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Anatomical redescription of two species of Philinoglossidae

(Gastropoda, Cephalaspidea)

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The organisations of two hitherto anatomically not investigated members of the Philinoglossidae, *Abavopsis latosoleata* Salvini-Plawen and *Philinoglossa praelongata* Salvini-Plawen, are described. The differences and similarities of both species compared with the other members of the family are presented. Accordingly, *A. latosoleata* resembles *Pluscula cuica* Marcus, 1953 in its midgut system and genital organs, but is clearly separated from this species among others by the presence of eyes, by a true penis formation and by the lack of a shell vestige. *Ph. praelongata* fits well into the diagnosis of its genus. It differs from all other congeners, however, by a pair of anterior foregut glands and by still distinctly separate subintestinal and visceral ganglia; in addition, certain characters respectively separate *Ph. praelongata* from each other species.

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Introduction

Animals living in interstices of marine sediments are members of a special realm and are generally characterised by a small body size and further particular adaptations. The fauna of this interstitial is best known from sands that are coarse and rinsed enough to enable the animals to live there permanently or complete parts of their life cycle within this habitat (mesopsammon). Excluding protists, most metazoan mesopsammonbionts are either preadapted by their small size (e.g. tardigrades, gastrotrichs) or have evolved a reduced size along with a restriction or simplification of their organisation (see Swedmark 1964 and compiled articles in "Styofauna mundi" ed. by L. Botosaneanu 1986). These latter adaptations, however, with respect to analogies and parallelisms imply difficulties in evaluating external as well as internal relationships of the taxa. This requires comprehensive investigation of all relevant aspects. This situation is also valid for the interstitial opisthobranch Mollusca (see Arnaud et al. 1986). Early investigations by Kowalevsky (1901a,b) on Pseudovermidae and Acochlidiomorpha were followed three decades later by Hertling (1932) with the first description of *Philinoglossa* with *Ph. helgolandica*. Currently six more species within four genera are known to belong to the interstitial Philinoglossidae: *Philinoglossa remanei* Marcus & Marcus,1958, *Ph. marcusi* Challis, 1969, *Ph. praelongata* Salvini-Plawen, 1973, *Pluscula cuica* Marcus, 1953, *Sapha amicorum* Marcus, 1959, and *Abavopsis latosoleata* Salvini-Plawen, 1973.

When Salvini-Plawen (1973) defined two new species from the Mediterranean Sea, *Abavopsis latosoleata* and *Philinoglossa praelongata* (Fig. 1) 40 years ago, they were characterised and roughly outlined, yet without anatomical-histological investigation. New interest in this animal group, both concerning their biodiversity and their relationships (see Brenzinger et al. 2013), requires more data. Among the seven species of philinoglossids, the anatomy of only the above two species is insufficiently known. Based on earlier studies (Weinbauer 1991), we focus in this contribution on describing the organisation

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of both species. This will help to better evaluate and clarify the internal relationships within this family of mesopsammobiont animals.

Material and methods

In various years between 1965 and 1990, investigations of the interstitial fauna of marine sands (mesopsammon) at European coasts were carried out. Among the molluscs, also the two species of philinoglossids treated in this contribution were collected. The presented material originates from off Rovigno/Istria (March/April 1965: Salvini-Plawen 1973; March 1989), off Ancona/E Italy (May 1989: Salvini-Plawen 1991), off Livorno/Liguria (Juni 1972: Salvini-Plawen 1973) and off Plymouth/S England (September 1982: Salvini-Plawen 1984).

The animals had been anaesthetised and therefore stretched in magnesium chloride ($MgCl_2$). Then mostly fixed with 75 % ethanol, occasionally with picric acid + formalin + acetic acid (Bouin's fluid), and preserved in 75 % ethanol. After embedding in paraffin or synthetic resin, serial cross sections of 5 µm were stained with azocarmine + aniline blue (AZAN); the 1–2 µm cross sections were stained with toluidine blue. Graphic reconstructions were drawn by hand on mm-scaled paper using standardised microscopes. Photographs were taken through a Nikon Eclipse E 800 microscope with a digital camera connected to a computer and processed with Adobe Photoshop.

Systematic descriptions

Philinoglossidae Hertling, 1832

Diagnosis. Small (up to 4 mm long) Cephalaspidea without external shell (either vestigial or entirely absent), head-shield largely fused with notum; reduced mantle cavity terminal without gill; radula with sickle-shaped teeth of 3.0.3 formula; without jaws and gizzard; central nerve ring prepharyngeal; copulatory apparatus anterior. Mesopsammobionts.

Genus *Abavopsis* Salvini-Plawen, 1973

Diagnosis. Philinoglossidae without vestige of shell; eyes present; stomach reduced, single left midgut gland sack-like; genital opening in the terminal body, with bursa copulatrix, without separate vagina.

Type species. *Philinoglossa (Abavopsis) latosleata* Salvini-Plawen, 1973.

Abavopsis latosoleata Salvini-Plawen, 1973
Figs 1A, 2–6

Philinoglossa (Abavopsis) latosoleata Salvini-Plawen, 1973: 115 ("Secche della Meloria" off Livorno/Italy; holotype in ethanol: NHM Wien/Natural History Museum Vienna, Mollusca 78701).
Abavopsis latosoleata – Salvini-Plawen 1983: 307.

Four specimens (A–D) from type locality and two from "Punta Croce" off Rovigno/Istria (1989) were series-sectioned; series Livorno B and C are deposited as voucher specimens in NHM Wien, Mollusca 81125/MP/326 and 81125/MP/327.

Diagnosis. Body stoutish up to 2.25 mm long; head-shield indicated, lateral body grooves along whole body, pedal sole wide and in part with upraised margin; eyes well visible, with pallial gland. All radula teeth with smooth margin. Cerebro-pleural ganglia fused, without parietal ganglia. Genital apparatus with ampulla. With penis and penis gland.

Redescription

External aspect (Fig. 1A)**.** The shell-less animals have a stoutish-oval body 1.5–2.25 mm in length and 0.5–0.6 mm in width (ratio = 3–3.5). They show a typical cephalaspid aspect with a head-shield separated from the notum by a pair of notches and – already visible in slightly contracted individuals – an anteriorly curved transverse furrow. The pedal sole (foot) is wide, laterally surpassing the body and locally presenting a medially upraised margin (parapodia). Its rounded terminal portion protrudes freely and encloses together with the overhanging rear of the notum a delimited space (area of the mantle cavity, without gill). The foot is separated from the head-shield and notum along its whole extension by a paired body groove. The animals are light-brown without pigmentation. The black eyes generally shine visibly through the head-shield (Figs 1A, 2A, 5A), whereas the light-orange pallial gland (Figs 1A, 2B, 6A) is vaguely discernible and only occasionally conspicuous as a bright spot.

The movement represents a homogeneous gliding without notable deformations of the body; no adhesion to the particles of the substratum was observed.

Body wall. All epidermis of the head-shield, notum and foot is homogeneously ciliated. The two lateral body grooves are almost devoid of cilia except for scattered cell groups of the Hancock's organs and the ciliated sperm tract in the right groove. The Hancock's organ in the anterior region of each groove is marked by an irregularly folded epithelium without distinct demarcation; they extend up to below the

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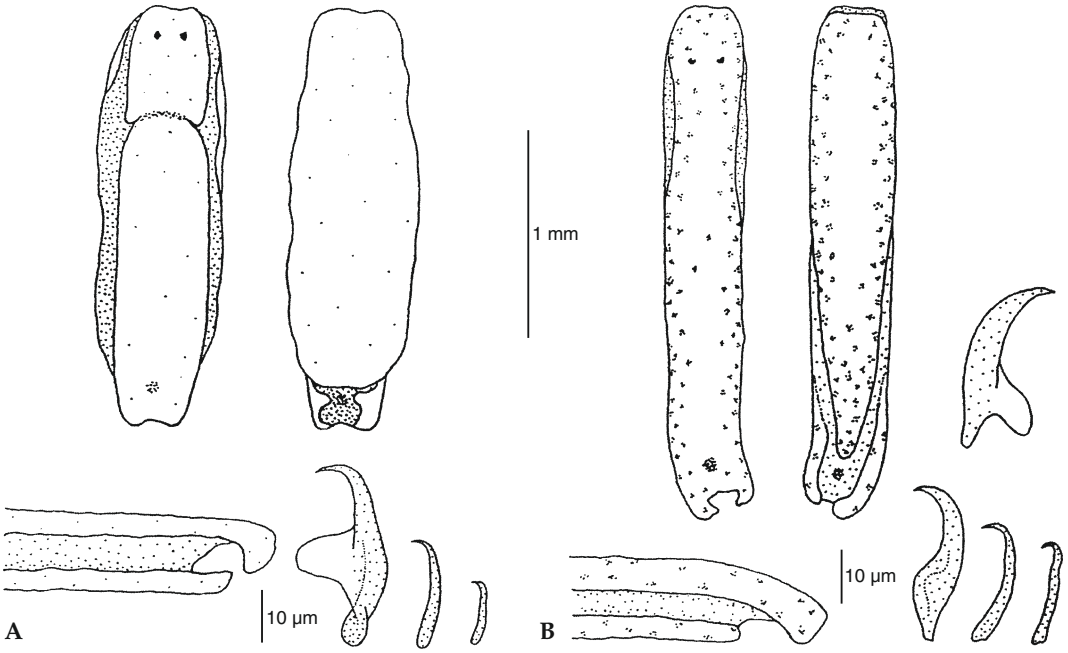

Fig. 1. Habitus from dorsal and ventral, posterior body from lateral, as well as radula teeth (right half of transverse row) of **A.** *Abavopsis latosoleata*, **B.** *Philinoglossa praelongata* (combined from Salvini-Plawen 1973).

posterior end of the accessory rhinophore ganglion. The epidermal cells are intermingled with small epithelial and larger subepithelial glands. These glands are more concentrated along the right groove (without correlation to the sperm tract) into which they empty dorsally and ventrally through narrow openings. There is no vestige of a shell. The loosely arranged connective tissue below the epidermis is provided with numerous spaces (lacunae) and scattered small pigment cells; the connective tissue is medially followed by a thin layer of circular musculature and several longitudinal fibres, laterally and ventrally more distinctly grouped into bands (Fig. 3A).

Pallial complex. The area of the mantle cavity lies nearly terminal and is delimited dorsally by the projecting notum, ventrally by the end of the foot (Fig. 1A). The anus is situated slightly to the right in the roof of the cavity, shortly behind the excretory pore. The genital opening is located somewhat more frontally within the ciliated sperm tract (Fig. 2B). There are no gill, osphradium or hypobranchial gland.

The pallial gland is embedded in the projecting notum, shortly behind the anus. It consists of 4–5 larger and several peripheral smaller cells (Fig. 6A). When emptied, the cells are longitudinally slender and difficult to delimit from the surrounding, thin connective tissue. The narrow outlet of the gland leads almost terminal into the mantle cavity area.

Another, small glandular formation is located in the terminal-most roof of the mantle cavity area (Fig. 6B). It represents a pit-like deepening of about 40 µm length characterised by a strong ciliation. The pit is surrounded by small, subepithelial gland cells which open intercellularly (see also the "fosette glandulaire" in *Philine auriformis*: Rudman, 1972: 171).

Alimentary tract. The alimentary tract begins, sunken in the transversal fold between notum and foot, with an outer opening surrounded by subepithelial glands; this opening thus represents also the outlet of the penis apparatus. The true mouth opening lies behind the junction with that outlet. The buccal cavity inbetween with its twofold function shows a strongly folded, low epithelium without cilia or glands.

