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The organization of the olfactory lobes in Euphausiacea and Mysidacea (Crustacea, Malacostraca)

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Summary. The structural organization of the olfactory lobes in representatives of euphausiid and mysid crustaceans was investigated and compared, also with these structures described in other crustaceans and in insects. In the investigated euphasiid and mysid species, the olfactory-globular tract and the position of cell clusters associated with the olfactory lobes show a similar arrangement. This arrangement is in agreement with that described in decapod crustaceans. The olfactory lobe neuropil in representatives of both taxa shows glomerular arrangement. These glomeruli are partly enclosed in a glial wrapping, and they represent the only site where synaptic contacts are established within the olfactory lobes. This glomerular arrangement appears similar to that described in the antennal lobe of insects, but differs from the columnar arrangement described in decapod crustaceans. Furthermore, about 15–20 FMRFamide-like immunoreactive globuli cells were labeled and they occupy a similar position in the investigated species. Neurites from these cells terminate only in the olfactory lobe glomeruli, and they are therefore regarded as intrinsic interneurons. The absence of serotonin-like immunoreactivity in the olfactory lobes is a feature only ascribed to the euphausiids and mysids. A specific neuropil area is present in male mysids, and it occupy a position forward of the olfactory lobe. The male-specific neuropil in mysids and the macro-glomerular in insects complex are interpreted as analogous structures.

A. Introduction

The olfactory lobes in crustaceans are thought of to constitute the site of olfactory processing between chemoreceptors and olfactory interneurons (Ache and Derby 1985). Earlier anatomical studies have shown that the olfactory lobes are prominent neuropil areas in the deutocerebral part of the brain in different crustacean species (Hanström 1928, 1947; Helm 1928; reviewed by Sandeman 1982). Since then, detailed information concerning the structural organization of the olfactory lobes in crustaceans has largely been obtained from different decapod species (see Sandeman and Luff 1973; Tsvileneva and Titova 1985; Blaustein et al. 1988). These studies show that the organization of the olfactory lobes share several morpholoical features, and that this organization probably represent a general structural plan.

Whether the general plan described in decapods is applicable to the organization of the olfactory lobes in other crustaceans, is a question yet to be determined. The presence of well-developed olfactory lobes is known in other crustaceans taxa, such as the Euphausiacea and Mysidacea (Hanström 1928, 1947). However, detailed information about the structural organization of their olfactory lobes is lacking.

B. Materials and methods

Animals. Adult males and females of the following species were used; *Meganyctiphanes norvegica* M. Sars, 1857 (Euphausiacea), *Boreomysis arctica* Kröyer, 1861, and *Neomysis integer* Leach, 1815 (Mysidacea). *Boreomysis* and *Meganyctiphanes* were obtained in waters near the Marine Biological Institute, Espegrend, Bergen, Norway. *Meganyctiphanes* specimens were also caught in waters near Tjärnö Marinbiological Station, Strömstad, Sweden. *Neomysis* were caught along the coast of the southern part of Sweden.

Golgi impregnation. A modified rapid Golgi impregnation was carried out as follows. Excised heads with eyestalks, antennae, and stomach removed were fixed in 2.5% glutaraldehyde in 0.15 M sodium cacodylate buffer (pH 7.3) for 4 h at 4° C. After several washes first in 0.15 M sodium cacodylate buffer (1.5 h) and then in 2.5% $Na_2Cr_2O_7$, an incubation in a solution consisting of 2.5% $Na_2Cr_2O_7$ and 0.1% OsO_4 followed for 24–48 h in darkness at room temperature. The specimens were then thoroughly washed in fresh 2.5% $Na_2Cr_2O_7$ at room temperature for 1–1.5 h, followed by an incubation in a solution consisting of 2.5% $Na_2Cr_2O_7$ and 5% glutaraldehyde for 48 h in darkness at room temperature. This incubation was followed by several washes first in fresh 2.5% $Na_2Cr_2O_7$, followed by short rinses in H_2O, and then washes in 0.75% $AgNO_3$. An incubation in 0.75% $AgNO_3$ followed for 3–

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4 days in darkness at room temperature. After a short rinse in H_2O, the specimens were dehydrated and embedded in Araldite (Durcupan, Fluka), and sectioned at 14–18 μm with an LKB pyramitome. The sections were stained with 1% Azur II and 1% methylene blue at 60° C for 5–15 min. Bodian-eosin impregnations from the collection of the Department of Zoology, Lund, Sweden, were also used.

Electron microscopy. Excised heads dissected as above were fixed overnight in 2.5% glutaraldheyde, with 2% NaCl added for fixation of *Meganyctiphanes,* in 0.15 M sodium cacodylate buffer (pH 7.3) at 4° C. The specimens were thoroughly washed in the same buffer, before postfixation in 1% OsO_4 in the same buffer for 1–2 h at 4° C. After embedding in Araldite, the specimens were sectioned with a diamond knife, stained in an LKB ultrastainer with lead citrate and uranyl acetate and examined with a JEOL 1200EX transmission electron microscope.

