brain of the horseshoe crab *Limulus polyphemus*. *J Morphol* 187:363–386
- Chambille I, Rospars JP (1981) Le deutocerebrum de la blatte *Blaberus craniifer* Burm. (Dictyoptera: Blaberidae). Étude qualitative et identification visuelle des glomerules. *Int J Insect Morphol Embryol* 10:141–165
- Clarkson ENK, Levi-Setti R, Horváth G (2006) The eyes of trilobites; the oldest preserved visual system. *Arthropod Struct Dev* 35:247–259
- Croset V, Rytz R, Cummins SF, Budd A, Brawand D, Kaessmann H, Gibson TJ, Benton R (2010) Ancient protostome origin of chemosensory ionotropic glutamate receptors and the evolution of insect taste and olfaction. *PLoS Genet* 6(8):e1001064. doi: [10.1371/journal.pgen.1001064](https://doi.org/10.1371/journal.pgen.1001064)
- Damen WGM, Hausdorf M, Seyfarth E-A, Tautz D (1998) A conserved mode of head segmentation in arthropods revealed by the expression pattern of *Hox* genes in a spider. *Proc Natl Acad Sci U S A* 95:10665–10670
- Denes AS, Jékely G, Steinmetz PRH, Raible F, Snyman H, Prud'homme B, Ferrier DEK, Balavoine G, Arendt D (2007) Molecular architecture of annelid nerve cord supports common origin of nervous system centralization in Bilateria. *Cell* 129:277–288
- Doeffinger C, Hartenstein V, Stollewerk A (2010) Compartmentalization of the precheliceral neuroectoderm in the spider *Cupiennius salei*: development of the arcuate body, optic ganglia, and mushroom body. *J Comp Neurol* 518:2612–2632
- Dohle W (2001) Are the insects terrestrial crustaceans? a discussion of some new facts and arguments and the proposal of the proper name 'Tetraconata' for the monophyletic unit Crustacea + Hexapoda. *Ann Soc Entom France (NS)* 37:85–103
- Douglas JK, Strausfeld NJ (2003) Anatomical organization of retinotopic motion-sensitive pathways in the optic lobes of flies. *Microsc Res Tech* 62:132–150
- Dreyer D, Vitt H, Dippel S, Goetz B, el Jundi B, Kollmann M, Huetteroth W, Schachner J (2010) 3D standard brain of the red flour beetle *Tribolium castaneum*: a tool to study metamorphic development and adult plasticity. *Front Syst Neurosci* 4:3. doi: [10.3389/neuro.06.003.2010](https://doi.org/10.3389/neuro.06.003.2010)
- Duman-Scheel M, Patel NH (1999) Analysis of molecular marker expression reveals neuronal homology in distantly related arthropods. *Development* 126:2327–2334
- Egelhaaf M (2006) The neural computation of visual motion information. In: Warrant E, Nilsson D-E (eds) *Invertebrate vision*. Cambridge University Press, Cambridge, pp 399–462

- Egelhaaf M, Kern R, Lindemann J, Braun E, Geurten B (2009) Active vision in blowflies: strategies and mechanisms of spatial orientation. In: Floreano D, Zufferey J-C, Srinivasan MV, Ellington C (eds) *Flying insects and robots*. Springer, Heidelberg, pp 51–61
- Eguchi E, Tominaga Y (1999) *Atlas of arthropod sensory receptors: dynamic morphology in relation to function*. Springer, Berlin
- Eisthen HL (2002) Why are olfactory systems of different animals so similar? *Brain Behav Evol* 59:273–293
- Elofsson R, Dahl E (1970) The optic neuropils and chiasmata of Crustacea. *Z Zellforsch mikrosk Anat* 107:343–360
- Elofsson R, Hagberg M (1986) Evolutionary aspects on the construction of the first optic neuropil (lamina) in Crustacea. *Zoomorphol* 106:174–178
- Elson RC (1996) Neuroanatomy of a crayfish thoracic ganglion: sensory and motor roots of the walking-leg nerves and possible homologies with insects. *J Comp Neurol* 365:1–17
- Eriksson BJ, Stollewerk A (2010) The morphological and molecular processes of onychophoran brain development show unique features that are neither comparable to insects nor to chelicerates. *Arthropod Struct Dev* 39:478–490
- Exner S (1891) *Die Physiologie der facettierten Augen von Krebsen und Insekten*. Deuticke, Leipzig
- Exner S, Hardie RC (1989) *The physiology of the compound eyes in insects and crustaceans*. Springer, Berlin
- Fahrenbach WH (1977) The brain of the horseshoe crab (*Limulus polyphemus*) II. Architecture of the corpora pedunculata. *Tissue Cell* 9:157–166
- Fahrenbach WH (1979) The brain of the horseshoe crab (*Limulus polyphemus*) III. Cellular and synaptic organization of the corpora pedunculata. *Tissue Cell* 11:163–200
- Fahrenbach WH, Chamberlain SC (1987) The brain of the horseshoe crab, *Limulus polyphemus*. In: Gupta AP (ed) *Arthropod brain: its evolution, development, structure, and functions*. Wiley, New York, pp 63–93
- Fanenbruck M, Harzsch S (2005) A brain atlas of *Godzillioognomus frondosus* Yager, 1989 (Remipedia, Godzilliidae) and comparison with the brain of *Speleonectes tulumensis* Yager, 1987 (Remipedia, Speleonectidae): implications for arthropod relationships. *Arthropod Struct Dev* 34:343–378
- Farris SM, Sinakevitch I (2003) Development and evolution of the insect mushroom bodies: towards the understanding of conserved developmental mechanisms in a higher brain center. *Arthropod Struct Dev* 32:79–101
- Farris SM (2005) Evolution of insect mushroom bodies: old clues, new insights. *Arthropod Struct Dev* 34:211–234
- Farris SM (2008) Tricerebral tract input to the insect mushroom bodies. *Arthropod Struct Dev* 37:492–503
- Farris SM (2011) Are mushroom bodies cerebellum-like structures? *Arthropod Struct Dev* 40:368–379
- Farris SM, Roberts NS (2005) Coevolution of generalist feeding ecologies and gyrencephalic mushroom bodies in insects. *Proc Natl Acad Sci U S A* 102:17394–17399
- Fonta C, Sun X-J, Masson C (1993) Morphology and spatial distribution of bee antennal lobe interneurons responsive to odours. *Chemi Senses* 18:101–119
- Franceschini N, Riehle A, Le Nestour A (1989) Directional selective motion detection by insect neurons. In: Stavenga DG, Hardie RC (eds) *Facets of vision*. Springer, Berlin, pp 360–390