The pharynx soon shows a triangular lumen and is here characterised by a strong musculature, consisting of bundles with transversal and longitudinal fibres, surrounded by a circular layer. The radula apparatus is differentiated in the posterior third of the pharynx upon a slender support. The radula teeth show, as typical for the family, a 3.0.3 arrangement

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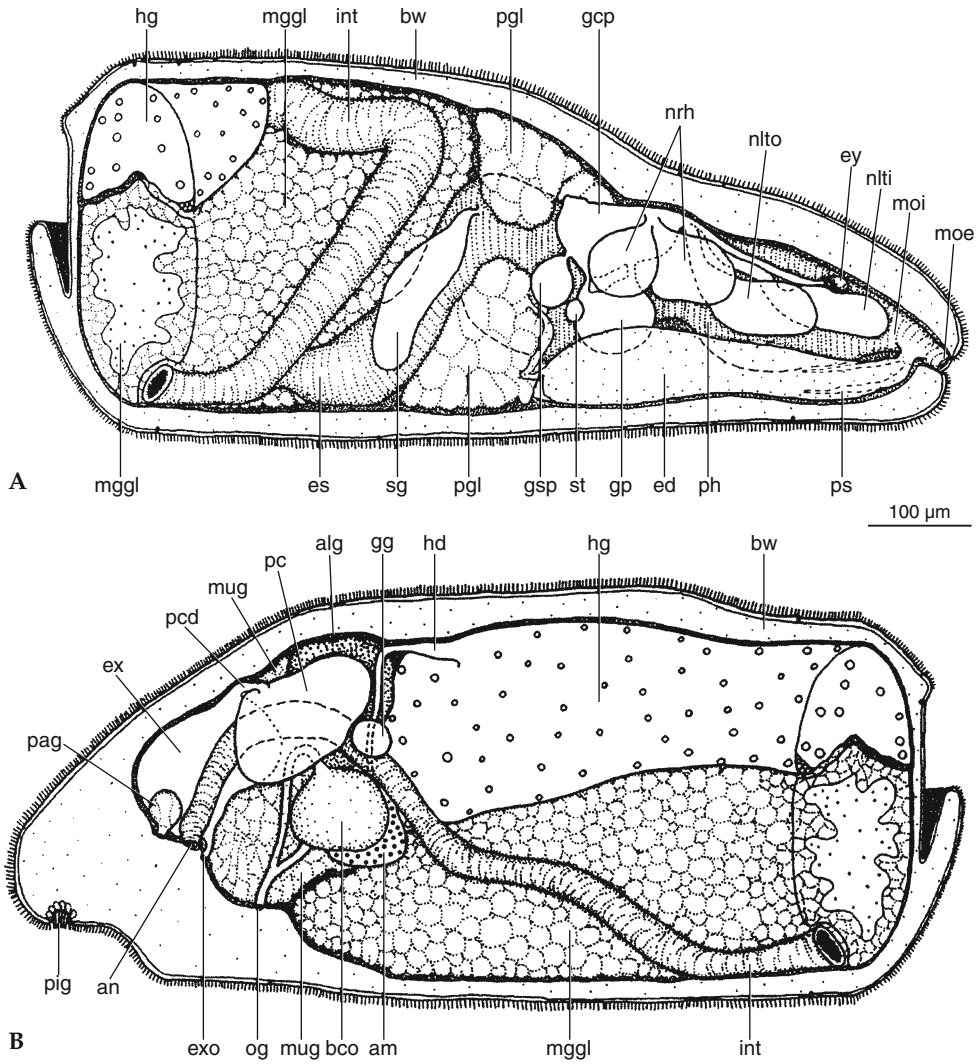

Fig. 2. *Abavopsis latosoleata*, general organisation viewed from the right. **A.** Anterior body half; **B.** posterior body half. Abbreviations: **alg**, albumen gland; **am**, ampulla; **an**, anus; **bco**, bursa copulatrix; **bw**, body wall; **ed**, ejaculatory duct; **es**, oesophagus; **ex**, excretory organ; **exo**, opening of excretory organ; **ey**, eye; **gcp**, cerebro-pleural ganglion; **gg**, genital ganglion; **gp**, pedal ganglion; **gsp**, supra-intestinal ganglion; **hd**, hermaphroditic duct; **hg**, hermaphroditic gland (gonad); **int**, intestine; **mggl**, left midgut gland; **moe**, external mouth opening; **moi**, internal mouth; **mug**, mucus gland; **og**, genital opening; **nlti**, inner labiotentacular nerve; **nrh**, rhinophoral nerve; **pag**, pallial gland; **pc**, pericardium; **pcd**, pericardioduct; **pgl**, penis gland; **ph**, pharynx; **pig**, glandular pit; **ps**, penis sheath; **sg**, salivary gland; **st**, statocyst.

in at least 20 transverse rows; in the present species all teeth lack denticles (Fig. 1A).

The pharynx continues dorsally in the oesophagus and at the transition the paired salivary glandular organs open from dorsal. They show voluminous gland cells with a big nucleus which are circularly arranged around the narrow lumen. The oesophagus curves ventrally and opens without formation of pouches or a gizzard directly into the bottom of the midgut gland (Fig. 3A). As in *Pluscula cuica* Marcus, 1953 (Marcus 1953, Brenzinger et al. 2013), there is thus no real stomach formation (contrast to Salvini-Plawen 1973) and the single (left) midgut gland represents an uniform, lobed to sack-like organ

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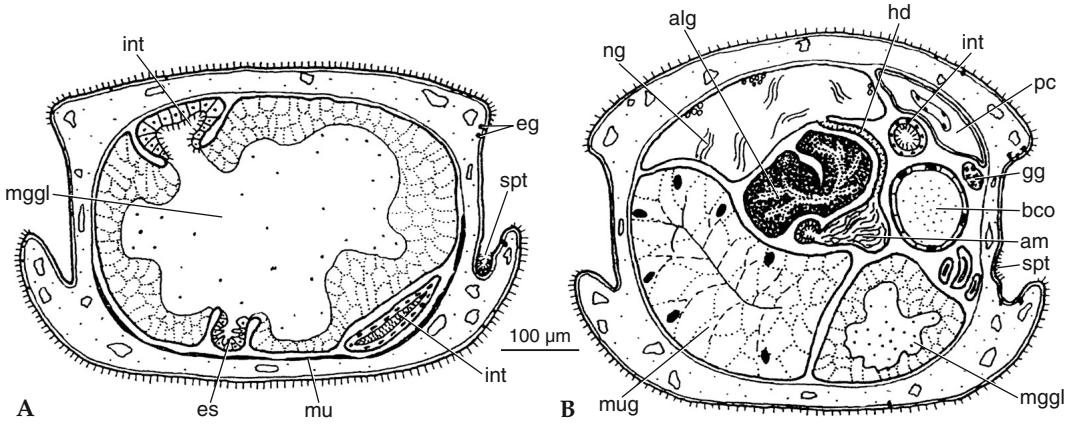

Fig. 3. *Abavopsis latosoleata*, schematised cross sections. **A.** Anterior region of midgut gland with opening of oesophagus and beginning intestine (Livorno B). **B.** Pericardium and organs of genital apparatus (Livorno D). Abbreviations: **alg**, albumen gland; **am**, ampulla; **bco**, bursa copulatrix; **eg**, epidermal gland; **es**, oesophagus; **gg**, genital ganglion; **hd**, hermaphroditic duct; **hg**, hermaphroditic gland (gonad); **int**, intestine; **mggl**, left midgut gland; **mu**, musculature; **mug**, mucus gland; **pc**, pericardium; **spt**, sperm tract.

with a smooth surface; it extends from the posterior end of the pharynx ventrally of the gonad up to the mucus gland of the gonoduct. Internally, the midgut gland shows a strong and irregularly folded, 20–50 µm high epithelium of strongly granulose, large cells. The content consists of glandular secretions; no food particles were discernible. The ciliated intestine emerges dorsally, fairly opposite to the opening of the oesophagus (Fig. 3A). It curves anteriorly to the right and ventral below the midgut gland (Fig. 3A), then running more at the right posteriorly (more or less twisted in case of body contraction) and dorsomedial (Fig. 3B) to meet the rectum and anus.

Sensory system (Fig. 4)**.** The main nervous system was analysed in detail by Huber (1993) and includes a prepharyngeal ring of separate cerebro-pleural ganglia with distinct cerebral commissure and the pedal ganglia with commissure; the cerebropedal and pleuropedal connectives are thin. Dorsolateral of the cerebropleural ganglia, the short rhinophoralis nerve leaves at each side; it splits and forms two ganglia (anterior, posterior) finely innervating the groove epithelium (posterior Hancock's organ); the clypei-capitis nerve has a common root with the rhinophoralis and runs dorsally into the head-shield. The labiotentacular nerve emerges ventrolateral from the cerebropleural ganglia to form an outer accessory ganglion providing the anterior portion of the Hancock's organ and an inner ganglion innervating the labial area. Both the optical nerve and the oral nerve originate anterior of the cerebral ganglia, the latter providing the anterior region of the head-shield.

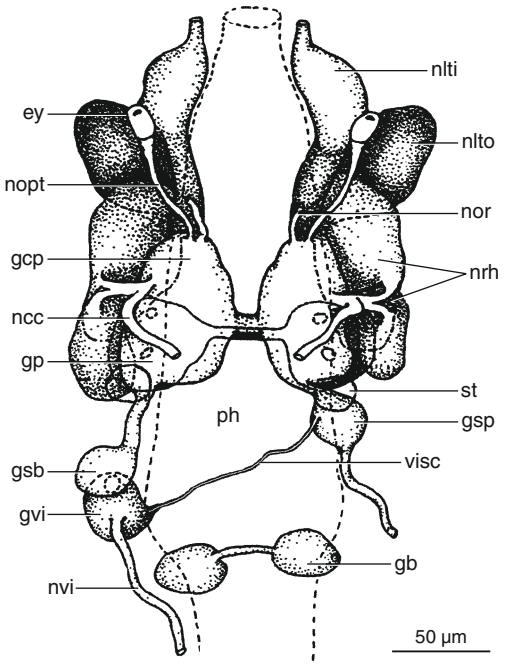

Fig. 4. *Abavopsis latosoleata*, nervous system (dorsal view). Abbreviations: **ey**, eye; **gb**, buccal gangion; **gcp**, Cerebro-pleural ganglion; **gp**, pedal ganglion; **gsb**, sub-intestinal ganglion; **gsp**, supra-intestinal ganglion; **gvi**, visceral ganglion; **ncc**, clypeo-capitis nerve; **nlti**, inner labiotentacular nerve; **nlto**, outer labiotentacular nerve; **nopt**, optic nerve; **nor**, oral nerve; **nrh**, rhinophoral nerve; **nvi**, visceral nerve; **ph**, pharynx; **st**, statocyst; **visc**, supraintestinal-visceral connective (visceral loop).

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The visceral loop shows three ganglia: the supraintestinal ganglion with a blind-ending (osphradial/gill?) nerve on the right close to the posterior cerebro-pleural ganglion; the visceral (abdominal) ganglion more posteriorly on the left, with a strong nerve and the close subintestinal ganglion. The thin connective runs obliquely below the pharynx between the supraintestinal and visceral ganglia. The cerebrobuccal connectives curve ventrally below the posterior end of the pharynx, where they differentiate the buccal ganglia with their commissure. A small genital ganglion (without connection discerned) is positioned in front of the female genital opening at the right side of the bursa copulatrix (Fig. 3B).

Apart from the Hancock's organs, only statocysts and photoreceptive sense organs are differentiated; an osphradium, such as in *Pluscula* (Bernzinger et al. 2012), could not discerned. The globular statocysts lie adjacent to the pedal ganglia. Each statocyst contains each one statolith and is innervated by the cerebropleural ganglia. Although deeply sunken below the epithelium of the head-shield, the eyes with lens are well visible due to their strongly stained pigment cup (Fig. 5A).They are generally positioned in front of the cerebral ganglia above the accessory labiotentacular ganglia.

Gono-pericardial system. The spacious pericardium lies at the right side above the bursa copulatrix and in front of the excretory organ (Figs 2B, 3B). The heart is separated into the posterior atrium (auricle) and the anterior ventricle; no aorta could be discerned. An almost transversely running pericardioduct connects with the excretory organ (emunctorium), which extends from the hindgut area to the left side of the body (Fig. 2B). The excretory organ opens through a short duct in the posterior-most right lateral body groove (area of mantle cavity), shortly in front of the anus.

