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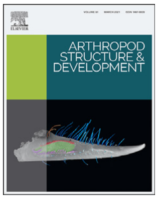

The lobula plate is exclusive to insects

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ABSTRACT

Just one superorder of insects is known to possess a neuronal network that mediates extremely rapid reactions in flight in response to changes in optic flow. Research on the identity and functional organization of this network has over the course of almost half a century focused exclusively on the order Diptera, a member of the approximately 300-million-year-old clade Holometabola defined by its mode of development. However, it has been broadly claimed that the pivotal neuropil containing the network, the lobula plate, originated in the Cambrian before the divergence of Hexapoda and Crustacea from a mandibulate ancestor. This essay defines the traits that designate the lobula plate and argues against a homologue in Crustacea. It proposes that the origin of the lobula plate is relatively recent and may relate to the origin of flight.

1. Introduction

It is uncontested that pancrustaceans (Crustacea + Hexapoda) equipped with prominent compound eyes respond behaviorally to visual motion of one kind or another (crustaceans: Berón de Astrada and Tomsic, 2002; Medan et al., 2007, 2015; Scarano et al., 2018; insects: Mu et al.,2014; Wu et al., 2016; Ribeiro et al., 2018; Rosner et al., 2019) and that stimuli eliciting those behaviors are reconstructed and encoded by circuits in the optic lobes. In crabs, neurons situated in the deepest levels of the optic lobe's lobula respond to optic flow (Horseman et al., 2011). In fast-flying insects, such as flies and moths, information about optic flow is encoded within a specific neuropil called the lobula plate (Borst et al., 2020). The neurons associated with this neuropil, and the network organization they provide, have been the subject of intense research for many years, the outcome of which is the recognition that the lobula plate responds to changes of optic flow over the retina and hence plays a crucial role in maintaining visual balance (e.g., Krapp et al., 1998; Krapp, 2000; Maimon et al., 2010). Information about those changes is relayed by fast conducting tangential neurons from the lobula plate to the thoracic ganglia, where it is integrated with signals provided by sensory systems detecting angular acceleration, airflow, and other relevant sensory cues, such as changes in odorant densities when the insect's flight is directed towards a relevant attractor (Frye and Dickinson, 2003; Sherman and Dickinson, 2003; Dickinson, 2005).

Arrangements of neurons contributing to the lobula plate's neuropil are known in great detail and have been identified across species of holometabolous insects, with particular attention paid to Diptera, represented by *Calliphora* and *Drosophila*. Recordings from, and dye fills of, the largest neurons in the lobula plate, known as "lobula plate tangential neurons," provided the first insights from *Calliphora* about relationships between the dendritic organization of these neurons and their responses to specific directions and orientations of visual motion across the retina (Hausen, 1982; 1984; Hengstenberg, 1982; Hengstenberg et al., 1982). Recordings from small neurons in *Calliphora,* called T4 and T5 neurons, that terminate on tangential neuron dendrites showed that the detection of motion is computed at the level of their dendrites at levels distal to the lobula plate, namely, in the innermost layer of the medulla and outermost layer of the lobula. Because the dendritic spread of a T4 or T5 neuron is small, supplied by relays representing just a few facets of the compound eyes, the detection of visual motion by a T4 or T5 neuron must be localized to just a small area in the visual field (Douglass and Strausfeld, 1995). That T4 and T5 neurons occur with great abundance and that their spacing represents every facet of the compound eye was first recognized in 1915 by the Spanish neuroanatomist Ramón y Cajal (Cajal and Sanchez, 1915). That organization meant that the entire retina is represented by those neurons across the entire lobula plate.

For the last 20 years or so *Drosophila* has been the workhorse on which genetic tools are used for dissecting, in great detail, the lobula plate's functional organization and development. In-depth confirmation and expansion of those early studies have greatly

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increased our knowledge about the biophysics and behavioral relevance of the fly's visual system (Joesch et al., 2010; Maimon et al., 2010; Chiappe et al., 2010; Maisak et al., 2013; Davis et al., 2020; Wei et al., 2020; Borst et al., 2020). We now recognize that the wide-field tangential neurons and the T4 and T5 neurons supplying them are two integral components of a set of traits that uniquely defines homologous centers across members of Holometabola thus far examined (Table 1). If lobula plate homologues exist in other pancrustacean lineages, they should be identifiable by those traits and the unique organization that they provide.

2. How old is the lobula plate?

Received opinion has it that lobula plates are ubiquitous to mandibulate arthropods. Studies on crustaceans claiming structural homologues of the insect lobula plate (e.g., Strausfeld, 2005; 2009; Bengochea et al., 2018) have contributed to the notion that this neuropil must have originated very early, possibly in the lower Cambrian (Shinomiya et al., 2015, 2019) before divergence to the three existing mandibulate lineages: Myriapoda, Crustacea, and Hexapoda, the last two comprising the subphylum Pancrustacea. An aim of this essay, therefore, is to consider whether there is evidence for the transphyletic occurrence of the lobula plate and thus whether an ancient origin of this neuropil is plausible.

3. The lobula plate is defined by conserved traits in holometabolous insects

An optic lobe of a mandibulate (Myriapoda + Pancrustacea) comprises a series of nested neuropils beneath the retina. In order, from distal to proximal, these neuropils are the lamina, medulla, and (in Pancrustacea) the lobula complex. The neuropils are connected by sequential chiasmata. Just one lineage of crustaceans, Malacostraca, has members that possess all three optic lobe neuropils (Bellonci, 1882; Hanström 1924). In insects, the lobula complex in different species can comprise between two and as many as five nested retinotopic neuropils proximal to the medulla (Rosner et al., 2017). Lobula plates (Fig. 1A) are defined by a set of distinct neuroanatomical features, called traits, the entire set of which, up to the time of writing, have been verified only in Holometabola (illustrated in Fig. 1, listed in Table 1). However, three traits in Table 1 are also mapped onto Odonata because, as described in the last section of this essay, they indicate neuroanatomical properties that suggest possible homology with three traits in Holometabola. Fig. 1A–H and 2A, B illustrate examples of defined lobula plate traits. Fig. 2C–G demonstrates the stark distinctions between these traits and features defining satellite neuropils adjacent to the medulla and lobula that have been claimed in earlier studies of Malacostraca (cited below) as lobula plate homologies or homoplasies.

The traits shown in Table 1 are organized to provide a shallow tectum-like neuropil, in which wide-field tangential neurons (trait #6, Fig. 1D) occupy distinct strata visited by the terminals of quartets of T4 and T5 neurons (traits #2, 3, 5, Fig. 1B,C,E) that converge onto them to establish a precise retinotopic representation of the retinal mosaic (trait #5, Fig. 2A and B), as predicted by Braitenberg's (1970) studies of the retinotopic organization of the fly (*Musca domestica*) optic lobes.

The disposition of the lobula plate with respect to the other retinotopic neuropils is shown in Fig. 3. Other than in hymenopterans, the lobula plate is situated alongside the lobula, with its outer surface facing that of the lobula. In the honeybee the corresponding neuropil is situated proximal to, and contiguous with, the lobula. Hymenoptera is the most basal holometabolous lineage (Misof et al., 2014), and it is reasonable to assume that this location is the lobula plate's ancestral location.

