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Can Brain Structures Help to Resolve Interordinal Relationships in Insects?

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> Abstract

While the monophyly of most insect orders is well supported by morphological data, relationships among orders are still largely undecided. Postulated interordinal relationships are often based on relatively few morphological characters or characters of questionable phylogenetic significance. In studies based on molecular evidence interordinal relationships are usually not significantly supported. Depending on the molecule under scrutiny or on the method of data analysis molecular studies often produced conflicting hypotheses on insect phylogeny. One organ that provides a large amount of independent morphological characters and that has as yet been scarcely utilized by insect phylogenists is the supraoesophageal ganglion or brain. Drawing from the vast literature on insect neuroanatomy, this review explores the value of neuronal characters for deriving relationships among insect orders.

> Key words

Insect phylogeny, interordinal relationships, brain, neuroanatomy, neuroarchitecture, histochemistry, arthropod evolution.

1. Introduction

The inference of phylogenetic relationships from shared neural characters is by no means a new approach. Early 20th century investigators like Holmgren (1916) and Hanström (1926) constructed arthropod phylogenies based on the identification of synapomorphic characters such as the presence and arrangement of neuropils in the central brain. Their neuroanatomical comparisons led both to suggest closer affinities between insects and malacostracan crustaceans than between insects and any other group of arthropods. These findings were for many years ignored in favor of a myriapod-insect clade, the "Tracheata-Atelocerata". Due to recent molecular and developmental studies (Edwards & Meyer 1989; Averof & Akam 1995, to name just two of many accounts), the Tracheata concept has been abandoned by many arthropod phylogenists in support of the Tetraconata hypothesis, which groups crustaceans and insects together (Dohle 2001; but also see Klass & Kristensen 2001). This late rehabilitation of Holmgren's and Hanström's results, accumulating data on brain architecture, and the opportunity to apply advanced cell-labeling techniques along with recent developments in imaging methods have led to a renaissance of a field that is now often referred to as "Neurophylogeny" (Harzsch 2002, 2006).

Until yet, comparative studies on neuroarchitecture have primarily focused on the relationships at higher taxonomic levels, where interesting, and in some cases surprising, findings have been achieved (for a brief synopsis see Loesel 2005). New systematic groupings such as the Tetraconata (Utting et al. 2000; Loesel et al. 2002) or the Ecdysozoa (Haase et al. 2001) have been found to be supported by neuroanatomical data. In other cases, the re-evaluation of existing views has been augmented or initialized by comparative studies of the central nervous system of the taxon scrutinized. A recent example are the Remipedia, a homonomously segmented subgroup of the Crustacea that have long been viewed to be "living fossils" and interpreted to be the most basal crustacean group. Fanenbruck & Harzsch (2005), however, discovered that their brains match the complexity of the brains of malacostracan crustaceans. These findings challenged the prevailing hypothesis that the Remipedia are an ancestral group.

While caution is certainly warranted when trying to resolve phylogenies based on a single organ, the study of