In mature animals (late June to August) the hermaphroditic gonad extends dorsally of the midgut gland from the region of the beginning intestine to the pericardium. It is composed of hermaphroditic follicles which are arranged symmetrically to the longitudinal body axis. Within the follicles the oocytes differentiate in the proximal and ventral areas, whereas the spermatogenesis takes place in the distal-dorsal areas. The genital products are led away via slender, non-ciliated ductules which unite medially to a dorsally running, ciliated hermaphroditic duct. This duct curves ventrally and widens to a U-shaped region, the ampulla, in adults filled with sperm. The duct continues dorsally to form the albumen gland, situated more to the right side and subdivided into several lobes with ciliated epithelium. No intermediate area ("membrane gland") could be specified and the subsequent portion represents the voluminous mucus gland. This fills the posterior-left body space up to the excretory organ and hindgut; the content of its big cells is scarcely structured. The emerging spermoviduct is ciliated, initially runs transversely through the mucus gland to the right body wall and then posteriorly. Shortly before its opening in front of the anus at the right side into the mantle cavity area, the spermoviduct is joined by the strongly wound, ciliated duct of the bursa copulatrix. This ball-shaped formation adjacent to the right body wall (Fig. 3B) is filled with a colourless secretion and provided with a low microvillous epithelium including big nuclei.

Copulatory apparatus. A ciliated sperm tract (rather than a gutter) runs from the genital opening along the right body groove, passes the Hancock's organ ventrally and continues to the mouth opening. Here, the copulatory apparatus opens. Posteriorly, it sometimes extends up to the midgut gland. Its anterior section represents a tube (penis sheath; Figs 5A,B) into which protrudes the free end of a narrow, ciliated duct surrounded by strong circular musculature (ductus ejaculatorius, Fig. 5C). This probably producible free end (penis), measuring over one third the length of whole duct, is distinctly cuticularised. The muscular penis duct sometimes shows without structural change a proximal, elongate bulbous enlargement (about three times in diameter, Fig. 5C; seminal vesicle?) and at its end opens the narrow, wound duct of the penis gland (prostate). This irregular sack-like organ may occupy the entire ventral and dorsal space around the posterior pharynx up to the midgut gland, depending on the state of the individual's maturity (Fig. 2A). Its epithelium consists of large, 30–40 µm high, non-ciliated cells with granules.

Distribution. The examined specimens come from the Secche della Meloria/Livorno/Ligurian Sea (type locality) and from off Rovigno/Istria/Adriatic Sea. Their conspecifity according to external characters and the radula (Salvini-Plawen 1973) corresponds with the internal organisation. The animals live interstitially (mesopsammic) in coarse and shell sands with some debris. Their known distribution currently is restricted to the Mediterranean Sea at 3–45 m depth only and includes also sands from off Banyuls-sur-Mer/Côte Vermeille/SE France (Salvini-Plawen 1973) and off Marseille/SE France (Poizat 1978, 1983).

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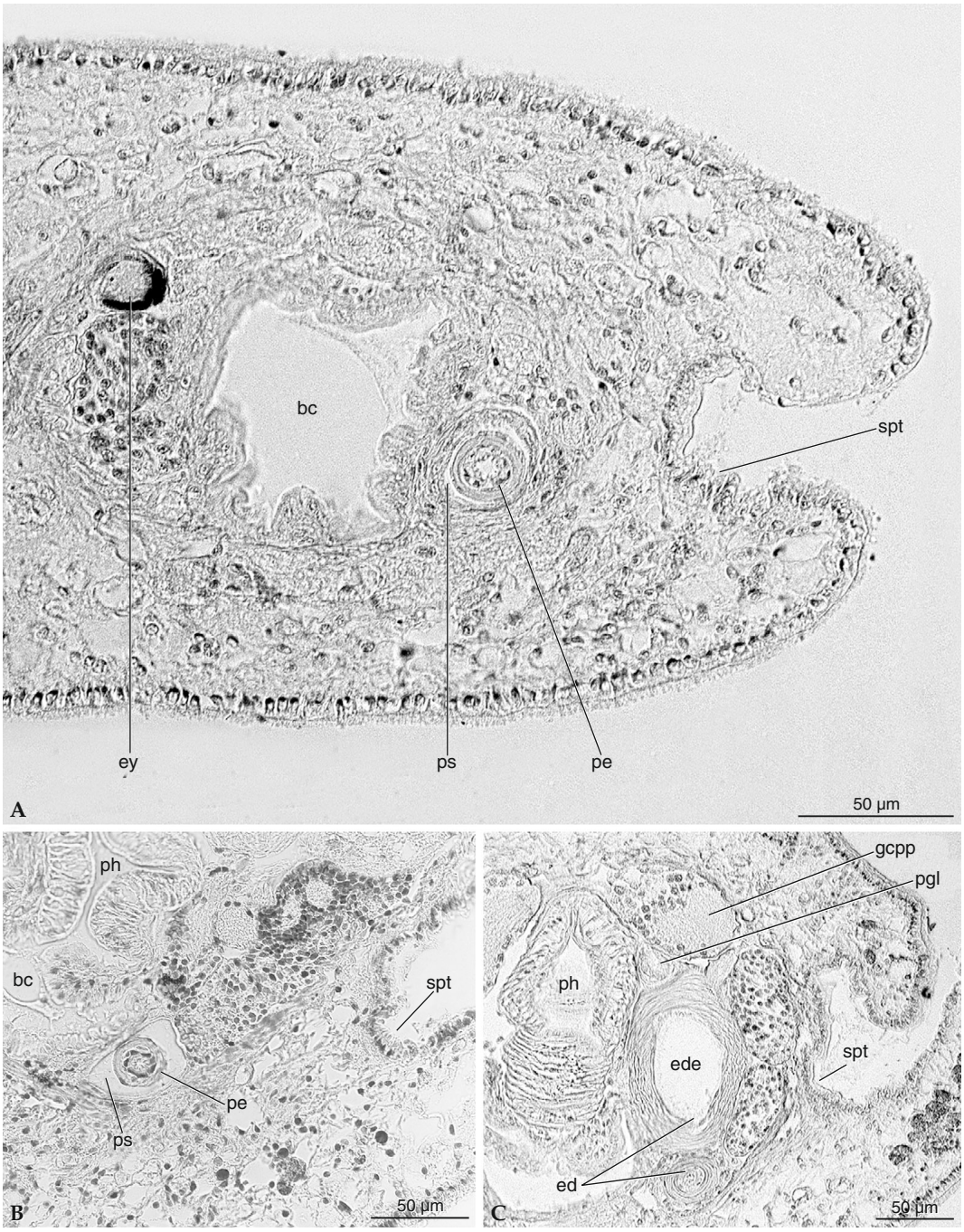

Fig. 5. *Abavopsis latosoleata*, cross sections through anterior body with copulatory apparatus. **A, B.** Precerebral region of two specimens (Livorno B & A); **C.** region with posterior ejaculatory duct (Livorno C). Abbreviations: **bc**, buccal cavity; **ed**, ejaculatory duct, **ede**, enlarged ejaculatory duct; **ey**, left eye; **gcp**, cerebro-pleural ganglion; **pe**, penis; **pgl**, duct from enlarged ejaculatory duct to penis gland; **ph**, pharynx; **ps**, penis sheath; **spt**, sperm tract.

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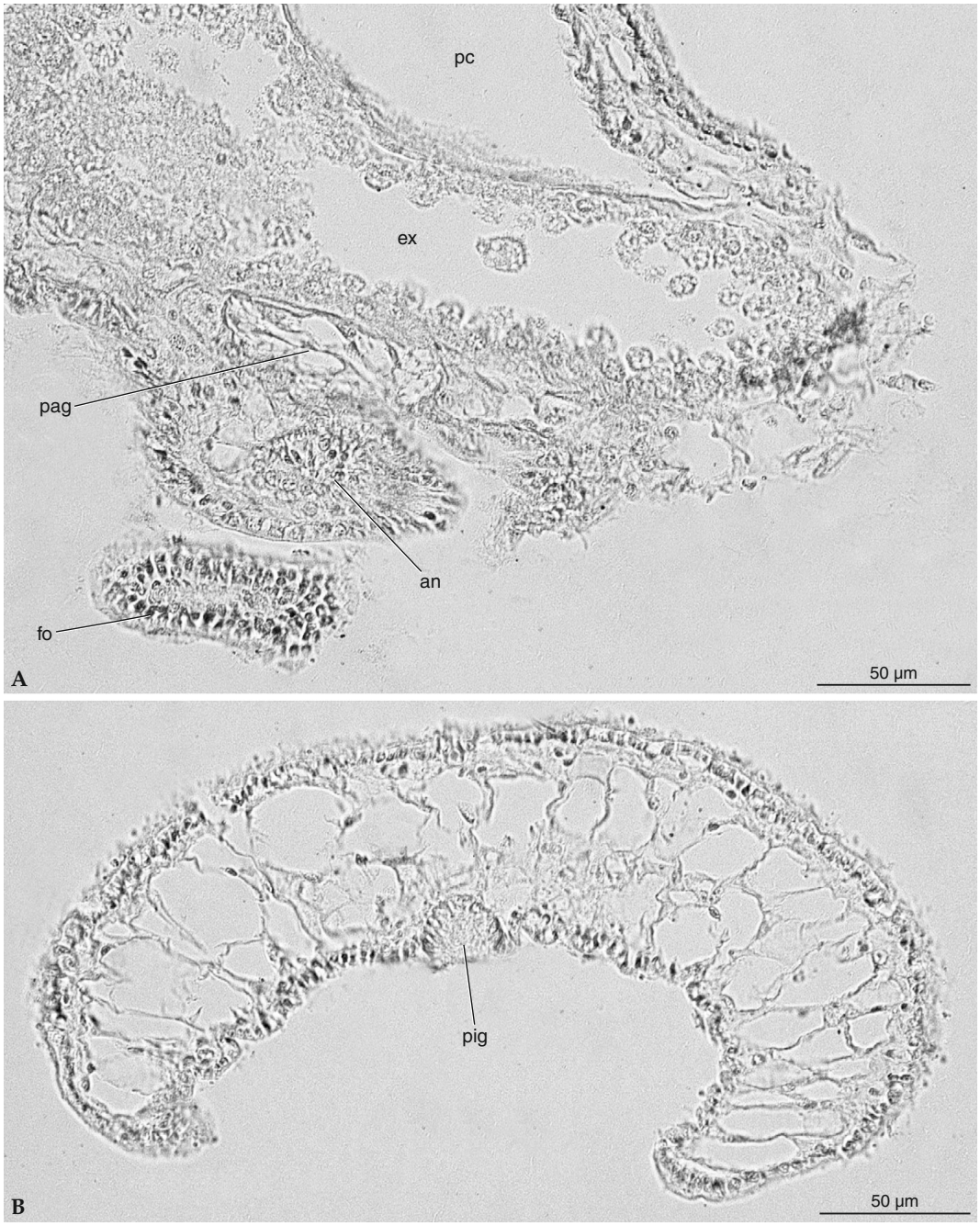

Fig. 6. *Abavopsis latosoleata*, cross sections through roof of overhanging notum. **A.** Body end with pallial gland (Livorno C); **B.** posterior notum with glandular pit (Livorno B). Abbreviations: **an**, posterior wall of anus; **ex**, excretory organ; **fo**, end of foot; **pc**, pericardium; **pag**, pallial gland; **pig**, glandular pit.

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Genus *Philinoglossa* Hertling 1932

Diagnosis. Philinoglossidae without vestige of shell; eyes and pallial gland present; midgut gland paired, elongate tube-like, right one short and directed anteriorly; genital opening at right in the anterior body, without bursa copulatrix or separate vagina.

Type species. *Philinoglossa helgolandica* Hertling, 1932.

