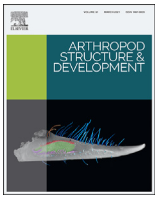
Arthropod Structure & Development 61 (2021) 101040

Contents lists available at ScienceDirect

Arthropod Structure & Development

journal homepage: www.elsevier.com/locate/asd



Convergent evolution of optic lobe neuropil in Pancrustacea

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ARTICLE INFO

Article history:
Received 16 September 2020
Received in revised form
2 February 2021
Accepted 3 February 2021
Available online 9 March 2021

Keywords:
Pancrustacea
Optic lobe
Ground pattern
Phylogeny
Convergence
Divergence

ABSTRACT

A prevailing opinion since 1926 has been that optic lobe organization in malacostracan crustaceans and insects reflects a corresponding organization in their common ancestor. Support for this refers to malacostracans and insects both possessing three, in some instances four, nested retinotopic neuropils beneath their compound eyes. Historically, the rationale for claiming homology of malacostracan and insect optic lobes referred to those commonalities, and to comparable arrangements of neurons. However, recent molecular phylogenetics has firmly established that Malacostraca belong to Multicrustacea, whereas Hexapoda and its related taxa Cephalocarida, Branchiopoda, and Remipedia belong to the phyletically distinct clade Allotriocarida. Insects are more closely related to remipedes than are either to malacostracans. Reconciling neuroanatomy with molecular phylogenies has been complicated by studies showing that the midbrains of remipedes share many attributes with the midbrains of malacostracans. Here we review the organization of the optic lobes in Malacostraca and Insecta to inquire which of their characters correspond genealogically across Pancrustacea and which characters do not. We demonstrate that neuroanatomical characters pertaining to the third optic lobe neuropil, called the lobula complex, may indicate convergent evolution. Distinctions of the malacostracan and insect lobula complexes are sufficient to align neuroanatomical descriptions of the pancrustacean optic lobes within the constraints of molecular-based phylogenies.

1. Introduction

Amongst its notable achievements – one being the invertebrate vision meeting that generated this special issue – Lund University provided the first published assertion that hexapods and crustaceans originated from a common ancestor. This came from Bertil Hanström (1891–1969), who entered the university in 1925 and retired from it 38 years later in 1963. A year into his appointment Hanström published a massive paper on invertebrate nervous system evolution that included what have become much-reproduced figures: relational trees depicting crustaceans (represented by Stomatopoda and Decapoda) and hexapods (represented by Insecta) as originating from a branchiopod-like ancestor, itself sister to Myriapoda (Fig. 1). A crucial decision by Hanström was to clearly define the arachnid lineage as entirely distinct, thus providing two divergent clades (in his view from a Trilobite grade ancestor), which today are termed Mandibulata and Chelicerata (Hanström, 1926).

Hanström did not derive his phylogenetic tree from comparisons of external morphology, as was the usual practice then in comparative morphology, but from comparing the organization of brains following the example of his mentor Nils Holmgren (1916). Both scientists adopted the rationale that when brains of different species share common arrangements of centers this indicates their phyletic relatedness, whereas differences of brain organization reveal divergence. Hanström was particularly attracted to the arrangement of visual neuropils beneath compound eyes, concluding that these are essentially identical in insects and decapods. These commonalities, and the comparable arrangements of crustacean nauplius eyes and insect ocelli, persuaded him that malacostracans and insects must have originated from a common ancestor. Their designation as the discrete taxon "Pancrustacea" was later established by molecular phylogenetics resolving their genomic relatedness (Regier et al., 2005).

The hypothesis that malacostracan crustaceans share a common ancestor with hexapods was emphasized later by other researchers who, like Hanström, were struck by commonalities of their nervous systems. In addition to describing similarities of pathways taken by pioneer neurons in the developing central nervous system of crustaceans and insects, an influential study in 1994 by Osorio and

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https://doi.org/10.1016/j.asd.2021.101040
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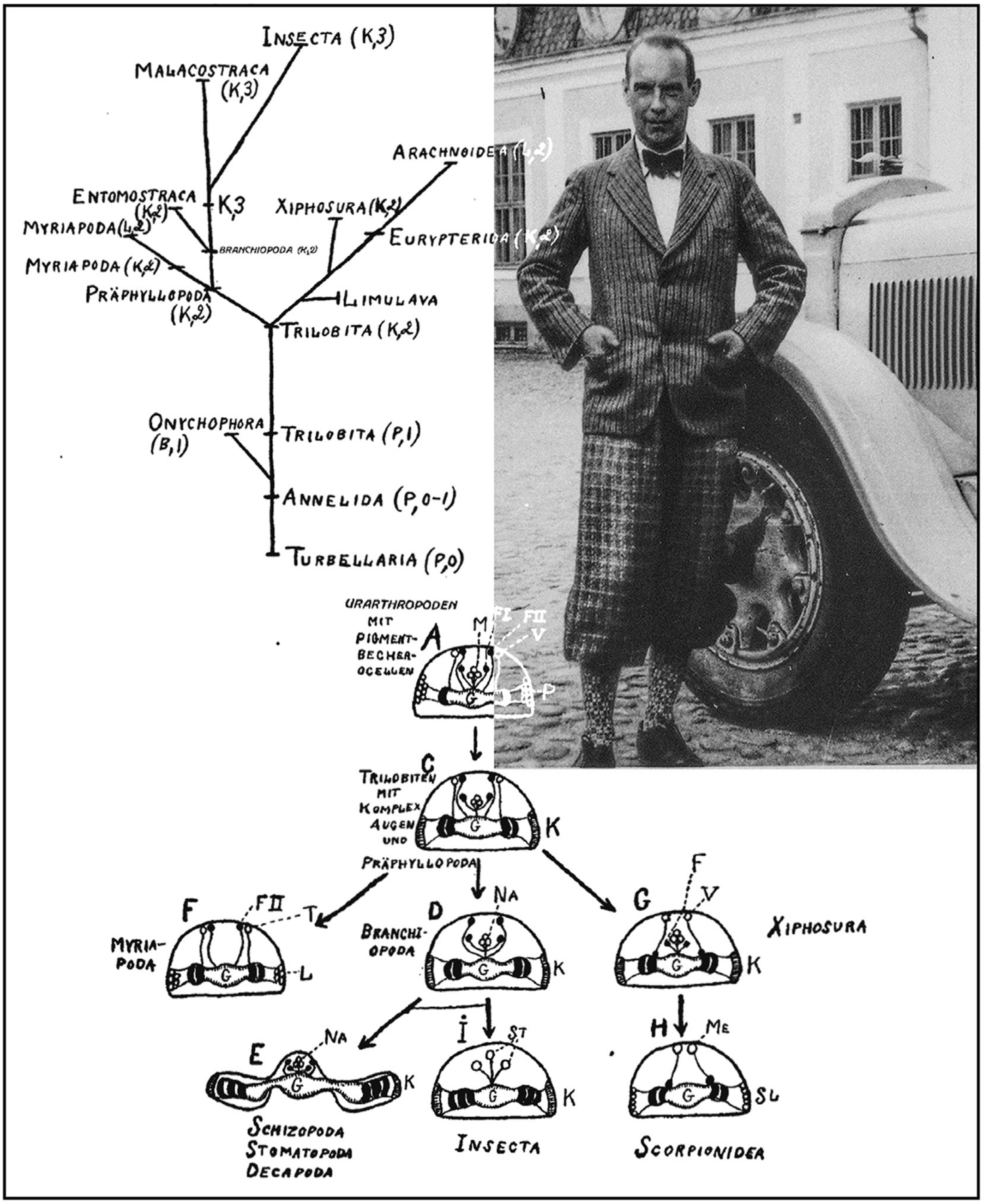

Fig. 1. The two crucial phylogenies based on comparing brain organization in extant arthropods with reference to proxy ancestor taxa such as Trilobita and Eurypterida. These phylogenies were published in 1926 by Hanström, here photographed shortly after assuming his appointment as professor at the University of Lund.

Bacon ("A good eye for arthropod evolution") directed attention to their corresponding optic lobe organization: three nested centers linked by chiasmata (Osorio and Bacon, 1994). Studies demonstrating shared patterns of optic lobe and compound eye development further strengthened the view that optic lobe organization common to decapods and hexapods indicated their ancestral arrangements (Harzsch and Hafner, 2006). That view has, until recently, been generally unchallenged other than sporadic concerns about taxon-specific differences of neural architecture pertaining to the second and third optic neuropils, the medulla and lobula, and their projections to the midbrain (Strausfeld, 1998).

Claiming optic lobe homology on the basis of neuroanatomical characters conflicts with molecular phylogenetics supported by fossil calibration (Oakley et al., 2013), which demonstrates a deep phyletic divide separating Multicrustacea, to which Malacostraca belongs, from Allotriocarida (Fig. 2). This second clade includes not only Hexapoda but also its sister taxon Remipedia (Von Reumont et al., 2011), and other morphologically uncomplicated taxa that possess extremely simple visual systems or lack them altogether, as do Remipedia and Cephalocarida (Oakley et al., 2013; Schwentner et al., 2017). Thus, there are serious challenges in reconciling phylogenies derived from genomics (Oakley et al., 2013; Lozano-Fernandez et al., 2019) with phylogenetic relationships suggested by neural arrangements (Strausfeld, 1998; Harzsch, 2002; Strausfeld and Andrew, 2011). Other efforts to resolve ancestral origins include those identifying commonalities of optic lobe development (Harzsch and Walossek, 2001; Wildt and Harzsch, 2002) and eye structure (Melzer et al., 1997; Paulus, 2000; Dohle,

