Published in final edited form as:

Ann N Y Acad Sci. 2009 July ; 1170: 487–496. doi:10.1111/j.1749-6632.2009.04020.x.

Dimorphic Olfactory Lobes in the Arthropoda

Nicholas Strausfeld and Carolina E. Reisenman

ARL Division of Neurobiology and Center for Insect Science, University of Arizona, Tucson, AZ 85721

Abstract

Specialized olfactory lobe glomeruli relating to sexual or caste differences have been observed in at least five orders of insects, suggesting an early appearance of this trait in insect evolution. Dimorphism is not limited to nocturnal species, but occurs even in insects that are known to use vision for courtship. Other than a single description there is no evidence for similar structures occurring in the Crustacea, suggesting that the evolution of dimorphic olfactory systems may typify terrestrial arthropods.

Although sex specific behaviors may be ubiquitous across phyla, obvious neural correlates are not easily recognized. Exceptions are centers that support sex-specific acoustic perception and song-released behaviors in birds^{1,2} and quite different but no less remarkable sensory dimorphism in orthopteran and dipterous insects^{3,4}; male-specific visual neuropils in flies that mediate target pursuit⁵⁻⁷; and, in insects, sex-specific olfactory organs and the neuropils that they serve⁸⁻¹². It is, however, insects, particularly those lepidopterans that we know as “moths”, that have provided such a wealth of experimental data demonstrating how complex blends that make up species-specific pheromones are processed by uniquely identifiable neurons and how these provide early information for odortactic flight¹³⁻¹⁶. Yet, while almost every moth investigated has been shown to possess sexually dimorphic antennae and sexually dimorphic olfactory lobes what is less secure is whether few or many other insect species, or even other land arthropods, are similarly endowed.

The olfactory (aka “antennal”) lobes of insects comprise discrete islets of neuropil, called glomeruli. In the moth *Manduca sexta*, which is often taken as a representative nocturnal lepidopteran, males and females possess in common a characteristic complement of glomeruli that have comparable topographic relationships with each other¹⁷. Indeed, it is typical for all insects examined that for any species there is a fixed number of antennal lobe glomeruli common to both sexes¹⁸⁻²⁰. These “ordinary glomeruli” serve specific populations of odorant receptors on the antennae that are selectively tuned to a range of odors that attract or repel both males and females of the species¹⁵. In males, however, a system of sex-specific glomeruli make up what has been termed the macroglomerular complex. Each male-specific glomerulus receives the terminals of a set of odorant receptor neurons specifically tuned to one of the components of the pheromone blend emitted by the female^{11,21}. Counterparts of these male-specific glomeruli also exist in females. They are much smaller, but are tuned to odors that are particularly relevant to female behavior^{8,22}.

Antennal lobe dimorphism, in which males have large and distinct glomeruli (Fig. 1), is not simply restricted to males versus females. Studies of social hymenopterans, for example honey bees, have shown that the antennal lobes of workers have a different number of glomeruli compared to those of drones²³. Likewise, there is evidence that in some species of ants the numbers of glomeruli vary according to caste²⁴⁻²⁶. Even from these few examples the observer is persuaded that within a species, in which there are clear sex- or task related differences of odorant-induced behaviors, there will likely be differences in the number and organization of glomeruli. Two other examples come to mind. Male and female *Anopheles gambiae*

mosquitoes have quite different food preferences and have sexually dimorphic antennae and glomeruli²⁷. These are not specializations of males to detect females. Rather, the male olfactory system detects floral odors so that the male can obtain nectar and hence the energy to acoustically locate and fly to females; the female olfactory system is tuned to human odors enabling her to obtain proteins for her eggs. In general, olfactory behaviors that are specific to each sex are driven by molecular features of odorants that are detected by specifically tuned odorant receptor cells on the antennae, the axons of which target specific glomeruli in the male and different but no less specific glomeruli in the female⁸. Another example comes from the Mutillidae. These are parasitic wasps, the females of which once fertilized lose their wings and spend weeks or even months searching out the burrows of solitary bees. The larvae of the bees, when large enough for the purpose (and, presumably smelling just right), receive a mutilid egg. Both male and female mutilids possess enormous antennal lobes, which like those of most other hymenopterans consist of scores of small ball-like glomeruli. However, the antennal lobe of a mutilid male looks quite different from that of the female: while males do not possess a small group of male-specific glomeruli as do moths, the two sexes have substantially different numbers of glomeruli arranged in sex-specific constellations²⁸.

