



REVIEW ARTICLE

A reconsideration of epipodial and cephalic appendages in basal gastropods: homologies, modules and evolutionary scenarios

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ABSTRACT

Basal gastropods have various types of body appendages. Besides pallial or cephalic tentacles, subocular tentacles, neck lobes and (occasionally) copulatory structures, there are epipodial tentacles and epipodial sense organs (ESOs), which have often been confused in the past. We provide clear definitions of these two different epipodial structures, describe various examples and reconsider literature data on their occurrence throughout basal gastropod clades, i.e. Patellogastropoda, Cocculiniformia, Neritimorpha, Neomphalina and (in particular) Vetigastropoda. So-called ‘epipodial tentacles’ of Patellogastropoda, Cocculiniformia, Neomphalina and of several vetigastropod subgroups are considered to represent a distinct and apomorphic gastropod organ, the ESO. In contrast, true epipodial tentacles are probably serial or iterative homologues of cephalic tentacles and are restricted to Vetigastropoda and certain caenogastropod taxa. In the light of these new data and interpretations, an evolutionary scenario is presented for epipodial structures in basal gastropods: a single pair of ESOs in a posterior position is considered as an apomorphic character of the gastropod stem lineage, which is retained in early juvenile Patellogastropoda, many Cocculiniformia and early juvenile Vetigastropoda. The various conditions in Neomphalina and Vetigastropoda can be explained by considering modularity of ESOs, cephalic/epipodial tentacles and sensory papillae. Each of these modules has become serially repeated in evolution and occurs in various combinations among basal gastropod clades.

INTRODUCTION

A single pair of cephalic tentacles is typical for the overwhelming majority of gastropods. In addition, the head, neck, mantle and the epipodium may be equipped with various kinds of appendages. Vetigastropoda in particular are known to bear a large variety of tentacles: accessory cephalic tentacles, subocular tentacles, copulatory organs, eyestalks, oral lappets and neck lobes, all varying significantly in shape and appearing in various combinations (see e.g. review by Hickman & McLean, 1990). After some discussion in the 19th century (summarized by Pelseener, 1887) it has been accepted for more than 120 years that epipodial structures are pedally (and not pallially) innervated, whereas the so-called neck lobes (if present) are cerebrally innervated and thus part of the head (Thiele, 1892).

Vetigastropoda (including the Lepetelloidea) are unique in showing distinct sensory papillae on the cephalic and epipodial tentacles, and often also at the mantle edge or even on the tentacular leaflets. This character has been variously described in the literature,

e.g. setose or papillate tentacles, ‘seta’-like projections and tentacles with (sensory) papillae (e.g. Flemming, 1884; Fretter & Graham, 1976, 1977; Warén & Bouchet, 1993; Fretter *et al.*, 1998; Okutani, Sasaki & Tsuchida, 2000; Künz & Haszprunar, 2001; Geiger, 2003). Tentacles without sensory papillae are usually described as smooth or nonpapillate (e.g. Haszprunar, 1993; Geiger, 2003).

Another sensory structure, which is connected with the epipodial tentacles in vetigastropods, has been well known for more than 130 years. Boutan (1885: pls 41, 42) first marked them as ‘x’ in the figures of early juveniles of *Scissurella* and *Fissurella*. Later, Pelseener (1899) and Robert (1902) called these ‘organs sensoriels lateraux’ in the trochid *Calliostoma zizyphinum*, Crofts (1929: 128) called them ‘subtentacular sense organs’ in *Haliotis tuberculata*. The term ‘epipodial sense organ’ was first applied by Fretter & Graham (1977) in their description of two *Gibbula* species, but the authors did not apply the term consistently, because they used just ‘sense organ’ for other species in the same paper. Crisp (1981) first introduced the acronym ESO, and described and depicted its fine

structure in detail (by SEM and TEM) for several trochid species. According to Crisp (1981) and Herbert (1984), the ESO of trochids is a knobbed structure at the base of an epipodial tentacle with a ciliated groove at the tip (Crisp, 1981: fig. 5A). TEM images revealed that the ESO is a mechanoreceptor with a distinct ultrastructure: its sensory cells bear so-called ‘collar receptors’, a unique structure characterized by a central cilium surrounded by eight or nine specialized microvilli (Crisp, 1981: fig. 6A; Herbert, 1984: pl. 17). Later, ESOs were reported in (almost) all vetigastropod superfamilies, although many authors did not describe them as ESOs or overlooked them (see below).