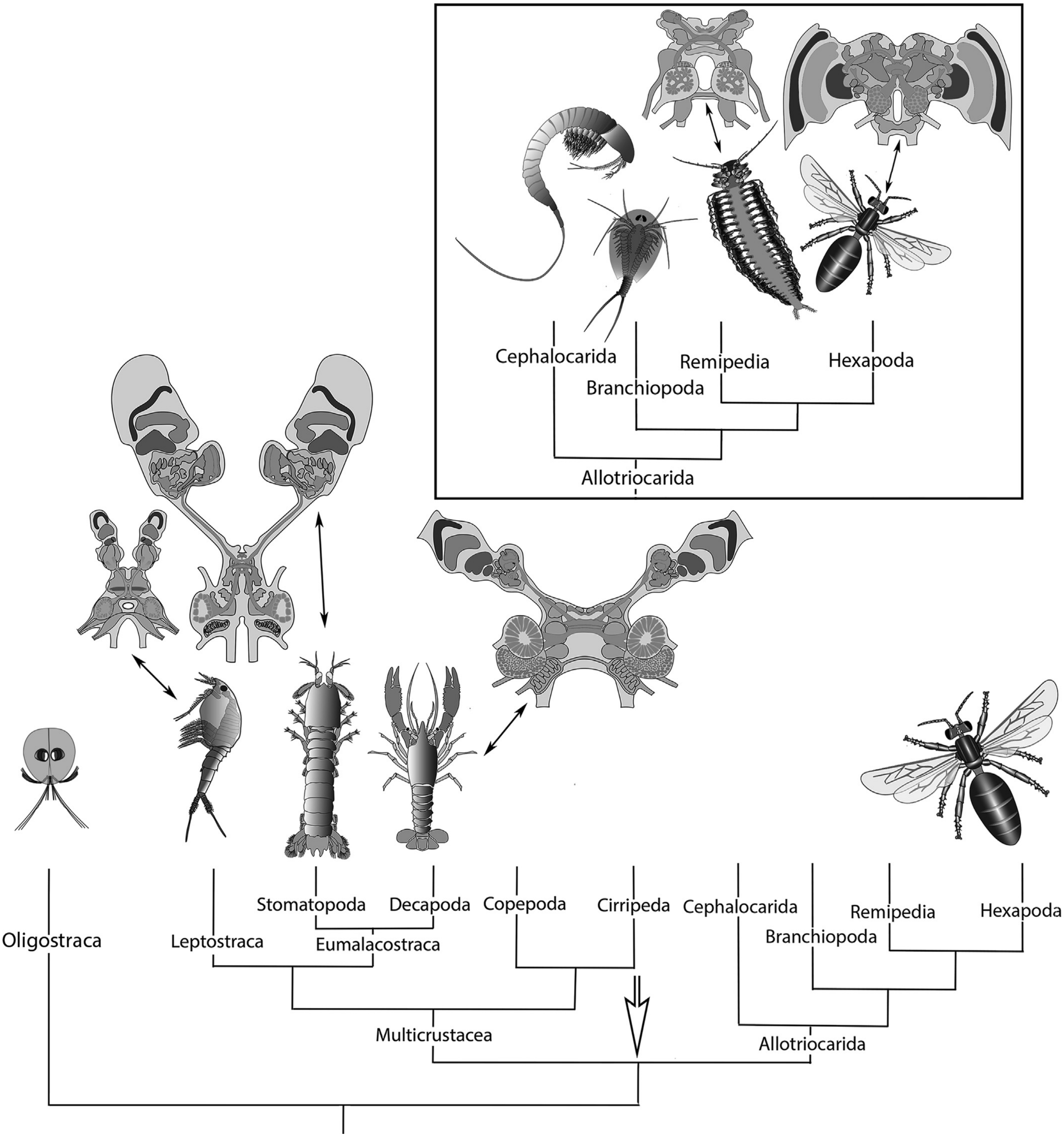

Fig. 2. An attenuated version of the Oakley et al. (2013) and Lozano-Fernandez et al. (2019). Molecular phylogenies show the major branches of Pancrustacea, with the deeply divided Superclasses Multicrustacea and Allotriocarida. The Superclass Oligostraca, represented here by Ostracoda, is the outgroup of Multicrustacea + Allotriocarida and thus offers possible insight into a hypothetical ancestry, although there is an absence of supporting neuroanatomical data. Insects are more closely related to remipedes than are either of these taxa to malacostracans, thereby challenging neuroanatomical analyses that suggested three nested optic neuropils were present in their common ancestor (Harzsch, 2002; Strausfeld and Andrew, 2011). The inset summarizes the four lineages of Allotriocarida (Lozano-Fernandez et al., 2019), of which only Branchiopoda and Hexapoda have compound eyes. Branchiopod brains possess just two optic lobe neuropils, but whether this is the consequence of an evolved loss cannot be established. Remipedes lack eyes and optic lobes, but the rest of their brain resembles that of a decapod crustacean, hence amplifying the idea of a malacostracan-like ancestor of Hexapoda (Fanenbruck et al., 2004; Fanenbruck and Harzsch, 2005).

1997, 2001). However, corresponding development of insect and branchiopod compound retinas may less reflect commonality across Pancrustacea than support both of these taxa belonging to Allotriocarida (Fig. 2). Similarities of insect and branchiopod lamina monopolar cell morphology contrast with equivalent but morphologically distinct lamina monopolar cells in eumalacostracans (Cajal and Sánchez, 1915; Nässel, 1975; Sztarker et al., 2009; Lessios et al., 2018). The growth and organization of the lamina and medulla are coupled with that of the retina (Meinertzhagen and Hanson, 1993; Wildt and Harzsch, 2002). Thus, in considering convergent or divergent evolution of the optic lobes it is notable that molecular phylogenetics, supported by the fossil record, shows that compound eyes have evolved numerous times during pancrustacean evolution. Ostracoda, belonging to the oldest eucrustacean crown group Oligostraca, is the most relevant taxon pertaining to such considerations (see, Oakley and Cunningham, 2002; Tinn and Oakley, 2008; Oakley et al., 2013).

The question asked in this article is whether hexapod visual systems evolved independently from those of their distant relatives in Multicrustacea, thus belying genealogical correspondence of optic lobe neuropils and instead admitting convergent evolution (Strausfeld, 1998). For even though traces of three nested optic neuropils are claimed in lower Cambrian stem mandibulates, such as fuxianhuiids (Ma et al., 2015; Yang et al., 2018), they cannot be definitively confirmed as mandibulate apomorphies. Claiming homology of the optic lobes thus presents a special challenge distinct from observations that forebrain centers, such as the central complex (Thoen et al., 2017a; Honkanen et al., 2019) and the mushroom bodies (Wolff and Strausfeld, 2015; Strausfeld et al., 2020; Modi et al., 2020), are highly conserved across Pancrustacea (Strausfeld et al., 2016; Thoen et al., 2017a).

Peripheral sensory centers provide information directly to the mushroom bodies and indirectly to the central complex, which are not only conserved across Pancrustacea (Strausfeld et al., 2016), but also appear to be unaffected by the evolved loss of sensory attributes. The absence of compound eyes in remipedes, for example, is not accompanied by an absence of the mushroom body or central complex neuropils (Fanenbruck and Harzsch, 2005; Stemme et al., 2016). The same applies to Copepoda (Andrew et al., 2012). The stability of central neuropils thus contrasts with the evolutionary lability of sensory neuropils.

A case in point refers to the bulb-like olfactory centers in the mandibulate brain's second segment, the deutocerebrum, which are targeted by olfactory sensory neuron axons. Olfactory lobes look superficially alike in crustaceans and insects, and relays from them supply homologous, albeit divergent, mushroom bodies in the lateral protocerebrum. Yet structural and molecular disparities in insects and crustaceans pertaining to the biology of their olfactory receptor neurons, and distinctions of their postsynaptic neuronal arrangements, have encouraged debate about whether divergent or convergent evolution is the more plausible explanation for these differences (Harzsch and Krieger, 2018; Strausfeld et al., 2020).

Here we inquire whether the optic lobes are similarly problematic, and we assess evidence for or against their convergent evolution in malacostracans and insects. A volume of neuroanatomical data relating to both groups allows a reexamination of which characters, if any, comprise an optic lobe ground pattern for Pancrustacea. There are now enough data from across many species to determine what neurological attributes support genealogical correspondence and whether those attributes are sufficient to conclude that ancestral circuits underlying comparable behaviors are shared by malacostracans and insects. For example crustaceans and insects possess large neurons at proximal levels in the optic lobes that similarly respond to the direction of object motion or visual flow (e.g., Medan et al., 2015; Horseman et al., 2011; Yamawaki, 2019; Borst et al., 2020). But it is not known if the circuits in which they participate, and which encode the same visual events, are homologous or the result of convergent evolution.

As a first approach to these questions, we review here aspects of optic lobe organization in crustaceans and insects that suggest their different evolutionary histories.

2. Materials and methods

Specimens used for this study were obtained from designated collection sites on San Juan Island, Washington, USA; the vicinity of Tucson, Arizona; the vicinity of Würzburg, Germany; and US commercial suppliers of marine fauna. With few exceptions, histological preparations shown here are Bodian reduced-silver stains that provide overviews of cytoarchitecture, and other distinctive arrangements which are revealed by anti-GAD immunocytology. The Bodian method (Buschbeck and Strausfeld, 1996) employed Roques silver proteinate (now discontinued). Immunocytological images employ antibodies raised against glutamic acid decarboxylase (GAD; rabbit polyclonal, Sigma—Aldrich CAT#: G5163) at a dilution of 1:500), and visualized using secondary IgG antibodies raised in donkey and conjugated to Cy3 fluorophore (Jackson ImmunoResearch; West Grove, PA). GAD has been previously used to identify GABAergic neurons in crustaceans (Stemme et al., 2016; Sayre and Strausfeld, 2019). Figures depicting examples of optic lobe neuropils are shown for species that are indicated with reference to a molecular phylogeny of Pancrustacea. Because there is so little variation of optic lobe neural architecture in Malacostraca, Multicrustacea is here abbreviated to just two lineages, Stomatopoda and Decapoda. To exemplify divergence of lobula organization across insects, Allotriocarida is represented by an expanded representation of Insecta, employing Misof et al.'s (2014) molecular-based phylogeny. Schematics of taxa and their phylogenetic relationships in Fig. 2 employ molecular trees published by Oakley et al. (2013) and Lozano-Fernandez et al. (2019).

Finally, a word of caution regarding terminology. For historical reasons, the same terminology is used to refer to optic lobe neuropils in insects and crustaceans. This does not imply their homology.

3. Results and discussion

3.1. General distinctions of insect and malacostracan optic lobes

Occasional studies have drawn attention to morphological differences that suggest homology of insect and crustacean optic lobes may not be as clear-cut as has been assumed (Strausfeld, 1998; Sinakevitch et al., 2003). With regard to their general neural architecture, major distinctions pertain to the malacostracan and insect medulla and lobula.

As shown in Fig. 3A, the malacostracan lobula is densely populated by neurons and has numerous computational strata that originate from lateral networks of anaxonal neurons (amacrines, local interneurons), as well as the layered dendrites and axon collaterals of through-going retinotopic output neurons. This stratified architecture also dominates the eumalacostracan medulla. But a comparable arrangement in insects is strictly limited to the medulla, particularly its outer two thirds, but does not so well define the medulla's inner third or the lobula (Fig. 3B).