Philinoglossa praelongata Salvini-Plawen, 1973
Figs 1B, 7–13

Philinoglossa (Philinoglossa) praelongata Salvini-Plawen, 1973: 113 ("Secche della Meloria" off Livorno/Italy; holotype in ethanol: NHM Wien/Natural History Museum Vienna, Mollusca 78702).

Several specimens series-sectioned: type locality, "Punta Croce" off Rovigno, "Torre di Porto Novo" south of Ancona, "Outer Cawsand Bay, Queens Ground" in Plymouth Sound. Two series ("Rovigno D" and "Livorno B") are deposited as voucher specimens in NHM Wien, Mollusca 81125/MP/328 and 81125/MP/329.

Diagnosis. Body slender up to 3 mm long; head-shield and notum continuous, notum posteriorly distinctly surpassing other body; pedal sole posteriorly narrowed, lateral body grooves in life along whole body. With a pair of anterior (buccopharyngeal) foregut glands, all radula teeth with smooth margin. Cerebro-pleural ganglia fused, without parietal ganglia; subintestinal and visceral ganglia separated but adjacent; genital apparatus without ampulla; with penis gland.

Redescription

External aspect (Fig. 1B)**.** The shell-less animals possess an elongate to slender, 1–3 mm long and 0.3–0.4 mm wide body (ratio = 5.5–6). Although members of the cephalaspids, their head-shield and notum represent a continuous dorsal surface, also maintained when the animals are disturbed and/or fixed (no contraction with transverse fold). The notum shows in its anterior third a slight narrowing through which in dorsal view the foot becomes visible in this region. The posterior notum is elongated, projecting far beyond the body and somewhat bent with both lateral ends tucked downwards-inside; together with glands, this projecting portion serves as an adhesive device. The pedal sole (foot) narrows already from the midbody (contrast to *Ph. helgolandica*) and ends tapered without free margin. In living specimens, the foot is separated throughout from the fused head-shield and notum by a paired body groove (contrast to *Ph. remanei* and *Ph. marcusi*); in preserved individuals, however, only the anterior body (head-shield section) distinctly retains its x-shaped cross section with lateral grooves (Figs 8A, 10A,B); the remainder of the body (notum section) assumes an inflated cross section up to a circular outline (Fig. 12B). The brownish-glassy animals are marked dorsally and at the foot by loosely arranged, olive-tinged to blackish spots, whose pigmentation is denser laterally in the posterior two-thirds of the body. In life, the entire notum is provided with prominent epithelial glands. The black eyes are well visible, as is in general the light-orange pallial gland in the protruding notum (it becomes black after ethanol fixation).

During free gliding within the substratum, the animals drag the protruding portion of the notum in a laterally bent or ventrally curved manner (on smooth surface they therefore move in circles). When resting, they posteriorly roll up somewhat and adhere with the protruding notum to a sand grain or similar particle (see Abb. 4 in Salvini-Plawen 1973).

Body wall. The fused head-shield and notum as well as the foot show homogeneous ciliation which is almost absent in the two lateral body grooves. The right groove is marked by the ciliated sperm tract. The Hancock's organ in the anterior region of each groove extends up to below the posterior end of the accessory rhinophore ganglion. Its epithelium is irregularly folded and provided with a dense seam of microvilli frequently interrupted by groups of ciliated cells. The common dorsal and ventral epidermal cells are interspersed by epithelial and subepithelial glands with increased density and size in the posterior region of the notum (adhesion). The loosely arranged connective tissue below the epidermis shows lacunae and includes numerous pigment cells; these cause the ornamentation of the body surface, intensified towards the borders and in the posterior body. The body musculature consists of longitudinal fibres below the connective tissue and is grouped into band-like bundles in ventral, lateral and dorsolateral positions (Figs 8A, 11B).

Pallial complex. The terminal mantle cavity is restricted to the space roofed by the overhanging portion of the notum (Fig. 1B). The anus lies medially in the anterior roof, the excretory opening slightly in front of it at the right side. There is no gill, osphradium or hypobranchial gland; also, no particular pit with glands (such as in *Abavopsis*) is present. The genital opening is located in the right groove in the anterior third of the body (Fig. 7A).

The pallial gland is embedded in the projecting notum and opens immediately behind the anus in the roof (Figs 7B, 13B). It measures about 50 µm in diameter and consists of 4–8 large cells filled with secretion; it is surrounded by a thin layer of con-

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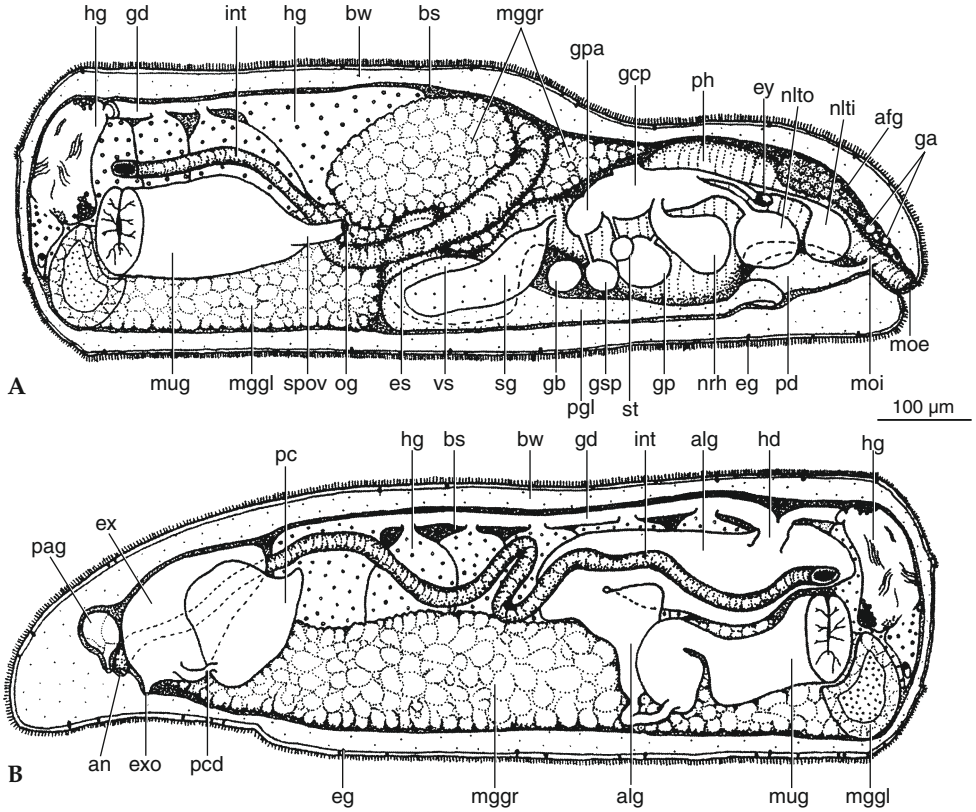

Fig. 7. *Philinoglossa praelongata*, general organisation viewed from right. **A.** Anterior body half; **B.** posterior body half. Abbreviations: **afg**, anterior foregut gland; **alg**, albumen gland; **an**, anus; **bs**, body space; **bw**, boda wall; **eg**, epidermal gland; **es**, oesophagus; **ex**, excretory organ; **exo**, opening of excretory organ; **ey**, eye; **ga**, accessory ganglia; **gb**, buccal ganglion; **gcp**, cerebro-pleural ganglion; **gd**, collecting gonoduct; **gp**, pedal ganglion; **gsp**, supra-intestinal ganglion; **hd**, hermaphroditic duct; **hg**, hermaphroditic gland (gonad); **int**, intestine; **mggl**, left midgut gland; **mggr**, right midgut gland; **mug**, mucus gland; **moe**, external mouth opening; **moi**, internal mouth; **nlti**, inner labiotentacular nerve; **nlto**, outer labiotentacular nerve; **nrh**, rhinophoral nerve; **og**, genital opening; **pag**, pallial gland; **pc**, pericardium; **pcd**, pericardioduct; **pd**, penis duct; **pgl**, penis gland; **ph**, pharynx; **sg**, salivary gland; **spov**, spermoviduct; **st**, statocyst; **vs**, seminal vesicle.

nective tissue. Occasionally, the cells show pigment granula adjacent to their periphery.

Alimentary tract. The outer mouth opens frontally, slightly ventral in the deepened transversal fold between notum and foot; here, numerous small (oral/buccal) glands are located subepithelially. The foregut is subdivided into three regions: the buccal cavity, the muscular pharynx ("buccal bulb/mass") and the simple posterior section or oesophagus into which the salivary glands open. Depending on the state of contraction, the position of the central nerve ring and the corresponding relations differ among specimens. The buccal cavity is lined by a low, in part folded epithelium; it extends far behind embracing the foremost anterior pharynx; anteriorly it receives at the right wall, such as in other *Philinoglossa* species, the outlet of the penis apparatus. The inner, true mouth opening with ciliated epithelium is located behind this outlet. Close to the posterior end of the extended buccal cavity, some accumulated gland cells with dark fine granules are ventrally present (Fig. 10A), but no openings could be discerned. The buccal cavity is laterodorsally overlain by a paired, lobed buccopharyngeal or anterior foregut glandular organ ("anterior salivary glands"; cf. Salvini-Plawen 1988) which is composed of irregularly arranged, packed gland cells of vitreous to delicately reticular aspect (Fig. 10A); these organs open dorsally into the beginning pharynx (Fig. 10B). This anteriormost pharynx is ciliated (Fig. 10A), elsewhere slightly cuticularised with triangular lumen. It is provided

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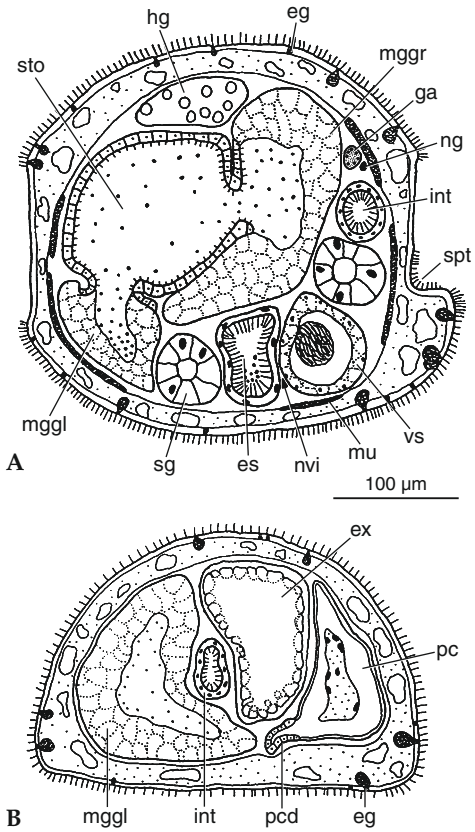

Fig. 8. *Philinoglossa praelongata*, schematised cross sections (Rovigno D). **A.** Region of stomach; **B.** region of pericardium, behind end of foot and in front of Fig. 12A. Abbreviations: **eg**, epidermal gland; **es**, oesophagus; **ex**, excretory organ; **ga**, accessory ganglion; **hg**, hermaphroditic gland (gonad); **int**, intestine; **mggl**, left midgut gland; **mggr**, right midgut gland; **mu**, musculature; **ng**, genital nerve; **nvi**, visceral nerve; **pc**, pericardium; **pcd**, pericardioduct; **sg**, salivary gland; **spt**, sperm tract; **sto**, stomach; **vs**, seminal vesicle.

