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Exploring Cerebral Features in Acochlidia (Gastropoda: Opisthobranchia)*

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Abstract. Histological semithin sections of the marine acochlidian species *Hedylopsis spiculifera* (Kowalevsky, 1901), *H. ballantinei* Sommerfeldt & Schrödl, 2005, *Microhedyle remanei* (Marcus, 1953) and *Asperspina murmanica* (Kudinskaya & Minichev, 1978) and of the limnic *Tantulum elegans* Rankin, 1979 were (re)examined for different cerebral features: 1) the number of cerebro-rhinophoral connectives, 2) the presence of Hancock s organs, 3) the relative position and size of the eyes, the length and diameter of the optic nerve, and the presence of an optic ganglion, and 4) cellular aggregates attached to the cerebral ganglia. We describe novel structures such as double cerebro-rhinophoral connectives in *T. elegans*, and "lateral bodies" in *H. spiculifera*, *H. ballantinei* and *A. murmanica*. Cerebral features are discussed as a promising additional set of characters for phylogenetic analysis. However, (ultra)structural comparisons of acochlidians with basal opisthobranchs and pulmonates are overdue.

Keywords. Cerebral nerves, "lateral bodies", dorsal bodies, Hancock's organ, optic ganglion.

1. INTRODUCTION

Acochlidian opistobranch gastropods show high morphological and biological diversity. However, the number of useful characters for phylogenetic analyses is still limited by the paucity of comparative data available. The central nervous system (cns) of several euthyneurous taxa was described (e.g. Haszprunar & Huber 1990; Huber 1993; Mikkelsen 2002), comprising data about cerebral nerves and sensory organs. The value of these data in phylogenetic studies is evident (Dayrat & Tillier 2002; Mikkelsen 1996). In contrast, several of the species (re)descriptions in Acochlidia do not include any information on the cns (e.g. Haynes & Kenchington 1991; Hughes 1991; Kirsteuer 1973; Marcus & Marcus 1955, 1959; Salvini-Plawen 1973; Wawra 1979, 1980, 1988). Other authors limited their descriptions of the cns to the main ganglia on the (pre)pharyngeal nerve ring and the visceral nerve cord (e.g. Bergh 1895; Bücking 1933; Challis 1968, 1970; Doe 1974; Hertling 1930; Kowalevsky 1901; Kudinskaya & Minichev 1978; Küthe 1935; Marcus 1953; Marcus & Marcus 1954; Morse 1976; Swedmark 1968; Wawra 1989; Westheide & Wawra 1974). Unfortunately, the identification of the small and hardly separated ganglia on the visceral nerve cord is problematic. Even detailed histological descriptions, such as that of *Tantulum elegans* by Rankin (1979), can be considerably misleading and thus cannot be trusted (see Neusser & Schrödl 2007). Furthermore, very few studies give data about cerebral nerves and sensory organs reflecting the complexity of the acochlidian cns. Huber (1993) gave a detailed overview of the cns in marine heterobranchs and determined the number of cerebral nerves in Acochlidia to only two (the labiotentacular nerve and the proximally joint oral and rhinophoral nerve) plus the static nerve. Sommerfeldt & Schrödl (2005) confirmed these three nerves plus optic nerves for *Hedylopsis spiculifera* and *H. ballantinei*. The authors emphasized the presence of large rhinophoral ganglia, from which the joint oral and rhinophoral nerve arise, and that was overlooked in *H. spiculifera* by Huber (1993). The terminology and the homology of the different cerebral nerves in Acochlidia are still uncertain.

Data about sensory organs are sparse, often consisting only in the affirmation of presence or absence of easily identified structures, such as eyes (e.g. Challis 1970; Marcus 1953; Marcus & Marcus 1955; Westheide & Wawra1974). Hancock's organs, the primary chemosensory organs in architectibranchs and cephalaspideans (Mikkelsen 1996, 2002), were thought to be absent in Acochlidia (e.g. Neusser et al. 2006; Sommerfeldt & Schrödl 2005; Wawra 1987). However, Hancock's organs like structures were reported from *Microhedyle glan-*

Table 1 . Comparison of cerebral features in different acochlidian species. +: present, –: absent, ?: not detected.

feature \ species	*Hedylopsis spiculifera*	*Hedylopsis ballantinei*	*Asperspina murmanica*	*Tantulum elegans*	*Microhedyle remanei*
Double cerebro-rhinophoral connective	?	?	?	+	?
Hancock´s organ	?	?	?	+	?
Eyes	+ pigmented	+ pigmented	–	+ reduced unpigmented	–
Eyes externally visible	dorsal and lateral well visible	dorsal and lateral hardly visible	–	not visible	–
Eyes position	posterior to the rhinophores (in some distance)	slightly posterior to the rhinophores (at their base)	–	slightly anterolateral to the cerebral ganglion	–
Eye size in diameter	25 µm	30 µm	–	20 µm	–
Optic nerve	long, undulated	long, undulated	–	short, not undulated	–
Optic nerve diameter	6–7 µm	6–7 µm	–	3 µm	–
Optic ganglion (diameter)	–	–	–	+ (18 µm)	–
Lateral bodies	+	+	+	–	–
Cells above cerebral commissure	?	?	+	?	?

dulifera (Kowalevsky, 1901) and *Pontohedyle milaschewitchii* (Kowalevsky, 1901) by EDLINGER (1980a, b), and recently confirmed for *P. milaschewitchii* (JÖRGER et al. in press). Additionally, our re-examination of *Tantulum elegans* revealed the presence of a small Hancock's organ in this species too (NEUSSER & SCHRÖDL 2007).