- Friedrich M, Wood EJ, Wu M (2011) Developmental evolution of the insect retina: Insights from standardized numbering of homologous photoreceptors. *J Eptl Zool* 316:484–499
- Fritsch M, Richter S (2010) The formation of the nervous system during larval development in *Triops cancriformis* (Bosc) (Crustacea, Branchiopoda): an immunohistochemical survey. *J Morphol* 271:1457–1481
- Galizia CG, Eisenhardt D, Giurfa M (2012) Honeybee neurobiology and behavior: a tribute to Randolph Menzel. Springer, New York
- Galizia CG, McIlwraith SL, Menzel R (1999) A digital three-dimensional atlas of the honey-bee antennal lobe based on optical sections acquired by confocal microscopy. *Cell Tissue Res* 395:383–394
- Galizia CG, Menzel R (2000) Odour perception in honeybees: coding information in glomerular patterns. *Curr Opin Neurobiol* 10:504–510
- Galizia CG, Menzel R (2001) The role of glomeruli in the neural representation of odours: results from optical recording studies. *J Insect Physiol* 47:115–129
- Galizia CG, Rössler W (2010) Parallel olfactory systems in insects: anatomy and function. *Annu Rev Entomol* 55:399–420
- Galizia CG, Szyska P (2008) Olfactory coding in the insect brain: molecular receptive ranges, spatial and temporal coding. *Entom Exp Appl* 128:81–92
- Ghaffar H, Larsen JR, Booth GM, Perkes R (1984) General morphology of the brain of the blind cave beetle, *Neaphaenops tellkampfi* Erichson (Coleoptera: Carabidae). *Int J Insect Morphol Embryol* 13:357–371
- Ghaninia M, Hansson BS, Ignell R (2007) The antennal lobe of the African malaria mosquito, *Anopheles gambiae*—innervations and three dimensional reconstruction. *Arthropod Struct Dev* 36:23–39
- Giribet G, Edgecombe GD, Wheeler WC (2001) Arthropod phylogeny based on eight molecular loci and morphology. *Nature* 413:157–161
- Glantz RM, Miller CS (2002) Signal processing in the crayfish optic lobe: contrast, motion and polarization vision. In: Wiese K (ed) *The crustacean nervous system*. Springer, Berlin, pp 486–498
- Glantz RM, Miller CS, Nässel DR (2000) Tachykinin-related peptide and GABA-mediated presynaptic inhibition of crayfish photoreceptors. *J Neurosci* 20:1780–1790

- Gronenberg W (2001) Subdivisions of hymenopteran mushroom body calyces by their afferent supply. *J Comp Neurol* 436:474–489
- Hafner GS, Tokarski TR (2001) Retinal development in the lobster *Homarus americanus*: comparison with compound eyes of insects and other crustaceans. *Cell Tissue Res* 305:147–158
- Hallberg E, Skog M (2011) Chemosensory sensilla in crustaceans. In: Breithaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 103–121
- Hansson BS, Harzsch S, Knaden M, Stensmyr MC (2011) The neural and behavioral basis of chemical communication in terrestrial crustaceans. In: Breithaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 149–173
- Hansson BS, Stensmyr MC (2011) Evolution of insect olfaction. *Neuron* 72:698–711
- Hanström B (1926) Das Nervensystem und die Sinnesorgane von *Limulus polyphemus*. *Lunds Univ Årsskr NF* 22:1–79
- Hanström B (1928) Vergleichende Anatomie des Nervensystems der wirbellosen Tiere unter Berücksichtigung seiner Funktion. Springer, Berlin
- Hardie RC (1989) Neurotransmitters in compound eyes. In: Stavenga DG, Hardie RC (eds) Facets of vision. Springer, Berlin, pp 235–256
- Hartenstein V (2006) The neuroendocrine system of invertebrates: a developmental and evolutionary perspective. *J Endocrinol* 190:555–570
- Harzsch S (2002) The phylogenetic significance of crustacean optic neuropils and chiasmata: a re-examination. *J Comp Neurol* 453:10–21
- Harzsch S (2003) Ontogeny of the ventral nerve cord in malacostracan crustaceans: a common plan for neuronal development in Crustacea and Hexapoda? *Arthropod Struct Dev* 32:17–38
- Harzsch S (2004a) Phylogenetic comparison of serotonin-immunoreactive neurons in representatives of the Chilopoda, Diplopoda, and Chelicerata: implications for arthropod relationships. *J Morphol* 259:198–213
- Harzsch S (2004b) The tritocerebrum of Euarthropoda: a “non-*drosophilocentric*” perspective. *Evol Dev* 6:303–309
- Harzsch S (2006) Neurophylogeny: architecture of the nervous system and a fresh view on arthropod phylogeny. *Integr Comp Biol* 46:162–194
- Harzsch S (2007) Architecture of the nervous system as a character for phylogenetic reconstructions: examples from the Arthropoda. *Species Phylog Evol* 1:33–57
- Harzsch S, Benton J, Darwirs RR, Beltz B (1999) A new look at embryonic development of the visual system in decapod crustaceans: neuropil formation, neurogenesis and apoptotic cell death. *J Neurobiol* 39:294–306
- Harzsch S, Glötzner J (2002) An immunohistochemical study of structure and development of the nervous system in the brine shrimp *Artemia salina* Linnaeus, 1758 (Branchiopoda, Anostraca) with remarks on the evolution of the arthropod brain. *Arthropod Struct Dev* 30:251–270
- Harzsch S, Hafner G (2006) Evolution of eye development in arthropods: phylogenetic aspects. *Arthropod Struct Dev* 35:319–340
- Harzsch S, Hansson BS (2008) Brain architecture in the terrestrial hermit crab *Coenobita clypeatus* (Anomura, Coenobitidae): neuroanatomical evidence for a superb aerial sense of smell. *BMC Neurosci* 9:1–35
- Harzsch S, Melzer RR, Müller CHG (2007) Mechanisms of eye development and evolution of the arthropod visual systems: the lateral eyes of myriapoda are not modified insect ommatidia. *Org Divers Evol* 7:20–32
- Harzsch S, Müller CHG, Wolf H (2005a) From variable to constant cell numbers: cellular characteristics of the arthropod nervous system argue against a sister-group relationship of Chelicerata and “Myriapoda” but favour the Mandibulata concept. *Dev Gen Evol* 215:53–68
- Harzsch S, Rieger V, Krieger J, Seefluth F, Strausfeld NJ, Hansson BS (2011) Transition from marine to terrestrial ecologies: changes in olfactory and tritocerebral neuropils in land-living isopods. *Arthropod Struct Dev* 40:244–257