As outlined above, the honey bee lobula plate resides proximal to the lobula and is visited by the terminals of T4 and T5 neurons (Fig. 3), morphologically identical to those found in flies (Cajal and Sanchez, 1915). These visit large diameter wide-field tangential

Table 1
Traits defining the lobula plate (LOP) are shown in bold typeface. Hemimetabolous neopteran insects are excluded from analysis (explanation in text), the exception being Odonata due to putative homologies with dipteran traits (italicized; explanation in main text). Traits 1–6 are also indicated in the legends for Figs. 1 and 2A, B. *Scutigera* is included as a proxy for the ancestral optic lobe (Strausfeld and Olea-Rowe, 2021).

OPTIC LOBE TRAITS LOP-DEFINING TRAITS 1-6	TAXA IN WHICH THESE TRAITS ARE EXPRSSED			
	MALACOSTRACA	HOLOMETABOLA	ODONATA	SCUTIGERA
Outer optic chiasma (Och 1)	✓	✓	✓	✓
Inner optic chiasma (Och 2)	✓	✓	✓	
Undivided medulla (ME)	✓			✓
#1. Inner medulla; ME(i)		✓	✓	
Multiple >2 lobula complex neuropils			✓	
#2. Quartets of T4 neuron dendrites in ME(i)		✓		
Quartets of T4-like neurons from ME(i)			✓	
#3. Quartets of T5 neurons dendrites in outer stratum of lobula		✓		
Quartets of "T5-like" neurons from outer stratum of lobula neuropil LO1			✓	
#4. Precise uncrossed retinotopic projections provided by T4 and T5 neuron axons into levels of large field tangential cells (#6)		✓		
#5. Segregation of T4 and T5 terminals onto layered wide-field tangential cells (#6).		✓		
Small satellite neuropil of ME and LO lacking traits 2-6	✓			
#6. Large-diameter, wide-field tangential neurons with layered dendritic trees		✓	✓	

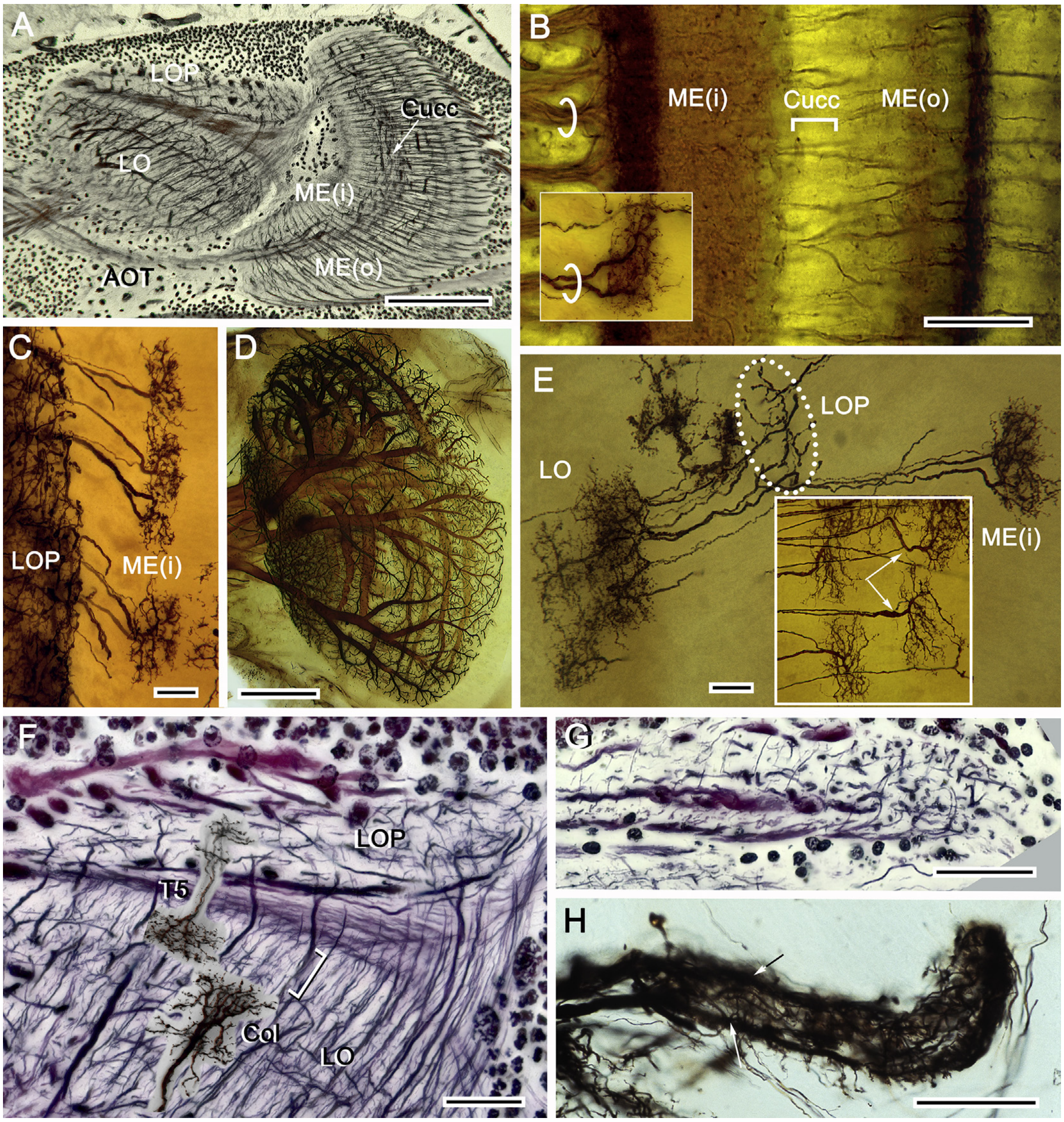

Fig. 1. Defining phenotypic traits of the lobula plate. A-E. The medulla and lobula complex of *Calliphora erythrocephala*. Axons from the Cuccati layer (arrowed Cucc) extend centrally as the anterior optic tract (AOT). The Cuccati layer separates the outer medulla [ME(o)] from the inner medulla [ME(i)] (trait 1, Table 1). The lobula plate (LOP) is linked to the medulla by uncrossed axons as it is to the lobula (LO) (trait 4, Table 1). B. Cobalt-silver stained medulla demonstrates the dense layer of T4 dendrites at the deepest level of ME(i) where pairs of columns give rise to two bundles each composed of four T4 axons (circled) that project to the lobula plate (trait 2, Table 1). The inset shows two corresponding Golgi-impregnated T4 neuron dendritic trees. C. T4 neurons axons maintain their retinotopic order between the medulla and lobula plate here shown extending into dense arrangements of tangential cell dendrites. D. Entire lobula plate stained with cobalt–silver showing layered the dendritic trees of wide diameter lobula plate tangentials (trait 6, Table 1) extending across the entire neuropil, thus subtending the entire projected retina. Here dendritic trees of three tangential cells provide horizontally oriented fields; dendritic fields of 10 tangential neurons provide vertically oriented fields. E. The axons of T4-neurons from the inner medulla (ME(i)) and T5-neurons (trait 3, Table 1) from the lobula (LO) shown converging to the same locus in the lobula plate (LOP, within dotted oval). The inset shows the characteristic asymmetry of T-neuron (here T5) dendritic fields (arrowed) aligned along the same orthogonal axis. F. Reduced silver stained section of the lobula complex of *Musca domestica*, showing the lobula plate's relationship with the lobula, the outer layer of which contains T5 neuron dendrites. Here one Golgi impregnated T5 neuron has been superimposed (upper) to illustrate distinctive separation of the specialized T5 layer from the lobula's columnar neurons at deeper levels, one here also superimposed (Col). This T5 neuron is shown ending at one of four orientation-direction specific layers (*Musca*) in the lobula plate (trait 5, Table 1), each receiving converging T5 and T4 terminals. G. Longitudinal section, corresponding to the orientation of the LOP in panel F, showing the layered arrangements of wide-diameter tangential neuron dendrites in an odonate optic neuropil (*Libellula saturata*) possibly corresponding to the holometabolan lobula plate. H. Lobula plate tangentials (arrowed) of the butterfly *Pieris brassicae*. This Golgi-impregnated specimen is one prepared by Domingo Sanchéz, Ramón y Cajal's collaborator, for their transformative 1915 paper. Scale bars: A, H, 100 μm; B, G, 25 μm; C, E, 10 μm; D, 50 μm; F, 20 μm. Panels B, D. modified from Strausfeld (2012).