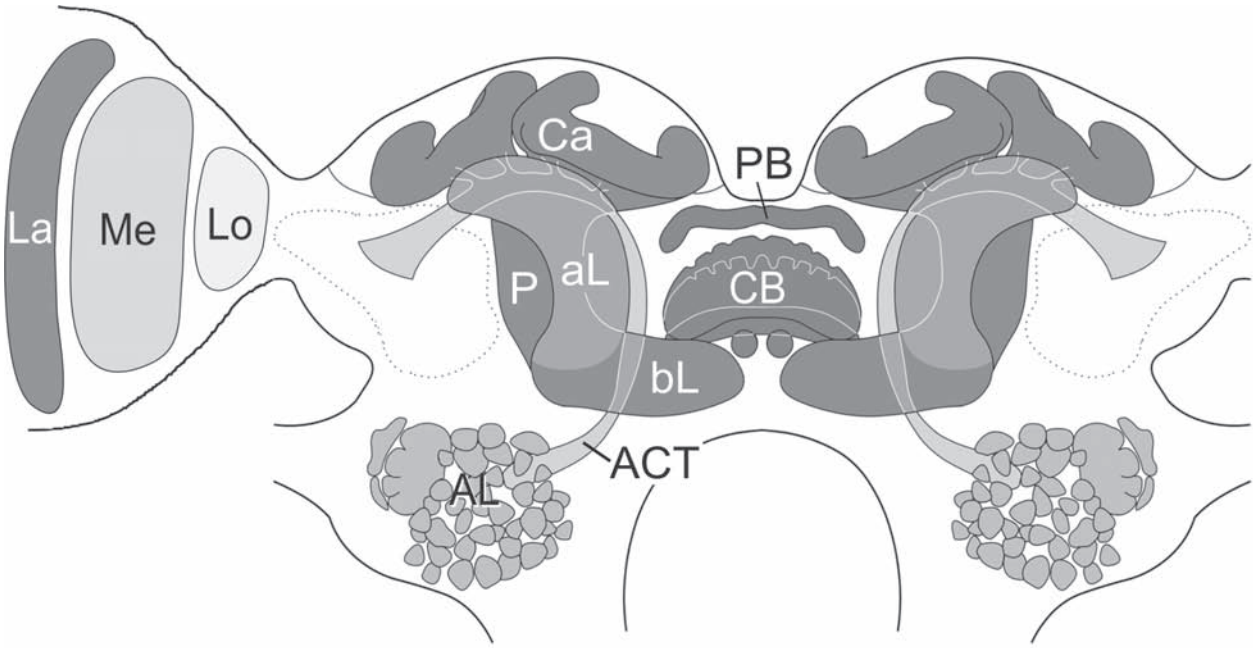

Fig. 1. Schematic drawing of a generalized insect brain. The optic lobes comprise the lamina (La), the medulla (Me), and the lobula (Lo). In this example, the lobula is a single neuropil. In some insect orders, however, it can be closely linked to an additional optic neuropil, the lobula plate. Main sensory integration and learning centers are the mushroom bodies which are subdivided into the calyx (Ca), the peduncle (P), and the alpha-, and beta-lobes (aL, bL, respectively). The calyx is the main input region of the mushroom body and can be subdivided into discrete zones that are characterized by their sensory input modality. In most insects, the mushroom bodies receive massive neuronal input from the antennal lobes (AL), primary olfactory brain areas which are subdivided into numerous glomeruli. The protocerebral bridge (PB) and the central body (CB) together form the central complex, the primary locomotion control center in the brain. ACT: antennocerebral tract. (Modified from STRAUSFELD 1998)

brain architecture has nevertheless been a rewarding enterprise, because the brain is such a complex structure that it provides the researcher with an enormous amount of independent characters. KUTSCH & BREIDBACH (1994) published a list of neural characters that can be exploited for phylogenetic comparisons. These range from a molecular (e.g. specific neurotransmitters or neuron-specific markers) through a cellular (size of the neuronal somata as compared to neighbouring somata, number and course of the neurites with respect to the ganglionic framework, target organs that certain neurons innervate, etc.) to a systemic level (position of neuropils in the brain, number of subunits, three-dimensional neuroarchitectural design). STRAUSFELD (1998), for example, scored one hundred independent neuroanatomical characters across the entire arthropods to study phylogenetic relationships using parsimony analysis.

2. Features of the insect brain that can be used for phylogenetic considerations

Can "Neurophylogeny" be of any help in clarifying as yet undecided interordinal relationships in insects? Is there maybe already enough information in the vast literature on the neuroanatomy of a wide variety of insect species that can be used for this endeavor? The insect brain – like all arthropod brains – is clearly divided into an outer cell cortex that contains the majority of neuronal cell bodies and into central neuropils that contain only dendritic and axonal ramifications of neurons (Fig. 2B). Neuropils are usually surrounded by a glial sheath which makes their demarcation from neighboring brain areas an easy task. Connections between neuropils are established by fiber tracts. Four brain regions (see Fig. 1) that will be examined in the following have been studied particularly well in recent accounts.

2.1. Antennal lobes

The antennal lobes are primary olfactory brain centers that receive direct input from olfactory receptor neurons of the antennae. Several authors have emphasized the common architecture of primary olfactory brain areas across animal phyla, most conspicuously their compartmentation into anatomical subunits termed glomeruli (HILDEBRAND & SHEPARD 1997; STRAUSFELD & HILDEBRAND 1999; EISTHEN 2002). These similarities could be the result of a common selective pressure to perform the same computational task across phyla. On the other hand, recent genetic analyses proposed a common evolutionary origin of the brain and brain