In order to clear up this confused terminology, we provide a survey of epipodial and cephalic structures in basal gastropod taxa with a focus on Vetigastropoda (Fig. 1). Epipodial tentacles are defined as serial/iterative homologues of the cephalic tentacles and thus show the same structure down to the ultrastructural level. In contrast, ESOs are different organs, characterized by a stout tentacle with a thick sensory epithelium at the tip (or laterally), which is ciliated (collar receptors). We distinguish two types of ESOs: (1) ‘simple ESO’ forming an entire tentacle; (2) ‘compound ESO’, i.e. a knob-like ESO located at the base of a (usually papillate) epipodial tentacle. We examined representatives of six vetigastropod superfamilies, of

various Neomphalina and of Cocculiniformia using SEM, histological sectioning, occasionally TEM and computer-aided 3D reconstruction. These new data were compared with the descriptions of tentacle conditions given in the literature. We discuss the evolution of cephalic and epipodial tentacles, sensory papillae and ESOs in basal gastropods and their systematic significance.

MATERIAL AND METHODS

Species investigated are listed in Table 1.

The SEM images were prepared according to Geiger *et al.* (2007) and Kunze (2011): animals were mechanically removed from the shell, dried in a graded ethanol series, critical-point dried, sputtered with gold and examined with a Hitachi SEM.

TEM studies on a *Diodora* species followed routine protocols with glutaraldehyde/osmium fixation, embedding in Spurr’s resin and staining of ultrathin (70–80 nm) sections (made by a Leica EM UC6) with uranyl acetate and lead citrate. The photographs were made in an FEI Morgagni TEM at 80 kV.

The histological sections were performed as follows: dissolution of the shell with acid (hydrochloric acid or Bouin’s fluid); dehydration