A major difference between eumalacostracan and insect optic lobes pertains to the spacing of neurons in the medulla and lobula complex (Fig. 3A and B). In both crustaceans and insects the mosaic of visual sampling units, each of which is provided by photoreceptors sharing the same optical alignment (Franceschini, 1975),

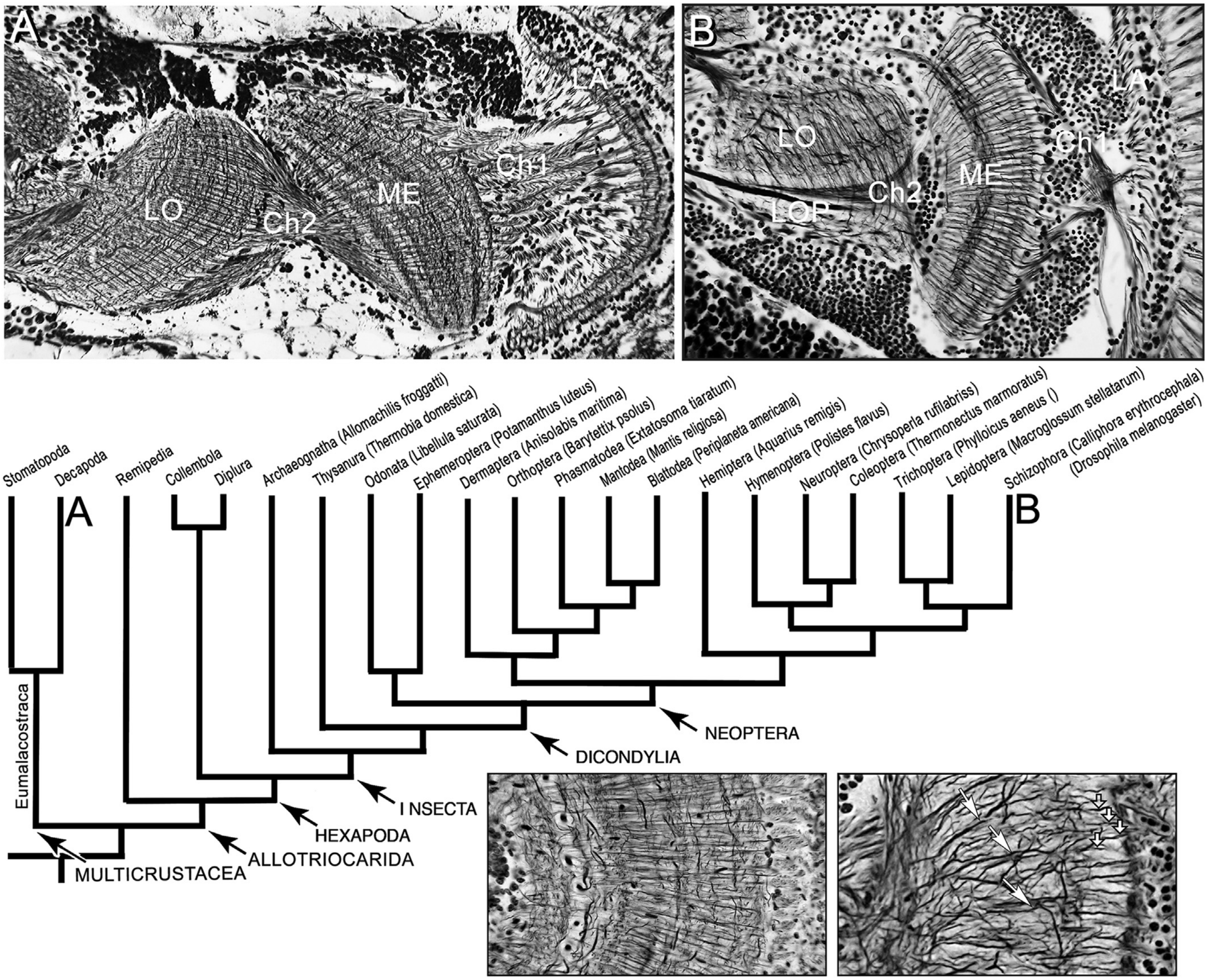

Fig. 3. The nested optic neuropil of Eumalacostraca (A) and Insecta (B) look similar yet reveal crucial taxon-specific distinctions. The eumalacostracan medulla is a single neuropil, whereas the insect medulla is divided into outer two thirds and an inner third by a prominent band of axons – the Cuccati bundle – belonging to tangential neurons associated with the outer part. Also, in contrast to the insect optic lobe, the retinotopic organization in the eumalacostracan lobula is at least as dense as in its medulla, and both are denoted by numerous synaptic strata through their depth. The two insets compare retinotopic organization in the lobula of the crab *Hemigrapsus nudus* (left) and the fruitfly *Drosophila melanogaster* (right). In the crab lobula, the spacing of retinotopic columns faithfully represents the retinal mosaic of visual sampling units. In the fruitfly, columnar neurons (large arrows) coarsen the incoming mosaic (small arrows). Many insect lineages possess a lobula plate that faces the lobula and is supplied by special arrangements of motion-sensitive neurons (see text). Eumalacostracan crustaceans have no corresponding neuropils. The relational tree pertaining to Insecta is adapted from Misof et al., (2014). Scale bars are omitted as they provide no relevant information. Abbreviations: Ch1, Ch2, first and second optic chiasmata; LO, lobula; LOP, lobula plate; LA, lamina; ME, medulla.

corresponds to the number of facets of the compound eye. This mosaic is generally represented across the surface of each of the nested visual neuropils where it is represented by a "retinotopic map." There are, however, important exceptions, discussed below, where this does not occur.

The first of these successive maps is established by the axons of visual sampling units (photoreceptor neurons) ending in the most distal optic neuropil, called the lamina. The points of the lamina map are relayed centripetally by neurons originating in the lamina entering the medulla. The relay neurons in the next level of the medulla extend the retinotopic map through its layers thereby conferring this region's columnar organization. Relays from the medulla columns impose the retinotopic mosaic into the lobula (Braitenberg, 1970). However, in the lobula the neural representation of retinotopy by its columnar neurons is very different in crustaceans compared with insects.

In insects, columnar neurons that relay information centrally from the lobula are arranged as palisades that extend from its outer layers to exit from its inner margin. There are numerous morphological classes of such neurons. As suggested by intracellular recordings of the insect lobula, each class of relay neurons leaving the lobula encodes a specific parameter of the insect's visual world and sends this information via its axons to a specific islet of neuropil, called an optic glomerulus, in the lateral protocerebrum (Okamura and Strausfeld, 2007; Mu et al., 2012; Aptekar et al., 2015; Keles and Frye, 2017). In the insect lobula, neurons comprising each class of outputs are spaced such that they coarsen the representation of the peripheral retinotopic mosaic, being spaced one to every six (or more) retinotopic inputs (Fig. 3B). Their overlapping dendritic trees subtend the whole of the relayed retina (Strausfeld and Okamura, 2007).

In crustaceans, inputs from the medulla likewise map the peripheral arrangement of visual sampling units into the lobula. The

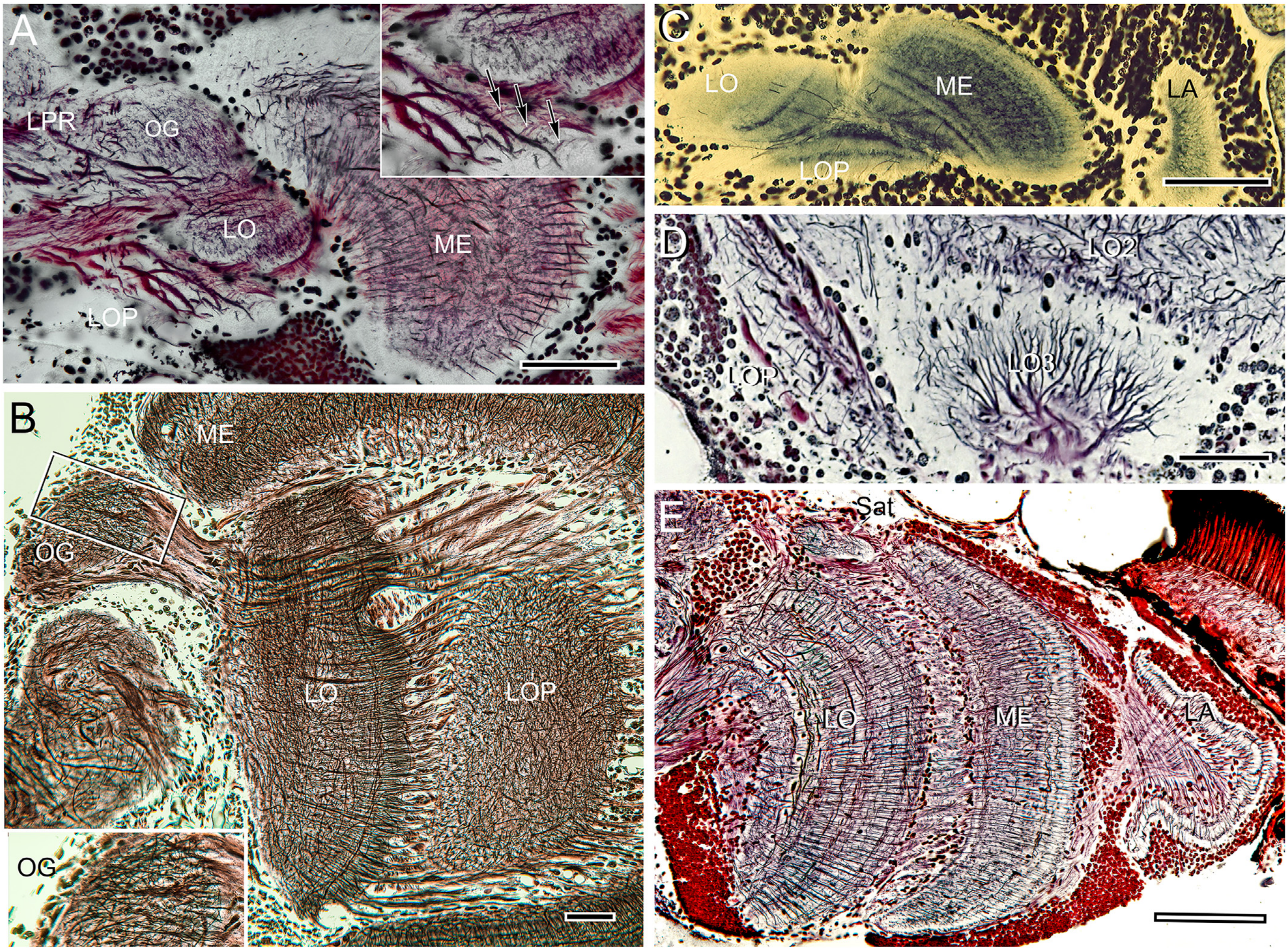

Fig. 4. Lobula plate in holometabolous insects (A–C) compared with a putative homologue in a dragonfly (D) and a homoplasic equivalent in a crab (E). A. Medulla (ME) and lobula complex in the neuropteran *Chrysoperla rufilabris* (green lacewing) showing the planar lobula plate (LOP) with large tangential neurons supplied by retinotopic inputs from the lobula (LO; arrowed in inset). Neuropil of a large optic glomerulus (OG) abutting the lateral protocerebrum (LPR) shows evidence of columnar organization, hence possible retinotopy. B. Lobula and lobula plate of *Macroglossum stellatarum* (hummingbird hawk moth). The lobula is connected to an optic glomerulus by bundles of axons (inset lower left) that confer a chunk-like retinotopy. C. The optic lobe of a pre-emergent trichopteran, likely a species of *Phylloicus*, showing its four nested optic lobe neuropils. D. Parts of the lobula "complex" of *Libellula saturata* (flame skimmer dragonfly), showing a cross section through the putative lobula plate denoted by its arrangement of horizontally and vertically oriented giant tangential neurons. LO2, LO3: two of four nested lobula neuropils typifying Odonata. E. Optic lobe of *Hemigrapsus nudus* showing a small lenticular-shaped neuropil (Sat) satellite to the medulla shows little evidence of retinotopy. LA, lamina. Scale bars: A–D 50 μm; E, 100 μm.

difference is that in malacostracans columnar neurons postsynaptic to those inputs do not coarsen this mosaic (Fig. 3A). For every visual sampling unit projected into the lobula, there is at least one of each of the many neuroanatomical (and thus physiological) classes of lobula output neurons. In a shore crab there are at least 60 distinct classes. A consequence of this organization is that the number of morphological types of efferent neurons extending centrally from the crustacean lobula is much greater than that from an insect's lobula. This suggests that the eumalacostracan visual system may encode a richer representation of its relevant visual ecology than does a morphologically similar but sparser arrangement of fewer cell types in an insect's visual system.