Immunocytochemistry. Excised heads destined for immunocytochemistry were fixed in 4% paraformaldehyde with 0.25% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2) for 4–6 h at 4° C. The heads were throroughly washed in phosphate buffer, dehydrated, embedded in paraffin, and sectioned at 15 μm. To block non-specific staining a preincubation in synthetic avidin (1:10000) (Sigma), biotin (1:10000) (Sigma), and normal goat serum (1:20), respectively, was carried out. The sections were then incubated in the primary antiserum against, either FMRFamide or serotonin (both from Incstar, Stillwater, U.S.A.), diluted 1:500 or 1:1000 in phosphate buffered saline (PBS) with 0.25% Triton X-100 and 1% bovine serum albumin (BSA). Incubation lasted overnight in a moisture chamber at room temperature. Visualization of the antisera was performed according to the ABC method using a Vectastain kit (Vector Labs). Preabsorption of the primary antisera in excess of synaptic FMRFamide (Peninsula Inc. U.K.) resulted in unstained sections.

A whole mount protocol was tested and performed as below. Fixed brains were dissected out and immersed in 0.1 M phosphate buffer (pH 7.2) with 20% dimethylsulfoxide (DMSO) for 1–2 h in cold at −70° C. After several washes in the same buffer and in 0.1 M PBS with 0.25% Triton X-100, the brains were incubated in FMRFamide antiserum diluted 1:1500 in PBS with 1% BSA for seven days at 4° C. As a secondary antiserum, unlabeled swine anti-rabbit immunoglobulins (Dakopatts, Copenhagen) diluted 1:50, were used. An incubation in peroxidase-antiperoxidase (PAP) complex (Dakopatts) also diluted 1:50 followed. Incubation time for both was 24 h at 4° C. After the PAP complex the brains were preincubated in 0.03% diaminobenzidine (DAB, Sigma) in 0.05 M TRIS-buffer (pH 7.6) for 30 min, whereupon 0.015% hydrogen peroxidase was added for another 10–15 min. Several washes were carried out between each incubation. The brains were then postfixed in 1% OsO_4 in sodium cacodylate buffer (pH 7.3) for 1 h at 4° C, and finally dehydrated, embedded in Araldite, and sectioned at 20–30 μm.

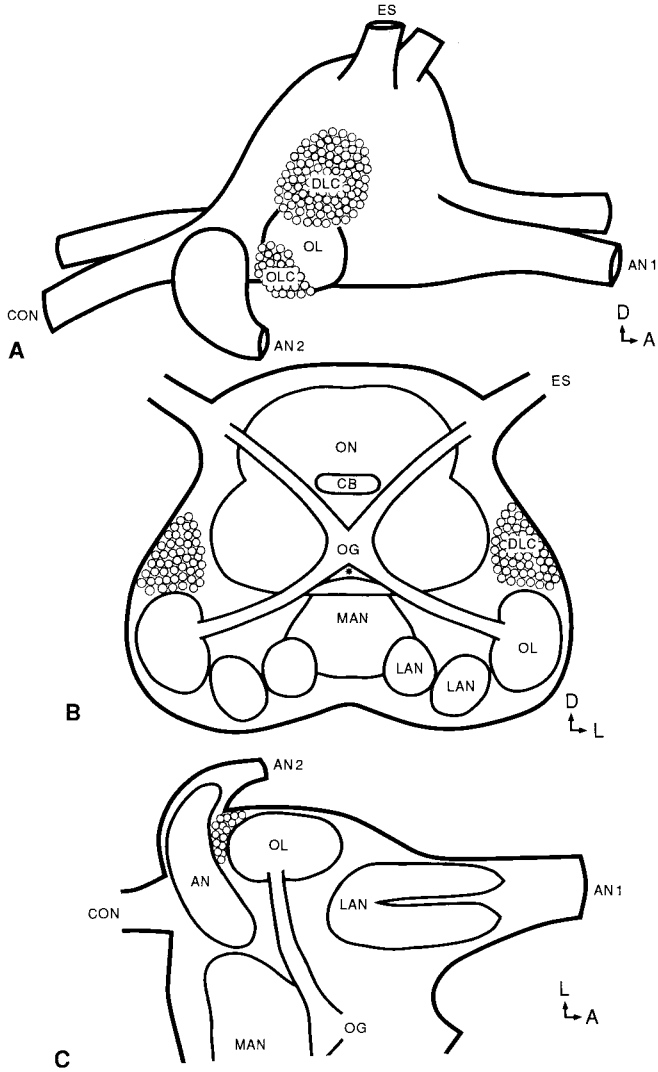

Fig. 1A–C. Schematic drawings representing a combined euphausiid and mysid brain, showing its external (**A**) and internal (**B, C**) gross morphology. **A** Lateral view, **B** Frontal section, and **C** horizontal section, of the left hemisphere. Abbreviations: *A* anterior; *D* dorsal; *L* lateral; *AN* antennulary neuropil (tritocerebrum); *AN1* antennular nerve; *AN2* antennulary nerve; *CB* central body; *CON* connective; *DLC* dorsal lateral cell cluster; *ES* connection (optic nerve) to eyestalk; *LAN* lateral antennular neuropil; *MAN* medial antennular neuropil; *OG* olfactory-globular tract; *OLC* olfactory lobe cell cluster; *OL* olfactory lobe; *ON* optic neuropils (protocerebrum). The deutocerebral commissure is indicated (*asterisk*) in **B**. Not to scale