- Harzsch S, Sandeman D, Chaigneau J (2012) Morphology and development of the central nervous system. In: Forest J, von Vaupel Klein JC (eds) Treatise on zoology—anatomy, taxonomy, biology. The Crustacea, vol. 3. Brill, Leiden, pp 9–236
- Harzsch S, Waloszek D (2000) Serotonin-immunoreactive neurons in the ventral nerve cord of Crustacea: a character to study aspects of arthropod phylogeny. *Arthropod Struct Dev* 29:307–322
- Harzsch S, Waloszek D (2001) Neurogenesis in the developing visual system of the branchiopod crustacean *Triops longicaudatus* (LeConte, 1846): corresponding patterns of compound-eye formation in Crustacea and Insecta? *Dev Genes Evol* 211:37–43
- Harzsch S, Wildt M, Battelle B, Waloszek D (2005b) Immunohistochemical localization of neurotransmitters in the nervous system of larval *Limulus polyphemus* (Chelicerata, Xiphosura): evidence for a conserved protocerebral architecture in Euarthropoda. *Arthropod Struct Dev* 34:327–342
- Heinze S, Homberg U (2007) Map-like representation of celestial E-vector orientations in the brain of an insect. *Science* 315:995–997
- Heisenberg M (2003) Mushroom body memoir: from maps to models. *Nature Rev Neurosci* 4:266–275
- Heuer CM, Kollmann M, Binzer M, Schachtner J (2012) Neuropeptides in insect mushroom bodies. *Arthropod Struct Dev* 41:199–226
- Heuer CM, Loesel R (2008) Immunofluorescence analysis of the internal brain anatomy of *Nereis diversicolor* (Polychaeta, Annelida). *Cell Tissue Res* 331:713–724
- Heuer CM, Loesel R (2009) Three-dimensional reconstruction of mushroom body neuropils in the polychaete species *Nereis diversicolor* and *Harmothoe*

- areolata* (Phyllococida, Annelida). Zoomorphol 128:219–226
- Heuer CM, Müller CHG, Loesel R (2010) Comparative neuroanatomy suggests repeated reduction of neuro-architectural complexity in Annelida. Front Zool 7:13. doi:10.1186/1742-9994-7-13
- Hoesle B (1989) Morphological and comparative studies on the second antennae of terrestrial isopods. Monitore Zoologico Italiano (N.S.) Monografia 4:127–152
- Holmgren N (1916) Zur vergleichenden Anatomie des Gehirns von Polychaeten, Onychophoren, Xiphosuren, Arachniden, Crustaceen, Myriapoden und Insekten. Kongl Svensk Vetenskap Akad Handl 56:1–303
- Homberg U (1985) Interneurons in the central complex in the bee brain (*Apis mellifera*, L.). J Insect Physiol 31:251–264
- Homberg U (1994) Distribution of neurotransmitters in the insect brain. Fischer, Stuttgart
- Homberg U (2008) Evolution of the central complex in the arthropod brain with respect to the visual system. Arthropod Struct Dev 37:347–362
- Homberg U, Christensen TA, Hildebrand JG (1989) Structure and function of the deutocerebrum in insects. Annu Rev Entomol 34:477–501
- Homberg U, Vitzthum H, Müller M, Binkle U (1999) Immunocytochemistry of GABA in the central complex of the locust *Schistocerca gregaria*: identification of immunoreactive neurons and colocalization with neuropeptides. J Comp Neurol 409:495–507
- Horridge GA (1975) The compound eye and vision of insects. Clarendon Press, Oxford
- Huetteroth W, Schachter J (2005) Standard three-dimensional glomeruli of the *Manduca sexta* antennal lobe: a tool to study both developmental and adult neuronal plasticity. Cell Tissue Res 319:513–524
- Ignell R, Dekker T, Ghaninia M, Hansson BS (2005) Neuronal architecture of the mosquito deutocerebrum. J Comp Neurol 493:207–240
- Ignell R, Hansson BS (2005) Projection patterns of gustatory neurons in the suboesophageal ganglion and tritocerebrum of mosquitoes. J Comp Neurol 492:214–233
- Johansson KUI, Hallberg E (1992) The organization of the olfactory lobes in Euphausiacea and Mysidacea (Crustacea, Malacostraca). Zoomorphol 112:81–90
- Kämper G, Murphey RK (1987) Synapse formation by sensory neurons after cross-species transplantation in crickets: the role of positional information. Dev Biol 122:492–502
- Keil TA, Steinbrecht RA (1984) Mechanosensitive and olfactory sensilla of insects. In: King RC, Akai H (eds) Insect ultrastructure, vol 1. Plenum, New York, pp 402–433
- Keil TA (2012) Sensory cilia in arthropods. ASD 41:515–534
- Kirschner S, Kleineidam CJ, Zube C, Rybak J, Grünwald B, Rössler W (2006) Dual olfactory pathway in the honeybee, *Apis mellifera*. J Comp Neurol 499:933–952
- Kloppenborg P (1995) Anatomy of the antennal motor neurons in the brain of the honeybee (*Apis mellifera*). J Comp Neurol 363:333–343
- Koenemann S, Hoenemann M, Stemme T, Jenner RA, v Reumont BM (2010) Arthropod phylogeny revisited, with a focus on crustacean relationships. Arthropod Struct Dev 39:88–110
- Kollmann M, Huetteroth W, Schachtner J (2011) Brain organization in Collembola (springtails). Arthropod Struct Dev 40:304–316
- Krieger J, Sandeman RE, Sandeman DC, Hansson BS, Harzsch S (2010) Brain architecture of the largest living land arthropod, the giant robber crab *Birgus latro* (Crustacea, Anomura, Coenobitidae): evidence for a prominent central olfactory pathway? Front Zool 7:25. doi:10.1186/1742-9994-7-25
- Krieger J, Sombke A, Seefluth F, Kenning M, Hansson BS, Harzsch S (2012) Comparative brain architecture of the European shore crab *Carcinus maenas* (Brachyura) and the common hermit crab *Pagurus bernhardus* (Anomura). Cell Tissue Res 348:47–69
- Kutsch W, Breidbach O (1994) Homologous structures in the nervous system of Arthropoda. Adv Insect Physiol 24:1–113
- Kutsch W, Heckmann R (1995a) Motor supply of the dorsal longitudinal muscles I: homonymy and ontogeny of the motoneurons in locusts (Insecta, Caelifera). Zoomorphol 115:179–195
- Kutsch W, Heckmann R (1995b) Motor supply of the dorsal longitudinal muscles II: comparison of motoneuron sets in Tracheata. Zoomorphol 115:197–211