A related distinction is apparent in the malacostracan and insect medullas. In insects the outer two thirds of the medulla are separated from the inner third by systems of tangentially directed axons that comprise the serpentine layer or, in older literature, the "Cuccati bundle," named after its discoverer (Cucatti, 1888). The Cuccati bundle carries heterolateral axons that connect the left and right medullas as well as some satellite neuropils disposed central to the optic lobes each side of the brain. A Cuccati bundle has never been resolved in a crustacean. The malacostracan medulla is undivided and densely stratified throughout its depth (Fig. 3A).

3.2. *The lobula plate and the absence of a homologue in crustaceans (Figs. 4–6)*

The lobula plate is a well-defined neuropil in which systems of neurons encode the direction of motion across the retina (optic flow), a computation that is crucial for visual stabilization in flight. The principal components of this circuit were first discovered in Lepidoptera and Diptera but accruing observations indicate that all holometabolous insects that fly have a lobula plate. Lepidoptera, here represented by the sphingid moth *Macroglossum stellatarum* (Figs. 4B and 6D), typifies an organization shared by Coleoptera (beetles), Lepidoptera (butterflies and moths), and Schizophora (flies). Neuropterans also possess a lobula plate (e.g., *Chrysoperla*, the green lacewing), as do Trichoptera (Fig. 4A, C).

The circuit's essential components comprise retinotopically organized quartets of small neurons called bushy T-cells (now called T4 neurons), the dendrites of which are constrained to the

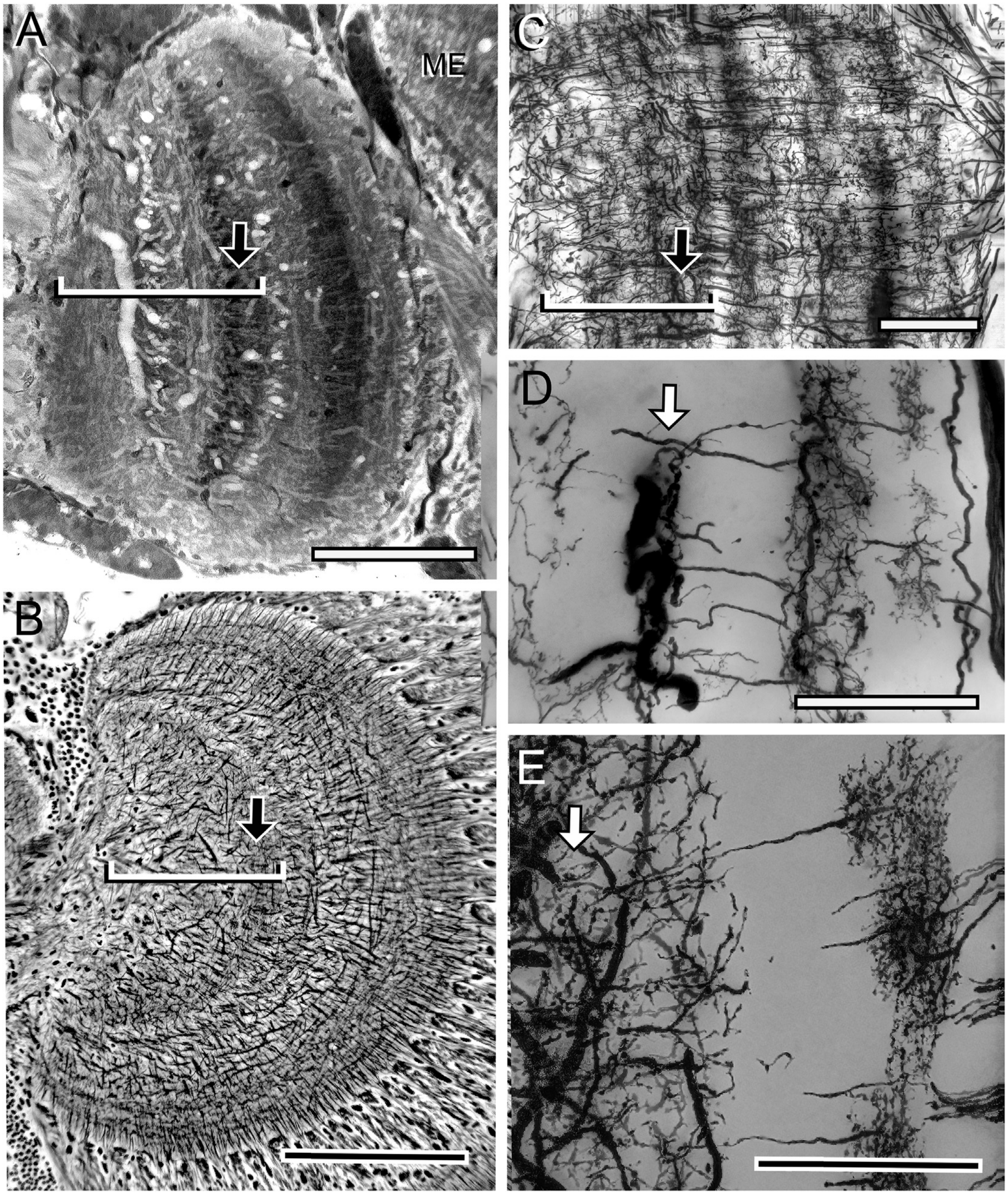

Fig. 5. Deep lobula organization in Eumalacostraca and Insecta. A. Ethyl gallate-stained lobula of the shore crab *Hemigrapsus nudus* showing a deep level (bracketed) containing systems of tangential neurons that subtend discrete overlapping domains of the retinal mosaic. B. Comparable arrangement in the lobula of *Apis mellifera* (honey bee), the innermost levels of which contain wide-field tangential cells that receive T4 and T5 neurons (see text). C. Golgi impregnation showing the same lobula level in *H. nudus*. Arrows in A-E indicate termination level of T5-like neurons originating in the outer two layers of the lobula. This organization is common to numerous eumalacostracan lineages. D. Two levels of T4/T5-like neurons terminate on wide-field tangentials of the inner lobula of *Pagurus hirsutiusculus* (hairy hermit crab). E. Golgi impregnation of *A. mellifera* showing T5 neurons in the outer layer of the lobula extending axons to deep levels of wide-field tangential neurons. ME, medulla. Scale bars: A, 100 μm; B-E, 50 μm.

most proximal stratum of the inner third of the medulla, below the Cuccati bundle. Each quartet maps into a distinctive neuropil called the “lobula plate” that is proximal to the medulla, aligned opposite the outer face of the lobula. T4 cell endings converge with the endings of a second similar set of neurons (T5 cells), the dendrites of which occupy the outermost layer of the lobula (Strausfeld, 1976; Buschbeck and Strausfeld, 1996). There are as many of these quartets as there are visual sampling units and together T4 and T5 neurons supply information about local motion across the retina (Borst et al., 2020). Their target neuropil, the lobula plate, is populated by systems of wide-field neurons that encode the direction of visual motion over large areas of the compound eye (Hausen, 1982; Hengstenberg, 1982; Borst et al., 2019). In Hymenoptera, the oldest endopterygote lineage (Misof et al., 2014), the lobula plate lies immediately beneath and is contiguous with the outer levels of the lobula. As originally shown by Cajal and Sanchez (1915), the axons of T4 and T5 neurons extend through the lobula to this deeper level, which is populated by wide-field tangential cells (Fig. 5E). Like wide-field tangential neurons of the dipteran lobula plate these also encode the direction of panoramic visual motion (Ibbotson, 1991). Whether the T4 and T5 neurons are organized as quartets in Hymenoptera has not yet been determined, however. In other holometabolous lineages, lobula plates are wholly separated from the lobula, the outer surfaces of both facing each other in perfect retinotopic register (Braitenberg, 1970).

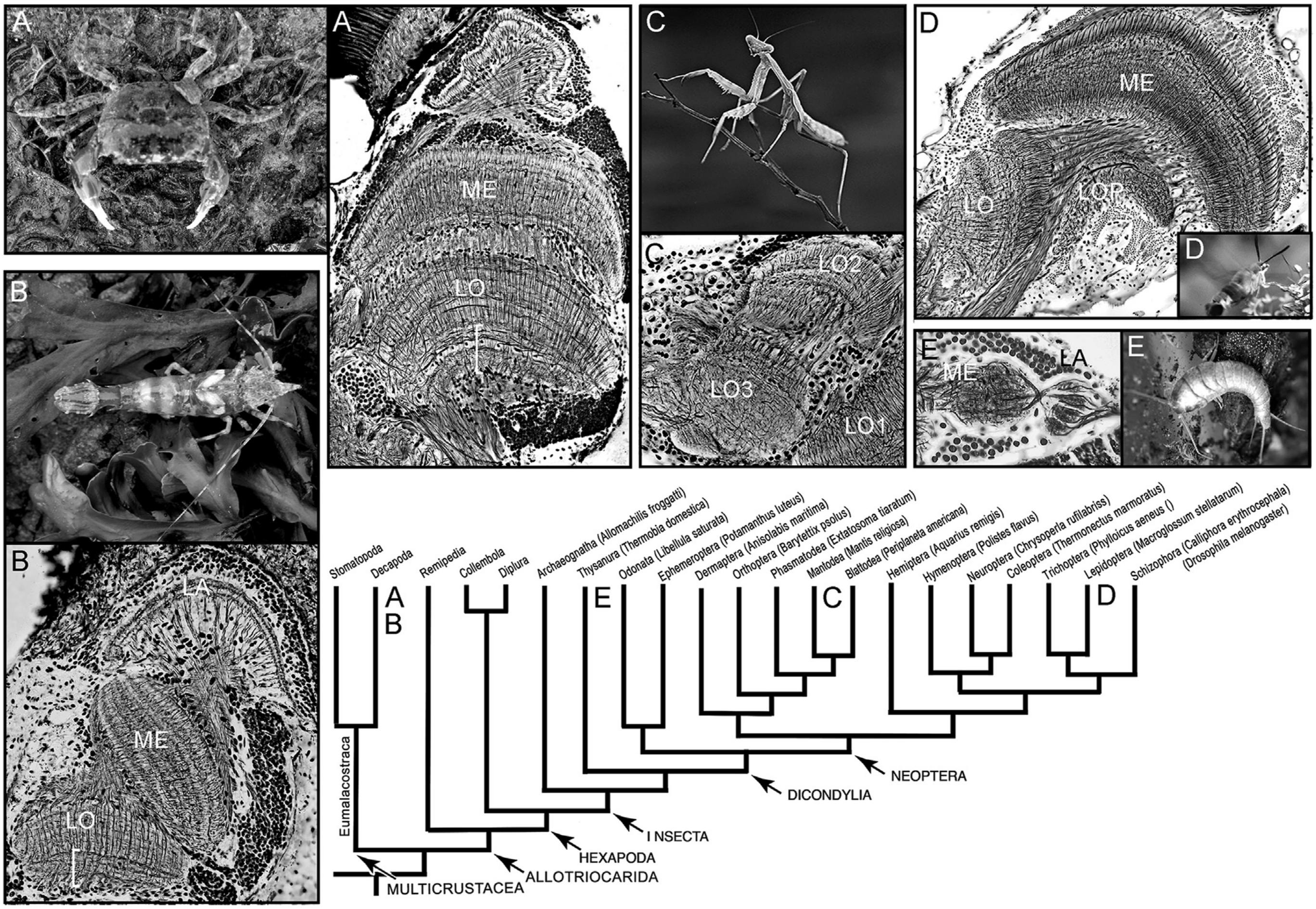

Fig. 6. Conserved versus divergent lobula organization in Eumalacostraca (A, B) and Insecta (C–E). The cognate lineages are indicated in the molecular phylogeny (Misof et al., 2014). For descriptions see main text. Species: A. *Hemigrapsus nudus*; B. *Lebbeus groenlandicus*; C, *Tenodera aridifolia*; D. *Macroglossum stellatarum*; E, *Thermobia domestica*. Abbreviations: LA, lamina; LO, lobula; LO1, LO2, LO3; multiple lobula complex neuropils in Mantodea, LOP, lobula plate; ME, medulla.