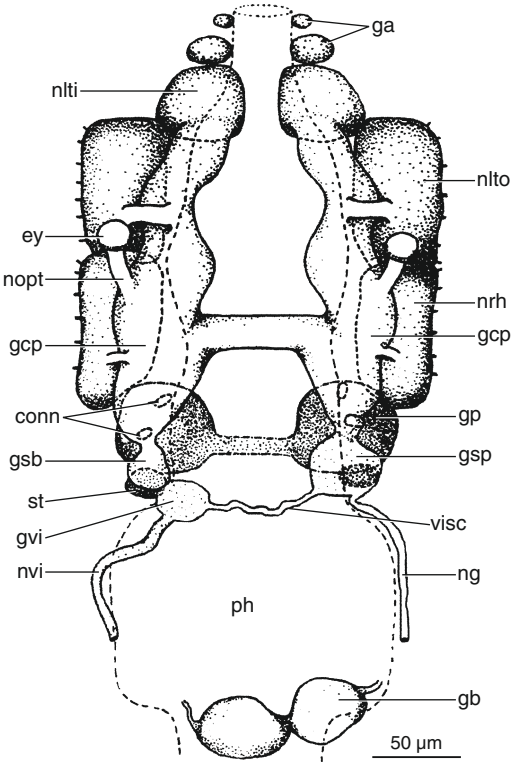

Fig. 9. *Philinoglossa praelongata*, nervous system (dorsal view). Abbreviations: **conn**, connectives; **ey**, eye; **ga**, accessory ganglia; **ga** accessory ganglion; **gb**, buccal ganglion; **gcp**, cerebro-pleural ganglion; **gp**, pedal ganglion; **gsb**, sub-intestinal ganglion; **gsp**, supra-intestinal ganglion; **ng**, genital nerve; **nlti**, inner labiotentacular nerve; **nlto**, outer labiotentacular nerve; **nopt**, optic nerve; **nrh**, rhinophoral nerve; **nvi**, visceral nerve; **ph**, pharynx; **st**, statocyst; **visc**, supraintestinal-visceral connective (visceral loop).

with longitudinal and transversal bundles of muscles, surrounded by a circular layer of musculature. In the posterior region the pharynx is ventrally connected by strong musculature with the radula sheath. The sheath opens in the preserved animals (in all specimens investigated) towards posterior, not into the pharynx but protruded into the oesophagus (Fig. 11B). Such a condition in preserved animals was also found at least in *Ph. helgolandica* (fig. 6c in Hertling 1932, region already with salivary glands) and in *Ph. marcusi* (fig. 1E in Challis 1969a: with radula sheath instead of "Ph." = pharynx, and fig. 2B,C with radula sheath within oesophagus instead of "Buc. m." = buccal mass). The radula shows a 3.0.3 arrangement of the teeth. As in *Abavopsis* and *Ph. marcusi* (Challis 1969a), the inner laterals of the present species have (in contrast to e. g. *Ph. helgolandica*) a smooth border devoid of denticles (Fig. 1B). Dorsal of the radula sheath the pharynx continues in the oesophagus which enlarges and surrounds the sheath (Fig. 11B). The anterior oesophagus receives at each side the opening of the duct (Fig. 11B) of the paired (posterior) salivary glandular organ; the gland cells of that organ show very large nuclei circularly arranged around a narrow lumen. The oesophagus with its ciliated epithelium curves to the left ventromedially and then opens from ventral into the stomach. This organ has a small, fairly globular outline and bears a low, ciliated epithelium. The openings of the two midgut glands are located in its

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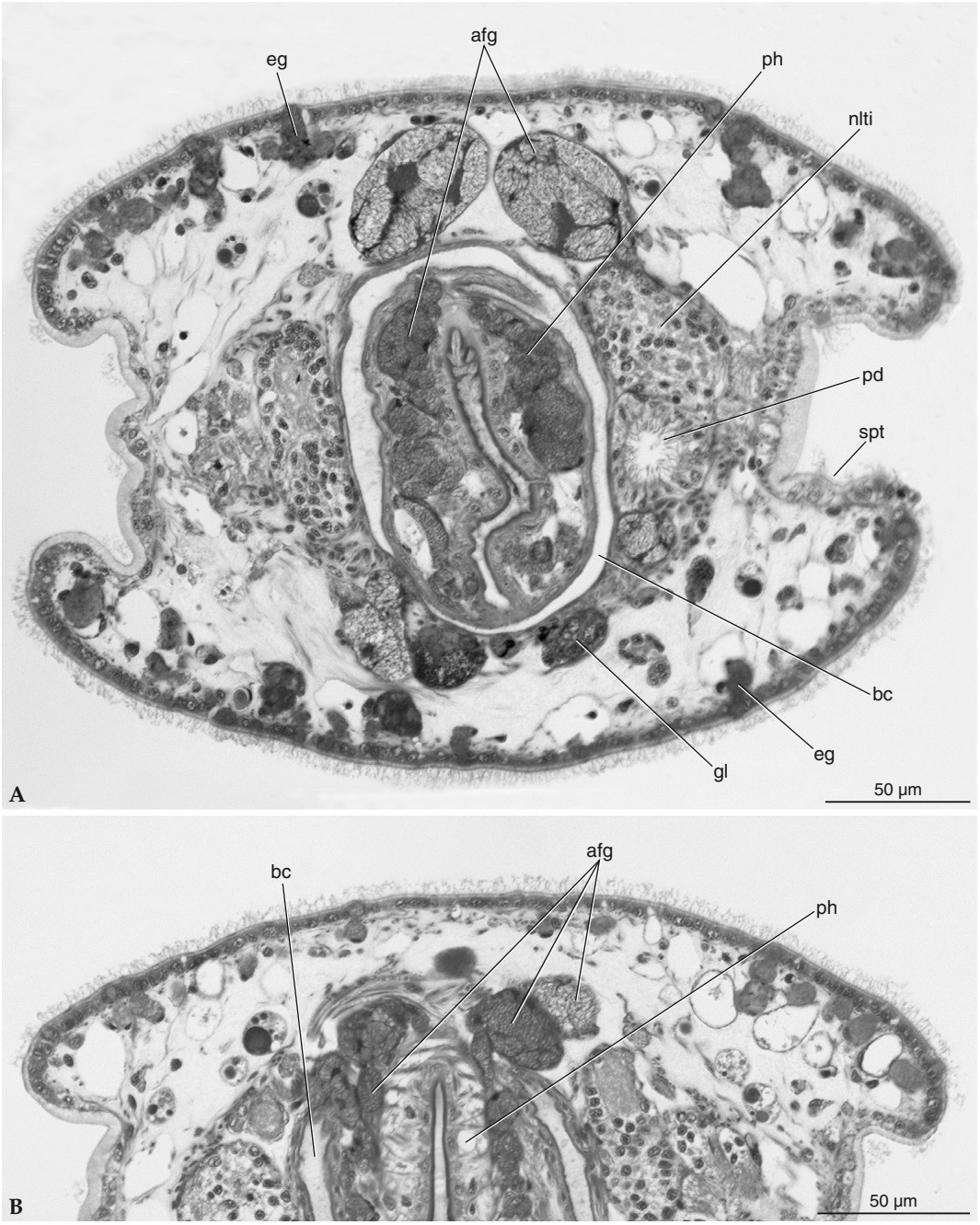

Fig. 10. *Philinoglossa praelongata*, cross sections through foregut I (Rovigno D). **A.** Cross section through anterior foregut glands; **B.** cross section through outleading anterior foregut glands into pharynx. Abbreviations: **afg**, anterior foregut gland; **bc**, buccal cavity; **eg**, subepidermal glands; **gl**, (posterior buccal?) gland; **nlti**, accessory ganglion of the inner labiotentacular nerve; **pd**, penis duct (ejaculatory duct); **ph**, pharynx; **spt**, sperm tract.

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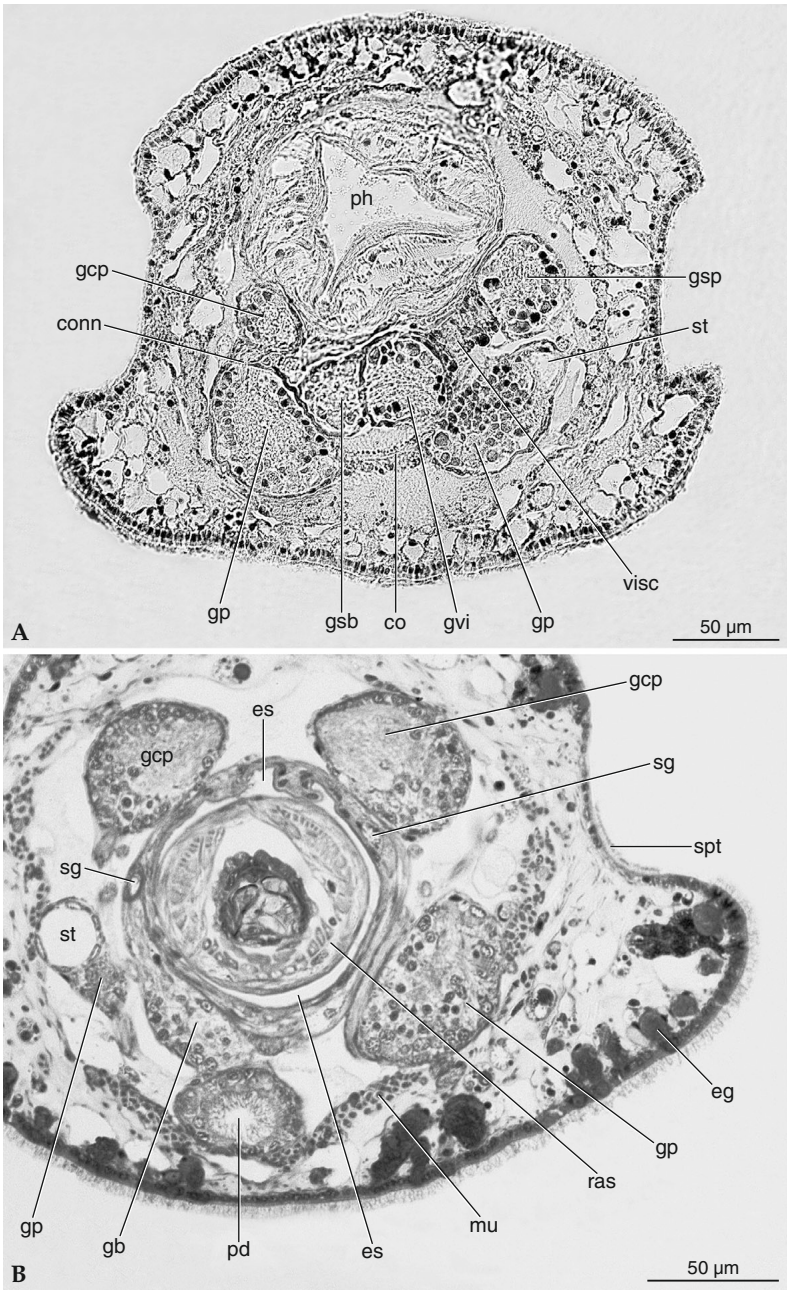

Fig. 11. *Philinoglossa praelongata*, cross sections through foregut II. **A.** Cross section through pharynx with visceral loop (Livorno B); **B.** slightly oblique cross section through region of anterior oesophagus (Rovigno D). Abbreviations: **co**, pedal commissure; **conn**, pleuro-pedal connective; **eg**, subepidermal glands; **es**, oesohagus; **gb**, buccal ganglion; **gcp**, cerebro-pleural ganglion; **gp**, pedal ganglion; **gsb**, subintestinal ganglion; **gsp**, supraintestinal ganglion; **gvi**, visceral (abdominal) ganglion; **mu**, longitudinal body wall musculature; **pd**, penis duct (ejaculatory duct); **ph**, pharynx; **ras**, radula sheath; **sg**, duct of salivary gland; **spt**, sperm tract; **st**, statocyst at posterior end of pedal ganglion; **visc**, supraintestinal-visceral connective.