Among representatives of four traditional acochlidian families (Hedylopsidae, Asperspinidae, Tantulidae and Microhedylidae), the present study (re)investigates a number of special cerebral nervous features using histological sections. As far as information is available, these characters are compared with other acochlidian species and are evaluated as a possible set of characters for future phylogenetic analysis.

2. MATERIAL

Serial semi-thin sections of five different acochlidian species were available for re-examination by light microscopy: one series (section thickness: 1.5 µm) of *Hedylopsis spiculifera*, Zoologische Staatssammlung München, ZSM N° 20070391 (Secche della Meloria, Livorno, Italy, September 2005) and one paratype series (section thickness: 2 µm) of *Hedylopsis suecica* Odhner, 1937, Swedish Museum of Natural History, SMNH N° 27211; *H. suecica* was considered as a synonym of *H. spiculifera* by WAWRA (1989) and confirmed by SOMMERFELDT & SCHRÖDL (2005). Five paratype series (section thickness: 2 µm) of *Hedylopsis ballantinei*, ZSM N° 20004766/1, 20004767, 20004768, 20004769 and N° 26X (Dahab, Gulf of Aqaba, northern Red Sea, October 1999). Six series (section thickness: 1.5 µm) of *Microhedyle remanei*, ZSM N° 20070079, 20070080, 20070081, 20070082, 20070083 and 20070084 (southwest of Castle Roads, Bermuda Islands, July 1999). Four series (section thickness: 1.5 µm) of *Asperspina murmanica*, ZSM N° 20062163, 20062164, 20062165 and 20062167 (Yarnyshnaya Bay, Barents Sea, Russia, August 2005). Four original paratype series (section thickness: 3 µm) and two recently prepared paratype series (section thickness: 1.5 µm) of *Tantulum elegans*, Royal Ontario Museum, Canada, ROM N° 8E1 and 2F0 (Golden Grove, St. Vincent, West Indies, July 1972). All sections, except the original paratype series of *T. elegans*, were stained with methylene blue-azure II according to RICHARDSON et al. (1960).

3. CEREBRAL FEATURES EXAMINED

3.1. Rhinophoral ganglia and cerebro-rhinophoral connectives

A comparative overview of all examined features in the different species is given in Table 1.

All species re-examined herein, except *Microhedyle remanei*, have a pair of true rhinophoral ganglia, i.e. large ganglia separated into a nuclei-free medulla and a cortex composed of cell bodies. The rhinophoral ganglia of *M. remanei* are not subdivided into cortex and medulla; instead the nuclei are distributed homogeneously all over the ganglion (see NEUSSER et al. 2006, fig. 3d). Serial sections of *Hedylopsis spiculifera*, *H. ballantinei* and *M. remanei* show only a single nerve (approx. 5–10 µm in diameter) that connects the cerebral ganglion to the rhinophoral one. In one specimen of *Tantulum elegans* examined, we found two nerves connecting the cerebral ganglion with the rhinophoral ganglion (Fig. 1). Both nerves are thin (approx. 7 µm in diameter) and lie close together (distance between them approx. 3µm). Nevertheless, the transition between the cerebral ganglion and the rhinophoral ganglion is well identifiable due to the presence of dark stained fibres (Fig. 1A, D).

3.2. Sensory organs

3.2.1. Hancock's organ and nerve

Paired, small and ciliated invaginations posterior to the head appendages and innervated by cerebral nerves are present in *Tantulum elegans* (see NEUSSER & SCHRÖDL 2007, fig. 4b). Neither such organs of similar shape could be detected in *Hedylopsis spiculifera*, *H. ballantinei* and *Microhedyle remanei*, or cerebral nerves innervating the region where Hancock's organs are present in other acochlidian species.

3.2.2. Eyes, optic nerves and optic ganglia

Asperspina murmanica and *Microhedyle remanei* are eyeless and lack any optic nerve or optic ganglion. Both *Hedylopsis* species have pigmented lens eyes (Fig. 3A, B) that, however, differ in size and relative position. The eyes of *H. spiculifera* are clearly visible externally (Fig. 2A, B) from dorsal and lateral and reach up to 25 µm in diameter (Fig. 3A). They are located on the rather lateral side of the head (Fig. 2B), and are in some distance posterior to the rhinophores (Fig. 2A, B) and anterior of the cerebral ganglia. In contrast, the eyes of *H. ballantinei* are hardly detectable by external view (Fig. 2C) even though they are slightly larger (approx. 30 µm in diameter) (Fig. 3B). Furthermore, they are situated closer together and are just posterior to the rhinophores (Fig. 2C). The optic nerves show approx. 6-7 µm in diameter in both species (Fig. 3A, B). They arise from the rhinophoral ganglia and are highly undulated. An optic ganglion is absent in *H. spiculifera* as well as in *H. ballantinei*. In contrast, *Tantulum elegans* develops a very short and thin optic nerve (approx. 3 µm in diameter) leading to a reduced unpigmented eye of approx. 20 µm in diameter (Figs. 1, 3C). The optic nerve arises from a small optic ganglion (approx. 18 µm in diameter) that is subdivided into the outer cortex and the inner medulla (Fig. 3D). It is attached laterally to the cerebral ganglion, both of which are surrounded by a thin layer of connective tissue (Fig. 3D). No nerves can be detected by light microscope examination connecting the cerebral with the optic ganglion.