Notably, lobula plate neuropils have large enough surfaces to accommodate the overlapping terminals of an eight-fold superimposed representation of the retinal mosaic (Fig. 4A–C). Although lobula plates typify Holometabola, Odonata also possesses lobula plate-like neuropils that are almost identical to those of Diptera (Fig. 4D) and count as one of five discrete retinotopic neuropils that comprise the elaborate lobula complex of dragonflies and darters (Fabian et al., 2020). Systems of T4- and T5-like neurons have been identified in the dragonfly (see accompanying paper in this issue; Strausfeld, 2021), suggesting that a T4 and T5 neuron system and its postsynaptic targets may have first appeared in the late Devonian, the time of origin of odonate insects according to molecular phylogenetics (Misof et al., 2014). The possible absence of T4 and T5 neurons in hemimetabolous insects would be ascribed to an evolved loss, unless further studies show otherwise.

Arrangements corresponding to T4 and T5 neurons are unknown in Crustacea, although satellite neuropils close to the medulla or lobula (Bengochea et al., 2018) have been referred to as “lobula plates” (Strausfeld, 2005, 2012), which with the benefit of hindsight has hindered rather than helped our understanding (Fig. 4E). For example, in the semiterrestrial isopod *Ligia occidentalis* the satellite is quite large. Its extensive planiform neuropil faces the lobula, as does the lobula plate in a fly. But in *Ligia*, the satellite receives chunk-like bundles of axons from the medulla that do not appear to confer any obvious retinotopy onto the neuropil's layer of tangential neurons (Strausfeld, 1998; Sinakevitch et al., 2003; see companion paper, Fig. 2C). Nor is there evidence of morphologically equivalent retinotopic neurons that in holometabolous insects characterize the lobula plate. Those differences further suggest that the satellite neuropil in *Ligia* is homoplasic (Strausfeld, 1998). Many eucaridid species have similar, usually smaller, satellite centers near the medulla that also lack features defining the holometabolan lobula plate (Fig. 4E).

Because there is no clear evidence that these satellite neuropils receive a precise point-for-point mapping of the retinotopic mosaic they bear greater similarity to optic glomeruli. These are common to both insects and malacostracan crustaceans (Strausfeld and Nässel, 1980). Optic glomeruli are discrete neuropils proximal to the medulla and lobula. They receive the terminals of columnar neurons, classes of which segregate to them from the lobula (Okamura and Strausfeld, 2007; Mu et al., 2012). Errors of interpretation can arise when the lobula or medulla provide neurons that terminate in an optic glomerulus to provide an approximation of retinotopy (Fig. 4A and B).

If malacostracans lack circuits comparable to those defining the holometabolan lobula plate, this does not exclude homoplasic arrangements of motion-detecting circuits in malacostracan and hexapod lobulas. Golgi studies of both Brachyura and Anomura (crabs and hermit crabs) show the lobula as divided tangentially into two distinct parts, the inner volume containing systems of large

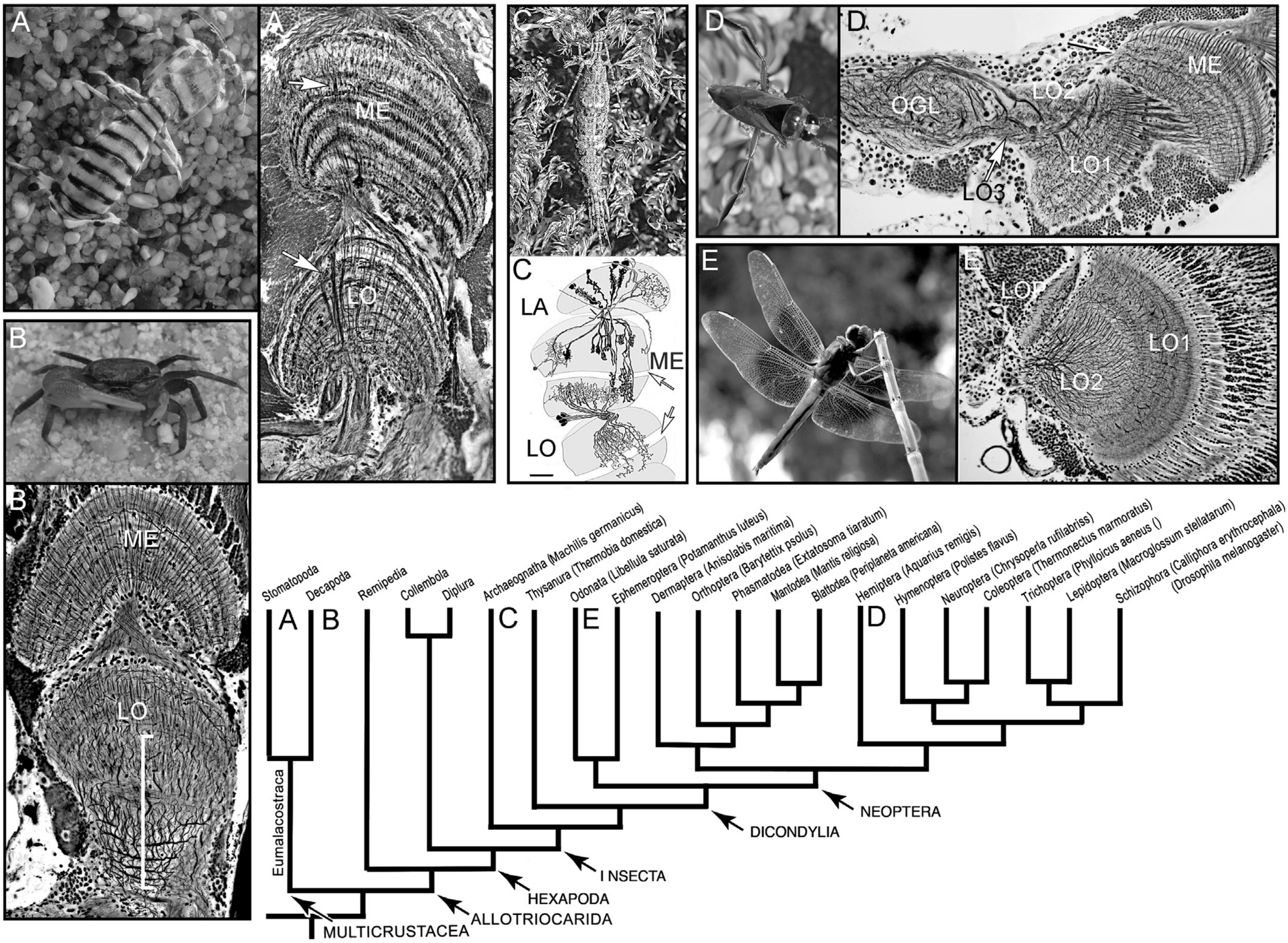

Fig. 7. Conserved versus divergent lobula organization in Eumalacostraca (A, B) and Insecta (C–E). Note the inclusion here of Archaeognatha (C). For descriptions see main text. Tree pertaining to Insecta is adapted from Misof et al., (2014). Taxa: A, Stomatopoda (*Lysiosquillina maculata*); B, Ocypodidae (*Uca minax*); C, *Machilis germanicus*; D, *Aquarius remigis*; E, *Libellula saturata*. OGL, optic glomerulus; other abbreviations as for Figure 6.

tangential neurons (Fig. 5A). This arrangement is comparable to the hymenopteran lobula (Fig. 5B) in which, as described above, tangential neurons in its inner volume receive inputs from T4 and T5 neurons. The eumalacostracan lobula is densely populated by small-field retinotopic neurons that extend from its outer level to deeper levels that are populated by large tangential neurons (Fig. 5C). When stained less densely (Fig. 5D), this arrangement demonstrates an organization similar to that in the honeybee where T5 neurons extend axons from their dendrites in the lobula's outer stratum to the deeper tangential neurons (Fig. 5E). As reported from intracellular recordings and dye-fills from two crab species, tangential neurons whose axons extend centrally from the inner volume of the lobula demonstrate selective responses to optic flow and to local visual motion (Berón de Astrada and Tomsic, 2002; Horseman et al., 2011; Medan et al., 2015). Such arrangements of wide-field and object motion-sensitive efferents from the decapod lobula are comparable to tangential neurons with centrally extending axons from comparable layers of the hymenopteran lobula that likewise encode wide-field and object motion (Ibbotson, 1991; Paulk et al., 2008). Both neuroanatomical and electrophysiological evidence thus support an interpretation that these arrangements in crabs and hymenopterous insects are examples of evolutionary convergence of dedicated motion-detecting circuits.

3.3. *Conserved optic lobe organization in Eumalacostraca but exuberant divergence in Insecta (Figs. 6 and 7)*

Here we describe examples of Stomatopoda and Decapoda that demonstrate conserved optic lobe organization within Multicrustacea. In Figs. 2, 6 and 7, the purposely attenuated Eumalacostraca (Multicrustacea) is attached to a much expanded Allotriocarida represented by insect lineages (from Misof et al., 2014), in which optic lobe evolution reveals prolific lobula divergence (Figs. 6 and 7).