C. Results

I. General morphology

In general, the following description of the olfactory lobes is applicable to all of the investigated species, but some differences will be noted. The paired olfactory lobes (OL) are distinct neuropil areas that occupy a lateral position in cerebral ganglia, or the brain. The paired, horseshoe-shaped lateral antennular neuropil (LAN) and the umpaired, ill-defined, medial antennular neuropil (MAN), lie medially to the olfactory lobes (Figs. 1A–C, 2A, B, 3A). These neuropil areas are here named according to their counterparts described in deca-

Fig. 2A–G. Micrographs of the olfactory lobes (*OL*) from different mysid species. **A, B** Horizontal section of *Boreomysis arctica* showing the difference between a male (**A**), with the male-specific neuropil (*asterisk*), and a female (**B**). **C** Frontal section of *Neomysis* showing a bundle of Golgi-impregnated interneurons that runs in the OG tract (*arrows*), and their arborizations that end in several glomeruli (*g*). The boundaries of the olfactory lobe are indicated (*dots*). **D, F** Electron micrographs of the olfactory lobes. **D** Part of a glomerulus showing a separating path (*arrows*) of fiber and glial elements and haemocoelic vessels as well as the synaptic area. **E** Micrograph showing the neural lamella (*white arrow*) and glial processes (*arrowhead*). Note the synaptic contact (*black arrow*) between the larger fiber elements (*asterisk*) in the glomerulus. **F** Micrograph of a layer of ensheathing glia processes (between *arrowheads*). **G** Frontal section of the olfactory lobe (*OL*) showing FMRF-ir terminals in the glomeruli

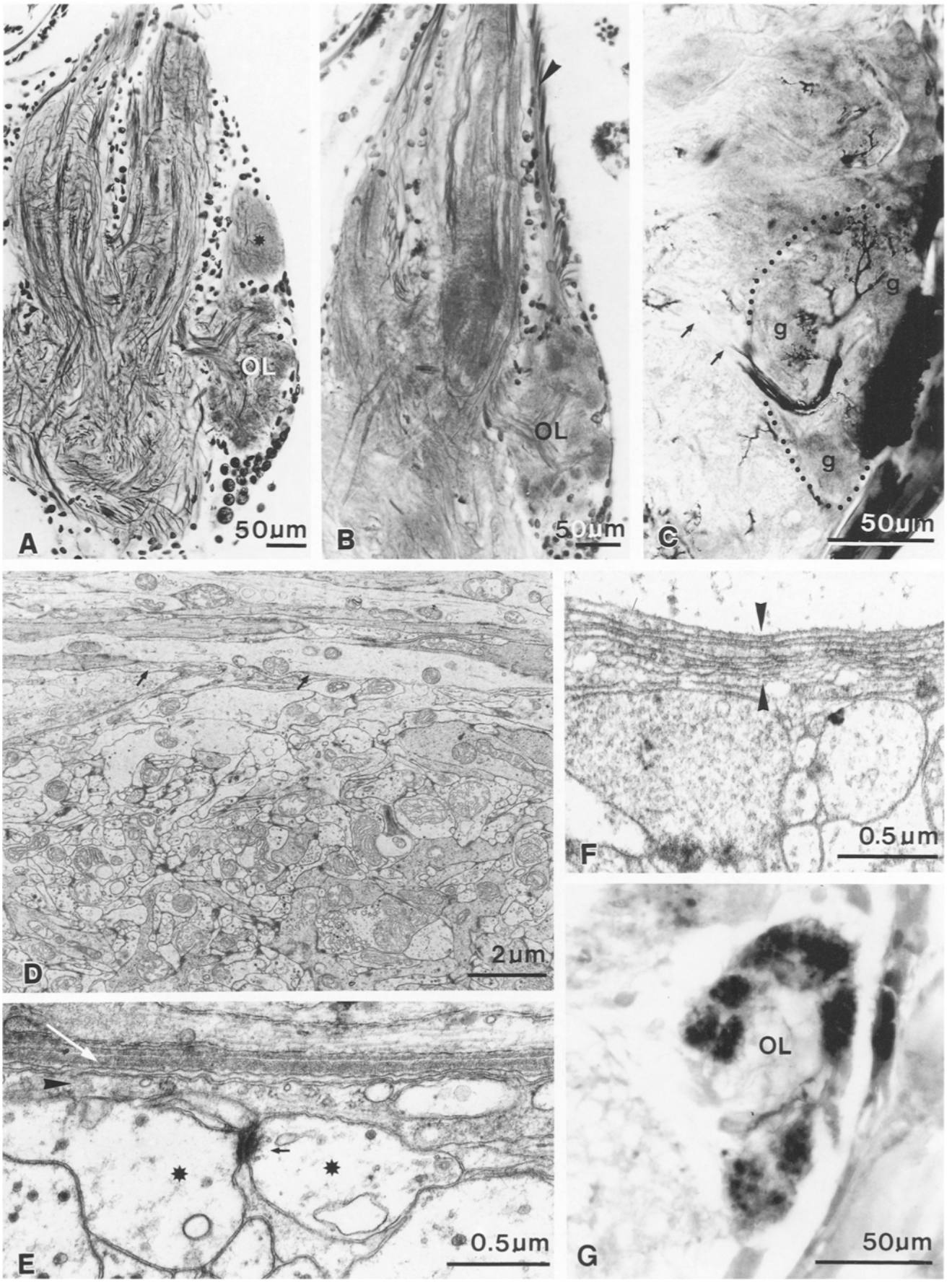

Fig. 2 A–G

pod crustaceans (reviewed by Sandeman 1982; see also Tsvileneva and Titova 1985; Blaustein et al. 1988), and together with the olfactory lobes they comprise the mass of the deutocerebral part of the brain in the investigated species.