neurons that encode the direction in panoramic visual motion (Ibbotson, 1991), corresponding to those parameters encoded by tangential cells in the dipteran lobula plate (Hausen 1982; Hengstenberg et al., 1982; Krapp et al., 1998). Genetic manipulations of *Drosophila* that block subsets of T4 and T5 neurons demonstrate that these, and only these neurons, drive the directionally selective responses of tangential neurons (Schnell et al., 2012), and it is probably safe to assume that the same is true for T4 and T5 neurons in Hymenoptera. The conclusion drawn from these observations is that traits defining the lobula plate appeared at least by the end of the Permian or Early Triassic, about 250 million years ago, the time of divergence of Hymenoptera from the pterygote stem (Misof et al., 2014). A morphogenic shift in location of the lobula plate to one where it faces the lobula may have evolved as a more efficient segregation of the flow-field pathway. In addition, evolved modifications of the number, stratification, and axon-specific variations of the dendritic organization of lobula plate tangential neurons (but not of T4 or T5 neurons) may

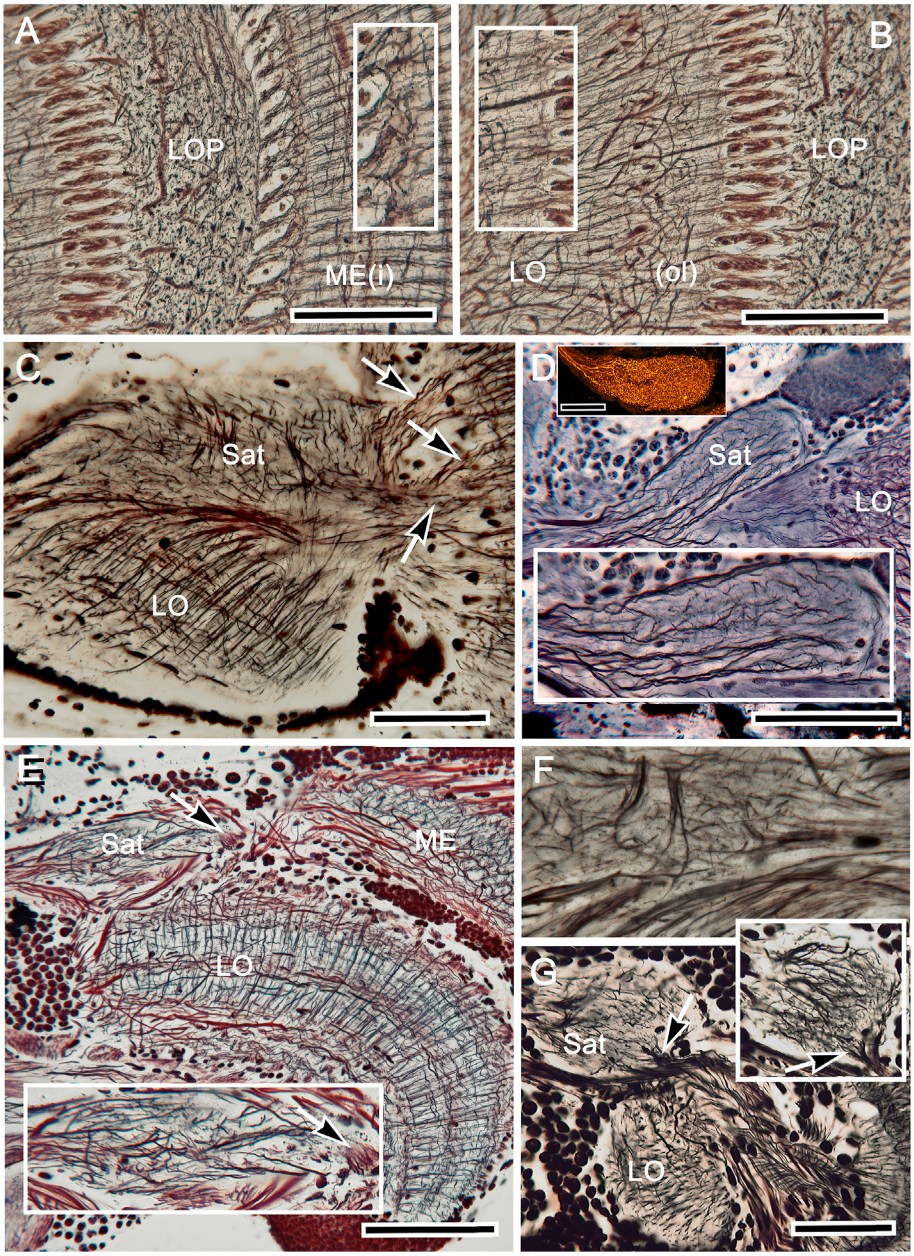

Fig. 2. Absence of lobula plate traits in decapod satellite neuropils. A. Reduced silver-stained lobula complex neuropil of the holometabolous insect *Calliphora erythrocephala* demonstrating retinotopic mappings (trait 4, Table 1) from the medulla's inner layer [ME(i)] (trait 1, Table 1) to the lobula plate (LOP). Inset shows axon bundles from pairs of adjacent columns. B. The same precision of projections is resolved between the lobula (LO) and LOP. Inset shows an enlargement of the lobula's outer layer (ol) from which T5 dendrites send their axons to the lobula plate (see Fig. 1F). C. Satellite (Sat) neuropil of the medulla and lobula of *Ligia occidentalis* linked to the medulla by chunked projections of axons (arrowed) lacking evidence of retinotopy. D. Lobula satellite neuropil of the fiddler crab (*Uca minax*) equipped with slender tangential fibers but lacking retinotopic inputs. The upper inset shows 5HT-labelling of this neuropil in *Hemigrapsus*, suggesting a role in visually-gated neuromodulation. E. Satellite neuropil of the medulla and lobula in the shore crab *Hemigrapsus nudus* showing chunk projections from the medulla (arrowed). Inset shows diffuse layers of slender tangential processes in the satellite neuropil that contrast with tangential organization of the holometabolan lobula plate (Fig. 1F). F. Detail of the lobula plate of *L. occidentalis* showing the absence of retinotopy (see also Sinakevitch et al., 2003 loc. cit. 8E, F) G. Two levels of the satellite neuropil in shrimp *Palaeomonetes pugio* showing dendritic trees associated with chunk projections from the medulla (arrows). Scale bars A–C, G, 50 μm; D, E, 100 μm; inset to G, 50 μm.

have been driven by different ecologically imposed requirements in flight performance (Buschbeck and Strausfeld, 1996, 1997; Buschbeck, 2000).