How general are sex-specific olfactory systems across the Insecta? Unfortunately, too few comparative studies have been done to answer this with anything approaching precision. Nevertheless, some assumptions can be made. One is that because sex-specific glomeruli occur in basal as well as crown groups, it is likely that a sex-specific organization of the antennal lobe may have evolved early in the evolution of the Insecta and may be a synapomorphy of at least the Neoptera. Thus far, sexually dimorphic antennal lobes have been documented in the Dictyoptera, Lepidoptera, Hymenoptera, Coleoptera, and Diptera. Nocturnal Lepidoptera, such as sphingid, heliothine, and noctuid moths are renowned for their sexually dimorphic antennae and antennal lobes^{17,20,29-30}. However, even diurnal species, such as the humming bird hawk moth *Macroglossum stellatarum* and the burnet moth *Zygaena filipendulae* possess antennal lobes that in males are equipped with three to five male-specific glomeruli (Fig. 2). Interestingly, unlike their nocturnal cousins, the antennae of these species show no obvious sexual dimorphism so one must assume that sensilla on the male antennae housing receptors tuned to components of the female pheromone are discrete, appearing little different from sensilla decorating the females' antennae.

It is sometimes suggested that sex pheromones confer a particular advantage for species that are nocturnal; or species that are sympatric yet are required to mate with the genetically appropriate partner; or species that need to attract conspecifics over long distances. Particularly beneath or within the canopy, acoustic communication or communication by odor are more effective over distance than visual communication. So it comes as something of a surprise that brightly colored diurnal moths equipped with color and form perception are also equipped with sexually dimorphic antennal lobes.

More surprising is that butterflies also have dimorphic antennal lobes, males being equipped with prominent male-specific glomeruli located at the same position in the lobes as those found in moths. So much, then, for the idea that visual sexual signals are most effective in daylight and odor-mediated ones are most effective at night. And, in this context, it is worth noting that studies on nocturnal Hymenoptera demonstrate that insects probably possess the most acute nocturnal vision of any group of animal³¹.

If antennal lobes are sexually dimorphic, then what about higher brain centers of the protocerebrum to which they send relay neurons? Insects can be categorized into three somewhat artificial groups: those that are equipped with antennal lobes and mushroom bodies, those that lack antennal lobes, and those that lack mushroom bodies. Absence of antennal lobes, as occurs in many aquatic genera, does not preclude a lack of mushroom bodies. Indeed, as far

as is known all dicondylic insects have them³². However, those that do have antennal lobes supply two protocerebral areas: the mushroom body calyces and a volume of the rostromedial protocerebrum called the lateral horn^{33,34}. In coleopterans, the males of which are equipped with at least two macroglomeruli (Fig. 3), the antennal lobes supply just one ascending pathway that extends to the lateral horn. En route, its projection neuron axons provide a massive collateral input to the mushroom body calyces. This, then, represents the simplest relationship between first order olfactory neuropil of the deutocerebrum (the second brain segment) and areas of the protocerebrum (the first brain segment). In contrast, the antennal lobes of flies provide at least five ascending pathways, although some comprise only a few axons³⁵. In honey bees there are also five such pathways and in both genera a subset of antennal lobe projection neurons in one of the ascending tracts supplies first the lateral horn and then sends prolongations into the calyx whereas another ascending tract first supplies collaterals to the calyces before terminating in the lateral horn³⁶. Studies on *Drosophila melanogaster* have shown that the calyx is parsed into three discrete zones, each of which is supplied by projection neurons arising from one of three characteristic ensembles of antennal lobe glomeruli. Similarly, the lateral horn neuropil is parsed into three discrete layer-like domains, each domain also representing one of the same three ensembles of glomeruli³⁵. A comparable representation has been described for ants and honey bees. Specific ensembles of antennal lobe glomeruli are differently represented in concentric domains of the lip region of the calyces³⁶⁻³⁷.