- Laissue PP, Reiter C, Hiesinger PR, Halter S, Fischbach KF, Stocker RF (1999) Three-dimensional reconstruction of the antennal lobe in *Drosophila melanogaster*. J Comp Neurol 405:543–552
- Land MF, Nilsson D-E (2012) Animal eyes. Oxford University Press, Oxford
- Langworthy K, Helluy S, Benton J, Beltz B (1997) Amines and peptides in the brain of the American lobster: immunocytochemical localization patterns and implications for brain function. Cell Tissue Res 288:191–206
- Laurent G, Naraghi M (1994) Odorant-induced oscillations in the mushroom bodies of the locust. J Neurosci 14:2993–3004
- Leise EM, Hall W, Mulloney B (1986) Functional organization of crayfish abdominal ganglia. I. The flexor systems. J Comp Neurol 253:25–45
- Leise EM, Hall WM, Mulloney B (1987) Functional organization of crayfish abdominal ganglia. II: sensory afferents and extensor motor neurons. J Comp Neurol 266:495–518
- Lichtneckert R, Reichert H (2005) Insights into the urbilaterian brain: conserved genetic patterning mechanisms in insect and vertebrate brain development. Heredity 94:465–477
- Linne V, Eriksson BJ, Stollewerk A (2012) *Single-minded* and the evolution of the ventral midline in arthropods. Dev Biol 364:66–76

- Loesel R (2004) Comparative morphology of central neuropils in the brain of arthropods and its evolutionary and functional implications. *Acta Biol Hung* 55:39–51
- Loesel R (2006) Can brain structures help to resolve interordinal relationships in insects? *Arthropod Syst Phylog* 64:101–106
- Loesel R (2011) Neurophylogeny—retracing early metazoan brain evolution. In: Pontarotti P (ed) *Evolutionary biology: concepts, biodiversity, macroevolution, and genome evolution*. Springer, Heidelberg, pp 169–191
- Loesel R, Heuer CM (2010) The mushroom bodies—prominent brain centers of arthropods and annelids with enigmatic evolutionary origin. *Acta Zool* 91:29–34
- Loesel R, Homberg U (1999) Histamine-immunoreactive neurons in the brain of the cockroach *Leucophaea maderae*. *Brain Res* 842:408–418
- Loesel R, Nässel DR, Strausfeld NJ (2002) Common design in a unique midline neuropil in the brains of arthropods. *Arthropod Struct Dev* 31:77–91
- Loesel R, Seyfarth EA, Bräunig P, Agricola HJ (2011) Neuroarchitecture of the arcuate body in the brain of the spider *Cupiennius salei* (Araneae, Chelicerata) revealed by allatostatin-, proctolin-, and CCAP-immunocytochemistry. *Arthropod Struct Dev* 40:210–220
- Masse NY, Turner GC, Jefferis GS (2009) Olfactory information processing in *Drosophila*. *Curr Biol* 19:R700–R713
- Mayer G (2006) Structure and development of onychophoran eyes—what is the ancestral visual organ in arthropods? *Arthropod Struct Dev* 35:231–245
- Mayer G, Koch M (2005) Ultrastructure and fate of the nephridialanlagen in the antennal segment of *Epeiripatus biolleyi* (Onychophora, Peripatidae)—evidence for the onychophoran antennae being modified legs. *Arthropod Struct Dev* 34:471–480
- Mayer G, Whittington PM, Sunnucks P, Pflüger H-J (2010) A revision of brain composition in Onychophora (velvet worms) suggests that the tritocerebrum evolved in arthropods. *BMC Evol Biol* 10:255. doi: [10.1186/1471-2148-10-255](https://doi.org/10.1186/1471-2148-10-255)
- Meinertzhagen IA (1991) Evolution of the cellular organization of the arthropod compound eye and optic lobe. In: Cronly-Dillon JR, Gregory RL (eds) *Vision and visual dysfunction, vol 2., Evolution of the eye and visual system*. Macmillan, London, pp 341–363
- Mellon Jr DeF (2007) Combining dissimilar senses: central processing of hydrodynamic and chemosensory inputs in aquatic crustaceans. *Biol Bull* 213:1–11
- DeF Mellon Jr, Reidenbach MA (2011) Fluid mechanical problems in crustacean active chemoreception. In: Barth F, Humphrey JAC, Srinivasan M (eds) *Frontiers in sensing*. Springer, New York, pp 159–170
- Melzer RR, Diersch R, Nicastro D, Smola U (1997) Compound eye evolution: highly conserved retinula and cone cell patterns indicate a common origin of the insect and crustacean ommatidium. *Naturwiss* 84:542–544
- Melzer R, Michalke C, Smola U (2000) Walking on insect paths: early ommatidial development in the compound eye of the ancestral crustacean *Triops cancriformis*. *Naturwiss* 87:308–311
- Melzer RR, Petyko Z, Smola U (1996) Photoreceptor axons and optic neuropils in *Lithobius forficatus* (Linnaeus, 1758) (Chilopoda, Lithobiidae). *Zool Anz* 235:177–182
- Milde JJ (1988) Visual responses of interneurons in the posterior median protocerebrum and the central complex of the honeybee *Apis mellifera*. *J Insect Physiol* 34:427–436
- Mißbach C, Harzsch S, Hansson B (2011) New insights into an ancient insect nose: the olfactory pathway of *Lepismachilis y-signata* (Archaeognatha: Machilidae). *Arthropod Struct Dev* 40:317–333
- Mittmann B, Scholtz G (2003) Development of the nervous system in the ‘head’ of *Limulus polyphemus* (Chelicerata: Xiphosura): morphological evidence for a correspondence between the segments of the chelicerae and of the (first) antennae of Mandibulata. *Dev Genes Evol* 213:9–17
- Müller CHG, Rosenberg J, Richter S, Meyer-Rochow VB (2003) The compound eye of *Scutigera coleoptrata* (Linnaeus, 1758) (Chilopoda: Notostigmophora): an ultrastructural reinvestigation that adds support to the mandibulata concept. *Zoomorphol* 122:191–209
- Nässel DR (1976) The retina and retinal projection on the lamina ganglionaris of the crayfish *Pacifastacus leniusculus* (Dana). *J Comp Neurol* 167:341–360
- Nässel DR (1977) Types and arrangement of neurons in the crayfish optic lamina. *Cell Tissue Res* 179:45–75
- Nässel DR, Elofsson R, Odselius R (1978) Neuronal connectivity patterns in the compound eyes of *Artemia salina* and *Daphnia magna* (Crustacea: Branchiopoda). *Cell Tissue Res* 190:435–457