1. Nerves and tracts

Afferents from sensory cells on the ipsilateral antennule (first antenna) are carried in the antennular nerve (AN1) (Fig. 1A, C) and, as this large nerve projects towards the brain, it splits up into smaller nerve branches. One branch of this nerve projects into the ipsilateral olfactory lobes (Figs. 2B, 4A) while the other branches project into the ipsilateral lateral antennular neuropil (Fig. 2A, B).

The large olfactory-globular tract (OG tract) arises from the medial part of each lobe, and forms a chiasm centrally in the brain just below the central body (CB) (Fig. 1B, C). From here the tract bifurcates and each branch of it projects towards protocerebral regions which are located in the eyestalks (Hanström 1928, 1947). During their course to the eyestalks the branches of the tract become less distinct. In some preparations a small commissure is partly discernible in the deutocerebrum, ventral to the olfactory-globular tract (Fig. 1B). It is suggested that this commissure corresponds to the deutocerebral commissure described in decapod crustaceans (Sandeman and Luff 1973).

2. Cell bodies

The cell bodies of the interneurons confined to the olfactory lobes are arranged in two clusters in the vicinity of each olfactory lobe (Figs. 1A–C, 2A, B, 3A). The majority of these cell bodies are characterized by their small diameter (10–20 μm) and nuclei that occupy the major part of the cell. This suggests that these interneurons can be interpreted as globuli cells (cf. Sandeman and Luff 1973). One cell cluster is located laterally to the brain proper on the dorsal part of the lobe. The other cell cluster is located on the ventroposterior part of the lobe. In analogy with similar cell body clusters in decapod crustaceans (reviewed by Sandeman 1982), the two clusters described here are referred to as the dorsal lateral cell cluster (DLC) and the olfactory lobe cell cluster (OLC), respectively (Figs. 1A–C, 3A).

II. Fine morphology

1. Glial elements

The olfactory lobes as well as the rest of the brain is surrounded by a neuronal lamella, an acellular layer that varies in thickness. It is less than 1 μm in *Meganyctiphanes* (Fig. 3C) and considerably thinner in *Neomysis* (Fig. 2E). Beneath the lamella there is a cellular layer, which also varies in thickness, consisting of different glial elements and occasionally haemocoelic vessels (cf. Abbot 1971b) (Figs. 2E, 3C). The glial elements are distinguished by their location and cellular components and they are here interpreted to correspond to the perineurium and cortical glia, respectively, as described in *Carcinus* by Abbott (1971a). In addition there are flattened glial processes that separate the olfactory lobe neuropil from the perineurium and cortical glia layer (Figs. 2E, 3D). Such glial processes also delimit the olfactory lobe from the olfactory lobe cell cluster. This type of glial process has similar morphological features to the ensheathing glia in *Carcinus*.

2. Organization of the olfactory lobes

Each olfactory lobe is essentially constructed of the following parts; a more or less pronounced central fibrous core region, surrounded by condensed neuropil areas in the form of spherical to irregular-shaped structures referred to as the glomeruli (Figs. 2A, B, 3A). At the medial part of the lobe there is an orifice for the passage of fibers to and from its interior region (Fig. 3A). The fibrous core region is composed of fibers from the olfactory-globular tract and neurites from cell bodies with a ventral position in the dorsal lateral cell cluster. These neurites join in a bundle that enters the lobe together with fibers in the olfactory-globular tract (Fig. 3A). Occasionally, neurites derived from cell bodies in the olfactory lobe cell cluster can be seen to enter the lobe. Bodian and Golgi impregnations of the lobe reveal that fibers and neurites enter at the central part of the glomeruli (i.e., the part that faces the core region) (Fig. 2A). Some fibers project via the olfactory-globular tract into the olfactory lobe where they arborize in several glomeruli (Fig. 2C). After entering into the separate glomerulus, the fibers ramify throughout the major part of it. The origin of these fibers is unknown.

3. Structure of glomeruli

Individual glomeruli lie irregularly arranged around the central core region of the lobe, and they are separated from each other by a less-stained interglomerular area (Figs. 2A, 3A). This area is mainly composed of haemocoelic vessels, different fibers, and sheaths of flattened glial processes (Fig. 2D). These last are processes from the surrounding ensheathing glia that extend into the neuropil and separate the glomeruli. Ensheathing glia form a complete layer around the peripheral part of the glomerulus (Fig. 2F). In some preparations this layer becomes progressively thinner as it continues towards the central face of the glomerulus, where neuronal elements enter.