If subsets of ordinary glomeruli are represented as discrete domains centrally then it should also be expected that projection neurons from sex-specific glomeruli would be differently represented in the calyces and lateral horn. This is confirmed from observations of dye-filled projection neurons from both types of glomeruli in *Manduca sexta*: there are two different terminal morphologies in the calyces and, in males, macroglomerular projection neurons terminate in a region situated directly beneath the lateral horn neuropils receiving terminals from ordinary glomeruli³⁴. The same type of spatial segregation has also been shown for the cockroach *Periplaneta americana*: male projection neurons end in a zone of the protocerebrum that is inferior to the lateral horn, which receives the layered terminals of projections neurons from ordinary glomeruli (Fig. 4). In *Drosophila melanogaster* projection neurons with arborizations in a uniquely identifiable glomerulus that in both sexes detects male pheromone terminate in different sex-specific domains in the lateral protocerebrum³⁸. While there as yet is too little data to generalize this sex-specific arrangement across taxa, the segregation documented for the four species above at least serves as a search image for further studies.

What about the third category of insects: those lacking mushroom bodies? These are the Machilidae, which comprise four families of monocondylic flightless insects, commonly known as bristletails, that were probably amongst the first hexapods to colonize land in the mid-Devonian³⁹. The brains of machilids are equipped with glomerular antennal lobes. Although it is not yet known if these are sexually dimorphic, these shrimp-like insects typically live as groups and are often found nestling together under moss or in rock crevices. They have splendidly long antennae and, like all insects, male machilids are required to locate females. The presence of sex-specific glomeruli in these primitive insects would be an interesting finding because machilid antennal lobes provide projection neurons to a substantial and clearly partitioned volume of the lateral protocerebrum. Indeed, this part of the brain is comparatively much larger than the lateral horn of a fruitfly or cockroach. As machilids lack mushroom bodies but have large target neuropils for their projection neurons, in this aspect their brains are more similar to those of malacostracan crustaceans than they are to the Dicondylia. In the Malacostraca, projection neurons from the antennular lobe send bilateral axons to two or three (depending on the species) discrete neuropils in the lateral protocerebrum. These are called the terminal medulla and the hemiellipsoid bodies⁴⁰. None of them are comparable to mushroom bodies but they are comparable to the lateral protocerebrum of machilids and the highly attenuated homologue in dicondylic insects, the lateral horn.

This brings us to the next question. If the malacostracan lateral protocerebrum is homologous to an equivalent region in insects, is there evidence for sexual dimorphism of the malacostracan antennular lobes? Thus far, there has been only one report of a putative sexual dimorphism in a mysid shrimp⁴¹. Although in many malacostracans the antennular lobes appear to be subdivided into two or more bulging ensembles of glomeruli, these have never been ascribed to sexual differences. However, with one glaring exception, these glomeruli are very different from those of the Insecta, a feature that alone suggests caution before claiming that crustacean antennular lobes are homologous to the olfactory lobes of insects⁴². And here it should be noted that we have avoided the term “antennal lobes” because even though insects only have one pair of cerebral appendages to the crustaceans' two, the single pair are the first antennae. This means that they are antennules, *sensu stricto*, and should be not confused with what crustacean biologists term “the antennae”⁴³. The latter comprise the second antenna pair, which does not exist in hexapods.

Antennular lobes are usually subdivided into column or wedge-shaped subunits that have termed glomeruli, though is somewhat misleading. Each subunit is clearly stratified, and in one representative taxon, the spiny lobster *Panulirus argus*, axons of olfactory receptor neurons can supply more than one subunit, something not observed in an insect olfactory lobe⁴⁴. Moreover, whereas insects have mainly uniglomerular projection neurons - that is, relay neurons whose dendrites are constrained to a single glomerulus (Fig. 1) - the malacostracan antennular lobe is populated by wide-field multiglomerular projection neurons⁴⁵. Thus far, no uniglomerular projection neuron has been described in a crustacean. If in some malacostracans it turns out that there is indeed sexual dimorphism of the olfactory system then it is likely that sex-specific morphologies would relate not to a few large glomeruli but to ensembles of many glomeruli that share the dendrites of a set of wide field projection neurons. Possible exceptions may be the Stomatopoda, commonly known as mantis shrimps. These have antennular lobes that are remarkably insect-like in that they are partitioned into discrete islet-like units (Fig. 5).