4. Lobula plates relate to the inner medulla, an exclusively hexapod trait

A fundamental difference in the organization of insect and crustacean medullas obviates homology between the holometabolan lobula plate and a neuropil in malacostracans that is satellite to the medulla and lobula. In insects, the medulla is a developmentally hybrid neuropil divided by the Cuccati layer. The two-thirds of the medulla distal to the Cuccati layer arise from progenitors that are distinct from those providing the inner third. This was demonstrated in 1983 (Fischbach, 1983) by observations of the eyeless (*ey*) mutation of *Drosophila*, which abolishes the development of the lamina and the outer two-thirds of the medulla, but spares the proximal

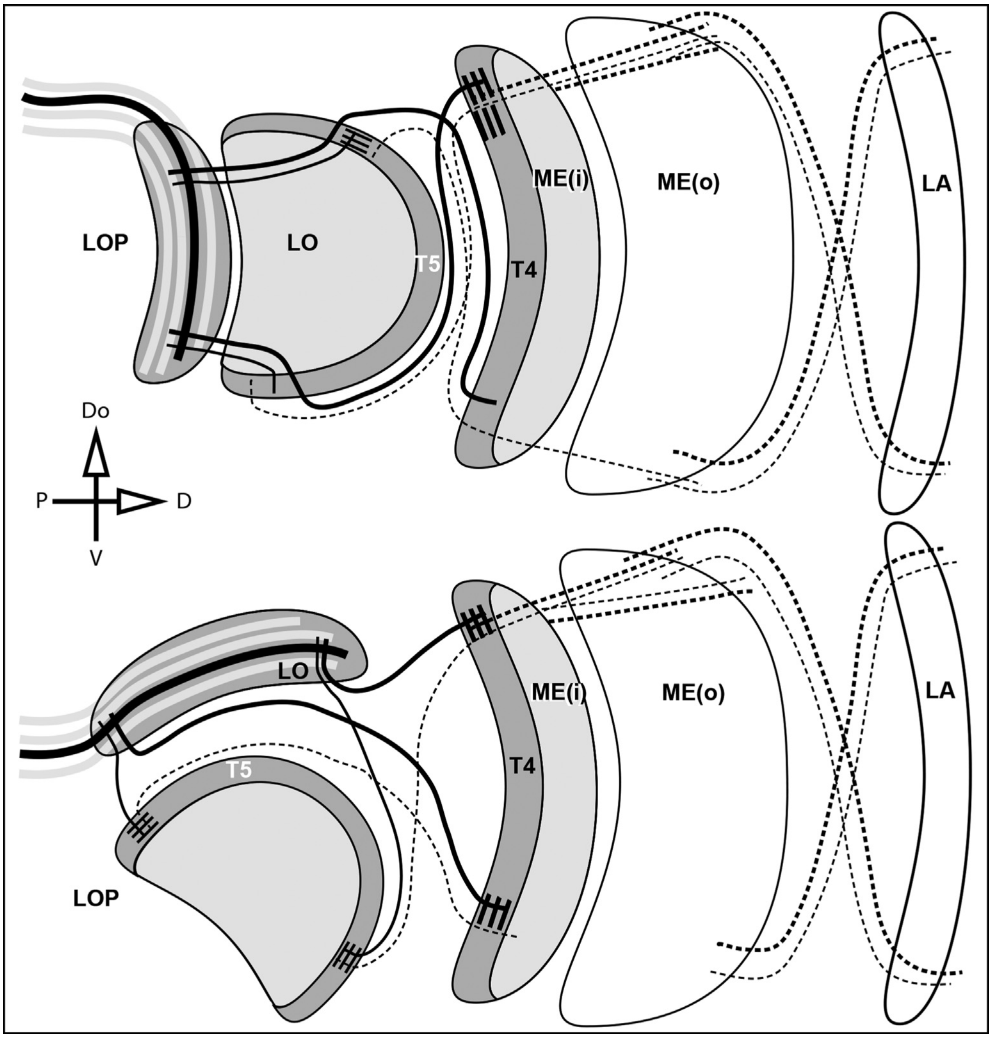

Fig. 3. The disposition of nested optic lobe neuropils in the honey bee (upper) and a dipteran (lower). Neuropils are shown from distal to proximal: LA, lamina (retina not shown); ME(o), ME(i), outer and inner medulla; LO, lobula; LOP, lobula plate. The hymenopteran lobula plate is also referred to as the inner lobula layer. Axes are idealized (dorsal, Do; ventral, V; distal, D; proximal, P) referring to the neuraxis. The T4 and T5 neuron dendrites in their respective levels of the inner medulla [ME(i)] and most distal lobula layer receive paired parallel channels relayed from the lamina (LA) through the outer [ME(o)] and inner medulla. One channel terminates in ME(i) in its T4 layer; the second extends to the T5 layer of the lobula plate. T4 and T5 axons originating from corresponding retinotopic loci in the medulla and lobula converge at layered wide-field tangential neurons that extend from the lobula plate centrally.

third of the medulla, the lobula, and the lobula plate. The inner third of the medulla is derived from the same embryonic population of neuroblasts (inner optic anlage) as that giving rise to the lobula and lobula plate (Hofbauer and Campos-Ortega, 1990). It is the inner third of the medulla and outermost stratum of the lobula that contain, respectively, the dendrites of T4 and T5 neurons. These neurons have been shown to be essentially identical, originating developmentally from a unique set of progenitor cells (Schilling et al., 2019). The characteristic quartet arrangement of each of these two cell types arising from that lineage relationship has been confirmed by genetic markers (Maisak et al., 2013; Schilling et al., 2019).

The decapod medulla lacks a Cuccati layer and is not divided into two distinct concentric regions. Studies on the developing decapod optic lobes (Harzsch and Dawirs, 1996; Harzsch et al., 1999; Harzsch, 2002) show no indication of lobula plate progenitors. A conclusion is that malacostracan optic lobe development does not provide lineages that would define an inner medulla neuropil, the consequence being that neurons genealogically corresponding to T4 neurons (and their sibling T5 neurons) do not exist. The absence of the latter is underscored by the apparent absence of a specialized outer layer of the malacostracan lobula.