The first two examples of decapods (Fig. 6) compare the optic lobes of a varunid shore crab, *Hemigrapsus nudus* (Infraorder Brachyura; 6A), with that of the spiny shrimp *Lebbeus groenlandicus* (6B), a member of Thoridae (Superfamily Alpheoidea, Infraorder Caridea). Molecular phylogenetics retrieves Eubrachyura as the most recent decapod clade, whereas Caridea is resolved as 250 million years older. Their geological ages, based on the fossil record of first appearance, are closer: Caridea appearing at the beginning of the Jurassic, Brachyura some 40 million years later (Wolfe et al., 2019). In both groups, lamina organization and stratification of the medulla and lobula revealed by Bodian staining is almost identical. The relative depth of their structurally matching lobulas is greater in *H. nudus* due to the

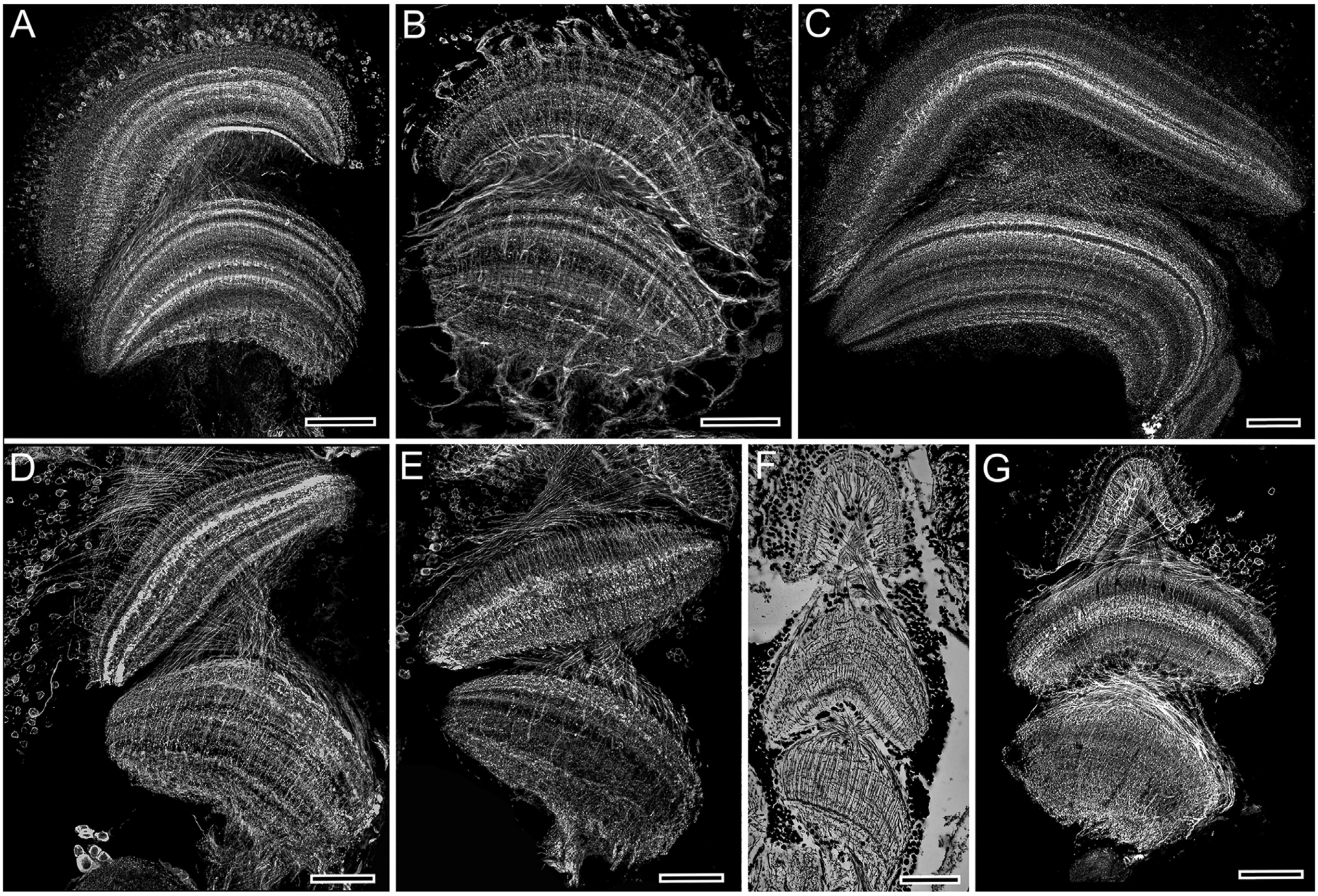

Fig. 8. Anti-GAD immunoreactivity in eumalacostracan medullas and lobulas. Bodian reduced-silver staining resolves common arrangements of neuroarchitectures across eumalacostracan optic lobes. However, as shown here, immunohistology reveals different distribution patterns of anti-GAD immunoreactivity within this common framework. A. *Uca minax* (Brachyura). B. *Hemigrapsus nudus* (Brachyura). C. *Penaeus vannamei* (Dendrobranchiata). D, E. *Lebbeus groenlandicus* and *Spirontocaris lamellicornis* (Caridea, Alpheoidea). F, G. *Palaemon pugio* (Caridea, Palaemonoidea) comparing typical eumalacostracan neuroarchitecture as revealed by Bodian reduced silver staining (F) with the organization of anti-GAD-immunoreactive arrangements (G). All scale bars indicate 100 μm.

accommodation of an expanded level of neuropil (bracketed in Fig. 6A and B) containing arrangements of large-diameter tangential neurons. Similarly, in the lobula of fiddler crabs (*Uca minax*), the eyes of which are acutely sensitive to visual motion (Zeil and Hemmi, 2006), the deep layers of the lobula (bracketed in Fig. 7B) reveal rectilinear arrangements of tangential neurons comparable with those described for varunid crabs (Berón de Astrada and Tomsic, 2002).

As in other crustaceans the photoreceptors of mantis shrimps detect linearly polarized light (Marshall et al., 1991) except where the two hemispheres of each eye are joined by a midband row of particular ommatidia, the photoreceptors of which provide specialized channels. Some detect circular polarization, others detect narrow bands of the visible and ultraviolet spectrum (Thoen et al., 2014). These midband photoreceptors are represented as a specialized retinotopic zone successively in all three optic neuropils. Despite these unique attributes (Fig. 7A), and a mantis shrimp's ability to move its eyes independently, the neuroarchitectures of the stomatopod medulla and lobula do not substantially depart from those of decapods except that the stomatopod lobula lacks a deep layer populated by wide-field tangential neurons (Thoen et al., 2017b, 2018).

Morphologies that appear to be standard to Decapoda contrast with the diversification of lobula organization in Insecta. For example, species of Mantodea (Fig. 6C) typically have four retinotopic neuropils organized in series LO1-LO4, the last receiving a diffuse input from the retinotopic LO3. A similar arrangement of neuropils has also been reported for its sister clade Blattodea, demonstrating that these arrangements of multiple retinotopic lobulas typify Dictyoptera, as originally reported by Rosner et al. (2017).

Studies of aquatic predatory insects, here represented by the hemipteran backswimmer *Aquarius remigis* (Fig. 7D), show elaborate lobula complexes comprising a substantial lobula (LO1) that adjoins two smaller territories (LO2, LO3), their typical arrangement. Although the hemipteran LO3 lobula is associated with a cluster of very small perikarya, suggesting correspondingly small interneurons populating it, there is no convincing evidence that this is a lobula plate-like organization: its surface area is likely too small to accommodate a full retinotopic representation, nor is there evidence of T4- or T5-like neuron ensembles supplying wide-field tangential neurons.

Apterygote insects comprise Archaeognatha and Thysanura, the latter represented here by the “silverfish” *Thermobia domestica* (Fig. 6E), which exhibits an evolved loss of ommatidia and hence its attenuated central representation: a much-reduced medulla and lamina retain their retinotopic connection by the outer optic chiasma, whereas there has been an evolved loss of the lobula. In Eumalacostraca, evolved loss of the lobula also occurs

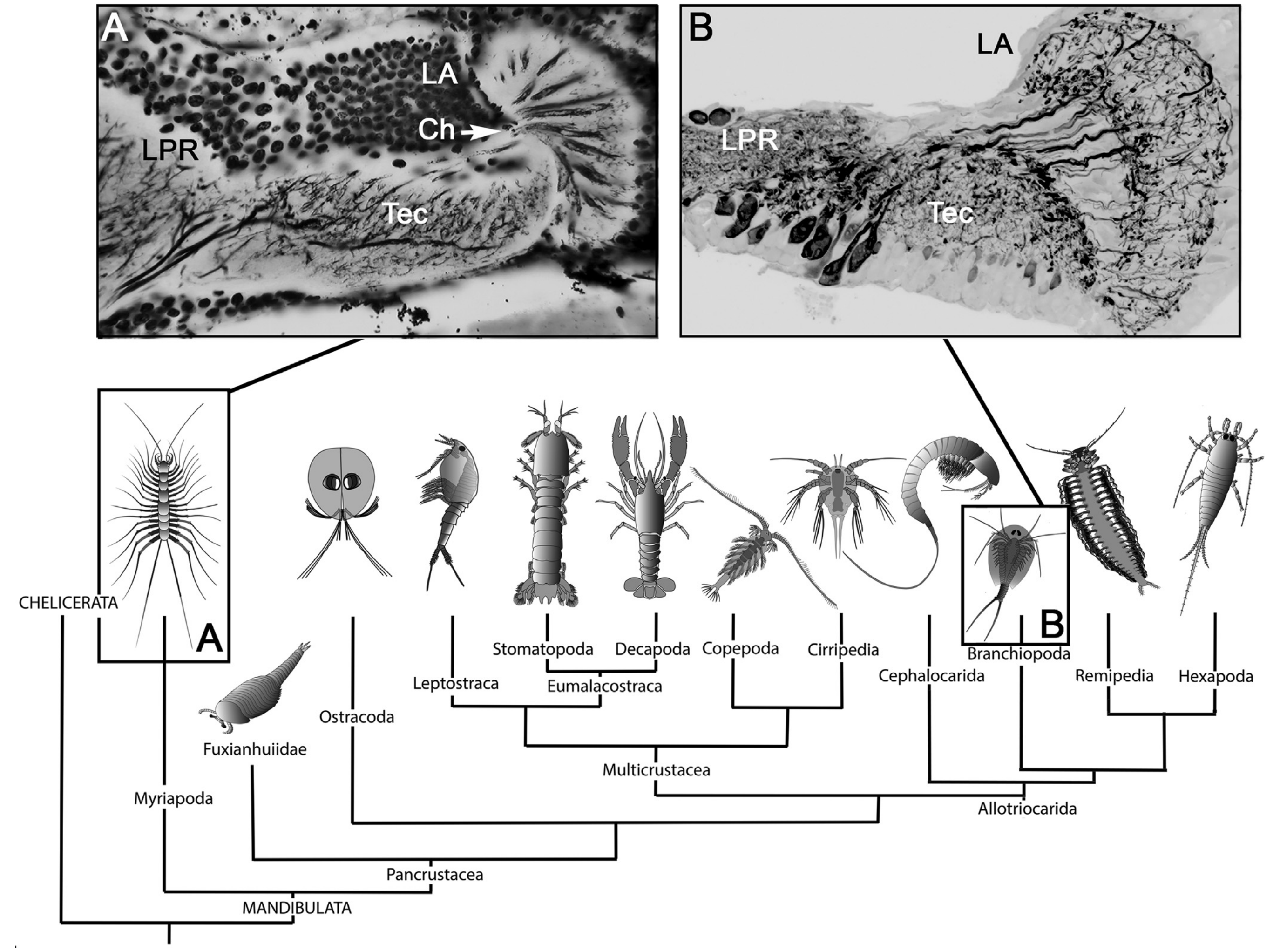

Fig. 9. Molecular phylogeny of Oakley et al., (2013) incorporating the basal position of Cephalocarida in Allotriocarida (Schwenter et al., 2017). The phylogeny is also extended to include one possible position of the stem (putatively mandibulate) *Fuxianhuia protensa* (Ma et al., 2012) and the extant basal myriapod *Scutigera coleoptrata* (A). Only the myriapod reveals a candidate ground pattern organization for total Mandibulata: its two neuropils, the lamina (LA) and a tectum-like second neuropil (Tec), connected by a chiasma (Ch; see Sombke and Harzsch, 2015). This contrasts with the allotriocarid Branchiopoda (B), representatives of which (here the notostracan *Triops longicaudatus*) possess similarly disposed optic lobe neuropils, but these are connected by a system of uncrossed axons and entirely different distributions of neuronal perikarya. LPR: lateral protocerebrum.

across lineages in both Eucarida and Pericarida, as in *Parhyale hawaiensis* (Ramos et al., 2019) although this is contested (Wittfoth et al., 2018). It is of considerable interest, however, that in the monocondylic Archaeognatha, here represented by the bristletail *Machilis germanicus* (Fig. 7C), optic lobe organization resembles that in dicondylic Holometabola. As Golgi impregnations attest, there is little to distinguish its lamina monopolar cells from those of *Drosophila*, a clade that is a mere 30-million-years old compared to Archaeognatha, fossils of which are claimed for the Devonian (Labandeira et al., 1988), about 330 million years earlier. The machilid medulla is also typical of Insecta: an outer two thirds separated by the Cuccati bundle from the inner third, which provides small retinotopic neurons to the lobula, suggesting comparison to holometabolan T3 neurons and thus the possibility that such arrangements evolved before the evolution of flight.