In summary, apart from the single description of a putative sex-specific glomerulus in a mysid shrimp, the occurrence of sex-specific glomeruli within the Tetraconata (Insecta+Crustacea) may be constrained to insects with terrestrial imagines. Within the Insecta, it is likely that sexual dimorphism of the antennal lobes occurs in many genera and even where obvious glomerular dimorphism is absent sex-specific differences can still be manifested by sex-specific projections into the protocerebrum, as described from *Drosophila melanogaster*³⁸. In insects where there are neither sex-specific glomeruli nor sex-specific projection neurons, this absence may indicate secondary loss or may suggest multiple evolution of sex-specific glomeruli in distantly related taxa. One key to our understanding of the evolution of sex-specific glomeruli will come from further studies on the primitive machilids. However, even if dimorphism is found in this group, it cannot resolve the question as to whether or not the trait has evolved independently in different insect lineages (Fig. 6).

The possibility that sexual dimorphic olfactory systems are typical of terrestrial arthropods needs still to be resolved. Studies on the Chelicerata have identified pheromones from three groups: the Acari (ticks), Araneae (spiders), and Scorpionida⁴⁶⁻⁴⁸. Preliminary studies on amblypygids (whip spiders) and solfugids (sun spiders), which are arid land chelicerates that have antenna-like appendages (the first leg pair and pedipalps, respectively), suggest that in these taxa their primary olfactory centers comprise two kinds of glomerular arrangements: small densely packed glomeruli reminiscent of those of Hymenoptera accompanying a very few large glomeruli, reminiscent of lepidopteran or dictyopteran macroglomeruli, or many small glomeruli alone. Such differences between individuals of the same species suggests that there is indeed dimorphism in these chelicerate olfactory systems (Fig. 7). If confirmed, this would be an intriguing example of parallel evolution of macroglomerular complexes in two

groups of arthropods, insects and chelicerates, whose last common ancestor probably existed about 540 million years ago.

Acknowledgments

Research for this article derives from support from the National Institutes of Health Grant R01-DC-02751 and from the John D. and Catharine T. MacArthur Foundation (NJS).