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anterior region at the same transverse level (Fig. 8A). The glands have an elongate, tube-like outline and their epithelium includes two different cell types (digesting and calciferous cells) without formation of diverticles or tubules. The obliquely arranged right midgut gland is short, extending anteriorly below the intestine curve in a fairly middorsal position adjoining the cerebro-pleural ganglia; its posterior portion extends shortly at the right side. The left midgut gland runs below the gonad posteriorly at the left side up to the excretory organ; in contracted animals it may be somewhat wound axially. The ciliated intestine emerges dorsally somewhat to the right and runs via with a wide curve over the right midgut gland towards the right body wall; here, it is more or less wound and occupies a fairly medial position up to the anus in the anterio-ventral area of the notum protrusion (mantle cavity).

Sensory system. The main nervous system was outlined by Salvini-Plawen (1973) and analysed in detail by Huber (1993), if his description concerns the same species. Depending on the state of contraction, the central nerve ring either surrounds the foregut at the beginning of the muscular pharynx (thus being really pre-pharyngeal; Fig. 11A) or behind it in the region of the anterior oesophagus with the salivary glands openings (thus being post-pharyngeal; Fig. 11B). Accordingly, the measured dimensions vary considerably: e. g. in a still immature specimen the distance between the cerebral commissure and the origin of the viscero-supraintestinal commissure from the abdominal ganglion was 135 µm, whereas in a mature, but contracted specimen it was only about 45 µm. The nerve ring includes the posteriorly elongate cerebropleural ganglia, the distinct cerebral commissure, the cerebropedal and pleuropedal connectives as well as the pedal ganglia with their commissure (Figs 9, 11A). In contrast to Huber (1993) and in coincidence with Salvini-Plawen (1973), no separate parietal ganglia could be discerned.

The innervation of the Hancock's organ has already been investigated by Edlinger (1980). The short rhinophoralis nerve leaves at each side of the elongate cerebropleural ganglia (Fig. 9). This nerve enlarges to a voluminous accessory ganglion innervating the posterior portion of the sense organ by numerous fine nerves; no connection to the pedal ganglion could be discerned (contrast to Salvini-Plawen 1973). The labiotentacular nerves are connected with a common root to the anterior area of the cerebropleural ganglia (Fig. 9). The outer nerve provides with its accessory ganglion the anterior portion of the Hancock's organ; the thick inner labiotentacular nerve and its frontally located ganglion innervates the labial area ("lip organ" in Edlinger 1980). Two pairs of isolated accessory ganglia, one behind another, are present in the connective tissue dorsally of the buccal cavity; they probably connect to the inner labiotentacular ganglia, but this was not detectable. The optic nerves originate behind the labiotentacular nerves dorsolaterally from the cerebral ganglia. In accordance with Huber (1993), neither clypei-capitis nerves nor oral nerves appear to be differentiated.

The visceral loop includes three ganglia (in contrast to the description by Huber, 1993) because behind the pleuro-pedal connective at right only one, fairly prominent ganglion is present: the supraintestinal ganglion, only a short distance away but distinctly separated, close to the statocyst (Fig. 11A). In continuation of the ganglion a strong (genital) nerve (Figs 9, 8A, 12A) runs at the right alongside the intestine and then along the right midgut gland. It extends posteriorly to the gonad. A small accessory ganglion (25 µm long, 25 µm × 15 µm across) is located at the level of the stomach (Fig. 8A), but no connection could be discerned. The subintestinal ganglion and the visceral (abdominal) ganglion are positioned in the left portion of the visceral loop; in contrast to fig. 10 in Huber (1993) which shows these ganglia totally fused, they are separate but adjacent (Fig. 11A). The subintestinal and the supraintestinal ganglia are positioned approximately at the same level, the visceral ganglion in general more posteriorly in a ventro-lateral position. Due to the distance of the supraintestinal and visceral ganglia, the connective below the gut is elongate (contrast to Huber 1993). The abdominal ganglion emits a strong visceral nerve posteriorly (Figs 9, 8A, 12A). The cerebrobuccal connectives end in the buccal ganglia with their about 5–10 µm short, free commissure (Fig. 9, contrast to Huber 1993); these ganglia are located ventrally of the anterior oesophagus (or radula sheath, Fig. 11B) in the region of the openings of the salivary glands.

Sense organs are represented by the Hancock's organs, the statocysts and the eyes. The oval to globular statocysts are located adjacent to the posterior pedal ganglia (Figs 11 A, B) and include one statolith each. The pigmented eyes lie below the epithelium of the head-shield, above the accessory ganglion of the outer labiotentacular nerves.

Gono-pericardial system. The spacious pericardium lies adjacent to the right dorsal body wall, in part lateral of the excretory organ (Figs 8B, 13A). The heart is subdivided into the posterior atrium (auricle) and the anterior ventricle; the aorta, if discernible, runs ventrally of the intestine towards anterior. In *Ph. helgolandica*, Marcus & Marcus (1958) mention the aorta alongside the intestine and an intra-pericardial

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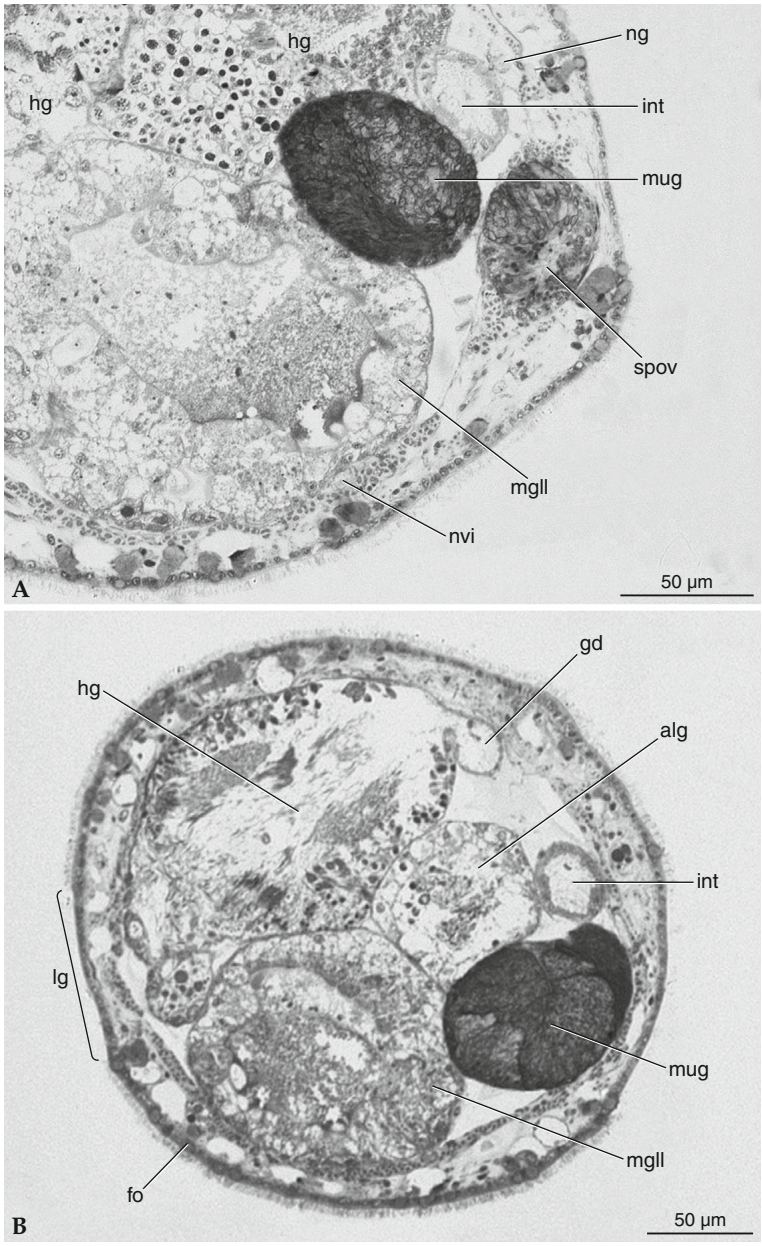

Fig. 12. *Philinoglossa praelongata*, cross sections through midbody (Rovigno D). **A.** Through anterior midbody close to genital opening; **B.** with genital organs. Abbreviations: **alg**, albumen gland; **fo**, pedal sole (foot); **gd**, collecting gonoduct; **hg**, hermaphroditic gland (gonad) follicle; **int**, intestine; **lg**, lateral body groove; **mgll**, left midgut gland; **mug**, mucus gland; **ng**, genital nerve; **nvi**, visceral nerve; **spov**, spermoviduct.

aorta trunk is apparently present (Bartolomaeus 1997); a distinct aorta is likewise present in *Ph. remanei* (Marcus & Marcus 1954). The pericardioduct emerges ventro-medially (Figs 8B, 13A) and connects with the excretory organ (emunctorium). This is sack-like and extends from behind the gonad to the end of the body cavity behind the pericardium (Fig. 7B), exclusively on the right side (the left side being

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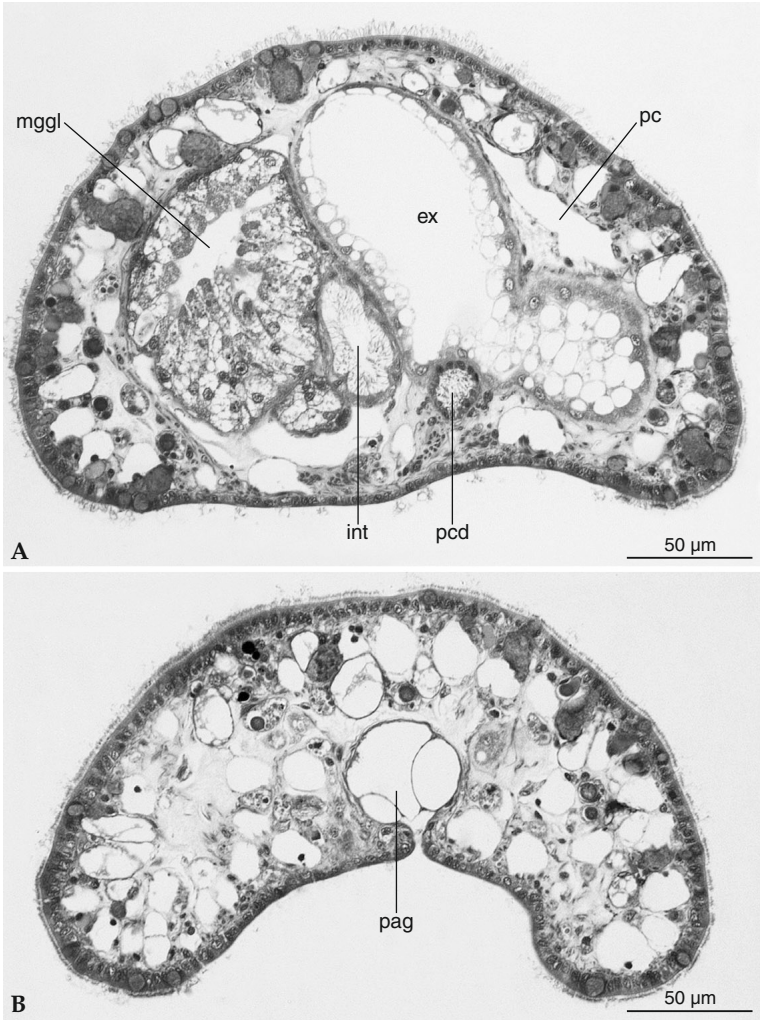

Fig. 13. *Philinoglossa praelongata*, cross sections through posterior body (Rovigno D). **A.** Behind Fig. 8B; **B.** through posteriorly overhanging notum with pallial gland. Abbreviations: **ex**, excretory organ; **int**, intestine; **pag**, pallial gland; **pc**, pericardium; **pcd**, pericardioduct.

occupied by the midgut gland). It opens through a short, median duct shortly in front of the anus in the anterio-ventral area of the notum protrusion (roof of the mantle cavity).