There is an outer region of larger diameter fiber profiles immediately below the ensheathing glia peripherally in the glomerulus. Synaptic contacts are occasionally found between these fiber elements (Fig. 2E). This outer region partly surrounds a denser central region, characterized by the abundance of synaptic contacts between

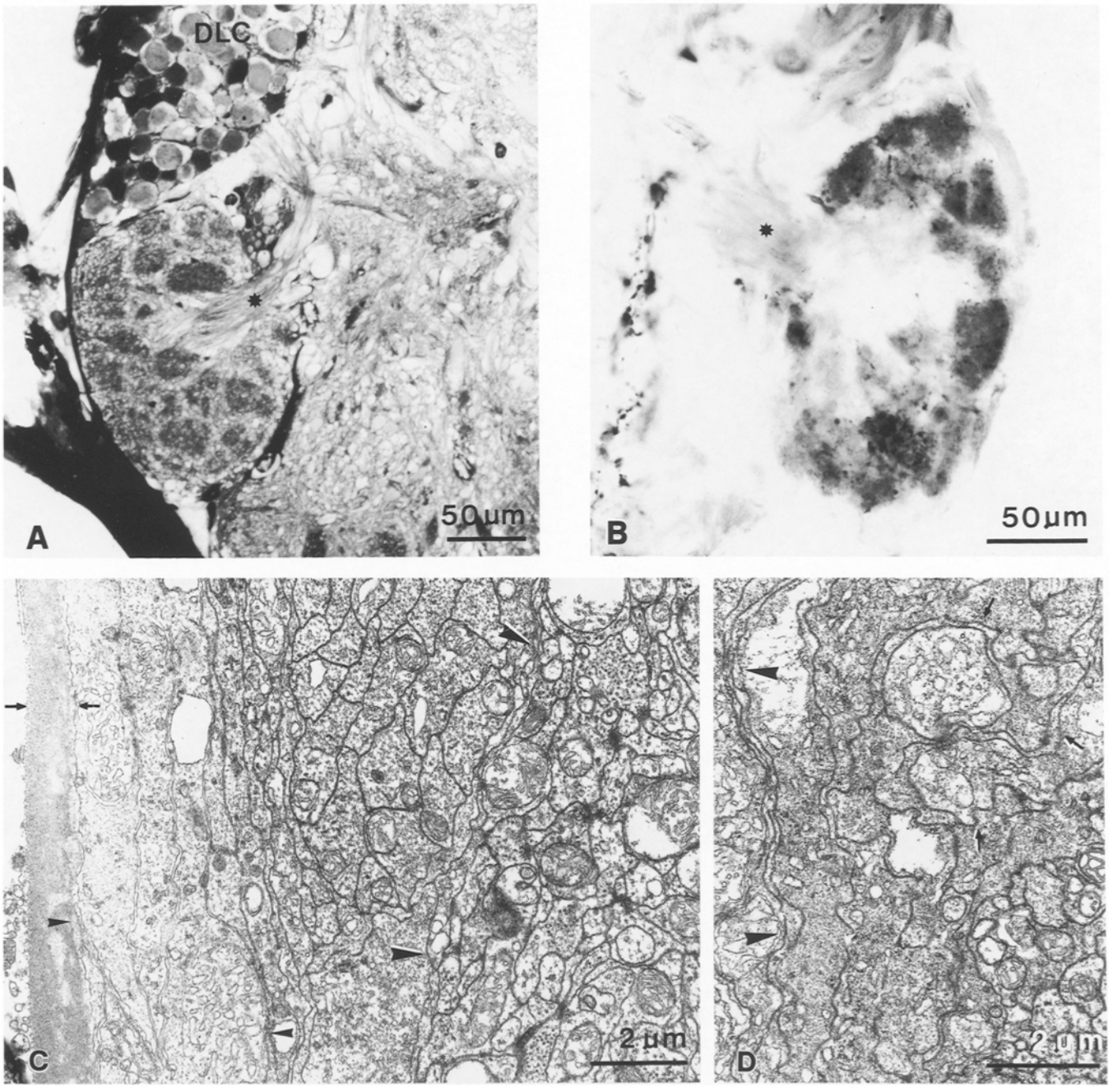

Fig. 3A–D. The olfactory lobe of *Meganyctiphanes norvegica*. **A–B** Micrographs of the lobe. **A** Frontal section showing the scattered, darkly stained glomeruli, the dorsal lateral cell cluster (*DLC*) and the olfactory-globular tract (*asterisk*). **B** Horizontal section of a whole-mount preparation showing FMRF-ir terminals in the glomeruli. The olfactory-globular tract is indicated (*asterisk*). **C, D** Electron micrographs of the olfactory lobes. **C** The neural lamella (between *arrows*) and the perineurium (small *arrowheads*) enclose the olfactory lobe. The glomeruli are partly enclosed by thin processes of ensheathing glia (large *arrowheads*). **D** In the glomerulus, a region of larger fiber elements (*arrows*) is present below the layer of ensheathing glia processes (*arrowheads*)

small diameter fiber elements (Figs. 2D, 3D). This suggests the presence of a regionalization within the glomerulus itself. In general, The synaptic terminals are characterizd by having a presynaptic density, which is apposed by a thickened membrane. A cluster of vesicles is often found near the synaptic density, to which it seems to be attached (Fig. 2E). The glomeruli are thus the only site in the olfactory lobes where synaptic contacts are established. It is suggested that each glomerulus constitutes a separated unit of synaptic contacts, incompletely enclosed in a glial wrapping.