References

1. Bottjer SW, Johnson F. Circuits, hormones, and learning: vocal behavior in songbirds. *J Neurobiol* 1997;33:602–618. [PubMed: 9369462]
2. Brauth SE, Liang W, Amateau SK, Robert TF. Sexual dimorphism of vocal control nuclei in budgerigars (*Melopsittacus undulatus*) revealed with Nissl and NADPH-d staining. *J Comp Neurol* 2005;484:15–27. [PubMed: 15717302]
3. Bailey WJ, Kamien D. Hearing dimorphism, trait variation and conflicts over space in the thorax of the bushcricket *Requena verticalis* (Listroselidinae: Tettigoniidae: Orthoptera). *J Comp Physiol A* 2001;187:647–652. [PubMed: 11763962]
4. Jackson JC, Robert D. Nonlinear auditory mechanism enhances female sounds for male mosquitoes. *Proc Natl Acad Sci USA* 2006;103:16734–16739. [PubMed: 17068125]
5. Zeil J. Sexual dimorphism in the visual system of flies: the divided brain of male Bibionidae (Diptera). *Cell Tissue Res* 1983;229:591–610. [PubMed: 6839353]
6. Gronenberg W, Strausfeld NJ. Descending pathways connecting the male-specific visual system of flies to the neck and flight motor. *J Comp Physiol A* 1991;169:413–426. [PubMed: 1723432]
7. Gilbert C, Strausfeld NJ. The functional organization of male-specific visual neurons in flies. *J Comp Physiol* 1991;169:395–411. [PubMed: 1723431]
8. King JR, Christensen TA, Hildebrand JG. Response characteristics of an identified, sexually dimorphic olfactory glomerulus. *J Neurosci* 2000;20:2391–2399. [PubMed: 10704513]
9. Lee JK, Strausfeld NJ. Structure, distribution and number of surface sensilla and their receptor cells on the olfactory appendage of the male moth *Manduca sexta*. *J Neurocytol* 1990;19:519–538. [PubMed: 2243245]
10. Matsumoto SG, Hildebrand JG. Olfactory mechanisms in the moth *Manduca sexta*: Response characteristics and morphology of central neurons in the antennal lobes. *Proc Roy Soc London B* 1981;213:249–277.
11. Christensen TA, Hildebrand JG. Male-specific, sex pheromone-selective projection neurons in the antennal lobes of the moth *Manduca sexta*. *J Comp Physiol A* 1987;160:553–569. [PubMed: 3612589]
12. Malun D, Waldow U, Kraus D, Boeckh J. Connections between the deutocerebrum and the protocerebrum, and neuroanatomy of several classes of deutocerebral projection neurons in the brain of male *Periplaneta americana*. *J Comp Neurol* 1993;329:143–162. [PubMed: 8454728]
13. Tumlinson JH, Brennan MM, Doolittle RE, Mitchell ER, Brabham A, Mazomenos BE, Baumhover AH, Jackson DM. Identification of a pheromone blend attractive to *Manduca sexta* (L.) males in a wind tunnel. *Arch Insect Biochem Physiol* 1989;10:255–271.
14. Leal WS. Chemical communication in scarab beetles: reciprocal behavioral agonist-antagonist activities of chiral pheromones. *Proc Natl Acad Sci USA* 1996;93:12112–12115. [PubMed: 8901541]
15. Vickers NJ, Christensen TA, Hildebrand JG. Combinatorial odor discrimination in the brain: attractive and antagonist odor blends are represented in distinct combinations of uniquely identifiable glomeruli. *J Comp Neurol* 1998;400:35–56. [PubMed: 9762865]
16. Vickers NJ, Poole K, Linn CE Jr. Plasticity in central olfactory processing and pheromone blend discrimination following interspecies antennal imaginal disc transplantation. *J Comp Neurol* 2005;491:141–156. [PubMed: 16127689]
17. Rospars JP, Hildebrand JG. Sexually dimorphic and isomorphic glomeruli in the antennal lobes of the sphinx moth *Manduca sexta*. *Chem Senses* 2000;25:119–129. [PubMed: 10781018]