3.3. Aggregates attached to the cerebral ganglia

3.3.1. "Lateral bodies"

A "lateral body" as defined herein consists of a more or less hemispherical cluster of cells that is lying laterally on the surface of each cerebral ganglion. Under a light microscope, the cells of the "lateral bodies" cannot be distinguished from the neuron bodies situated in the cortex of the cerebral ganglion. Each "lateral body" is surrounded by a separate, relatively thin sheath of connective tissue and together with the cerebral ganglion by a second common and thick one. "Lateral bodies" are present in *Hedylopsis spiculifera* (Fig. 4A), *H. ballantinei* (Fig. 4B) and *Asperspina murmanica* (Fig. 4C). The "lateral body" lacks any subdivision. The nuclei are more or less uniformly distributed over the entire "lateral body". There are no nerves visible under the light microscope connecting the cerebral ganglion with the "lateral body", and there are no nerves arising from the latter. None of the specimens examined of *Microhedyle remanei* and *Tantulum elegans* had "lateral bodies".

3.3.2. Cells near the cerebral commissure

Additionally, we could find several cells of uncertain origin and function dispersed in the connective tissue above the cerebral commissure in *Asperspina murmanica* (Fig. 4D). In contrast to the "lateral bodies", these cells are not tightly attached to each other, and are not enclosed by an individual sheath of connective tissue. No data about the presence or absence of these cells can be given for *Hedylopsis spiculifera*, *H. ballantinei* and *Tantulum elegans*, due to very compressed tissue layers.

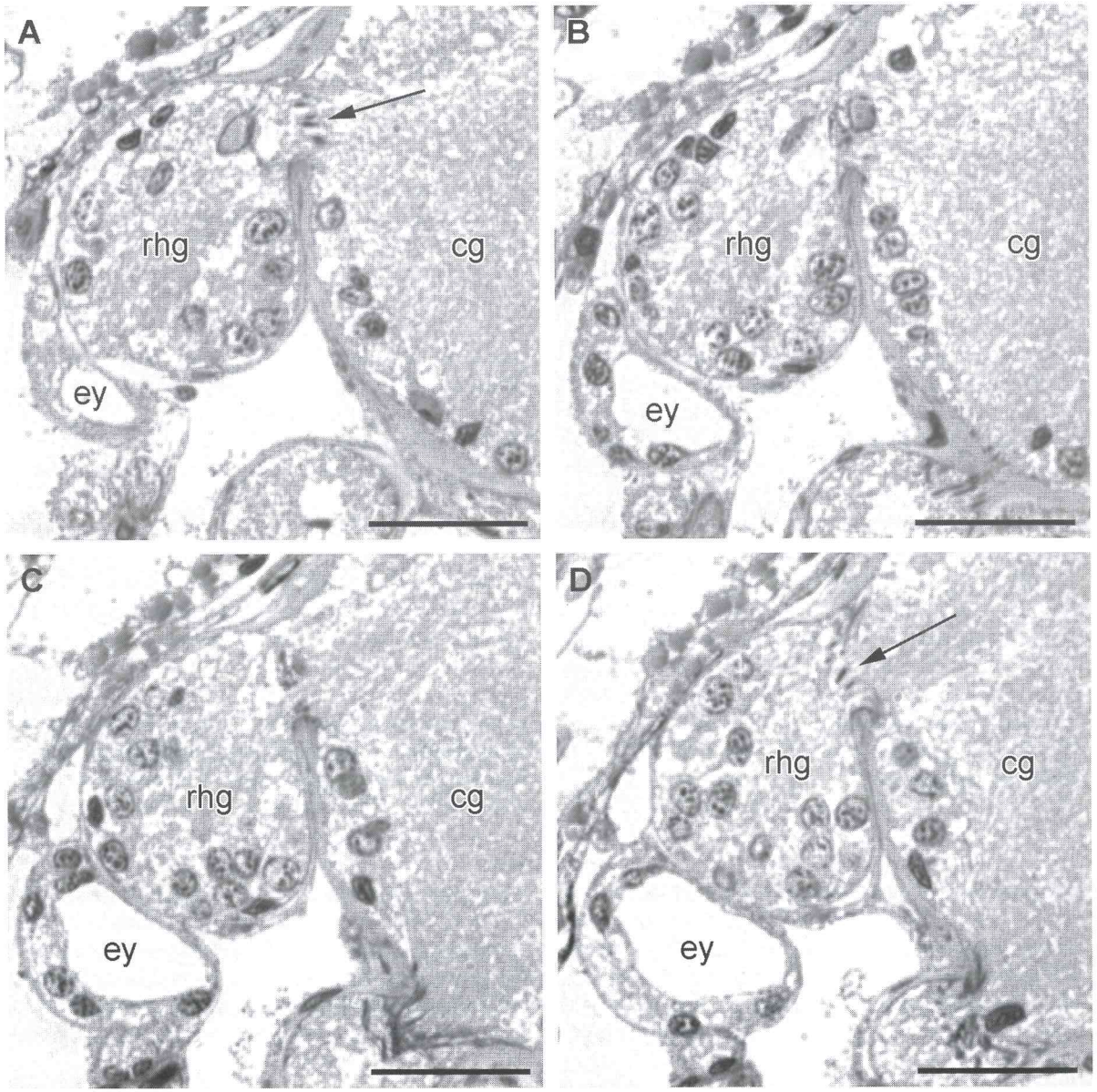

Fig. 1. Double cerebro-rhinophoral connective in *Tantulum elegans*. Four consecutive cross sections of series ROM N° 8E1, 3.slide, 6. ribbon, section N° 17–20. A: section N° 17, first cerebro-rhinophoral connective. B and C: section N° 18 and 19, respectively, without connective. D: section N° 20, second cerebro-rhinophoral connective. cg cerebral ganglion; ey eye; rhg rhinophoral ganglion; arrow, indicates fibres of the cerebro-rhinophoral connective. Scale bars A–D: 15 µm.