3.4. *A hidden divergence of eumalacostracan optic neuropils (Fig. 8)*

Whereas the optic lobes of insects have undergone much diversification regarding the neural arrangements in and divisions of their lobulas, neuroanatomical evidence thus far demonstrates highly conserved arrangements of neural architecture across eumalacostracan optic lobes. For example, despite the localized region in the stomatopod's lamina, medulla and lobula representing the eye's retinal midband, the stratified organization of the medulla and all of the lobula exemplified in *Gonodactylus smithii* is hardly different from the medulla of the varunid crab *Neohelice granulata* and most of its lobula (compare: Thoen et al., 2017a, 2018; Sztarker and Tomsic, 2014). If the degree to which the visual world is reconstructed by a visual system is reflected by the number of computational strata within the medulla and lobula, then if these strata are similarly organized in widely different decapod crustaceans, this could suggest that optic lobes uniformly encode the same parameters of visual space independent of a species' local ecology. This seems implausible, however, because marine ecologies can differ starkly, so it is therefore revealing that differences of neural circuitry across Eumalacostraca become most apparent after revealing the organization of inhibitory elements within seemingly equivalent neuroarchitectures. As demonstrated earlier (Sinakevitch et al., 2003), neurons containing the inhibitory transmitter gamma-aminobutyric acid (GABA)

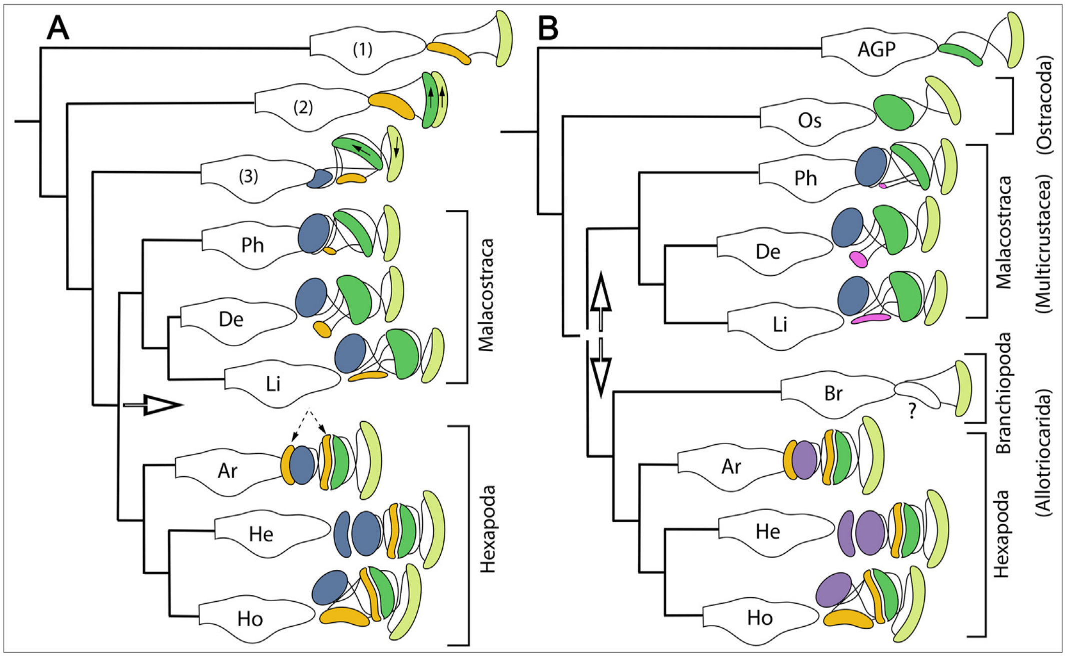

Fig. 10. Conjectured evolution of nested optic lobe neuropils before (A) and after (B) congruence of neuroanatomical data with molecular phylogenetics. (**A**) Summarizes proposed evolution of chiasmata and optic lobe neuropils (from, Strausfeld, 2005). A hypothetical branchiopod-like ancestral organization (1) would have been equipped with a lamina (light green) generated by the outer proliferation zone connected by uncrossed axons to a lobula plate-like tectum (orange) generated by the inner proliferation zone. Successive transformations involved lamina duplication (2), counter directional development of the subsequent layers (2) resulting in crossed retinotopic connections (3), and the separated inner layer (the medulla - dark green) retaining its uncrossed axons to the ancestral tectum. Subsequent outgrowth of the lateral protocerebrum was proposed as the origin of the lobula (3 - dark blue). This phyllocarid-like organization was suggested as ancestral to both Malacostraca and Hexapoda (outward arrow at node), subsequent differences within each lineage explained as evolved divergences, e.g., Phyllocarida (Ph), Decapoda (De) and Peracarida (*Ligia*; Li in malacostracans), and a novel inner medulla (orange) originating from the inner optic anlage in insects. Alternative locations of the insect lobula plate are immediately beneath the lobula (Archaeognatha; Ar), or opposite it (Holometabola; Ho), or its evolved loss/diminution (Hemimetabola; He). The inner medulla is retained, however. (**B**) A modern reassessment: congruence of neuroanatomical data with genomic relationships (Oakley et al., 2013; Schwentner et al., 2017). A chilopod-like ancestral ground pattern (AGP) with a chiasma linking the lamina and medulla (light and darker green) may typify extant visual Ostracoda (Os), belonging to Oligostraca, the outgroup of Multicrustacea + Allotriocarida. Currently, although still open to re-examination, the ancestral lamina ground pattern and first chiasma is shown persisting through pancrustacean evolution, as is the entire medulla in malacostracans and its homologue in insects – the volume of medulla distal to the Cuccati bundle. The insect's inner medulla derives from the inner optic anlage as do the lobula plate (orange) and lobula (purple). Branchiopoda (Br) is recognized as basal to Hexapoda. Its optic lobes may have evolved convergently or, alternatively, its optic lobes have retained the medulla and lobula plate and their uncrossed connections but have lost the lamina and lobula. In Multicrustacea, the medulla is undivided. The lobula (dark blue) is suggested to have evolved convergently as have various satellite neuropils (magenta) adjacent to the medulla and lobula. Early divergence from a hypothetical ostracod-like ancestor (see text) is indicated by the expanded arrows (see text).

are plentiful in the pancrustacean optic lobes and their organization reveals intriguing differences across species of insects. For example, the distribution of GABA in the lobula plate of a fly is markedly different from that of a sphingid moth even though silver stains suggest close similarities of neural architectures (Sinakevitch et al., 2003).

Application of antibodies raised against GAD, the enzyme that catalyzes decarboxylation of glutamate to GABA, shows that where Bodian methods suggest closely corresponding organization, GAD immunoreactivity reveals taxon-specific distinctions (Fig. 8). For example, silver staining resolves the optic lobe of the fiddler crab *Uca* as barely distinguishable from that of the shore crab *Hemigrapsus* (compare Figs. 6A and 7B). Yet these two species, resolved by anti-GAD immunohistology show major differences of immunoreactive distributions and intensities (Fig. 8A and B). Likewise, two sister species belonging to Thoridae, *L. groenlandicus* and *Spirontocaris lamellicornis*, both benthic rock dwellers but only one reported as a cleaner shrimp, show specific differences of GAD immunoreactivity in their layering (Fig. 8D and E). In contrast, the glass shrimp *Palaemon pugio*, despite reduced silver revealing layers in the medulla and lobula typical of caridean shrimps, shows further differences of anti-GAD immunoreactivity (Fig. 8F and G). The optic lobe of the whiteleg shrimp *Penaeus vannamei* (Fig. 8C) shows constrained anti-GAD immunoreactivity in the medulla, but multiple immunoreactive layers in the lobula. Such immunohistological distinctions suggest divergent evolution of inhibitory circuitry in what appear to be almost indistinguishable neuroarchitectures revealed by silver impregnation.

3.5. *The ancestral pancrustacean optic lobe and elaboration through convergence*

Not only Hanström (1926) envisaged a branchiopod-like ancestor of insects. In proposing a similar ancestor for the freshwater emergence of Hexapoda, Glenner et al. (2006) found support from molecular data initially resolving the sister relationship of Crustacea and Hexapoda (Giribet et al., 2001). However, proposing Branchiopoda as a proxy ancestor has had to take into account that there is no chiasma between its first (lamina) and its second optic neuropil. Various arguments have been deployed to account for the evolution of chiasmata, one of which argued for an inversion of the branchiopod-like second optic neuropil and hence the formation of a chiasma (Elofsson and Dahl, 1970; Wildt and Harzsch, 2002). A second hypothesis (Strausfeld, 2005) argued for a duplication of an outer proliferation zone in a branchiopod-like ancestor to provide two neuropils growing in opposite directions thereby connected by crossing axons: the outer neuropil a *de novo* neuropil; the inner layer populated by more neurons but retaining its uncrossed connections to the now more deeply displaced (erstwhile) second neuropil of the branchiopod-like ancestor. The lobula, which originates from an inner proliferation zone (Fischbach, 1983), was proposed to have