5. Lobula plate homologues are not identifiable in crustacea

To promote the idea that the lobula plate, as defined by the traits in Table 1, is an ancient neuropil that originated in the lower Cambrian requires that these neuropils exist not only in insects such as flies but broadly across Pancrustacea and in mandibulate outgroups that possess compound eyes and optic lobes. Consequently speculation about an ancient lobula plate has found encouragement from neuroanatomical observations that identify small satellite neuropils associated with the decapod or isopod lobula and medulla. Examples are in *Pandalopsis dispar* (Strausfeld, 2005), and in *Nebalia pugettensis*, *Palaeomonetes pugio*, and *Ligia occidentalis* (Strausfeld, 1998; Sinakevitch et al., 2003). Those accounts suggested that these satellite neuropils, also called lobula plates, were in all probability homoplasic (i.e., convergent with the insect lobula plate; Strausfeld, 1998; Sinakevitch et al., 2003) and that their organization is distinct from that defining the holometabolan lobula plate (Fig. 2C–G). The single commonality is that holometabolan lobula plates and the decapod satellite neuropils are situated close to the medulla and lobula and have connections to one or both. Two studies of malacostracan optic lobes have, however, referred to these satellite neuropils as lobula plate homologues (Strausfeld 2005, 2009). This is here recognized as untenable. Studies of the shore crab *Neohelice granulata* (Bengochea et al., 2018) also propose lobula plate homology; however, its satellite neuropil appears to receive only a crude representation of the medulla's columnar organization by what appears to be “chunk representation” of its retinotopy, a term also employed for bulk retina-lamina projections in strepsipteran optic lobes identified by Buschbeck et al. (1999). A comparable representation is provided by visual neuron projections into insect optic glomeruli (Strausfeld and Nässel, 1981; Otsuna and Ito, 2006; Mu et al., 2012) and for inputs to the “lobula plate” analogue of semi-terrestrial isopods (Fig. 2C, F; and Strausfeld, 1998).

6. Optic flow is detected in the malacostracan lobula

If in malacostracan crustaceans there is no lobula plate as defined in Holometabola, then where are the circuits in malacostracans that encode information about optic flow? Large neurons responding to directional motion across the retina have been described as situated deep in the crab's lobula (e.g., Medan et al., 2015) at a level suggested as possibly analogous to the hymenopteran lobula plate (Strausfeld 2005, loc. cit. Fig. 13). Yet the crab's satellite neuropil, referred to as a lobula plate by Bengochea et al. (2018) has been suggested to be anatomically relevant to encoding visual flow. Intracellular recordings and dye fills (Scarano et al., 2020) demonstrate neurons with extensive planar dendritic fields in the lobula that respond to directional visual motion. These neurons terminate in a discrete neuropil in the lateral protocerebrum from where each sends a slender collateral process across the entire lateral protocerebrum. Their terminals in the Bengochea et al.‘s satellite neuropil appear equipped with varicosities suggesting presynaptic identity (Scarano et al., 2020, loc. cit. Fig. 3E). The question remains whether this satellite neuropil has any equivalence to the holometabolan lobula plate. It is relevant that this center in *Hemigrapsus nudus* is packed with anti-5HT (serotonin)–immunoreactive processes (Fig. 2D, upper inset). One possible interpretation is that activity in certain lobula efferent neurons, such as those described by Scarano et al. (2020), gates neuromodulatory activity in the satellite neuropil via their centrifugal collaterals.

The detection and encoding of optic flow across the decapod retina, that up to now is most comparable to that encoded by the fly lobula plate, has been demonstrated in the crab *Carcinus maenas* by Horseman et al. (2011) from intracellular recordings of centrally projecting tangential neurons originating deep in the lobula. This location corresponds to the comparable level of the honey bee lobula complex, in which tangential neurons respond to optic flow (Ibbotson, 1991). As historically documented (Cajal and Sanchez, 1915), and shown in Fig. 3 here, this proximal level of the honey bee lobula complex is the likely ancestral location of the holometabolan lobula plate. The conclusion that can be drawn is that the deep lobula of malacostracans may be the functional analogue of the insect lobula plate as proposed in Strausfeld and Olea-Rowe (2021. loc. cit. Fig. 5A–E).

7. Molecular phylogenetics speaks against an ancestral lobula complex common to malacostraca and hexapoda

Molecular phylogenetic analyses have determined that Malacostraca and Hexapoda are widely separate, as shown by the deep division of Multicrustacea (to which Malacostraca belongs) and Allotriocarida, whose Hexapoda are more closely related to Remipedia than either are to Malacostraca (Von Reumont et al., 2011; Oakley et al., 2013; Schwentner et al., 2017; Lozano-Fernandez et al., 2019). This implies that similarities of sensory neuropils previously considered as homologues in the brains of insects and malacostracans should in future be considered as a possible consequence of convergent evolution (Strausfeld and Olea-Rowe, 2021). Neuropils that can, however, be considered as comprising the optic lobes of the ancestral pancrustacean are the lamina and medulla, which today define the optic lobes of the sister mandibulate group Myriapoda. A proxy for an ancestral organization is *Scutigera coleoptrata* belonging to the oldest chilopod lineage Scutigeromorpha (Edgecombe and Giribet, 2019), the morphologically simple optic lobes of which consist of a lamina connected by an optic chiasma to an undivided medulla lacking a Cuccati layer (Sombke and Harzsch, 2015).

The proposal that the lobula plate must have originated in the lower Cambrian, before insects and crustaceans diverged (Shinomiya et al., 2015, 2019) is, therefore, extremely unlikely as it implies that the lobula plate, as defined by the traits in Table 1, would have to have been present in stem euarthropods before divergence of the stem providing the two existing mandibulate lineages, Myriapoda and Pancrustacea. Advocates of a Cambrian origin (Shinomiya et al., 2015, 2019), have looked for support also from *Fuxianhuia protensa*, a euarthropod from the lower Cambrian that shows evidence of fossilized soft tissues associated with the compound eyes (Ma et al., 2012). Although those fossil traces may correspond to the optic lobes, there is no evidence of traits indicative of a lobula plate.

8. Does the lobula plate relate to the origin of insect flight?

Holometabolous insects are renowned for their extraordinary versatility of flight behavior and control. But they are not alone: a far older clade is equally adept. This is Odonata (dragonflies, damselflies, skimmers, and darters), predators acclaimed both for their ability to calculate interception trajectories and for their spatial memory of their perches (Switzer, 1997; Eason et al., 2006; Olberg, 2012; Gonzalez-Bellido et al., 2016). Recordings from dragonfly optic lobes resolve units that differentiate the motion of a small target from background visual noise and neurons that “lock-onto” a moving visual target (Wiederman and O'Carroll, 2011; Lancer et al., 2019). Recent studies resolve neurons that respond to optic flow, although those cells are situated not in a neuropil that has been suggested to be the dragonfly's lobula plate, but rather in a region here designated as lobula #3 (LO3 in Fig. 4E; Evans et al., 2019).

Flies that chase each other possess circuits that maintain their target within their binocular field (Land and Collett, 1974; Collet and Land, 1978; Gronenberg and Strausfeld, 1991). Forward flight interrupted by intermittent bouts of aerobatic pursuit implies that neurons encoding optic flow coordinate with channels encoding small-field object detection (Nicholas et al., 2018). In view of similarities between the chasing behavior of flies and odonates, it might be expected that Odonata, in which optic lobe neurons respond to optic flow (Evans et al., 2019), possess circuits that, if not identical to those defining the holometabolan lobula plate, might show close similarities.