- Nässel DR, Geiger G (1983) Neuronal organization in fly optic lobes altered by laser ablations early in development or by mutations of the eye. *J Comp Neurol* 217:86–102
- Nässel DR, Waterman TH (1977) Massive diurnally modulated photoreceptor membrane turnover in crab light and dark adaptation. *J Comp Physiol A* 131:205–216
- Newland PL, Rogers SM, Gaaboub I, Matheson T (2000) Parallel somatotopic maps of gustatory and mechanosensory neurons in the central nervous system of an insect. *J Comp Neurol* 425:82–96
- Nilsson D-E (1989) Optics and evolution of the compound eye. In: Stavenga DG, Hardie RC (eds) *Facets of vision*. Springer, Berlin, pp 30–73
- Nilsson D-E, Kelber A (2007) A functional analysis of compound eye evolution. *Arthropod Struct Dev* 36:373–385
- Nilsson D-E, Osorio D (1997) Homology and parallelism in arthropod sensory processing. In: Fortey RA, Thomas RH (eds) *Arthropod relationships*. Chapman and Hall, London, pp 333–347

- Nishino H, Nishikawa M, Yokohari F, Mizunami M (2005) Dual, multilayered somatosensory maps formed by antennal tactile and contact chemosensory afferents in an insect brain. *J Comp Neurol* 493:291–308
- North G, Greenspan RJ (2007) *Invertebrate neurobiology*. Cold Spring Harbor Laboratory Press, New York
- Oldfield BP (1988) Tonotopic organization of the insect auditory pathway. *Trends Neurosci* 11:267–270
- Osorio D (2007) *Spam* and the evolution of the fly's eye. *BioEssays* 29:111–115
- Pareto A (1972) Die zentrale Verteilung der Fühlerafferenz bei Arbeiterinnen der Honigbiene, *Apis mellifera*, L. *Ztschr Zellforsch mikr Anat* 131:109–140
- Patel NH, Kornberg TB, Goodman CS (1989a) Expression of *engrailed* during segmentation in grasshopper and crayfish. *Development* 107:201–212
- Patel NH, Martin-Blanco E, Coleman KG, Poole SJ, Ellis MC, Kornberg TB, Goodman CS (1989b) Expression of *engrailed* proteins in arthropods, annelids, and chordates. *Cell* 58:955–968
- Paulus HF (2000) Phylogeny of the Myriapoda—Crustacea—Insecta: a new attempt using photoreceptor structure. *J Zool Syst Evol Res* 38:189–208
- Pflüger HJ, Stevenson P (2005) Evolutionary aspects of octopaminergic systems with emphasis on arthropods. *Arthropod Struct Dev* 34:379–396
- Rathmayer W (1990) Inhibition through neurons of the common inhibitory type (CI-neurons) in crab muscles. In: Wiese K (ed) *Frontiers in crustacean neurobiology*. Birkhäuser, Basel, pp 271–278
- Regier JC, Shultz JW, Kambic RE (2005) Pancrustacean phylogeny: hexapods are terrestrial crustaceans and maxillopods are not monophyletic. *Proc R Soc B* 272:395–401
- Regier JC, Shultz JW, Zwick A, Hussey A, Ball B, Wetzer R, Martin JW, Cunningham CW (2010) Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* 463:1079–1083
- Reichert H (1988) Control of sequences of movements in crayfish escape behavior. *Experientia* 44:395–401
- Richter S (2002) The Tetraconata concept: hexapod-crustacean relationships and the phylogeny of Crustacea. *Org Divers Evol* 2:217–237
- Richter S, Loesel R, Purschke G, Schmidt-Rhaesa A, Scholtz G, Stach T, Vogt L, Wanninger A, Brenneis G, Doring C, Faller S, Fritsch M, Grobe P, Heuer CM, Kaul S, Moeller OS, Müller CHG, Rieger V, Rothe BG, Stegner MEJ, Harzsch S (2010) Invertebrate neurophylogeny: suggested terms and definitions for a neuroanatomical glossary. *Front Zool* 7:29. doi: 10.1186/1742-9994-7-29
- Roberston RM, Pearson KG, Reichert H (1982) Flight interneurons in the locust and the origin of insect wings. *Science* 217:177–179
- Römer H, Marquart V, Hardt M (1988) Organization of a sensory neuropile in the auditory pathway of two groups of orthoptera. *J Comp Neurol* 275:201–215
- Rospars JP (1983) Invariance and sex-specific variations of the glomerular organization in the antennal lobes of a moth, *Mamestra brassicae* and a butterfly, *Pieris brassicae*. *J Comp Neurol* 220:80–96
- Rospars JP (1988) Structure and development of the insect antennodeutocerebral system. *Int J Insect Morphol Embryol* 17:243–294
- Rospars JP, Hildebrand JG (1992) Anatomical identification of glomeruli in the antennal lobes of the male sphinx moth *Manduca sexta*. *Cell Tissue Res* 270:205–227
- Rospars JP, Hildebrand JG (2000) Sexually dimorphic and isomorphic glomeruli in the antennal lobes of the sphinx moth *Manduca sexta*. *Chem Senses* 25:119–129
- Rössler W, Zube C (2011) Dual olfactory pathway in Hymenoptera: evolutionary insights from comparative studies. *Arthropod Struct Dev* 40:349–357
- Rota-Stabelli O, Campbell L, Brinkmann H, Edgecombe GD, Longhorn SJ, Peterson KJ, Pisani D, Philippe H, Telford MJ (2011) A congruent solution to arthropod phylogeny: Phylogenomics, microRNAs and morphology support monophyletic Mandibulata. *Proc R Soc B* 278:298–306
- Sachse S, Krieger J (2011) Olfaction in insects—the primary processes of odor recognition and coding. *E-Neuroforum* 2:49–60
- Sandeman D, Kenning M, Harzsch S (in press) Adaptive trends in malacostracan brain form and function related to behaviour. In: Derby C, Thiel M (eds) *Crustacean nervous system and their control of behaviour. The natural history of the Crustacea*, vol. 3
- Sandeman DC, Luff SE (1973) The structural organization of glomerular neuropile in the olfactory and accessory lobes of an Australian freshwater crayfish, *Cherax destructor*. *Ztschr Zellforsch mikr Anat* 142:37–61
- Sandeman DC, Beltz BS, Sandeman RE (1995) Crayfish brain interneurons that converge with serotonin giant cells in accessory lobe glomeruli. *J Comp Neurol* 352:263–279
- Sandeman D, DeF Mellon Jr (2002) Olfactory centers in the brain of freshwater crayfish. In: Wiese K (ed) *The crustacean nervous system*. Springer, Berlin, pp 386–404
- Sandeman DC, Sandeman RE (1994) Electrical responses and synaptic connections of giant serotonin-immunoreactive neurons in crayfish olfactory and accessory lobes. *J Comp Neurol* 341:130–144