The specimens from Livorno (late June 1972) and Plymouth (Sept. 1982) were not yet fully mature, in contrast to the animals from Rovigno (March/April 1965) and Ancona (late May 1989). The hermaphroditic gonad extends dorsally of the midgut gland from the region of the stomach to the excretory organ. It consists of 9–10 follicles each opening by a short, narrow outlet to the right into the dorsal, collecting gonoduct (Fig. 12B), which is devoid of cilia. This duct shows an anterior and a posterior branch (Figs 7A,B), the latter being longer with six follicles. Each follicle is hermaphroditic (contrast to Salvini-Plawen 1973) and regionated into a wider, dorsal space in which spermatogenesis takes place and a smaller, ventral lobe for oogenesis (Fig. 12B). In the anterior third to half of the length of the gonad, both branches of the gonoduct join in a very short hermaphroditic duct which leads ventrally into the albumen gland. There is no formation of an ampulla. The albumen gland represents a wide duct with cubical, glandular and ciliated cells; it shows a blind anterior portion and extends about 120–170 µm pos-

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teriorly (Fig. 7B), where it curves anterioventrally. At the end of this (first) glandular section, a very narrow, ciliated and twisted duct emerges, which opens into the voluminous mucus gland (second section, Fig. 7B). This extends below the albumen gland along the right body wall anteriorly (Fig. 12B), almost up to the genital opening; its narrow lumen is lined by a high glandular epithelium without cilia. Anteriorly, a laterally separated, short ciliated spermoviduct (Figs 7A, 12A) opens as a genital opening directly behind the region of the stomach in the anterior third of the body; this opening is in the right body groove. There is no bursa copulatrix (spermatheca, receptaculum seminis).

Copulatory apparatus. The ciliated sperm tract runs from the genital opening along the right body groove to reach the mouth opening. The copulatory apparatus opens from right into the buccal cavity and extends to below the stomach region. Its anterior section turns from the right opening (Fig. 10A) posteriorly to a midventral position and represents here the strongly ciliated outleading penis duct surrounded by a thin layer of circular musculature (ductus ejaculatorius, Fig. 11B). The subsequent penis gland (prostate) is wide and tubular in outline, and may be wound. Its glandular epithelium increases towards posterior. Here, the lumen widens somewhat and continues in the sack-like vesicula seminalis (Fig. 7A) which in adults is filled with sperm. It is lined by a simple non-glandular epithelium without cilia.

Distribution. The animals occur interstitially (mesopsammic) in coarse and shell sands below the tidal zone. Their known distribution includes Rovigno/Istria and Marijan/Split/Croatia, Secche della Meloria/Livorno and La Spezia/Liguria (Salvini-Plawen 1973), Ancona/E Italy/Adriatic (Salvini-Plawen 1991), Almería/SE Spain (Salvini-Plawen & Templado 1990), Plymouth/S England (Salvini-Plawen 1984), Skagerrak/W-Sweden (Poizat 1991); 3–22 m depth.

The conspecifity of the animals from Rovigno and Plymouth with the type material from Livorno according to external characters and the radula (Salvini-Plawen 1973, 1984) is confirmed herein by the corresponding internal organisation, even if the Livorno and Plymouth specimens were not yet mature; the investigated specimens from Ancona likewise coincide.

Comparative remarks (discussion)
Figs 14–16

The members of Philinoglossidae clearly belong to the Cephalaspidea, which are characterised by the formation of a head-shield with paired Hancock's organ, a prepharyngeal nerve ring and a monaulic genital system. Among the cephalaspid taxa, the radula type and the lack of jaws in Philinoglossidae refers to Philinoidea. Particularly the radula as well as the larval shell and the black mantle gland of the veliger (Rudman 1972, Horikoshi 1967, Swedmark 1968) coincide with Philinidae. The latter group also contains species without gizzard plates (Rudman 1972, Horikoshi 1967); the glandular pit below the posterior margin of the notum in *Philine* and *Abavopsis* is also of interest for further comparative considerations. Molecular studies place *Philinoglossa praelongata* differently as sister taxon to Aglajidae (Vonnemann et al. 2005; Philinidae not included), to Gastropteridae (Malaquias et al. 2009, Göbbeler & Klussmann-Kolb 2011) or to Scaphandridae (Jörger et al. 2010) and are thus roughly consistent with the morphological evidence. The interstitially living Philinoglossidae may thus be classified within Cephalaspidea as a family of Philinoidea (Salvini-Plawen 1973, Brenzinger et al. 2013).

A comparison within the family Philinoglossidae, with its seven species, points to *Pluscula cuica* as being the more conservative member (Marcus 1953, Salvini-Plawen 1973, Brenzinger et al. 2013). In detail, however, the organisations of the species reflect a mosaic differentiation of characters (Table 1), specifically the external adaptations, the nervous system and the copulatory apparatus. The likewise mesopsammic *Philine exigua* Challis, 1969, represents in some aspects intermediate, parallel adaptations (Challis 1969b, Arnaud et al. 1986, Jörger et al. 2010): this species is therefore also considered here (Fig. 15, Table 1) to point to the problem of plesiomorphies vs. analogies. Among the characters, the alimentary tract offers some valuable features (Fig. 14) for evaluation. The general trend within Philinoglossidae appears to be the simplification of the anatomical structures of this organ system. There is coincidence among the *Philinoglossa* species in that they have a stomach area and a paired midgut gland; both are plesiomorphic conditions among Cephalaspidea (e. g. Brenzinger et al. 2013). The midgut glands, however, are tube-like and their epithelium is smooth without particular intrusions (diverticles or tubules); the right gland in *Ph. remanei* shows a blind portion towards posterior (Marcus & Marcus 1954). Similar tube-like midgut glands are known for other mesopsammobionts such as *Philine exigua* (Challis 1969b), Pseudovermidae (Nudibranchia-Aeolidoidea-Heteroprocta),

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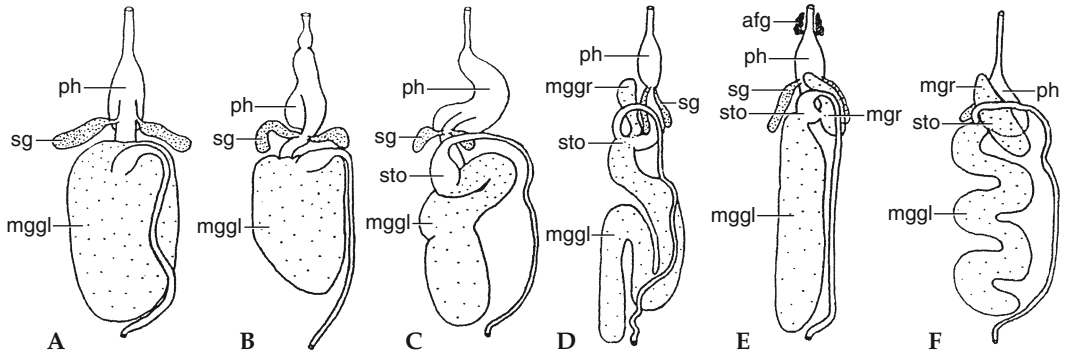

Fig. 14. Philinoglossidae. Schematic organisation of the alimentary tracts: **A.** *Abavopsis latosoleata*; **B.** *Pluscula cuica* (see Marcus 1953, Brenzinger et al. 2013); **C.** *Sapha amicorum* (see Marcus 1959); **D.** *Philinoglossa helgolandica* (see Hertling 1932, Marcus & Marcus 1958); **E.** *Philinoglossa praelongata*; **F.** *Philinoglossa remanei* (see Marcus & Marcus 1954). Abbreviations: **afg**, anterior foregut gland; **mggl**, left midgut gland; **mggr**, right midgut gland; **ph**, pharynx; **sg**, salivary gland; **sto**, stomach.

Microhedylidae (Acochlidiomorpha) or Rhodopidae (Rhodopemorpha). This may point to parallel adaptations within the biotope (Hoffmann 1939: 1129–1130, 1157–1158). In contrast, the right midgut gland as well as the stomach area in *Pluscula cuica* and *Abavopsis latosoleata* are reduced (synapomorphy?) and the single gland is sack-like, which points to a shared plesiomorphy. *Sapha amicorum* represents an intermediate condition, possessing a stomach area but the left midgut gland only, which is tube-like and smooth-walled (Marcus 1959). Moreover, the almost identical genital organs in *A. latosoleata* and

Table 1. Comparison of main characters in Philinoglossidae and *Philine exigua*.

	Pluscula cuica	*Abavopsis latosoleata*	*Sapha amicorum*
References	Marcus 1953, Brenzinger et al. 2013	present contribution	Marcus 1959
(Vestige of) shell	+	–	–
Lateral body grooves	whole body	whole body	anterior fourth
Pallial gland	+	+	+
Parietal ganglia	absent?[1]	absent	absent
Subintestinal-visceral ganglia	separate?[1]	separate	separate
Eyes	–	+	+
Oral/buccal glands	+	+	+
Anterior foregut glands	–	–	–
Inner lateral radula tooth	smooth?[2]	smooth	about 20 denticles
Stomach	–	–	+
Midgut gland	only left, sack-like	only left, sack-like	only left, tube-like
Follicles of the gonad	hermaphroditic	hermaphroditic	♂/♀ separate
Genital opening	posterior	posterior	at right anterior
Ampulla	+	+	+
Bursa copulatrix	+	+	–
Vagina	–	–	+
Penis gland	+	+	+
Penis	–	+	–

1 see text: "Comparative remarks (discussion)"
2 according to Marcus & Marcus (1954) with about 20 denticles

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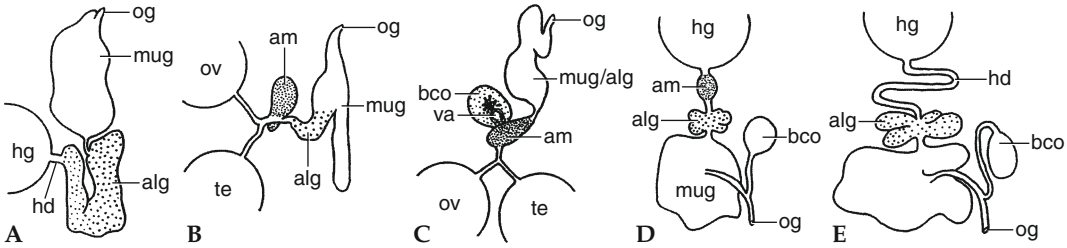

Fig. 15. Schematic organisation of the genital organs in Philinoglossidae and *Philine exigua*. **A.** *Philinoglossa praelongata*; **B.** *Philinoglossa remanei* (see Marcus & Marcus 1954); **C.** *Sapha amicorum* (see Marcus 1959); **D.** *Abavopsis latosoleata* and *Pluscula cuica* (see Marcus 1953, Brenzinger et al. 2013); **E.** *Philine exigua* (see Challis 1969b). Abbreviations: **alg**, albumen gland; **am**, ampulla; **bco**, bursa copulatrix; **hd**, hermaphroditic duct; **hg**, hermaphroditic gland (gonad); **mug**, mucus gland (in *Pluscula* including a "membrane gland"); **og**, genital opening; **ov**, ovarium; **te**, testis; **va**, vagina.

P. cuica also support the closer relationship of both (synapomorphy), though those of *Philine exigua* are similar (Fig. 15) and could point to analogies. The condition of the genital organs does not, however, pertain to the copulatory apparatus, which shows a different adaptation; in *Abavopsis* a true penis within a sheath is differentiated, whereas in *Pluscula* the distal penis duct functions as a penis papilla effected by a sphincter (Marcus 1953, Brenzinger et al. 2013). In *Abavopsis* no seminal vesicle appears to be present; Marcus (1953) describes a distinct seminal vesicle (with sperm) at the rear of the penis gland (prostata) in *Pluscula*, which bulbous terminal portion, however, is not specified as such by Brenzinger et al. (2013).