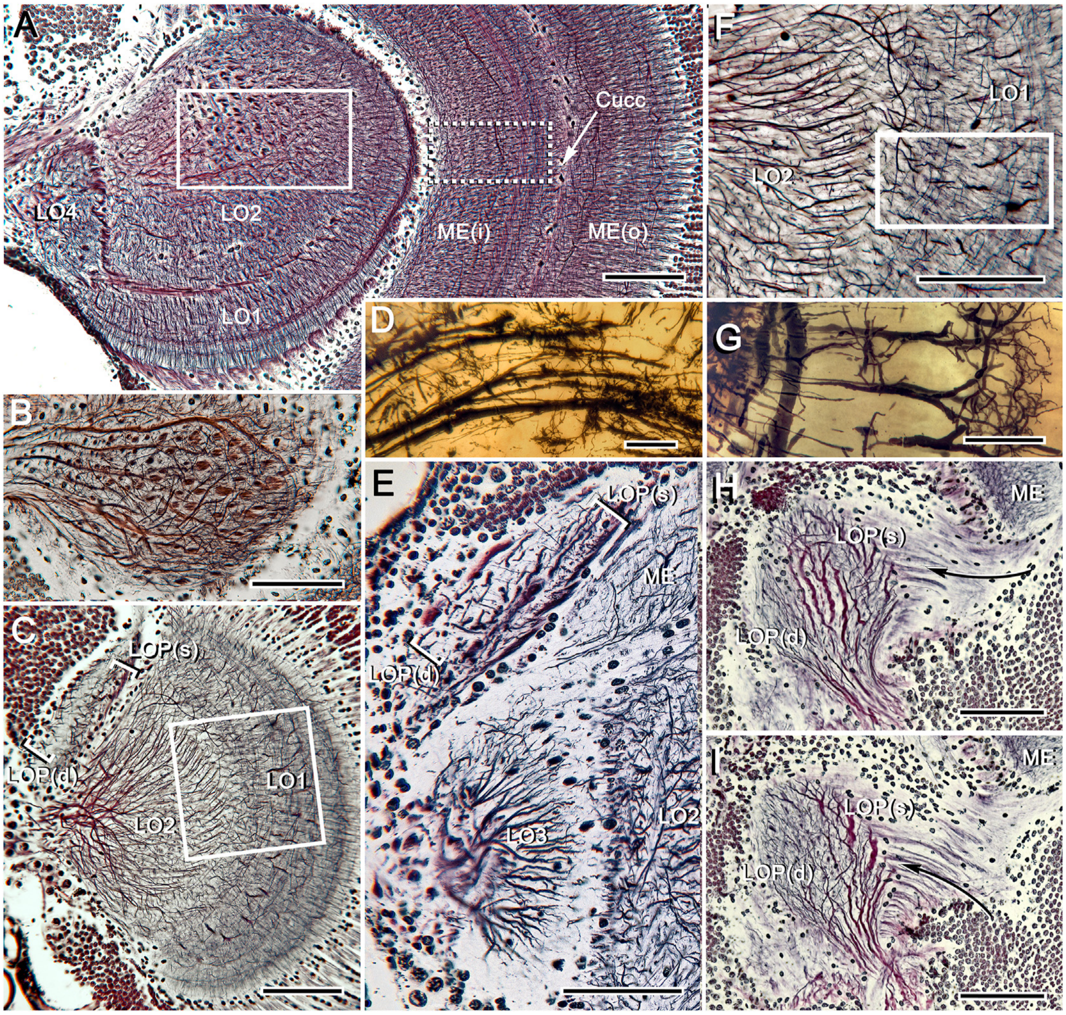

Fig. 4. The odonate medulla and lobula complex (*Libellula saturata*). A. Bodian-stained odonate optic lobe showing the succession of neuropils belonging to the outer and inner medulla [ME(o), ME(i)] separated by the Cuccati layer (Cucc, arrowed); and the first and second lobula neuropils (LO1, LO2) similarly separated, the second abutting a fourth neuropil situated proximally (LO4). The dotted area beneath the Cuccati layer (Cucc) corresponds to the level shown in Fig. 5B. B. Enlargement of an equivalent area boxed in A but at a slightly deeper level, showing tangential cell dendrites extending amongst regularly spaced retinotopic columns. C. LO1 with retinotopic projections to LO2, here shown with numerous axons of tangential cells converging to project from the optic lobe centrally. The cross-sectional profile of the lobula plate, which lies dorsally near the back of the optic lobe shows a clear division into a superficial and a deep layer [brackets, LOP(s), LOP(d)]. D. LOP tangential neurons resolved by Golgi impregnation. E. Details of the lobula plate and a third lobula neuropil (LO3) lying beneath LO4 (panel A) denoted by large regularly branching tangential neurons. F. An area of LO1, boxed in panel C, showing ensembles of columnar neurons and, beneath, arrangements of tangential neurons. G. Golgi-impregnated elements corresponding to neurons boxed in panel F. H, I. Two “top-down” oblique views of the lobula plate, the first (panel H) illustrates the swathe of axons (arrowed) extending into it from the inner medulla. The second (panel I) illustrates cell body fibers (arrowed) sweeping into it from a crowded population of minute cell bodies that form a posterior rind lining the optic lobe. Annotations in Fabian et al., (2020) differ from those present here, which may have to be revised accordingly: LO1 = PLO(o) + PLO(i); LO2 = ILO; LO3 = SLO; LO4 = MLO; LOP = LOP. Scale bars: A, C, 100 μm; B, E, F, G, H, 50 μm; D, G, 20 μm.

Confocal analysis of the brains of three dragonfly species labeled with an antibody raised against synapsin have demonstrated four discrete nested retinotopic centers proximal to the medulla (Fabian et al., 2020). These are described as lobulas, each linked to the next by retinotopic relays. Some of these neuropils contain large tangential neurons that respond to wide-field visual motion (Fabian et al., 2020); others possess palisades of small-field efferents indicative of neurons with similar morphologies that in *Drosophila* respond to small objects (Keleş et al., 2020).

Odonate optic lobes stained with reduced silver demonstrate the characteristic neural architecture of each lobula neuropil: columnar palisades; systems of extremely slender tangential neurons; other large tangential neurons with robust dendritic trees arranged in a manner suggesting retinotopic inputs from just part of the relayed retinal mosaic (Fig. 4A–C, E,F H,I). A fifth neuropil identified by Fabian et al. (2020) was accorded the identity of a lobula plate. Reduced silver staining shows the neuropil possesses large-diameter tangential neurons (Fig. 2G) arranged in two distinctive layers (Fig. 4C, E). Oblique views of this neuropil (Fig. 4H and I) suggest that swathes of axons sweeping around the posterior margin of the medulla (direction arrowed in Fig. 4H) might correspond to a lobula plate on the basis of dense ensembles of such extremely small axons, although this is not a secure identification. A similar swathe extends from a dense cluster of minute cell bodies that lies behind the lobula plate (Fig, 4I, indicated by the arrow). The posterior locations of these cell body clusters near the optic lobe's margin approximate the locations of T4 and T5 neuron cell bodies in flies, but again these afford only approximate comparisons. Golgi impregnations also resolve systems of narrow but robust tangential cell dendrites extending across the neuropil suggested as a lobula plate (Fig. 4D).