- Sandeman DC, Sandeman RE, Derby C, Schmidt M (1992) Morphology of the brain of crayfish, crabs, and spiny lobsters: a common nomenclature for homologous structures. *Biol Bull* 183:304–326
- Sandeman DC, Scholtz G (1995) Ground plans, evolutionary changes and homologies in decapod crustacean brains. In: Breidbach O, Kutsch W (eds) *The nervous systems of invertebrates: an evolutionary and comparative approach*. Birkhäuser, Basel, pp 329–347

- Sandeman DC, Scholtz G, Sandeman RE (1993) Brain evolution in decapod crustacea. *J Exptl Zool* 265:112–133
- Sandeman DC, Varju D (1988) A behavioral study of tactile localization in the crayfish *Cherax destructor*. *J Comp Physiol A* 163:525–536
- Sanes JR, Zipursky SL (2010) Design principles of insect and vertebrate visual systems. *Neuron* 66:15–36
- Schachtner J, Schmidt M, Homberg U (2005) Organization and evolutionary trends of primary olfactory brain centers in Tetraconata (Crustacea + Hexapoda). *Arthropod Struct Dev* 35:257–299
- Schmalfuss H (1998) Evolutionary strategies of the antennae in terrestrial isopods. *J Crustac Biol* 18:10–24
- Schmidt H, Rickert C, Bossing T, Vef O, Urban J, Technau GM (1997) The embryonic central nervous system lineages of *Drosophila melanogaster*. II. Neuroblast lineages derived from the dorsal part of the neuroectoderm. *Dev Biol* 189:186–204
- Schmidt M, Ache BW (1992) Antennular projections to the midbrain of the spiny lobster. II. Sensory innervation of the olfactory lobe. *J Comp Neurol* 318:291–303
- Schmidt M, Ache BW (1993) Antennular projections to the midbrain of the spiny lobster. III. Central arborizations of motoneurons. *J Comp Neurol* 336:583–594
- Schmidt M, Ache BW (1996a) Processing of antennular input in the brain of the spiny lobster, *Panulirus argus*. II. The olfactory pathway. *J Comp Physiol A* 178:605–628
- Schmidt M, Ache BW (1996b) Processing of antennular input in the brain of the spiny lobster, *Panulirus argus*. I. Non-olfactory chemosensory and mechanosensory pathway of the lateral and median antennular neuropils. *J Comp Physiol A* 178:579–604
- Schmidt M, Ache BW (1997) Immunocytochemical analysis of glomerular regionalization and neuronal diversity in the olfactory deutocerebrum of the spiny lobster. *Cell Tissue Res* 287:541–563
- Schmidt M, DeF Mellon Jr (2011) Neuronal processing of chemical information in crustaceans. In: Breithaupt T, Thiel M (eds) *Chemical communication in crustaceans*. Springer, New York, pp 123–147
- Schmidt M, van Ekeris L, Ache BW (1992) Antennular projections to the midbrain of the spiny lobster. I. Sensory innervation of the lateral and medial antennular neuropils. *J Comp Neurol* 318:277–290
- Scholtz G, Edgecombe GD (2006) The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. *Dev Genes Evol* 216:395–415
- Sinakevitch I, Douglass JK, Scholtz G, Loesel R, Strausfeld NJ (2003) Conserved and convergent organization in the optic lobes of insects and isopods, with reference to other crustacean taxa. *J Comp Neurol* 467:150–172
- Skinner K (1985a) The structure of the fourth abdominal ganglion of the crayfish, *Procambarus clarki* (Girad). I. Tracts in the ganglionic core. *J Comp Neurol* 234:168–181
- Skinner K (1985b) The structure of the fourth abdominal ganglion of the crayfish, *Procambarus clarki* (Girad). II. Synaptic neuropils. *J Comp Neurol* 234:182–191
- Sombke A, Harzsch S, Hansson BS (2011a) Organization of deutocerebral neuropils and olfactory behavior in the centipede *Scutigera coleoptrata* (Linnaeus, 1758) (Myriapoda: Chilopoda). *Chem Senses* 36:43–61
- Sombke A, Lipke E, Kenning M, Müller CHG, Hansson BS, Harzsch S (2012) Comparative analysis of deutocerebral neuropils in Chilopoda (Myriapoda): implications for the evolution of the arthropod olfactory system and support for the Mandibulata concept. *BMC Neurosci* 13:1. doi: 10.1186/1471-2202-13-1
- Sombke A, Rosenberg J, Hilken G (2011b) Chilopoda—the nervous system. In: Minelli A (ed) *Treatise on zoology—anatomy, taxonomy, biology—the Myriapoda*, vol I. Brill, Leiden, pp 217–234
- Sombke A, Rosenberg J, Hilken G, Westermann M, Ernst A (2011c) The source of chilopod sensory information: external structure and distribution of antennal sensilla in *Scutigera coleoptrata* (Chilopoda, Scutigeroforma). *J Morphol* 272:1376–1387
- Spreitzer A, Melzer RR (2003) The nymphal eyes of *Parabuthus transvaalicus* Purcell, 1899 (Buthidae): an accessory lateral eye in a scorpion. *Zool Anz* 242:137–143
- Staudacher E (1998) Distribution and morphology of descending brain neurons in the cricket. *Cell Tissue Res* 294:187–202
- Staudacher E, Schildberger K (1999) A newly described neuropile in the deutocerebrum of the cricket: antennal afferents and descending interneurons. *Zoology* 102:212–226
- Stavenga DG, Hardie RC (1989) *Facets of vision*. Springer, Berlin
- Stavenga DG, Melzer RR, Harzsch S (eds) (2006, 2007) Origin and evolution of arthropod visual systems. *Arthropod Struct Dev* 35(4) (2006), 36(4) (2007)
- Stegner MEJ, Richter S (2011) Morphology of the brain in *Hutchinsoniella macracantha* (Cephalocarida, Crustacea). *Arthropod Struct Dev* 40:221–243
- Stollewerk A (2008) Evolution of neurogenesis in arthropods. In: Minelli A, Fusco G (eds) *Evolving pathways*. Cambridge University Press, Cambridge, pp 359–380
- Stollewerk A, Chipman AD (2006) Neurogenesis in myriapods and chelicerates and its importance for understanding arthropod relationships. *Integr Comp Biol* 46:195–206
- Stollewerk A, Simpson P (2005) Evolution of early development of the nervous system: a comparison between arthropods. *BioEssays* 27:874–883
- Strausfeld NJ (1976) *Atlas of an insect brain*. Springer, Berlin
- Strausfeld NJ (1989) Beneath the compound eye: neuro-anatomical analysis and physiological correlates in the study of insect vision. In: Stavenga DG, Hardie