4. DISCUSSION

4.1. Rhinophoral ganglia and number of cerebro-rhinophoral connectives

The presence of rhinophoral ganglia were reported for *Hedylopsis spiculifera* and *Tantulum elegans* (see RANKIN 1979; WAWRA 1989), but both descriptions lack histological data of the rhinophoral ganglia. Recently, rhinophoral ganglia were described in detail for *Hedylopsis ballantinei* (see SOMMERFELDT & SCHRÖDL 2005), *Microhedyle remanei* (see NEUSSER et al. 2006), *T. elegans* (see NEUSSER & SCHRÖDL 2007) and *Pontohedyle milaschewitchii* (see JÖRGER et al. in press). Due to their position anterodorsally of the cerebral ganglia and their similar innervation the homology of the rhinophoral ganglia can be assumed for all acochlidian species studied herein. In contrast to *Hedylopsis* species, *Asperspina murmanica* and *T. elegans*, rhinophoral ganglia of *P. milaschewitchii* and *M. remanei* are not separated into medulla and cortex. The presence

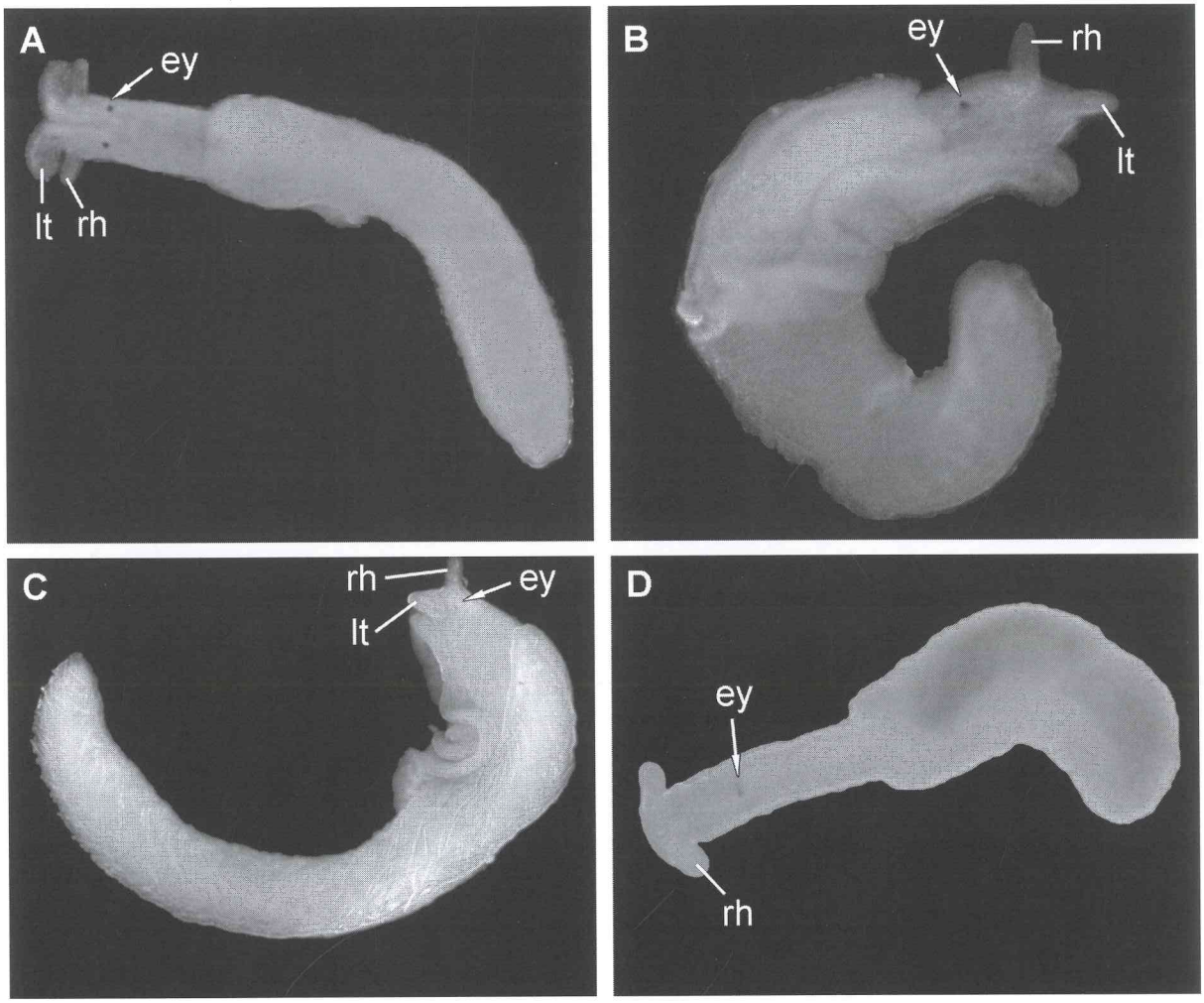

Fig. 2. Position of eyes in different acochlidian species, external view. A: *Hedylopsis spiculifera*, dorsal view, length 3.5 mm. B: *Hedylopsis spiculifera*, lateral view, length 3.5 mm. C: *Hedylopsis ballantinei*, lateral view, length 5 mm. D: *Pontohedyle milaschewitchii*, dorsal view, length 2.5 mm. ey eye; lt labial tentacle; rh rhinophore.

of rhinophoral ganglia within *P. milaschewitchii* that is lacking any rhinophores might be explained by a modified, e.g. neurosecretory function. *Microhedyle remanei*, however, possesses rhinophores and cell bodies evenly distributed within the rhinophoral ganglia.