4. Sexual dimorphism

In front of each olfactory lobe a small neuropil area appears in male mysids, where it occupies a position laterally to the lateral antennular neuropil and ventrally

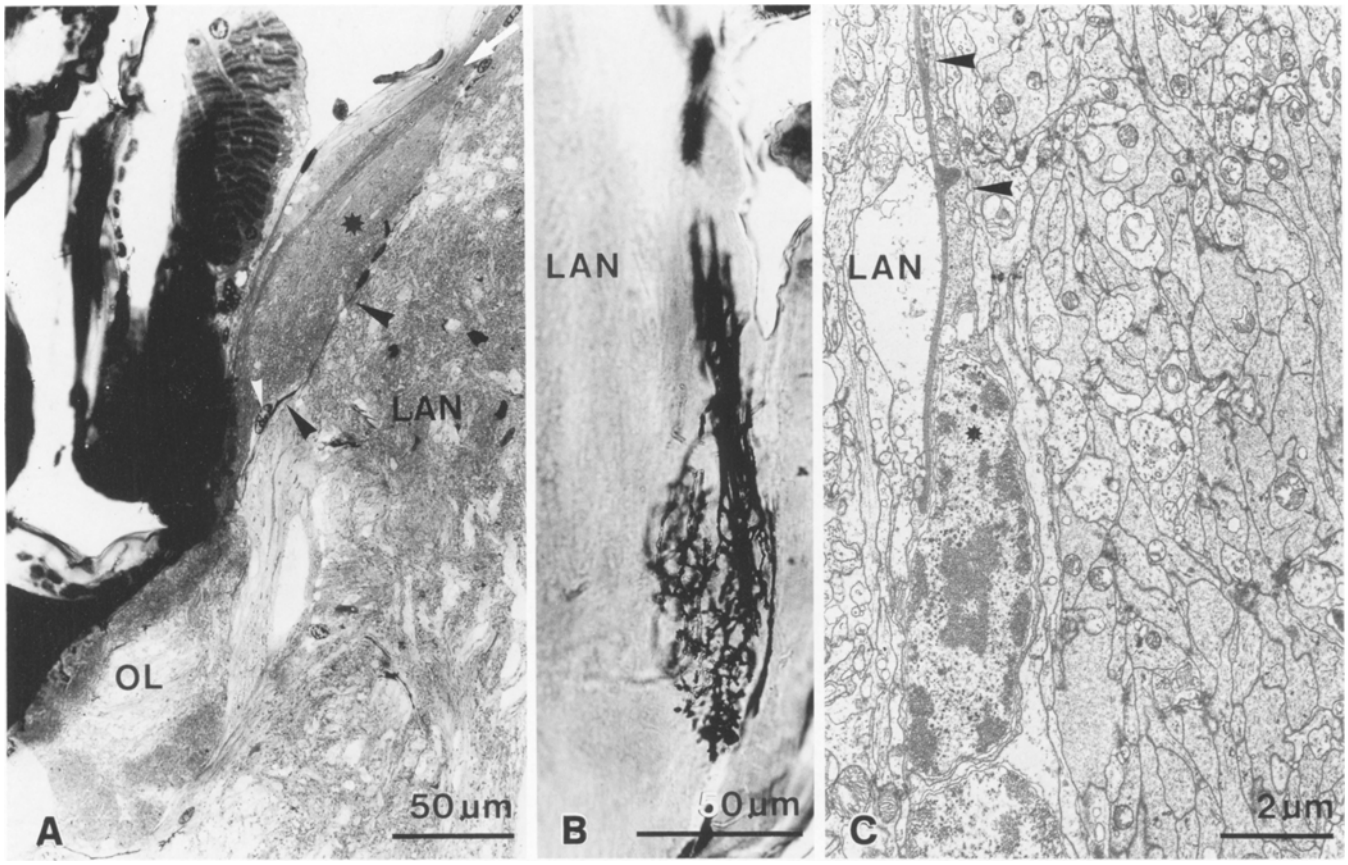

Fig. 4A–C. The male-specific neuropil of *Neomysis integer*. **A, B** Horizontal section of the neuropil. **A** The position of the neuropil (*asterisk*) in front of the olfactory lobe (*OL*) and lateral to the lateral antennular neuropil (*LAN*) is shown. Part of the antennular nerve is also visible (*white arrow*). Note also the boundaries of the neuropil (*black arrowheads*) and the glial cell body (*white arrowhead*). **B** Micrograph showing the termination of Golgi-impregnated sensory afferents in the male-specific neuropil. Abbreviations as in above. **C** Electron micrograph showing the vessels (*arrowheads*) that deline the male-specific neuropil from the lateral antennular neuropil (*LAN*). Note the vessel glia cell body is also shown (*asterisk*)

to the branch of the antenna nerve that enters the olfactory lobe (Figs. 2A, 4A). Depending on speices, the form of the male-specific neuropil varies from being elongated in *Neomysis* (Fig. 4A) to a spherical form in *Boreomysis* (Fig. 2A). In *Neomysis*, processes of haemocoelic vessels at the medical face of the neuropil enclose this side, as well as the anterior and posterior edge of the neuropil (Fig. 2A, C). The lateral side of the neuropil is occupied by neural elements. This implies that the major part of the male-specific neurpil is separated from the surrounding tissue, and it may be regarded as a separate unit analogous to the macro-glomerular complex in insects (cf. Matsumoto and Hildebrand 1981).

Golgi impregnations of *Neomysis* reveal that presumed sensory afferents enter at the lateral face of the male-specific neuropil. Branching of their delicate endings is rather sparse, but they ramify throughout the neuropil area (Fig. 4B). Similarly, electron micrographs show that synaptic contacts are distributed over the whole neuropil mass (Fig. 4C).