- RC (eds) Facets of vision. Springer, Berlin, pp 317–359
- Strausfeld NJ (1998) Crustacean–insect relationships: the use of brain characters to derive phylogeny amongst segmented invertebrates. *Brain Behav Evol* 52:186–206
- Strausfeld NJ (1999) A brain region in insects that supervises walking. *Progr Brain Res* 123:273–284
- Strausfeld NJ (2005) The evolution of crustacean and insect optic lobes and the origins of chiasmata. *Arthropod Struct Dev* 34:235–256
- Strausfeld NJ (2009) Brain organization and the origin of insects: an assessment. *Proc R Soc B* 276:1929–1937
- Strausfeld NJ (2012) Arthropod brains. Evolution, functional elegance, and historical significance. The Belknap Press of Harvard University Press, Cambridge, MA
- Strausfeld NJ, Andrews DR (2011) A new view of insect–crustacean relationships I. Inferences from neural cladistics and comparative neuroanatomy. *Arthropod Struct Dev* 40:276–288
- Strausfeld NJ, Barth FG (1993) Two visual systems in one brain: neuropils serving the secondary eyes of the spider—*Cupiennius salei*. *J Comp Neurol* 328:43–62
- Strausfeld NJ, Buschbeck E, Gomez RS (1995) The arthropod mushroom body: its functional roles, evolutionary enigmas and mistaken identities. In: Breidbach O, Kutsch W (eds) The nervous system of invertebrates—an evolutionary and comparative approach. Birkhäuser, Basel, pp 349–381
- Strausfeld NJ, Douglas J, Campbell H, Higgins C (2006a) Parallel processing in the optic lobes of flies and the occurrence of motion computing circuits. In: Warrant E, Nilsson D-E (eds) Invertebrate vision. Cambridge University Press, Cambridge, pp 349–399
- Strausfeld NJ, Hansen L, Li Y, Gomez RS, Ito K (1998) Evolution, discovery, and interpretation of arthropod mushroom bodies. *Learn Mem* 5:11–37
- Strausfeld NJ, Hildebrand JG (1999) Olfactory systems: common design, uncommon origins? *Curr Opin Neurobiol* 9:634–939
- Strausfeld NJ, Nässel DR (1981) Neuroarchitecture of brain regions that subserve the compound eyes of Crustacea and insects. In: Autrum H (ed) Handbook of sensory physiology, vol VII/6B. Invertebrate visual center and behaviors I. Springer, Berlin, pp 1–132
- Strausfeld NJ, Reisenman CE (2009) Dimorphic olfactory lobes in the Arthropoda. *Ann NY Acad Sci* 1170:487–496
- Strausfeld NJ, Sinakevitch I, Brown SM, Farris SM (2009) Ground plan of the insect mushroom body: functional and evolutionary implications. *J Comp Neurol* 513:265–291
- Strausfeld NJ, Strausfeld CM, Loesel R, Rowell D, Stowe S (2006b) Arthropod phylogeny: onychophoran brain organization suggests an archaic relationship with a chelicerate stem lineage. *Proc R Soc B* 273:1857–1866
- Strausfeld NJ, Strausfeld CM, Stowe S, Rowell D, Loesel R (2006c) The organization and evolutionary implications of neuropils and their neurons in the brain of the onychophoran *Euperipatoides rowelli*. *Arthropod Struct Dev* 35:169–196
- Strausfeld NJ, Weltzien P, Barth FG (1993) Two visual systems in one brain: neuropils serving the principal eyes of the spider *Cupiennius salei*. *J Comp Neurol* 328:63–75
- Strauss R (2002) The central complex and the genetic dissection of locomotor behaviour. *Curr Opin Neurobiol* 12:633–638
- Strauss R (2003) Control of *Drosophila* walking and orientation behavior by functional subunits localized in different neuropils in the central brain. In: Elsner N, Zimmermann H (eds) Proceedings of the 29th Göttingen neurobiology conference. Thieme, Stuttgart, p 206
- Strauss R, Hanesch U, Kinkelin M, Wolf R, Heisenberg M (1992) No-bridge of *Drosophila melanogaster*—portrait of a structural mutant of the central complex. *J Neurogenet* 8:125–155
- Strauss R, Heisenberg M (1990) Coordination of legs during straight walk and turning in *Drosophila melanogaster*. *J Comp Physiol A* 167:403–412
- Strauss R, Heisenberg M (1993) Higher control center of locomotor behavior in the *Drosophila* brain. *J Neurosci* 13:1852–1861
- Strotmann J (2001) Targeting of olfactory neurons. *Cell Mol Life Sci* 58:531–537
- Sullivan JM, Beltz BS (2005) Integration and segregation of inputs to higher-order neuropils of the crayfish brain. *J Comp Neurol* 481:118–126
- Sun X-J, Fonta C, Masson C (1993) Odour quality processing by bee antennal lobe interneurons. *Chem Senses* 18:355–377
- Szlendak E, Oliver JH (1992) Anatomy of synganglia, including their neurosecretory regions, in unfed, virgin female *Ixodes scapularis* Say (Acari: Ixodidae). *J Morphol* 213:349–364
- Sztarker J, Strausfeld NJ, Tomsic D (2005) Organization of optic lobes that support motion detection in a semiterrestrial crab. *J Comp Neurol* 493:396–411
- Tautz J, Müller-Tautz R (1983) Antennal neuropile in the brain of the crayfish: morphology of neurons. *J Comp Neurol* 218:415–425
- Telford MJ, Thomas RH (1998) Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. *Proc Natl Acad Sci U S A* 95:10671–10675
- Tichy H, Barth FG (1992) Fine structure of olfactory sensilla in myriapods and arachnids. *Microsc Res Tech* 22:372–391
- Tomer R, Denes A, Tessmar-Raible K, Arendt D (2010) Profiling by image registration reveals common origin of annelid mushroom bodies and vertebrate pallium. *Cell* 141:800–809
- Trautwein MD, Wiegmann BM, Beutel R, Kjer KM, Yeates DK (2012) Advances in insect phylogeny at

- the dawn of the postgenomic era. *Annu Rev Entomol* 57:449–468
- Tsuneki K (1992) Endocrine System of arthropods other than crustaceans and insects. In: Matsumoto A, Ishii S (eds) Atlas of endocrine organs. Springer, Berlin, pp 227–229
- Tyrer NM, Gregory GE (1982) A guide to the neuroanatomy of locust suboesophageal and thoracic ganglia. *Phil Trans R Soc B* 297:91–123
- Ungerer P, Scholtz G (2008) Filling the gap between identified neuroblasts and neurons in crustaceans adds new support for Tetraconata. *Proc R Soc B* 275:369–376