Of all the specimens here studied, the double connection between the cerebral ganglia and rhinophoral ganglia could only be detected in one specimen of *Tantulum elegans*, and is only clearly visible on the right side of the nervous system. Unfortunately, the identification of these thin nerves depends critically upon preservation and staining conditions as well as on the cutting plane. Tiny nerves can thus be overlooked and easily misinterpreted, or be invisible even on semi-thin serial sections. While "detected" usually means "present", "not detected" does not necessarily mean "absent". The cerebro-rhinophoral connective has been identified by the presence of dark stained fibres. HASZPRUNAR (1985, figs. 19, 20) described similar fibres occurring at the transition between two different ganglia in *Discotectonica discus* Philippi, 1844. A double cerebro-rhinophoral connective has also been found in *Pontohedyle milaschewitchii* (see JÖRGER et al. in press); both nerves are even thinner than those in *T. elegans*. There is no reliable data on further acochlidians.

HASZPRUNAR & HUBER (1990) described a double cerebro-rhinophoral connective for the enigmatic opisthobranchs *Rhodope veranii* Kölliker, 1847 and *Rhodope transtrosa* Salvini-Plawen, 1989, as well as a double connective attaching the cerebral ganglion with the procerebrum in the pulmonate *Smeagol manneringi* Climo, 1980. In fact, the double cerebro-rhinophoral connective of the acochlidian cns resembles the general pulmonate condi-