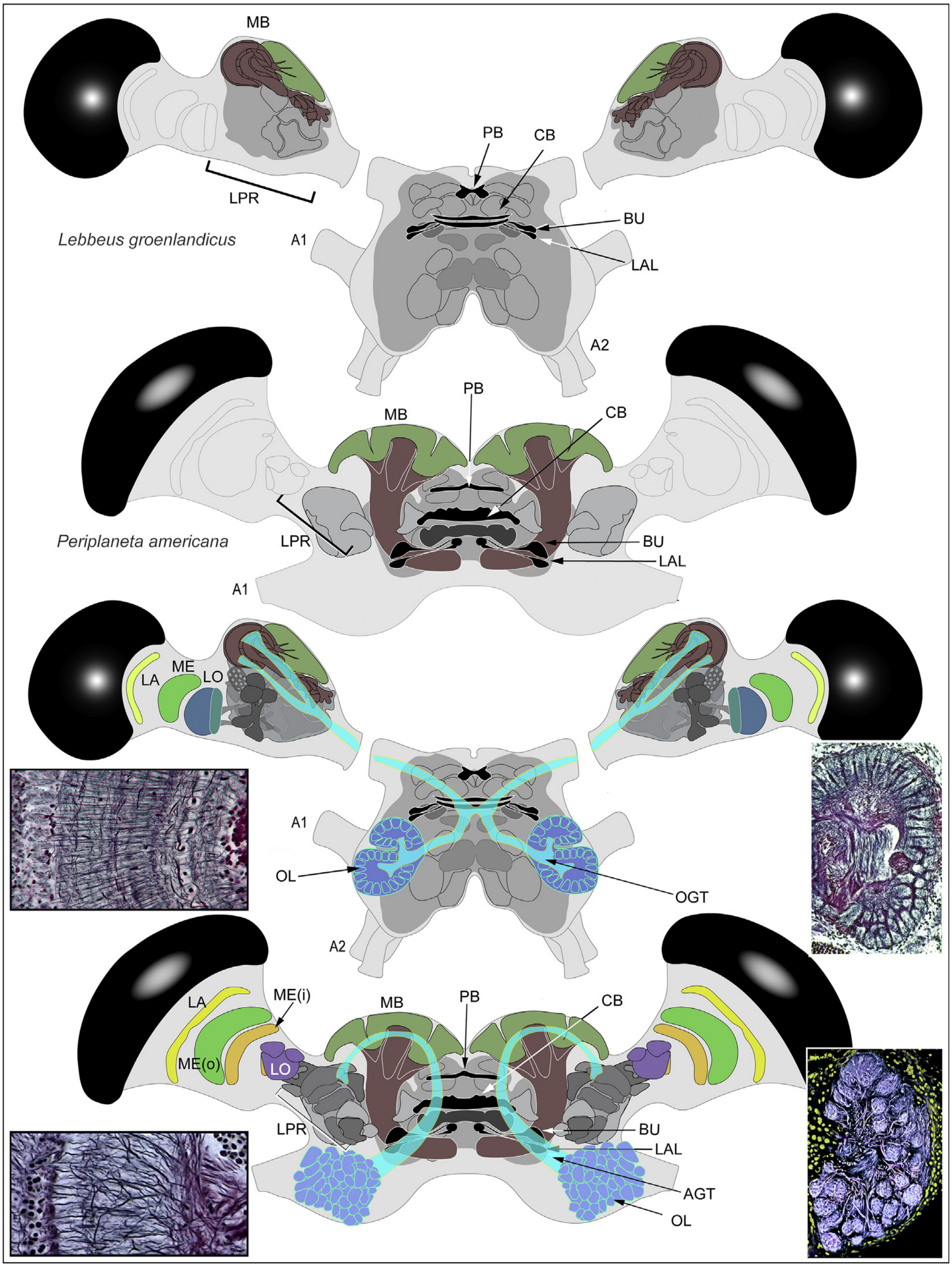

Fig. 11. Genealogical correspondence, homoplasy and divergence. Correspondence of the central complex and mushroom bodies (upper two figures) in Eumalacostraca (*Lebbeus groenlandicus*) and Insecta (*Periplaneta americana*) reflect the evolutionary stability of the mandibulate protocerebrum. Here the homologous protocerebral centers are the mushroom bodies (MB) and the central complex, comprising the central body (CB), protocerebral bridge (PB), buttress (BU), and the lateral accessory lobe (LAL). These corresponding arrangements across Pancrustacea contrast with evolution of sensory systems and their cognate neuropils. Here differences of sensory neuropil organization (lower two figures, same species) speak against assumptions of common ancestral arrangements (see text). Divergent evolution of the optic lobe medullas (ME) is indicated by the insect medulla being divided into an outer two thirds and inner third [ME(o), ME(i)], the latter derived from the inner optic anlage, as is the lobula complex (LO). Convergent evolution is revealed at the level of the lobula here exemplified by the spacing of retinotopic efferent neurons in a crustacean (upper left inset) and an insect (lower left inset). Neural architectures of the olfactory lobes (OL) reflect divergent organization between crustaceans (upper right inset) and insects (lower right inset). These differences relate to genetic distinctions of their olfactory receptor neurons, the circuitry within the lobes, and thus the encoding of odorants. Other abbreviations: OGT, AGT, olfactory globular tract, antennal glomerular tract; A1, A2, first, second antennae.

evolved later thus suggesting a younger age than the neuropil supplied by uncrossed axons (Strausfeld, 2005).

At this juncture, it is important to refer here to the influential 1997 paper by Nilsson and Osorio, proposing that, although Branchiopoda and Malacostraca shared a common ancestor, their compound eyes and optic lobes may have evolved separately (Nilsson and Osorio, 1997). Retinotopy hallmarks the optic lobes of both but only in malacostracans and insects are there three successive neuropils linked by chiasmata and equipped with morphologically similar neurons. Nilsson and Osorio (1997) thus advocated that these commonalities indicate that Malacostraca and Insecta likely shared a common ancestor possessing chiasmata. Neural cladistics likewise came to a similar conclusion (Strausfeld and Andrew, 2011).

However, we here return to the fact that these views have since been displaced by genetic analyses demonstrating that Hexapoda is most closely related to Remipedia, a class of blind homonomous anchialine crustaceans (Regier et al., 2010). Further advances by Oakley et al. (2013) which defined two major pancrustacean clades, Multicrustacea and Allotriocarida, showed that the latter also include Branchiopoda and Cephalocarida in addition to the insect-remipede lineage. Cephalocarida have been subsequently identified as the most stemward lineage of Allotriocarida (Schwentner et al., 2017; Lozano-Fernandez et al., 2019), thus supporting the cephalocarid—branchiopod—remipede trajectory and the marine origin of Hexapoda.

Apart from Hexapoda, the only allotriocarid lineage possessing compound eyes and possessing retinotopic neuropils is Branchiopoda, species of which, such as *Triops* and *Artemia*, possess just two nested neuropils. These are not connected by a chiasma, suggesting either independent evolution of the branchiopod optic lobes or a diminution and modification of an ancestral organization that was closer to that of Insecta (Fig. 9). Figure 10 compares the now defunct scenario of malacostracan + insect optic lobe evolution (Fig. 10A) from a branchiopod-like ancestor (Strausfeld, 2005) with the current assignation of optic lobe morphologies (Fig. 10B) to pancrustacean lineages defined by molecular phylogenetics (Oakley et al., 2013; Schwentner et al., 2017; Lozano-Fernandez et al., 2019).

Branchiopoda are excluded as a proxy for an ancestral pancrustacean visual system. However, Eucrustacea is sister to Myriapoda, one lineage of which is equipped with a visual system comprising two optic neuropils linked by an optic chiasma (Fig. 9). This is exemplified in the basal chilopod *Scutigera coleoptrata* (Sombke and Harzsch, 2015). Sombke and Harzsch make the crucial suggestion that because optic lobe organization in *Scutigera* is essentially not different from a eucrustacean lamina and medulla, absent a lobula, it could be considered as a proxy for the mandibulate optic lobe ground pattern (Fig. 10B). Although poorly documented, histology of the ostracod *Cypridina (Doloria) livis* (Cannon, 1931), belonging to Oligostraca, which is the earliest group to diverge from the eucrustacean stem (Oakley et al., 2013), likewise suggests just two nested optic neuropils as a possible ancestral optic lobe.

Where does this take us? The answer is to reject one (Fig. 10A), but to entertain three alternative scenarios that could reconcile neuroanatomy with eucrustacean divergence as resolved by molecular phylogenetics. One is the scenario shown in Fig. 10B, which can as plausibly invoke a scutigeromorph-like common ancestor of Pancrustacea (Oligostraca + Multicrustacea + Allotriocarida) that lacked a lobula or an oligostracan-like ancestor of Multicrustacea + Allotriocarida that, if sightless, lacked all optic neuropils. One proposed alternative is to invoke an ancestral organization corresponding to the malacostracan-like ground pattern: namely, already comprising three nested neuropils (Harzsch, 2002; see also Fig. 4: in Fanenbruck et al., 2004: Harzsch, 2006). This rationalizes the presence of a lobula plate and inner medulla as constituting an apomorphy of Insecta. A third, and possibly most attractive alternative for Fig. 10B, is introduced by the finding from molecular phylogenetics of multiple losses and re-evolution of compound eyes in Ostracoda belonging to Oligostraca, which is the outgroup of Multicrustacea + Allotriocarida. In extant ostracods, the absence or presence of eyes is correlated, respectively, with abyssal (unlit) or shallow (lit) water habitats. Certain shallow water species equipped with eyes have descended from eyeless ancestors (Oakley and Cunningham, 2002; Syme and Oakley, 2012). If the common ancestor of Multicrustacea + Allotriocarida was an eyeless ostracod-like taxon that lacked optic lobes (as does Remipedia), might the first stem representatives of Multicrustacea and of Allotriocarida have been eyeless as well? Compound eye growth and hence neural organization is coupled with that of the underlying lamina and medulla (see, Courgeon and Desplan, 2019). If eyes re-evolved independently in Multicrustacea and Allotriocarida, so would their two outer optic neuropils, with corresponding convergent evolution of their lobulas. Further studies are needed to determine whether neuronal types and connectivities generated by the outer proliferation zones in malacostracans, branchiopods, and insects suggest convergent evolution at those more distal levels of the optic lobe.

In conclusion, differences between the malacostracan and insect optic lobes amplify a phenomenon that has been much discussed, namely the distinction between the evolutionary stability of the arthropod protocerebrum and the evolutionary lability of its sensory interfaces. Comparisons across extant arthropods suggest that even before the early divergence of chelicerates and mandibulates, central brain organization has remained stable over hundreds of millions of years (Strausfeld et al., 2016). In contrast, it is sensory surfaces and their immediate neuropils that are evolutionarily labile. Consider the two examples shown in Fig. 11. Allowing for minor differences, the protocerebrum and its cardinal centers — the central complex and mushroom bodies — of a decapod crustacean and a neopteran insect exemplify stable genealogical correspondence. But despite their apparent similarities, across Pancrustacea sensory neuropils supplying information to those higher centers do not necessarily correspond. Distinctions of eumalacostracan and insect sensory neuropils exemplified by their lobulas can be suggested to be a consequence of convergent evolution. Other distinctions suggest not convergence but divergence, where computational substrates of an ancestral ground pattern evolve modifications in response to innovations in their sensory surface, such as the departure of the insect olfactory lobes from the crustacean ground pattern reflecting the innovation of ligand-gated olfactory sensory neurons (see also: Harzsch and Krieger, 2018).

Acknowledgements

We thank Camilla Strausfeld for discussion and advice in improving iterations of the manuscript leading to this final version. We thank Greg Edgecombe for his observations and suggestions, and two reviewers for their constructive opinions. This research was supported by the US National Science Foundation Grant no. 1754798.

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