18. Chambille I, Rospars JP. Neurons and identified glomeruli of antennal lobes during postembryonic development in the cockroach *Blaberus craniifer* (Dictyoptera, Blaberidae). *Int J Insect Morphol* 1985;14:203–226.
19. Laissue PP, Reiter C, Hiesinger PR, Halter S, Fischback KF, Stocker RF. Three-dimensional reconstruction of the antennal lobe in *Drosophila melanogaster*. *J Comp Neurol* 1999;405:543–552. [PubMed: 10098944]
20. Berg BG, Galizia CG, Brandt R, Mustaparta H. Digital atlases of the antennal lobe in two species of tobacco budworm moths, the oriental *Helicoverpa assulta* (male) and the american *Heliothis virescens* (male and female). *J Comp Neurol* 2002;446:123–134. [PubMed: 11932931]
21. Hansson BS, Ljungberg H, Hallberg E, Löfstedt C. Functional specialization of olfactory glomeruli in a moth. *Science* 1992;256:1313–1315. [PubMed: 1598574]
22. Hillier N, Kleineidam C, Vickers N. Physiology and glomerular projections of olfactory receptor neurons on the antenna of female *Heliothis virescens* (Lepidoptera: Noctuidae) responsive to behaviorally relevant odors. *J Comp Physiol A* 2006;192:199–219.
23. Arnold G, Masson C, Budharugsa S. Comparative study of the antennal lobes and their afferent pathway in the worker bee and the drone (*Apis mellifera*). *Cell Tissue Res* 1985;242:593–605.
24. Kleineidam CJ, Obermayer M, Halbich W, Rössler W. A macroglomerulus in the antennal lobe of leaf-cutting ant workers and its possible functional significance. *Chem Senses* 2005;30:383–392. [PubMed: 15843501]
25. Nishikawa M, Nishino H, Misaka Y, Kubota M, Tsuji E, Satoji Y, Ozaki M, Yokohari F. Sexual dimorphism in the antennal lobe of the ant *Camponotus japonicus*. *Zool Sci* 2008;25:195–204. [PubMed: 18533751]
26. Zube C, Rössler W. Caste- and sex-specific adaptations within the olfactory pathway in the brain of the ant *Camponotus floridanus*. *Arthropod Struct Dev* 2008;37:469–479. [PubMed: 18621145]
27. Ghaninia M, Hansson BS, Ignell R. The antennal lobe of the African malaria mosquito, *Anopheles gambiae* - innervation and three-dimensional reconstruction. *Arthropod Struct Dev* 2007;36:23–39. [PubMed: 18089085]
28. Strausfeld, NJ. Insect Brain. In: Wullman, M.; Roth, G., editors. *Brain, Evolution and Cognition*. Wiley International; 2001.
29. Karpati Z, Dekker T, Hansson BS. Reversed functional topology in the antennal lobe of the male European corn borer. *J Exp Biol* 2008;211:2841–2848. [PubMed: 18723543]
30. Greiner B, Gadenne C, Anton S. Three-dimensional antennal lobe atlas of the male moth, *Agrotis ipsilon*: a tool to study structure-function correlation. *J Comp Neurol* 475:202–210. [PubMed: 15211461]
31. Greiner B. Visual adaptations in the night-active wasp *Apoica pallens*. *J Comp Neurol* 2006;495:255–262. [PubMed: 16440299]
32. Strausfeld NJ, Li Y, Gomez R, Kei K. Evolution, discovery, and interpretations of Arthropod mushroom bodies. *Learn Memory* 1998;5:11–37.
33. Strausfeld, NJ. *Atlas of an insect brain*. Springer; Berlin, Heidelberg, New York: 1976.
34. Homberg U, Christensen TA, Hildebrand JG. Structure and function of the deutocerebrum in insects. *Ann Rev Entomol* 1989;34:477–501. [PubMed: 2648971]
35. Tanaka NK, Awasaki T, Shimada T, Ito K. Integration of chemosensory pathways in the *Drosophila* second-order olfactory centers. *Curr Biol* 2004;14:449–457. [PubMed: 15043809]
36. Kirschner S, Kleineidam CJ, Zube C, Rybak J, Grünewald B, Rössler W. Dual olfactory pathway in the honeybee, *Apis mellifera*. *J Comp Neurol* 2006;499:933–952. [PubMed: 17072827]
37. Gronenberg W. Modality-specific segregation of input to ant mushroom bodies. *Brain Behav Evol* 1999;54:85–95. [PubMed: 10529521]
38. Datta SR, Vasconcelos ML, Ruta V, Luo S, Wong A, Demir E, Flores J, Balonze K, Dickson BJ, Axel R. The *Drosophila* pheromone cVA activates a sexually dimorphic neural circuit. *Nature* 2008;452:473–477. [PubMed: 18305480]
39. Labandeira CC, Beal BS, Hueber FM. Early insect diversification: evidence from a Lower Devonian bristletail from Quebec. *Science* 1988;242:913–916.

40. Sullivan JM, Beltz BS. Integration and segregation of inputs to higher-order neuropils of the crayfish brain. *J Comp Neurol* 2005;481:118–126. [PubMed: 15558720]
41. Johansson KUI, Hallberg E. Male-specific structures in the olfactory system of mysids (Mysidacea; Crustacea). *Cell Tissue Res* 1992;268:359–368.
42. Schachtner J, Schmidt M, Homberg U. Organization and evolutionary trends of primary olfactory brain centers in Tetraconata (Crustacea+Hexapoda). *Arthropod Struct Dev* 2005;34:257–299.
43. Boxshall GA. The evolution of arthropod limbs. *Biol Rev Camb Philos Soc* 2005;79:253–300. [PubMed: 15191225]
44. Schmidt M, Ache BW. Antennular projections to the midbrain of the spiny lobster: sensory innervation of the olfactory lobe. *J Comp Neurol* 1992;318:291–303. [PubMed: 1583164]
45. Schmidt M, Ache BW. Immunocytochemical analysis of glomerular regionalization and neuronal diversity in the olfactory deutocerebrum of the spiny lobster. *Cell Tissue Res* 1997;287:541–563. [PubMed: 9027299]
46. Kuwahara, Y. Chemical ecology of astigmatid mites. In: Cardé, RT.; Miller, JG., editors. *Advances in Insect Chemical Ecology*. Cambridge University Press; Cambridge: 2004. p. 76-109.
47. Schulz S, Toft S. Identification of a sex pheromone from a spider. *Science* 1993;260:1635–1637. [PubMed: 17810206]
48. Gaffin, DD.; Brownell, PH. Chemosensory behavior and physiology. In: Brownell, PH.; Plois, GA., editors. *Scorpion Biology and Research*. Oxford University Press; New York: 2000. p. 223-245.