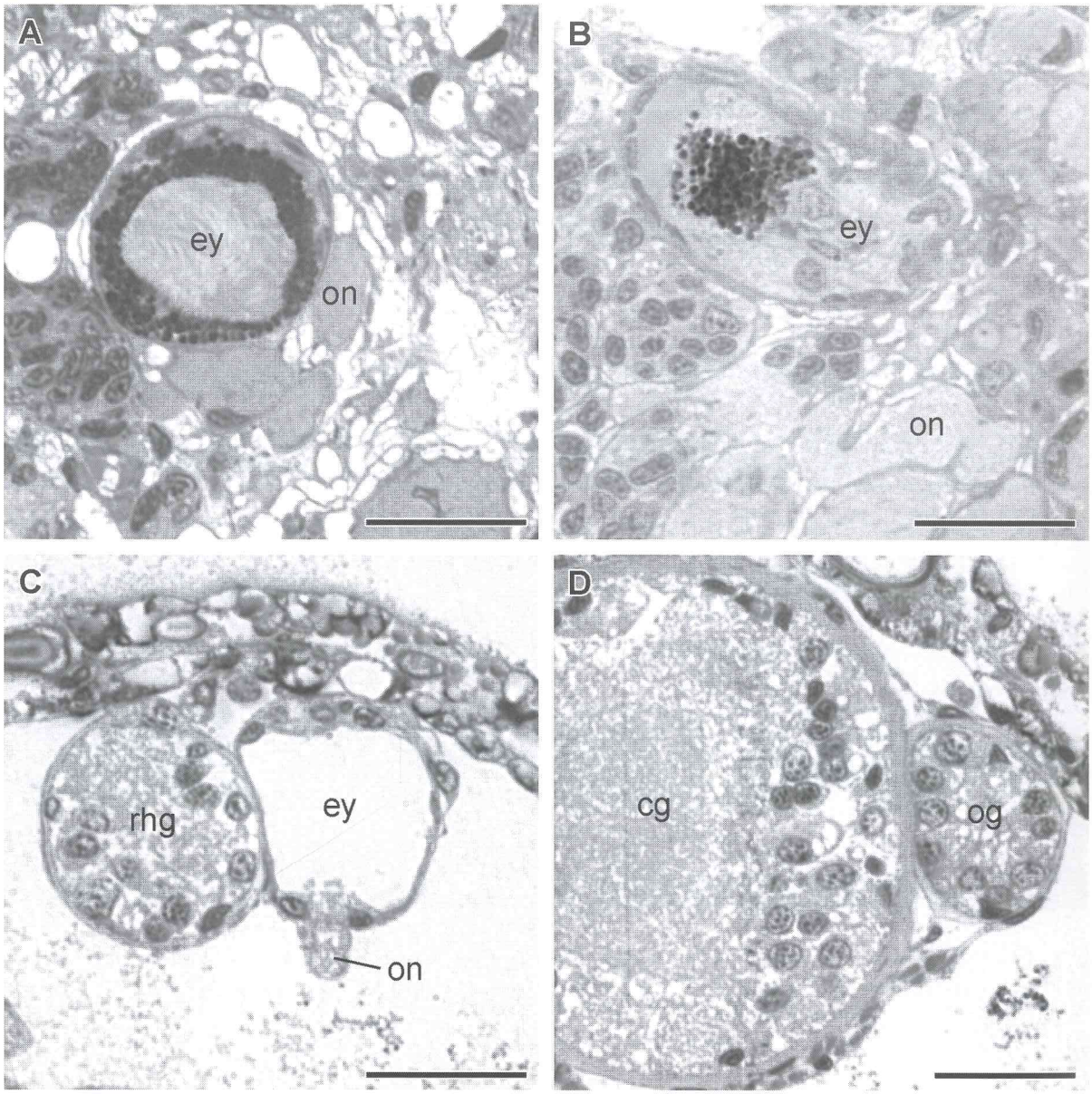

Fig. 3. Eyes and optic ganglion (cross sections). A: Pigmented eye in *Hedylopsis spiculifera* ZSM N° 20070391. B: Pigmented eye in *Hedylopsis ballantinei* ZSM N° 20004766/1. C: Unpigmented eye in *Tantulum elegans* ROM N° 8E1. D: Optic ganglion attached to the cerebral ganglion in *Tantulum elegans* ROM N° 8E1. cg cerebral ganglion; ey eye; og optic ganglion; on optic nerve; rhg rhinophoral ganglion. Scale bars A–D: 15 μm.

tion (VAN MOL 1967). Therefore, the potential homology of acochlidian rhinophoral ganglia to the procerebrum of pulmonates should be investigated in detail.

4.2. Sensory organs

4.2.1. Hancock's organ

We were not able to detect any Hancock's organ like structures in the species examined herein except for *Tantulum elegans* which shows a pair of epidermal folds on the side of the head (NEUSSER & SCHRÖDL 2007). Such folds were reported for *Pontohedyle milaschewitchii* and *Microhedyle glandulifera* and regarded as Hancock's organs by EDLINGER (1980a, b), i.e. as true homologues of the primary chemosensory organs in architectibranchs and cephalaspids (see MIKKELSEN 1996). According to their similar position, cerebral innervation, (although more tiny) structure, and probable sensory function, a general homology can be suspected. Some doubts persist, such as the