Within the *Philinoglossa* species, in contrast, the simplified copulatory apparatus (without penis gland in *Ph. remanei* and *Ph. marcusi*, Fig. 16) parallels the common lack of a bursa copulatrix (spermatheca, receptaculum seminis). *Ph. praelongata* has a penis gland (prostate), also present in *Ph. helgolandica* as a short glandular interconnection to the seminal vesicle

Philinoglossa helgolandica	*Ph. remanei*	*Ph. marcusi*	*Ph. praelongata*	*Philine exigua*
Hertling 1932, Marcus & Marcus 1958	Marcus & Marcus 1954, 1958	Challis 1969a	present contribution	Challis 1959b
–	–	–	–	internal
whole body	anterior third	anterior half	whole body	whole body
+	+	+	+	+
absent	absent	absent	absent	absent
scarcely separate	scarcely separate	scarcely separate	separate adjacent	separate adjacent
+	+	+	+	+
?	+	–	+	+
–	–	–	+	–
about 20 denticles	10–12 denticles	smooth	smooth	10–13 denticles
+	+	+	+	+
paired, tube-like	paired, tube-like	paired, tube-like	paired, tube-like	only left, lobed
hermaphroditic	♂/♀ separate	hermaphroditic	hermaphroditic	♂/♀ separate
at right anterior	at right anterior	at right anterior	at right anterior	posterior
+	+	–	–	+
–	–	–	–	+
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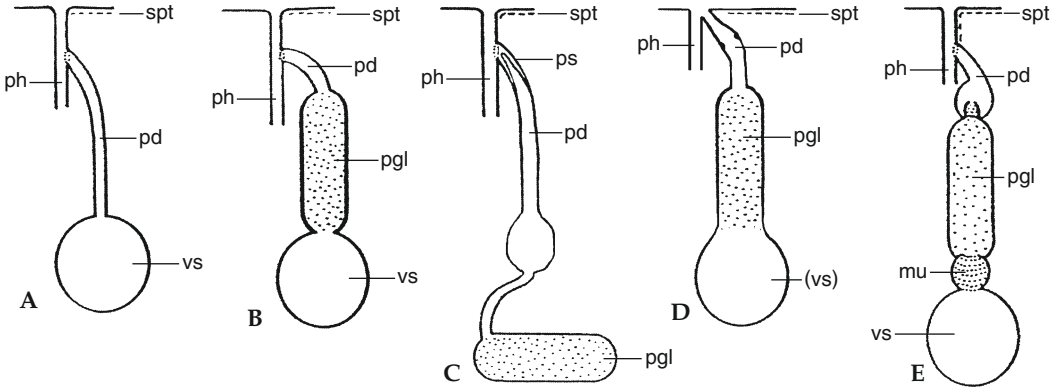

Fig. 16. Schematic organisation of the copulatory apparatus in Philinoglossidae. **A.** *Philinoglossa marcusi, Ph. remanei* (see Challis 1969a, Marcus & Marcus 1954); **B.** *Philinoglossa praelongata, P. helgolandica* (see Hertling 1932, Marcus & Marcus 1958, and present contribution); **C.** *Abavopsis latosoleata*; **D.** *Pluscula cuica* (see Marcus 1953, Brenzinger et al. 2013); **E.** *Sapha amicorum* (see Marcus 1959). Abbreviations: **mu**, musculature (sphincter); **ph**, foregut (pharynx); **pd**, penis duct; **pgl**, penis gland; **ps**, penis sheath; **spt**, sperm tract; **vs**, seminal vesicle.

(Marcus & Marcus 1958). Nonetheless, *Ph. praelongata* has the smooth radula teeth in common with *Ph. marcusi* (as well as *Abavopsis* and, according to Brenzinger et al. 2013, also *Pluscula).* At the same time, within *Philinoglossa,* only *Ph. praelongata* has a paired anterior (buccopharyngeal) foregut gland (Fig. 10) and still shows distinctly separate subintestinal and visceral ganglia (Fig. 11A) such as *Abavopsis, Sapha* and *Philine exigua.* For *Pluscula,* the situation is still unclear: according to Marcus (1953) both ganglia are almost fused, whereas Brenzinger et al. (2013) describe at left two separate ganglia, which they designate as parietal and fused subintestinal-visceral ganglia, but could represent the separate subintestinal and visceral ganglia (no parietal ganglia: the synapomorphic presence of parietal ganglia in "Pentaganglionata", see Haszprunar 1985, and their fusion with other ganglia where they are absent, remains hypothetical). *Ph. helgolandica* and *Ph. remanei* possess an ampulla (Marcus & Marcus 1954, 1958), as do *Pluscula*, *Sapha* and *Philine exigua*; *Ph. remanei* is additionally characterised by producing eggs and sperm in separate follicles (Marcus & Marcus 1954). The ventral vagina in *Sapha amicorum* underlines the special anagenesis of this species within Cephalaspidea and separates it from other Philinoglossidae. Closing up, this family apparently reflects three evolutionary lines (clades) represented by *Pluscula* and *Abavopsis*, by *Sapha amicorum* and by the *Philinoglossa* species.

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References

Arnaud, P. M., Poizat, C. & Salvini-Plawen, L. v. 1986. Marine-interstitial Gastropoda (including one freshwater interstitial species). Pp. 153–176 in: L. Botosaneanu (ed.). Stygofauna Mundi. Leiden (E. J. Brill/W. Backhuys).

Bartolomaeus, T. 1997. Ultrastructure of the renopericardial complex of the interstitial gastropod *Philinoglossa helgolandica* Hertling, 1932 (Mollusca: Opisthobranchia). Zoologischer Anzeiger 235: 165–176.

Botosaneanu, L. (ed.) 1986. Stygofauna mundi. 740 pp., Leiden (E. J. Brill/W. Backhuys).

Brenzinger, B., Padula, V. & Schrödl, M. 2013. Insemination by a kiss? Interactive 3D-microanatomy, biology and systematics of the mesopsammic cephalaspidean sea slug *Pluscula cuica* Marcus, 1953 from Brazil (Gastropoda: Euopisthobranchia: Philinoglossidae). Organisms, Diversity & Evolution. 13(1): 33–54.

Challis, D. A. 1969a. *Philinoglossa marcusi* n. sp. (Mollusca: Opisthobranchia: Philinoglossacea) from the British Solomon Islands Protectorate. Transactions of the Royal Society of New Zealand, Biological Sciences 11: 169–175.

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– – 1969b. *Philine exigua* (Opisthobranchia: Bullomorpha), a minute interstitial species from Melanesia. Transactions of the Royal Society of New Zealand, Biological Sciences 11: 177–186.

Edlinger, K. 1980. Zur Phylogenie der chemischen Sinnesorgane einiger Cephalaspidea (Mollusca – Opisthobranchia). Zeitschrift für Zoologische Systematik und Evolutionsforschung 18: 241–156.

Göbbeler, K. & Klussmann-Kolb, A. 2011. Molecular phylogeny of the Euthyneura (Mollusca, Gastropoda) with special focus on Opisthobranchia as a framework for reconstruction of evolution of diet. Thalassas 27(2): 121–154.

Haszprunar, G. 1985. The Heterobranchia – a new concept of the phylogeny of the higher Gastropoda. Zeitschrift für Zoologische Systematik und Evolutionsforschung 23: 15–37.

Hertling, H. 1932. *Philinoglossa helgolandica*, n. g., n. sp., ein neuer Opisthobranchier aus der Nordsee bei Helgoland. Wissenschaftliche Meeresuntersuchungen, N.F., Abteilung Helgoland 19(2): 1–9.

Hoffmann, H. 1939. Opisthobranchia 1. Bronns Klassen und Ordnungen des Tierreichs 3/II/3. 1247 pp., Leipzig (Akademische Verlagsgesellschaft).

Horikoshi, M. 1967. Reproduction, larval and life history of *Philine denticulata* (J. Adams) (Mollusca: Tectibranchia). Ophelia 4: 43–84.

Huber, G. 1993. On the cerebral nervous system of marine Heterobranchia (Gastropoda). Journal of Molluscan Studies 59: 381–420.

Jörger, K. M., Stöger, I., Kano, Y., Fukuda, H., Knebelsberger T. & Schrödl, M. 2010. On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. BMC Evolutionary Biology 10: 323. doi:10.11186/1471-2148-10-323.

Kowalevsky, A. 1901a. Études anatomiques sur le genre *Pseudovermis*. Mémoires de l'Académie Impériale des Sciences de St.-Pétersbourg, Classe Physico-Mathématique 12(4): 1–28.

– – 1901b. Les Hédylides, étude anatomique. Mémoires de l'Académie Impériale des Sciences de St.-Pétersbourg, Classe Physico-Mathématique 12(6): 1–32.

Malaquias, M. A. E., Mackenzie-Dodds, J., Bouchet, P., Gosliner, T. & Reid, D. G. 2009. A molecular phylogeny of the Cephalaspidea sensu lato (Gastropoda: Euthyneura): Architectibranchia redefined and Runcinacea reinstated. Zoologica Scripta 38: 23–41.

Marcus, E. 1953. Three Brazilian sand-Opisthobrancha. Boletim da Faculdade de Filosofía, Ciencias e Letras Univ. Sao Paulo 165 (Zoologia 18): 165–203.

– – 1959. Eine neue Gattung der Philinoglossacea. Kieler Meeresforschungen 15: 117–119.

– – & Marcus, E. 1954. Über Philinoglossacea und Acochlidiacea. Kieler Meeresforschungen 10: 215–223.

– – & Marcus, E. 1958. Opisthobranchia aus dem Schill von Helgoland. Kieler Meeresforschungen 14: 91–96.

Poizat, C. 1978. Gastéropodes mésopsammiques du fonds sableux du Golfe de Marseille. Thèse doctorale à la Faculté des Sciences et Techniques de l'Université d'Aix-Marseille III (France), Fasc. I: 1–301; Fasc. II: figs 1–84, pls 1–17.

– – 1983. Mesopsammic opisthobranchs from the provencal coast (Marseilles, Bouches du Rhône, France): long term variations of the populations. Journal of Molluscan Studies 12A: 126–135.

– – 1991. New data on the interstitial opisthobranch assemblage and other meiofauna from the Skagerrak, Sweden. Journal of Molluscan Studies 57: 167–177.

Rudman, W. B. 1972. The genus *Philine* (Opisthobranchia, Gastropoda). Proceedings of the Malacological Society London 40: 171–187.

Salvini-Plawen, L. v. 1973. Zur Kenntnis der Philinoglossacea and der Acochlidiacea mit Platyhedylidae fam. nov. (Gastropoda, Cephalaspidea). Zeitschrift für Zoologische Systematik und Evolutionsforschung 11: 110–133.

– – 1983. Stamm: Mollusca (Weichtiere). Pp. 248–390 in: Riedl, R. (ed.). Fauna und Flora des Mittelmeeres. Hamburg/Berlin (P. Parey).

– – 1984. Notes on molluscan meiofauna from Plymouth. Journal of the Marine Biological Association U.K. 64: 497–502.

– – 1988. The structure and function of molluscan digestive systems. Pp. 301–379 in: Trueman, E. R. & Clarke, M. R. (eds). The Mollusca, Vol. 11. Form and Function. London (Academic Press).

– – 1991. *Pseudovermis thompsoni* new species (Nudibranchia, Aeolidoidea) from the northern Adriatic Sea. Journal of Molluscan Studies 57: 179–187.

– – & Templado, J. 1990. Nota sobre los moluscos mesopsammicos del Sudeste de España. Iberus 9: 527–528.

Swedmark, B. 1964. The interstitial fauna of marine sand. Biological Reviews 39: 1–42.

– – 1968. The biology of interstitial Mollusca. Symposia of the Zoological Society London 22: 135–149.

Vonnemann, V., Schrödl, M., Klussmann-Kolb, A. & Wägele, H. 2005. Reconstruction of the phylogeny of the Opisthobranchia (Mollusca: Gastropoda by means of 18S and 28S rRNA gene sequences. Journal of Molluscan Studies 71: 113–125.

Weinbauer, C., 1991. Anatomie und Verwandtschaft von Philinoglossacea. 82 pp., Diploma thesis Mag. rer. nat., Formal- & Naturwissenschaftliche Fakultät der Universität Wien (Vienna/Austria).

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