Figure 1.
Laser-scanning confocal microscopic images of output neurons in the antennal lobe of male *M. sexta* with arborizations confined to one of the male-specific glomerulus (leftmost neuron) and a sexually isomorphic glomerulus (rightmost).

Figure 2. Macroglomerular complexes (boxed) of two diurnal Lepidoptera, the sphingid moth *Macroglossum stellatarum* (A, C) and the six-spot burnet moth *Zygaena filipendulae stephensi* (B, D). Ordinary glomeruli are indicated at one glomerulus (OG).

Figure 3. Macroglomeruli in the antennal lobe of the social beetle *Odontotaenius disjunctus* (inset to Panel B). Most of the antennal lobe consists of isomorphic ordinary glomeruli (OG) that are similar in appearance (Panel A). However, dorsally in the female antennal lobe is one distinctive glomerulus (bracketed) that lies above a large isomorphic glomerulus (Panel B).

Figure 4.

Sex-specific termination areas of antennal lobe projection neurons, exemplified here by *Periplaneta americana*. Male-specific neurons from the macroglomerulus (MG) ascend in front of the mushroom body's medial lobe (M) to beneath the calyces (ca) where axons provide collaterals decorated with small bead-like specializations. The axon terminates as a dense brush-like ending in the inferior lateral protocerebrum (i l pro). Projection neurons (example shown in grey) from ordinary glomeruli (OG) provide larger varicose specializations in the calyces and a field of varicose endings in the lateral horn (I ho), caudal to the i l pro.

Figure 5.

Comparisons of crustacean and insect olfactory lobe glomeruli. A. Islet-like glomeruli of the stomatopod *Pseudosquilla ciliata*. B. Wedge-shaped “glomeruli” of the ghost shrimp *Callinassa californiensis*. C. An “antennal” lobe of the housefly, *Musca domestica*, in which each glomerulus is clearly defined and has a unique location. Similar unique identities may also be typical of stomatopod antennular lobes. However, if there are unique identities in decapod antennular lobes these are more likely to reflect ensembles of small subunits, such as indicated by the bracket in B.

Figure 6.

Occurrence of glomeruli and sexual/caste dimorphism. Within the Eucrustacea, only malacostracan taxa are reported to be equipped with antennular lobes (character 1). These appear to comprise isomorphic subunits (see Fig. 4A, B). Uniquely identifiable glomeruli (2) are first recognized in the most basal extant insects, the Machilidae. Sex-specific glomeruli (3) are recognized across neopteran species. Caste/sex specific glomerular clusters (4) are typical of the Hymenoptera. In many groups, antennal lobes have been secondarily lost (5), thus making it impossible to determine whether antennal lobe sexual dimorphism originated deeper than the Neoptera.

Figure 7.

Primary olfactory neuropils of chelicerates show dimorphism. A. Solfugids are equipped with olfactory receptors on their pedipalps (black), which provide several dozen glomeruli in the brain that have connections to the paired mushroom bodies (B: central nervous system outline). The glomerular complexes (one of the bilaterally paired complex bracketed in C, D) are equipped with small or, in some individuals (interpreted as males) large glomeruli (arrowed in C). As in insects, glomeruli are uniquely identifiable. The first leg pair of Amblypygidae (colored black in E) are specialized to provide highly sensitive tactile and olfactory organs. These supply many hundreds of minute glomeruli that extend across three neuromeres, as far rostrally as the paired and highly folded mushroom bodies (F: central nervous system outline). In some individuals the small glomeruli are flanked by groups of larger ones (bracketed in G), whereas in others (sex undetermined) there are single large glomerulus (arrow) or a cluster of medium sized glomeruli (bracketed in H).