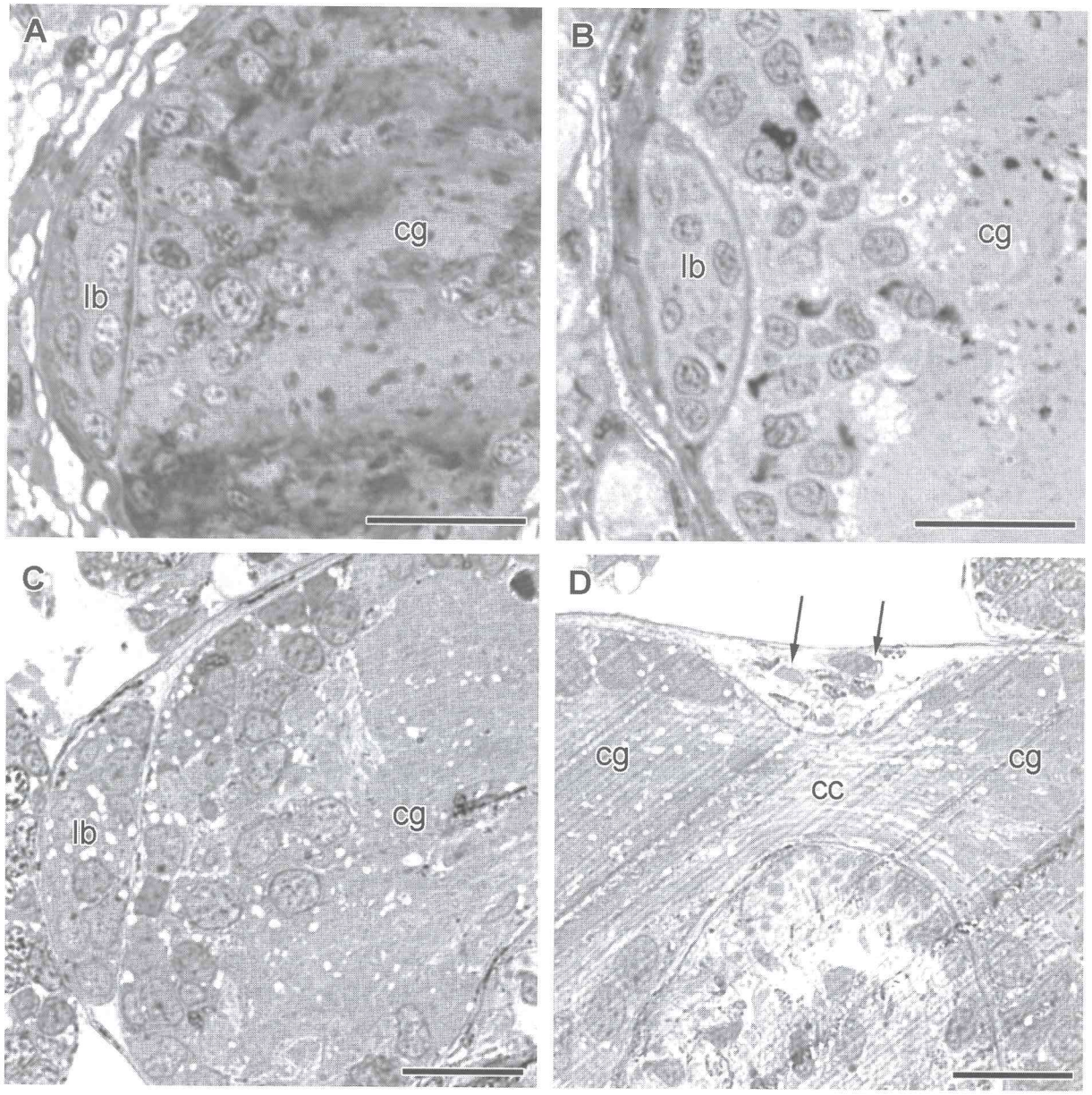

Fig. 4. Aggregates attached to the cerebral ganglia (cross sections). A: "Lateral body" in *Hedylopsis spiculifera* ZSM N° 20070391. B: "Lateral body" in *Hedylopsis ballantinei* ZSM N° 20004766/1. C: "Lateral body" in *Asperspina murmanica* ZSM N° 20062163. D: Cells above cerebral commissure in *Asperspina murmanica* ZSM N° 20062163. cc cerebral commissure; cg cerebral ganglion; lb "lateral body"; arrow, cells near cerebral commissure. Scale bars A–D: 15 µm.

yet unclear homology of euthyneuran cerebral nerves, the unknown origin of the Acochlidia and reports of acochlidian "Hancock's organs" from only a few and supposedly derived microhedylid species, i.e. *P. milaschewitchii* and *M. glandulifera,* and the enigmatic *T. elegans*.

4.2.2. Eyes, optic nerves and optic ganglia

In the past, the description of acochlidian eyes often was limited to the affirmation of presence or absence of these sensory organs. Eyes are absent in all *Asperspina* species, *Microhedyle remanei*, *Ganitus evelinae* Marcus, 1953, *Paraganitus ellynnae* Challis, 1968 and *Pontohedyle verrucosa* Challis, 1970 (see Challis 1968, 1970; Kudinskaya & Minichev 1978; Marcus 1953; Morse 1976; Salvini-Plawen 1973; Swedmark 1968). Our results show that the position, size and development of eyes in Acochlidia examined herein differ considerably.

The eyes of *Hedylopsis spiculifera* are clearly visible externally from a dorsal and lateral view. In the freshwater acochlidian species *Strubellia paradoxa* (Strubell, 1892) and *Acochlidium fijiense* Haynes & Kenchington, 1991 the eyes are clearly observable only in lateral view (unpubl. data of MS). In contrast, the eyes of the marine *Microhedyle glandulifera* (see KOWALEVSKY 1901; MARCUS & MARCUS 1955; ODHNER 1952), *Hedylopsis ballantinei* (Fig. 2C) and *Pontohedyle milaschewitchii* (Fig. 2D) are externally not that clearly visible through the head tissue. WESTHEIDE & WAWRA (1974) observed that eyes of *Parhedyle cryptophthalma* (Westheide & Wawra, 1974) were not visible externally in living specimens, and only as two small pigmented spots in preserved specimens. Eyes in *Pseudunela cornuta* (Challis, 1970) are poorly developed and not visible externally (CHALLIS 1970, as *Hedylopsis cornuta*).

The eyes of *Hedylopsis spiculifera* and *H. ballantinei* are both located dorsolaterally in the body cavity; while the eyes of *H. ballantinei* are situated at the base of the rhinophores, in *H. spiculifera* they are somewhat more posteriorly. A similar dorsolateral eye position at or close to the base of the rhinophores is already known from the limnic acochlidian species *Acochlidium amboinense* Strubell, 1892, *Palliohedyle weberi* (Bergh, 1895) and *Strubellia paradoxa* (see BERGH 1895; BÜCKING 1933; KÜTHE 1935). In contrast, the eyes of *Pontohedyle milaschewitchii* are located more posteriorly and closer together (Fig. 2D). WESTHEIDE & WAWRA (1974) described a similar eye position in the marine acochlidian *Parhedyle cryptophthalma*.

The optic nerve is short in *Strubellia paradoxa* (see KÜTHE 1935). The well-developed eyes of *Acochlidium amboinense*, *Palliohedyle weberi* and *S. paradoxa* were described as attached anterodorsally to anterolaterally on the cerebral ganglia (BERGH 1895; BÜCKING 1933; KÜTHE 1935), thus the optic nerves are probably short as well. The eyes of *Pontohedyle milaschewitchii* are directly attached to the cerebral ganglia (JÖRGER et al. in press), as are the eyes of *Parhedyle cryptophthalma*, *Microhedyle nahantensis* (Doe, 1974), *M. glandulifera* and *M. odhneri* (Marcus, 1955) (see DOE 1974; MARCUS & MARCUS 1955; WESTHEIDE & WAWRA 1974). The optic nerve is moderately long but thin in *Tantulum elegans*, while long and thick in both *Hedylopsis* species. The long optic nerves observed herein may be phylogenetically informative in Acochlidia.

All eyes described for Acochlidia are pigmented, except those of *Tantulum elegans* (present study) and of *Microhedyle nahantensis* (see DOE 1974). The "poorly developed" eyes of *Pseudunela cornuta* described by CHALLIS (1970) should be reinvestigated.

The eye size differs within the species: whereas eyes of *Hedylopsis spiculifera* and *H. ballantinei* measure approx. 25 and 30 µm, respectively, eyes in *Pontohedyle milaschewitchii* reach approx. 20 µm (JÖRGER et al. in press). The largest eye size known from an acochlidian species is 0.52 mm and was reported for the limnic *Palliohedyle weberi* (see BERGH 1895).