- Utting M, Agricola H, Sandeman RE, Sandeman DC (2000) Central complex in the brain of crayfish and its possible homology with that of insects. *J Comp Neurol* 416:245–261
- van Wijk M, Wadman WJ, Sabelis MW (2006a) Gross morphology of the central nervous system of a phytoseiid mite. *Exptl Appl Acarol* 40:205–216
- van Wijk M, Wadman WJ, Sabelis MW (2006b) Morphology of the olfactory system in the predatory mite *Phytoseiulus persimilis*. *Exptl Appl Acarol* 40:217–229
- Vitzthum H, Müller M, Homberg U (2002) Neurons of the central complex of the locust *Schistocerca gregaria* are sensitive to polarized light. *J Neurosci* 22:1114–1125
- von Békésy G (1967) Sensory inhibition. Princeton University Press, Princeton, NJ
- von Reumont BM, Jenner RA, Wills MA, Dell'Ampio E, Pass G, Ebersberger I, Meusemann K, Meyer B, Koenemann S, Iliffe TM, Stamatakis A, Niehuis O, Misof B (2012) Pancrustacean phylogeny in the light of new phylogenomic data: support for Remipedia as the possible sister group of Hexapoda. *Mol Biol Evol* 29:1031–1045
- Wachowiak M, Diebel CE, Ache BW (1997) Local interneurons define functionally distinct regions within olfactory glomeruli. *J Exptl Biol* 200:989–1001
- Warrant E, Nilsson D-E (2006) Invertebrate vision. Cambridge University Press, Cambridge
- Watson AHD (1986) The distribution of GABA-like immunoreactivity in the thoracic nervous system of the locust *Schistocerca gregaria*. *Cell Tissue Res* 246:331–341
- Wegerhoff R, Breidbach O (1995) Comparative aspects of the chelicerate nervous system. In: Breidbach O, Kutsch W (eds) The nervous systems of invertebrates: an evolutionary and comparative approach. Birkhäuser, Basel, pp 159–179
- Wehner R (1972) Information processing in the visual system of arthropods. Springer, Berlin
- Wertz A, Rössler W, Obermayer M, Bickmeyer U (2006) Functional anatomy of the rhinophore of *Aplysia punctata*. *Front Zool* 3:11. doi:10.1186/1742-9994-3-6
- Whittington PM (1996) Evolution of neuronal development in arthropods. *Semin Cell Dev Biol* 7:605–614
- Whittington PM (2004) The development of the crustacean nervous system. In: Scholtz G (ed) Evolutionary developmental biology of Crustacea, Crustacean Issues, vol 15. Balkema, Lisse, pp 135–167
- Whittington PM (2006) The evolution of arthropod nervous systems: insights from neural development in the Onychophora and Myriapoda. In: Striedler GF, Rubenstein JLR, Kaas JH (eds) Theories, development, invertebrates. Academic, Oxford, pp 317–336
- Whittington PM, Bacon JP (1997) The organization and development of the arthropod ventral nerve cord: insights into arthropod relationships. In: Fortey RA, Thomas RH (eds) Arthropod relationships. Chapman and Hall, London, pp 295–304
- Whittington PM, Mayer G (2011) The origins of the arthropod nervous system: Insights from the Onychophora. *Arthropod Struct Dev* 40:193–209
- Whittington PM, Meier T, King P (1991) Segmentation, neurogenesis and formation of early axonal pathways in the centipede, *Ethmostigmus rubripes* (Brandt). *Roux's Arch Dev Biol* 199:349–363
- Wiens TJ (1989) Common and specific inhibition in leg muscles of decapods: sharpened distinctions. *J Neurobiol* 20:458–469
- Wiens TJ, Wolf H (1993) The inhibitory motoneurons of crayfish thoracic limbs: structures and phylogenetic comparisons. *J Comp Neurol* 336:61–278
- Wiersma CAG, Roach J, Glantz RM (1982) Neuronal integration in the optic system. In: Sandeman DC, Atwood HL (eds) The biology of Crustacea, vol 4., Neuronal integration and behavior. Academic Press, New York, pp 1–31
- Wiese K (2001) The crustacean nervous system. Springer, Berlin
- Wiese K (2002) Crustacean experimental systems in neurobiology. Springer, Berlin
- Wildt M, Harzsch S (2002) A new look at an old visual system: structure and development of the compound eyes and optic ganglia of the brine shrimp *Artemia salina* Linnaeus, 1758 (Branchiopoda, Anostraca). *J Neurobiol* 52:117–132
- Wolf H (1990) Activity patterns of inhibitory motoneurons and their impact on leg movement in tethered walking locusts. *J Exptl Biol* 152:281–304
- Wolf H (2008) The pectine organs of the scorpion, *Vaejovis spinigerus*: structure and central (glomerular) projections. *Arthropod Struct Dev* 37:67–80
- Wolf H, Harzsch S (2002a) The neuromuscular system in the walking legs of a scorpion. 1. Arrangement of muscles and innervation in the walking legs of a scorpion: *Vaejovis spinigerus* (Wood, 1863) Vaejovidae, Scorpiones, Arachnida. *Arthropod Struct Dev* 31:185–202
- Wolf H, Harzsch S (2002b) The neuromuscular system in the walking legs of a scorpion. 2. Inhibitory innervation of the walking legs of a scorpion: *Vaejovis spinigerus* (Wood, 1863), Vaejovidae, Scorpiones, Arachnida. *Arthropod Struct Dev* 31:203–215
- Wolf H, Harzsch S (2012) Serotonin-immunoreactive neurons in the scorpions' pectine neuropils:

- similarities to insect and crustacean olfactory centers? *Zoology* 115:151–159
- Wolff G, Harzsch S, Hansson BS, Brown S, Strausfeld NJ (2012) Neuronal organization of the hemiellipsoid body of the land hermit crab *Coenobita clypeatus*: correspondence with the mushroom body ground pattern. *J Comp Neurol* 520:2824–2846
- Zeil J, Layne J (2002) Path integration in fiddler crabs and its relation to habitat and social life. In: Wiese K (ed) *Crustacean experimental systems in neurobiology*. Springer, Heidelberg, pp 227–246
- Zeil J, Sandeman RE, Sandeman DC (1985) Tactile localisation: the function of active antennal movements in the crayfish *Cherax destructor*. *J Comp Physiology A* 157:607–617
- Zube C, Kleineidam CJ, Kirschner S, Neef J, Rössler W (2008) Organization of the olfactory pathway and odor processing in the antennal lobe of the ant *Camponotus floridanus*. *J Comp Neurol* 506:425–441