5. Immunocytochemically identified olfactory interneurons

Of the two applied antisera, only the one raised against FMRFamide labeled any neuronal structures in the olfactory lobes. Absence of serotonin-like immunoreactivity in the olfactory lobes is in agreement with results in the study of Aramant and Elofsson (1976): with the use of the Falck-Hillarp fluorescence method, they could not demonstrate any monoaminergic structures in the olfactory lobes of the mysids *Neomysis integer* and *Praunus flexuosus*.

In the investigated specimens, cell bodies of the FMRFamide-like immunoreactive (FMRF-ir) interneurons associated with the olfactory lobes are mainly located in the dorsal lateral cell cluster. The number of FMRF-ir cell bodies in this cluster varies between 15 and 20, but they are of similar size (diameter 10–20 µm).

In the mysids, neurites emanating from the FMRF-ir cell bodies run between the lobe and the brain proper toward the entrance of the olfactory-globular tract. Inside the lobe the neurites separate and run unbranched toward the glomeruli. Due to the low number of FMRF-

ir globuli cells compared to innervated glomeruli, their neurites are believed to branch and ramify in several glomeruli. The immunoreactive terminals are distributed in the whole mass of each glomerulus (Fig. 2G). In males of *Boreomysis* immunoreactive terminals also appear in the male-specific neuropil, but they could not be traced to their origin.

In *Meganyctiphanes,* neurites originating from the FMRF-ir cell bodies were not sufficiently stained to be followed completely. Some of FMRF-ir fibers in the lobe are interpreted to be derived from these FMRF-ir cell bodies, and their terminals ramify in the mass of the glomeruli (Fig. 3D). In addition, a few FMRF-ir fibers appear in the lobe, representing arborizations from larger fibers running in the brain proper. The origin of these fibers is unknown.

D. Discussion

This study demonstrates that a general structural plan of the olfactory lobes of the investigated euphausiid and mysid species exists, though they represent different taxa of malacostracan Crustacea (Bowman and Abele 1982). Similarities in this plan are manifested not only in the position of their olfactory lobes and the connection of tracts and cell clusters, but also in the glomerular arrangement of the lobe neuropil. Furthermore, the distribution of FMRF-ir olfactory interneurons and their connectivity patterns show some differences, while the absence of serotonin-like immunoreactive olfactory interneurons is a common feature. However, the presence of a sexual dimorphism is a feature only ascribed to the mystid species. Compared with the general plan described for the olfactory lobes in decapod crustaceans (Tsvileneva and Titova 1985; Blaustein et al. 1988; reviewed by Sandeman 1982), there are similarities which indicate that a general structural plan of the olfactory lobes is present in crustaceans. Thus, similarities exist in the position of the olfactory lobes and the related cell clusters, as well as for the olfactory-globular tract. Despite the similarities in this plan, there are differences in the structure of the olfactory lobes of some euphausiids and mysids, especially in finer details such as the glomerular arrangement and the nature of immunoreactive interneurons.

I. Glomerular neuropil

According to Maynard (1962), the olfactory lobe of crustaceans can be regarded as containing a structural neuropil. However, the organization of this structured neuropil is more variable among crustaceans than in insects. Including this study, three different morphological types of olfactory neuropil are discernible in crustaceans, which indicate a diverse construction of their olfactory lobes. Firstly, a very specific neuropil organization has recently been described in the olfactory lobes of the cephalocarid, *Hutchinsoniella macracantha* (Elofsson and Hessler 1990). Each lobe consist of several sublobes, where the neuropil compartments are interspersed with microvilli-like terminals. Secondly, among the Decapoda, the olfactory lobes contain tapered structures of dense neuropil called columns. The columns are peripherally arranged in the lobes, surrounding a large central core of neurites (Sandeman and Luff 1973; Blaustein et al. 1988). These studies also show the presence of a regionalization of the columns in the form of an outer cap and an inner base (column). Finally, in the investigated euphausiid and mysid species the olfactory lobe neuropil is thus suggested to be of a glomerular nature, with individual glomeruli more or less scattered around a central core. Each glomerulus has a spherical shape and it is separated from the other glomeruli by layers of ensheathing glia. The glomeruli constitute the only site in the olfactory lobes were synaptic contacts are established, a feature also ascribed to the columns in decapods (Sandeman and Luff 1973).

It is evident that the olfactory lobes of Malacostraca Crustacea show a structural variation in the form of a columnar or a glomerular organized neuropil. The main question is if these structures only differ in shape, or if they also reflect a functional difference. On the one hand, as pointed out by Sandeman and Luff (1973), the arrangement of the columns of decapods deviates from conventional glomeruli. The differences are displayed by the presence of a cap and a base region, and how neuronal elements connect to the columns (see Blaustein et al. 1988). It has been shown that sensory afferents that converge into the columns end and form contacts in the cap (Sandeman and Luff 1973), as well as in the base (Schmidt and Ache 1990). However, knowledge is lacking to verify if this feature reflects an organizational layering of the columns. If so, each column may be regarded as a functional unit as its name implies, and the glomerulus may represent a morphological unit. On the other hand, there are some similarities between the two structures, such as the delicate regionalization within the glomeruli itself of euphausiids and mysids. This regionalization is however not so pronounced as in the columns of decapods. Like the glomeruli in insects (see below), there is a nontopographic representation of sensory afferents in the columns in decapods (Mellon and Munger 1990).