The optic ganglion in *Tantulum elegans* was first described by NEUSSER & SCHRÖDL (2007) and is regarded to be a true ganglion with subdivision into cortex and medulla (see NEUSSER et al. 2006). More specifically, it is enclosed in a thin layer of connective tissue together with and attached to the cerebral ganglion. This feature should not be confused with the "lateral bodies" described in the present study, since the latter are lying inside the thick layer of connective tissue from the cerebral ganglion (see below). So far there are only two reports of ganglia being surrounded by a common layer of connective tissue with the cerebral ganglia: the rhinophoral ganglia of *T. elegans* (see NEUSSER & SCHRÖDL 2007), and the rhinophoral ganglia of *Pontohedyle milaschewitchii* (JÖRGER et al. in press).

The presence of an optic ganglion only in *T. elegans* is surprising, since eyes are unpigmented in this species, while for species possessing more well-developed eyes (e.g. both *Hedylopsis* species and *Pontohedyle milaschewitchii*) this character is lacking. Either there are some unknown sensory abilities involved in at least one ontogenetic stage, or both eyes and optic ganglia are evolutionary remnants of organs in the process of being reduced. The optic ganglia of *Tantulum* do no more fuse with the rhinophoral ganglia, as may be the case in both *Hedylopsis* species with large rhinophoral ganglia bearing optic nerves. We urgently need ontogenetic evidence for the development of acochlidian central nervous structures.

The presence of optic ganglia, the origin and length of optic nerves, eye position in terms of situation and proximity to the cerebral ganglion, as well as eye size and structure should be reinvestigated in all acochlidian species, since these may be easily accessible and phylogenetically informative characters (see MIKKELSEN 1996).

4.3. Aggregates attached to the cerebral ganglia

4.3.1. "Lateral bodies"

SOMMERFELDT & SCHRÖDL (2005) described "dorsal bodies" attached to the cerebral ganglion in the acochlidian *Hedylopsis ballantinei*. We herein confirm the presence of such organs for both *Hedylopsis* species and *A. murmanica*. Their position is, however, more lateral than dorsal. We thus propose to use the term "lateral bodies" for

such acochlidian structures until more detailed and comparative data are available to assess their homology to pulmonate dorsal bodies.

The "lateral bodies" of the re-examined acochlidian species are characterized by a group of neuronal cells that are enclosed within the thick connective tissue layer surrounding the cerebral ganglion. The dorsal bodies of basommatophoran pulmonates consist of a pair of similar neuronal cell clusters that are, however, enclosed in a thin sheath of connective tissue, and are situated dorsally on the cerebral ganglia. Basommatophoran dorsal bodies can lie close together and appear as one group in *Helisoma* Swainson, 1840 and *Planorbarius* Duméril, 1806, or they can be distinguished as two separate tissue masses, as in *Ancylus* Mueller, 1774, *Lymnaea* Lamarck, 1801 and *Siphonaria* Sowerby, 1823 (SALEUDDIN 1999; SALEUDDIN et al. 1997; TAKEDA & OHTAKE 1994).

SOMMERFELDT & SCHRÖDL (2005) described the "lateral bodies" of *Hedylopsis spiculifera* and *H. ballantinei* being subdivided into an outer cortex and an inner medulla. According to SALEUDDIN (1999), most of the dorsal bodies of basommatophoran pulmonates develop a cortex with nuclei and an inner medulla with cell processes that lie very close to the cerebral ganglia. In "lateral bodies" of *H. spiculifera*, *H. ballantinei* and *Asperspina murmanica*, no such clear subdivision into cortex and medulla was found; instead all nuclei are distributed more or less uniformly. Similarly, the basommatophoran pulmonate *Siphonaria pectinata* Linnaeus, 1758 is described to possess dorsal bodies without clear separation into cortex and medulla (SALEUDDIN et al. 1997).

The function of the "lateral bodies" in *Hedylopsis spiculifera*, *H. ballantinei* and *Asperspina murmanica* is unclear. Due to the absence of visible nerves arising from these aggregations, the "lateral bodies" are possibly not sensory but secretory organs. The role of dorsal bodies in pulmonates as an endocrine organ involved in female reproduction is quite well known (SALEUDDIN 1999). Furthermore a putative endocrine gland, called the juxtaganglionar organ, has been described in several opisthobranch species (e.g. SWITZER-DUNLAP 1987). However, the homology of these structures is still unclear. Future studies by means of transmission electron microscopy and (immuno)histochemical studies are needed to understand homologies and functions. Disregarding our deficient knowledge, within acochlidians the presence of "lateral bodies" in members of Hedylopsidae, Asperspinidae and Tantulidae versus their absence in two members of Microhedylidae (*Pontohedyle milaschewitchii, Microhedyle remanei)* may represent characters with a phylogenetic signal.

4.3.2. Cells near the cerebral commissure

For the first time in an acochlidian species we describe several cells that are loosely dispersed within the connective tissue above the cerebral commissure in *Asperspina murmanica*. Due to its position such a cell aggregation resembles the dorsal bodies of stylommatophoran pulmonates (e.g. *Theba pisana* Mueller, 1774, *Helix aspersa* Mueller, 1774 and *Achatina fulica* Ferussac, 1821) which were described as diffusely scattered cells within the connective tissue sheath of the cerebral ganglion and located near the cerebral commissure (SALEUDDIN 1999; SALEUDDIN et al. 1997; TAKEDA & OHTAKE 1994). The presence, structure, origin and function of these cells in acochlidians cannot be revealed by light microscopy alone but requires ultrastructural studies.

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