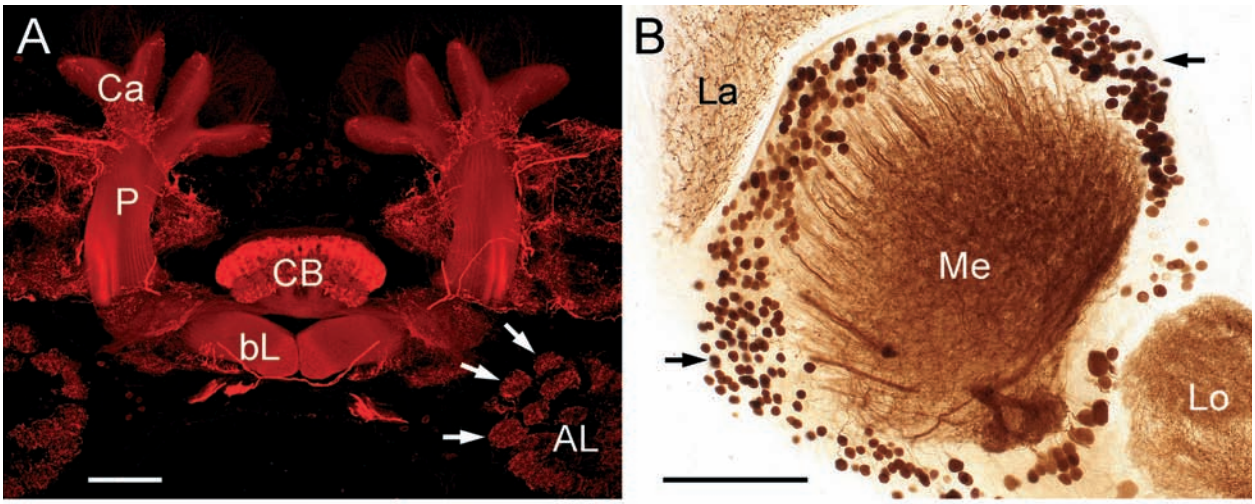

Fig. 2. The major cerebral areas as depicted in Fig. 1 exemplified by two standard staining procedures carried out on the brain of the cockroach *Leucophaea maderae*. **A**: Confocal Laser scanning image of an allatostatin immunofluorescence labeling of the midbrain showing the central body (CB). Substructures of the mushroom bodies are the calyces (Ca), the peduncle (P), and the β-lobe. The antennal lobe (AL) comprises approx. 100 glomeruli (arrows) in this species. For details of the staining method see Loesel et al. (2002). **B**: Details of the optic lobe revealed by GABA-immunostaining. As is typical for arthropod neuropils, the medulla (Me) is surrounded by a cortex of neuronal cell bodies (arrows) while the actual neuropil consists of dendritic and axonal arborizations but not cell bodies of neurons. The medulla is flanked by the lamina (La) and the lobula (Lo). For details of the staining method see Petri et al. (2002). Scale bars: 200 μm.

areas across bilaterian phyla, which might include the olfactory centers (Arendt & Nübler-Jung 1996; Kammermeier & Reichert 2001; Sprecher & Reichert 2003).

In insects, glomeruli are usually arranged in one or two layers around a central coarse neuropil (Fig. 2A). The number of glomeruli is species-specific and ranges from about 40 in Diptera and Ensifera to approximately 250 in ants. In some groups a glomerular organization is completely absent, while in other groups (Caelifera) individually identifiable glomeruli have been replaced by several thousand isomorphic so called microglomeruli. Can these numbers be of any help in clarifying interordinal relationships, e.g. do putatively closely related orders have a similar number of glomeruli? Unfortunately this is not the case. No trends linking the glomerular number to systematic units or any physiological or ecological parameter have been found. As mentioned above, within a single order, the Orthoptera, numbers range from 40 glomeruli in Ensifera to approx. 3000 microglomeruli in certain Caelifera. In addition, the number of glomeruli can differ in different casts of the same species. In drones of *Apis mellifera* 104 glomeruli have been counted whereas antennal lobes of workers of the same species contain up to 166 glomeruli. Moreover, glomerular organization has been lost several times during insect evolution. There are representatives in the Hemiptera, in the Coleoptera, and in the Trichoptera that exhibit no glomerular organization of their antennal lobes. [Numbers in this chapter are cited from a detailed review by Schachtner et al. (2005) on evolutionary trends in olfactory brain centers of arthropods.]