With the structural characteristics given above for glomeruli in some euphausiids and mysids, it is obvious that these structures have several features in common with the antennal lobe glomeruli described in insects (Prillinger 1981; Tolbert and Hildebrand 1981; reviewed by Rospars 1988; Homberg et al. 1989). Insect glomeruli are described as rounded structures partly enclosed in glia, in which synaptic contacts are established (Tolbert and Hildebrand 1981). A delicate regionalization of the glomeruli appears to be a feature also present in the glomeruli of some insects (Boeckh et al. 1970; Homberg et al. 1989). Further, it has been shown that there is a functional rather than a topographic representation of sensory afferents in insect glomeruli (Stocker et al. 1983), which is why they are regarded as separated functional units.

Taken together, this implies that glomeruli in the in-

vestigated euphausiid/mysid crustaceans and insects have several morphological features in common, while the columns are units only described in decapods. The two structures differ morphologically, but may be similar in function. It should be kept in mind that ontogenetic studies are lacking, which is why it is possible that morphologically differences between columns and glomeruli are of a developmental nature.

II. Neuronal organization

The olfactory lobes in the investigated euphasiid and mysid species are thus provided with a set of FMRF-ir globuli cells that exhibit similar morphological features. Their neurites are restricted to the ipsilateral olfactory lobe where each glomerulus is homogenously innervated. The FMRF-ir globuli cells are interpreted as olfactory interneurons that are intrinsic to the olfactory lobes, and thus act as local interneurons.

Olfactory interneurons exhibiting FMRFamide-like immunoreactivity have also been described in insects (Homberg et al. 1990) and decapods (Schmidt and Ache 1990). The FMRF-ir olfactory interneurons in insects are regarded as local interneurons, and show similar characteristics to those described here for euphausiids and mysids. In decapods however, the FMRF-ir globuli cells are local interneurons, but their connectivity pattern in the columns is of a regionalized nature, that is, the cap and the base of the columns differ in staining. Thus, the distribution of FMRF-ir terminals in columns and glomeruli is another feature that reflects differences between the two structures.

Interneurons of the olfactory lobes exhibiting serotonin-like immunoreactivity is a common feature both in decapods (Sandeman et al. 1988; Johansson 1991) and in insects (Nässel 1987). In the decapods, there are two morphological classes of 5-HT-ir olfactory interneurons; globuli cells and large interneurons (Sandeman et al. 1988; Johansson 1991). The termination pattern in the columns of these interneurons differs as described above. Similarily, these two morphological classes of decapod olfactory interneurons are labeled by antiserum raised against substance P (Sandeman et al. 1990). Thus, the lack of 5-HT-ir olfactory interneurons is a feature only ascribed to euphausiid and mysid species.

III. Sexual dimorphism

The presence of sexual dimorphic neuropil units is known from several insect species (Bretschneider 1924; Matsumoto and Hildebrand 1981; Prillinger 1981; for reviews see Rospars 1988; Homberg et al. 1989), while such units have hitherto not been described in crustaceans. In insects, this neuropil is referred to as the macro-glomerular complex (Matsumoto and Hildebrand 1981), and is located in the antennal lobes of males near the entrance of the antennal nerve. As the name suggests this complex develops as a fusion of several neuropil units (Prillinger 1981). The presence of the macro-glomerular complex corresponds to a peripheral dimorphism in the form of specific olfactory sensilla on the antennae of males (see Steinbrecht 1987).

In this initial study, sexual dimorphic neuropil units are shown to be present at the same position in the deutocerebral part of the brain of male mysids. As in insects, there is a correlation between the male-specific neuropil and the presence of a peripheral dimorphism displayed by specific sensilla (Guse 1983; Johansson and Hallberg 1992). Despite their varying form, the organization of the male-specific neuropil indicates that it represents a glomerulus, similar to the macro-glomerular complex described in insects. However, it is not known if the male-specific neuropil develops and constitutes a part of the olfactory lobe as the macro-glomerular complex (Prillinger 1981). Similarities thus exist between males from mysids and some insect species in the presence of sexually dimorphic structures. It can not be excuded that these structures in mysids are involved in pheromone detection as corresponding structure are in insects (Matsumoto and Hildebrand 1981; reviewed by Rospars 1988), Thus, the male-specific neuropil and the macro-glomerular complex may be analogous structures that have evolved in animals that occupy different habitats.

IV. Concluding remarks

The general structural plan of the olfactory lobes shows large similarities in several Malacostraca Crustacea. However, upon closer examination these similarities tend to conceal the presence of finer variations in the construction of the olfactory lobe neuropil and related olfactory interneurons. Differences in finer structural details of the olfactory lobes are present, not only between different malacostracan crustaceans but also in non-malacostracans, and can referred to taxonomic groups. Whether these differences are the product of different evolutionary paths or represent developmental transformations is unanswered. In addition, the presence of male-specific neuropils is a feature in common for Mysidacea and some Insecta, and they are suggested to represent analogous structures. Also, the glomerular arrangement of the olfactory neuropil appears to be a feature that is common for some Euphausiacea/Mysidacea and Insecta.

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