Golgi impregnations of odonate optic lobes also reveal palisades of retinotopic columnar neurons that provide efferents from the LO1 lobula (Fig. 4F and G) as well as tangentially directed dendrites that extend across their axons (Fig. 4G). More distally, Golgi impregnations resolve systems of small T4-like neurons, the dense bush-like dendrites of which are arranged beneath the medulla's Cuccati layer (Fig. 5A, C-E; levels indicated in Fig. 4A). Bodian preparations suggest that these neurons may be organized as quartets (Fig. 5B); and quartets can occasionally be resolved in Golgi-impregnated material (Fig. 5D). The same quartet arrangement is observed for lobula neurons suggested here as T5-like (Fig. 5J). The dendritic trees of the T4-like neurons extend unilaterally from their axons, as they do in Diptera, intersecting 2—3 retinotopic columns, representing a small patch of facets. Each of a pair of T4 dendrites extends either in one or the other direction, indicating a morphological orientation that may play a role in the directional selectivity of a T4 neuron's local circuitry (Fig. 5E). Corresponding dendritic asymmetries also typify T4 and T5 neurons in dipterous insects (Fig. 1E, inset). Neurons reminiscent of dipteran T5 neurons originate from the outermost layer of the most distal lobula (LO1; Fig. 5F). Their dendritic trees are visited by the shallow-ending terminals from columnar neurons projecting through both levels of the medulla (double arrowhead, Fig. 5G). This arrangement corresponds to the fly lobula, where the outermost stratum of the lobula contains T5 neuron dendrites supplied by relays from the medulla. In the dragonfly these neurons originate from cell bodies that flank the posterior margin of the optic lobe (Fig. 5H and I).

Individual axons of neurons possibly corresponding to holometabolan T4 and T5 neurons have not yet been followed through to their terminus due to interference imposed by mass staining of other neurons that obscure extremely thin axons. Nevertheless, that these T4- and T5-like neurons have axons that appear to bypass lobulas LO1, LO2 and LO4, suggests the large tangentials of LO3 (Fig. 4H) and the lobula plate-like neuropil as putative targets.

The presence in odonates of T4- and T5-like neurons and wide-field tangential cells as their possible postsynaptic targets would

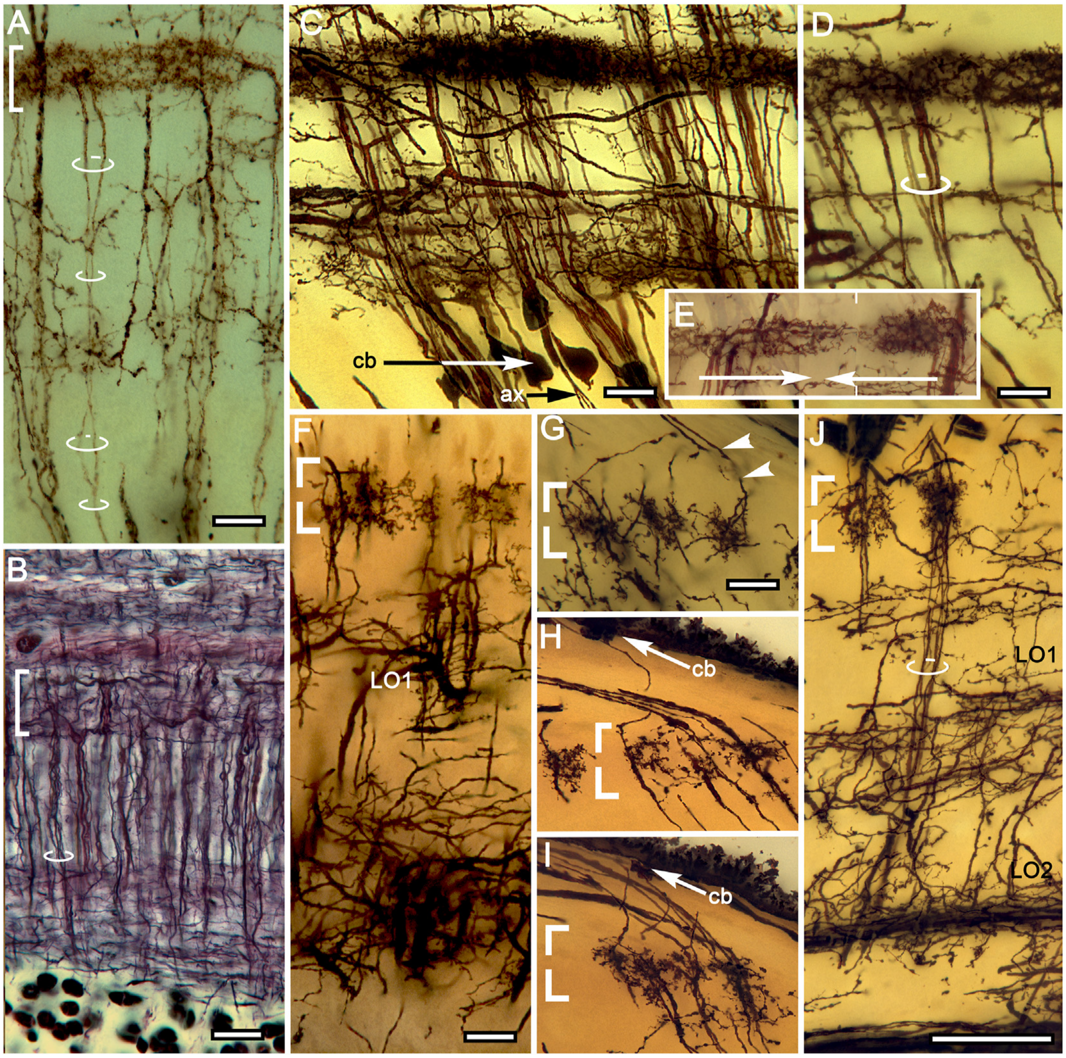

Fig. 5. T4-like and T5-like neurons in the odonate optic lobe (*Libellula saturata*). A. T-neuron dendritic trees are layered (bracket) within the inner medulla, but not as deeply as in the fly optic lobes. Paired axons (example ringed) often demonstrate two neurons with oppositely directed dendritic trees extending unilaterally from the initial stem of their axon. B. Bodian-stained medulla showing the layer (bracketed) of dendrites and clusters of axons ascribed to quartets of T4-like neurons (one quartet ringed). C. Golgi impregnation of T4-like neurons showing their cell bodies (cb) beneath the medulla sending neurites distally to join the T-neuron axons (ax) immediately beneath their dendritic trees. D. Quartets of T4-like neurons are occasionally revealed by Golgi impregnation (ringed). E. Unilaterally extending dendrites of T4-like cells oriented in two directions within the retinotopic mosaic. F. Golgi impregnation of LO1 and LO2, showing T5-like dendrites limited to the outermost stratum of LO1 (open bracket). G. T5-like dendrites (open bracket) showing their lateral extents and depth relationships with terminals from the medulla (one indicated by arrowheads). H, I. T5-like dendritic trees and axons extending centrally (downwards in panel) in the direction of the lobula plate (not shown), with their cell bodies (cb) close to the posterior margin of the optic lobe. J. A quartet of T5-like neurons (ringed). Scale bars: A-I, 20 μm; J, 50 μm.

correspond to three of the six traits that define a holometabolan lobula plate. Even with the absence of the full set of traits, the presence of T4- and T5-like neurons and a putative postsynaptic neuropil allows speculation that a system for controlling visual balance in flight may have evolved approximately 360 million years ago at a time when insects evolved active flight (Misof et al., 2014).