2.2. Mushroom bodies

The mushroom bodies (Fig. 2A) are prominent protocerebral neuropils that act as centers for sensory integration (Gronenberg 2001) and memory formation (Heisenberg 2003). They are the neuronal basis for associative and flexible behaviors (Farris & Roberts 2005). Evidence suggests that mushroom bodies may have been acquired twice in the Hexapoda: in the non-insect Diplura and in the Dicondylia. Until the phylogenetic position of the Diplura is resolved, however, it must also be considered that mushroom bodies arose only once within the hexapods and were secondarily lost in the archaeognathans (Farris 2005). Within the remaining insect taxa (Zygentoma and Pterygota), the mushroom bodies share a common groundplan in terms of cellular architecture and connectivity. Mushroom bodies consist of several thousand parallel fibers of intrinsic neurons, called Kenyon cells. Dendritic arborizations of these neurons form the calyces, the major synaptic input region to the mushroom bodies. 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 antennocerebral tract (Fig. 1). Mushroom bodies, 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 β-lobe), the major

output regions of the mushroom bodies (for a synopsis of the literature on mushroom body morphology and connectivity see FARRIS 2005).

Although all insect mushroom bodies share this basic groundplan, substantial morphological modifications, especially with regard to the number, the shape and size, and the complexity of the calyces are observed. In the social Hymenoptera (ants, bees, and wasps) the calyx is partitioned into discrete zones that are characterized by their sensory input modality. Two of these calyx zones, the lip and the collar, receive olfactory and visual input, respectively. In ants, the relative size of the lip and collar vary with the size of their primary sensory input neuropil, the antennal and optic lobes, and also with the importance of each sensory modality for the life of the animal (GRONENBERG & HÖLLDOBLER 1999). Even greater morphological differences can be found in insects outside the Hymenoptera. Calyces, originally termed this way because of their cup-like appearance in some species, can be present as single or double calyces per mushroom body, if doubled they can be either fused or unfused, they can have a globular shape, or be totally absent. As is the case with the number in antennal lobe glomeruli, these variations do not follow any taxonomic borders, as exemplified in the anatomical diversity of coleopteran mushroom body calyces: In this order, almost the entire range of external calyx morphologies that can also be found in other insect groups has been described. Coleopteran calyces vary from single to double, from fused to unfused, from globular to cup shaped, and they are absent in certain aquatic species (FARRIS 2005). On the other hand, similar architectural features like an increase in calycal surface area and volume along with an increase in Kenyon cell number have been acquired independently in several insect lineages. These large, "gyrencephalic" mushroom bodies are characteristic of generalist feeders, social insects and long-lived species with a flexible behavior. FARRIS & ROBERTS (2005) have argued that gyrencephalic calyces may represent an adaption for enhancing the computational capacity of the mushroom bodies in several ways: by increasing the number of sensory input neurons, by subcompartmentalization for segregation of different sensory modalities, and by providing additional neuronal substrate for complex learning computations and memory storage. In this context the mushroom bodies have been viewed as the insect's equivalent to the cerebral cortex in mammals.

2.3. Optic lobes

The optic lobes of the Pterygota contain a set of at least three retinotopic neuropils. These are the lamina, the medulla, and the lobula (Figs. 1, 2B). The outermost of these neuropils, the lamina, receives direct inputs from photoreceptor axons of the compound eye. An outer and an inner chiasma (interneurons crossing each other) link the lamina to the medulla and the medulla to the lobula, respectively. The lobula as a third order optic neuropil is pivotal for higher computational tasks such as object discrimination and movement detection (EGELHAAF & BORST 1993). This arrangement is likely a symplesiomorphic character state since malacostracan crustaceans share the same architecture of their optic system. In the Pterygota, however, this basic design is more elaborate with respect to the medulla, which is divided into an outer and inner medulla.