But questions remain. One is whether the presence of several retinotopic neuropils proximal to the medulla, as in Odonata (Fabian et al., 2020), represents a basal optic lobe organization, or an elaboration derived from a simpler arrangement. The earliest known insect lineage is Archaeognatha, ascribed by molecular phylogenetics to the late Silurian, about 440 million years ago (Misof et al., 2014) preceding the origin of flying insects by about 80 million years. The extant representatives of Archaeognatha are bristletails (Machilidae), which as shown in Fig. 6A possess an optic lobe comprising four nested centers. The medulla is divided into an outer two thirds and an inner third by the Cuccati layer (arrowed in Fig. 6A, C). The lobula is divided into two distinct components

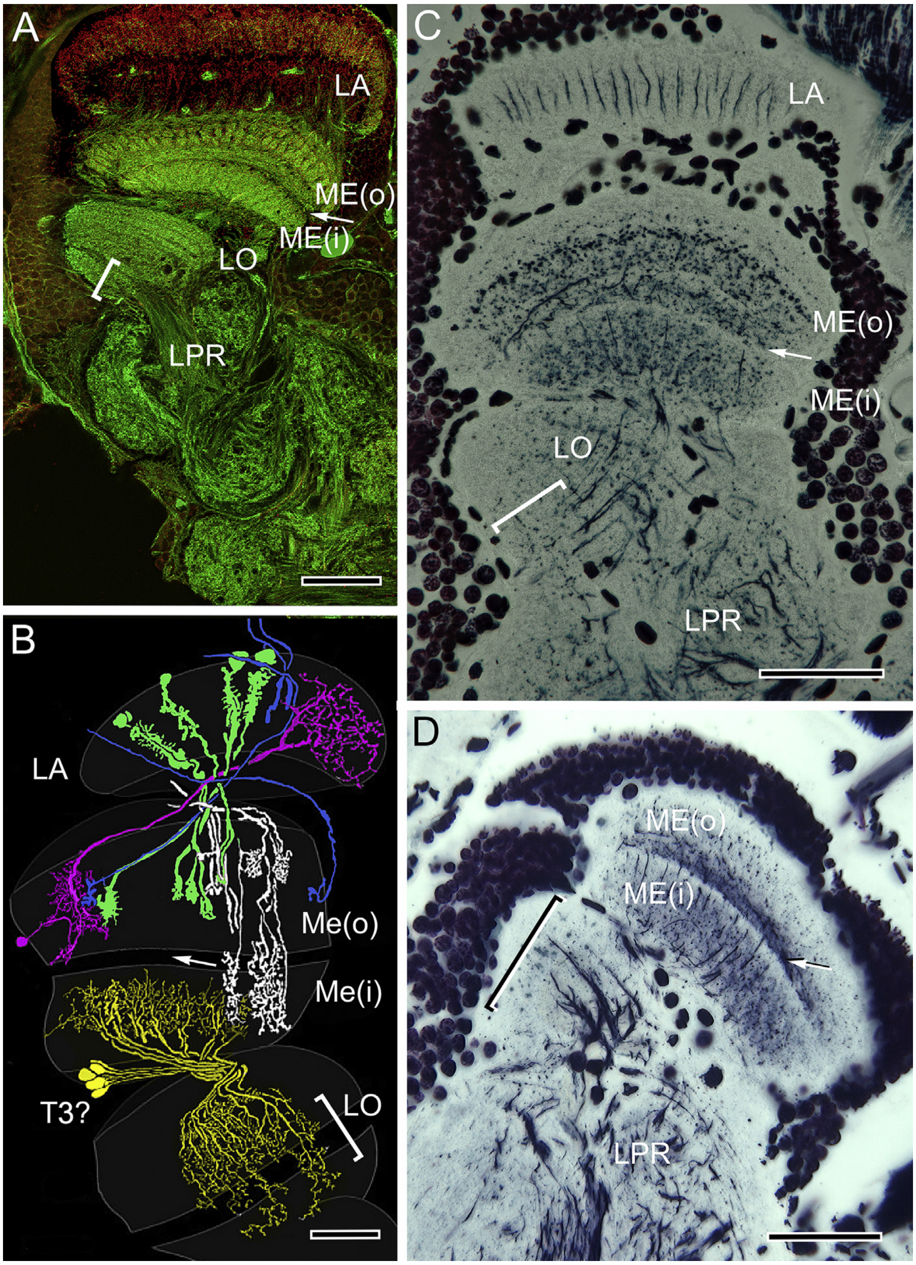

Fig. 6. Optic lobes of Archaeognatha: *Allomachilis froggatti* (A), *Machilis germanicus* (B) and (C, D) *Petrobius* sp. A. The nested optic lobe neuropil and the attachment of the lobula (LO) to the lateral protocerebrum (LPR) shows an organization corresponding to that in Hymenoptera. The medulla's outer and inner neuropil [ME(o), ME(i)] (trait 1, Table 1) are divided by the Cuccati layer (arrowed). A proximal level in the lobula (bracketed) is distinguishable from the more distal neuropil. B. Correspondence with the optic lobes of basal holometabolans is supported by the morphologies of neurons. These include lamina monopolar cells (green), centrifugal neurons projecting to the lamina from the outer medulla (purple), and small retinotopic columnar neurons (white). Retinotopic columnar neurons provide relays between the lamina and the dendrites of T-neurons (yellow), the dendrites of which are constrained to the medulla's inner layer, with some terminals just reaching the lobula's inner layer. C, D. The Bodian method does not provide high-definition staining of this insect. However, it demonstrates the layering of the outer medulla as distinct from the denser inner layer. Panel D illustrates an oblique view of the lobula showing large tangential cells (bracketed) (trait 6, Table 1) occupying its inner volume, as they do in Hymenoptera. Scale bars: A, C, D, 100 μm; B, 50 μm. Panels B and D from Sinakevitch et al. (2003).

(Fig. 6A, C), the inner component comparable to the level occupied by the lobula plate in honey bees. In Machilidae this level contains systems of large diameter tangential neurons, the dendrites of which extend across the whole of the neuropil (Fig. 6D). Together, these are two traits amongst others defining the hymenopteran lobula plate homologue (Fig. 3). Neurons with dense dendritic trees in the inner medulla (Fig. 6B) are suggestive of T3-like cells described from Lepidoptera and Diptera (Strausfeld and Blest, 1970; Fischbach and Dittrich, 1989) that extend axons as far as the inner component of the lobula, which is equipped with systems of large-diameter tangential neurons (Fig. 6C). If further specimens provide additional evidence of the remaining traits, then a network encoding optic flow would already have existed in the Devonian (420-360 mya), to which fossilized fragments of machilids have been ascribed (Labandeira et al., 1988). Machilidae also suggest that the two-component lobula and two component medulla are the ancestral condition in insects, implying that compound lobulas comprising more than two retinotopic neuropils, as in Odonata, Dictyoptera and Hemiptera (see companion paper, Strausfeld and Olea-Rowe, 2021) are derived morphologies.

To conclude: a small but unique set of traits define the organization of the holometabolan lobula plate. Whether some of these traits are present in the other two neopteran clades, Polyneoptera and Condylognatha (Misof et al., 2014) has not been determined, despite abundant evidence for behaviors driven by optic flow and other motion parameters (e.g., O'Shea and Williams, 1974; Wang et al.,2018; Rosner et al., 2019). There is no lobula plate homologue in crustaceans, yet the numerous examples of neurons in Brachyura encoding parameters of visual motion suggest convergent neuronal arrangements particularly at the level of the deep lobula (e.g., Horseman et al., 2011; Oliva and Tomsic, 2014). It is these that offer unexplored aspects of convergent evolution and possible insights into commonalities of underlying network organization that have evolved independently in diverging subphyla.

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