Deviations of this scheme are extremely sparse in Pterygota. The only pronounced difference between orders is the presence (Odonata, Ephemeroptera, Trichoptera, Lepidoptera, Diptera, Coleoptera, and Hymenoptera) or absence (all other hexapods investigated, including the Archaeognatha) of a separate fourth optic neuropil, the lobula plate. The analysis of optic lobe evolution has been complicated by the finding that certain malacostracan crustaceans contain a fourth optic neuropil comparable to the lobula plate in the Pterygota. A pronounced fourth optic neuropil is present in some Pericarida, such as the littoral isopod *Ligia occidentalis*, and can also be found in other malacostracans, where it is often diminutive (STRAUSFELD 1998, 2005). The question arises whether lobula plates of isopods and insects have evolved convergently or whether they derive from a common ancestor and are therefore a plesiomorphic character in insects. Recent comparative studies (SINAKEVITCH et al. 2003; STRAUSFELD 2005) suggest that the presence of a distinct lobula plate is an ancient feature of the ground plan of Tetraconata. Those hexapod orders that do not possess a distinct fourth optic neuropil have nevertheless the equivalent of a lobula plate only that it is fused with the lobula and therefore hard to identify. This fusion may be a derived character state for a clade comprising all non-holometabolous Neoptera. In this case the Archaeognatha would have acquired this fusion independently. Alternatively, a fused lobula/lobula plate could be a derived character of hexapods, with Palaeoptera and Holometabola having secondarily split the lobula again into two discrete neuropils. Other than that, the neuroarchitecture of the optic lobe of hexapods is of ancient origin and highly conserved so that no conclusion as to the phylogenetic position of individual orders can be drawn.

2.4. Central complex

The central complex is a set of protocerebral midline neuropils that plays a role in limb coordination (STRAUSFELD 1999), locomotion control (STRAUSS

2003) and navigation (Homberg 2004). In insects, the main components of the central complex are the central body and the protocerebral bridge (Figs. 1, 2A). The neuroarchitecture of the central body is characterized by several layers, the most prominent of which are the ellipsoid body (lower division) and the fan-shaped body (upper division). Williams (1975) described the fan-shaped and ellipsoid bodies of the locust as comprising reiterative columns. These columns are spread out like the staves of a fan (hence the name fan-shaped body). Columnar neurons provide connections with the protocerebral bridge via a complicated arrangement of chiasmata. These features are highly conserved in neopteran insects and have been described to be principally identical in the locust *Schistocerca gregaria* (Williams 1975), the flies *Musca domestica*, and *Drosophila melanogaster* (Strausfeld 1976; Hanesch et al. 1989; Renn et al. 1999), the cockroach *Periplaneta americana* (Loesel et al. 2002) and the wasp *Polistes canadensis* (Strausfeld 1999). Unpaired midline neuropils that resemble the neuroarchitectural design of the insect central body are present in all arthropod groups (including the Onychophora, where the central body is remarkably chelicerate-like, see Loesel & Strausfeld 2003) but the diplopods. Shared features include the presence of distinct layers and of columnar fibers that form a chiasm after leaving the central body. Even the equipment with certain neurotransmitters like allatostatin and tachykinin is conserved in most arthropod taxa investigated (Loesel et al. 2002). The available data suggest that the neuroanatomical *Leitmotiv* of the central body has been highly conserved during arthropod evolution and evolved at least 600 million years ago, before the first terrestrial arthropods emerged. In fact, the basic neuroarchitecture of this locomotor control center might even be more ancient than the phylum Arthropoda itself.

3. Conclusion

We have examined the usefulness of four of the best studied areas of the brain for resolving interordinal relationships in insects. While in principle the neuroarchitectural design of the hexapod brain is quite conserved, two of these regions, the antennal lobes and the mushroom bodies display a wide range of variations of these conserved themes within orders, so that no conclusion as to sister group relationships of individual insect taxa can be derived. At least regarding the mushroom bodies, this variety seems to be linked to differences in ecology and behavioral complexity. In contrast, neuroanatomical features of the optic lobe neuropils and the central complex are highly conserved among hexapods and shared with other arthropod groups, specifically with the Malacostraca. Does this imply that the neurophylogenetic approach is a futile attempt to resolve interordinal relationships in insects? Not necessarily, but comparative studies on neuroarchitecture have primarily focused on the relationships at higher taxonomic levels. The researcher that is interested in insect phylogeny would first have to identify novel characters that could be used for this task. The apparent diversity between and conservancy within insect orders concerning their external morphology should be reflected in some parts of the central nervous system, maybe if not in the brain then in other neuronal centers like the thoracic or abdominal ganglia. On the other hand, major radiations of insects, for example those that came about related to the evolution of vascular plants or angiosperms, occurred within a relatively short geological time period (Grimaldi & Engel 2005). Most modern insect orders had evolved until the Triassic. Since then, evolution had more than 200 million years to "work" on the neuroanatomy of the brain. This long time period may have blurred the traces of evolutionary events that occurred within a relatively short time scale. If this is the case, it might not be possible to definitely resolve relationships between insect orders, neither with anatomical nor with molecular methods.

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