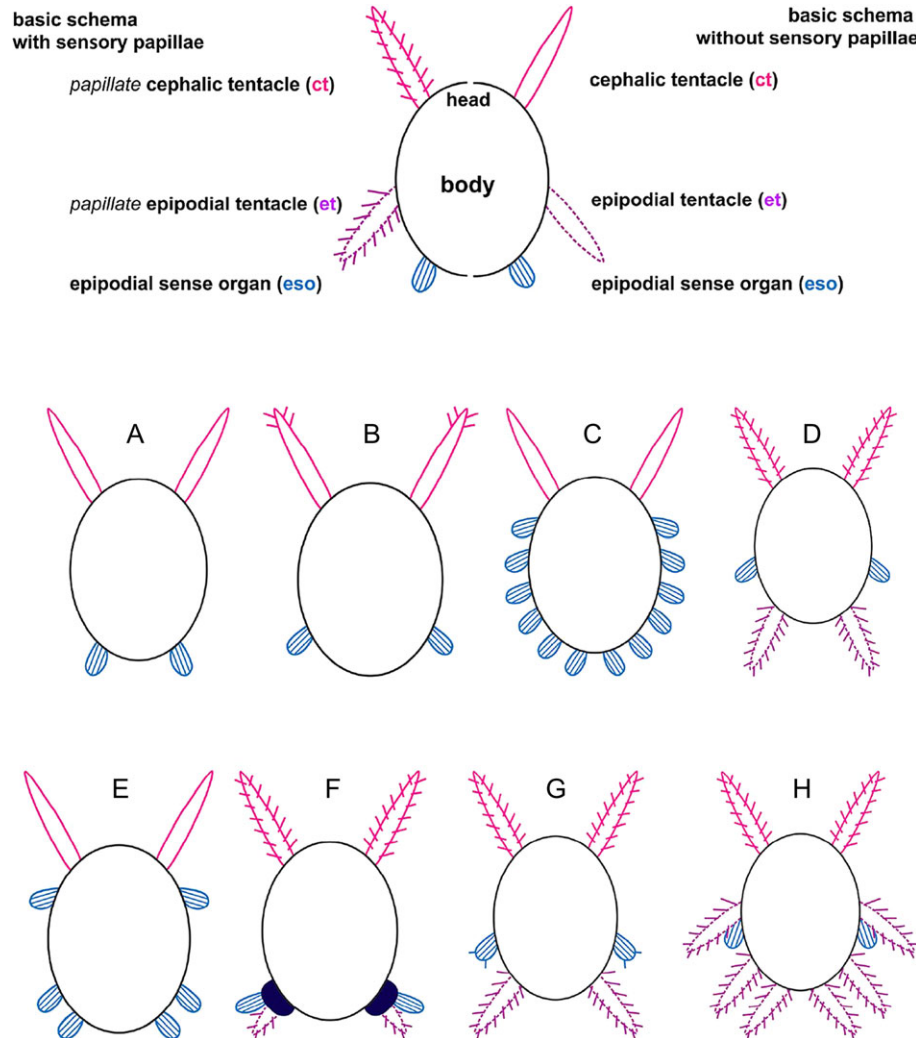


Figure 1. Diagrammatic scheme of the taxa included in this study, showing the arrangement of tentacles and ESOs. **A.** *Patella* and *Notacmaea* early juveniles (Patellogastropoda), most adult Cocculinidae (Cocculiniformia), several adult Lepetelloidea, juvenile *Clypeosectus* (Lepetodriloida: Clypeosectidae). **B.** Juvenile *Diodora* (Fissurellidae) and *Haliotis* (Haliotidae). **C.** Most Neomphalina and most adult Fissurellidae. **D.** *Ventsia* (Seguenziidae). **E.** *Lepetodrilus* (Lepetodrilidae). **F.** The Pseudococculinidae (incl. *Kaiparapelta*) and Caymanabyssiidae clade (Lepetelloidea). **G.** Scissurellidae. **H.** *Skenea* (Trochoidea: Skeneidae).

Table 1. Studied taxa, their tentacular conditions and applied methods.

Systematics	Species	Cephalic tentacles	Epipodial tentacles	ESO conditions	Methods applied	Vouchers	Figures
Cocculiniformia							
Cocculinidae	<i>Cocculina</i> sp.	Smooth	None	1 posterior pair	SEM	SMNH	1A, 2A–C
Cocculinidae	<i>Teuthirostria cancellata</i> Moskalev, 1976	Smooth	None	1 posterior pair	hist	ZSM, paratype	1A, 2D
Neomphalina							
Peltospiridae	<i>PeltoSPIra operculata</i> McLean, 1989	Smooth	None	Several along the epipodial ridge	SEM	SMNH 81063	1C, 3A, B
Peltospiridae	<i>PeltoSPIra smaragdina</i> Warén & Bouchet, 2001	Smooth	None	Several along the epipodial ridge	SEM	SMNH 50408	1C, 3C, D
Neomphalidae	<i>Cyathermia naticoides</i> Warén & Bouchet, 1989	Smooth	None	Several along the epipodial ridge	SEM	SMNH 43065	3E, F
Vetigastropoda							
Pseudococculinidae	<i>Kaiparapelta</i> sp.1, 2	Papillate	1 pair of posterior bifid tentacles: epipodial tentacle and ESO combined		hist, 3D, SEM	MNHN	1F, 4A–F
Fissurellidae	<i>Diodora</i> sp. (aquarium)	Papillate (juv.)	None	Several along the epipodial ridge	hist, 3D, SEM	ZSM	1B, C, 5A–I
Lepetodrilidae	<i>Lepetodrilus</i> cf. <i>pustulosus</i> McLean, 1988	Smooth	None	3 pairs	SEM	SMNH	1E, 6A–F
Lepetodrilidae	<i>Lepetodrilus fucensis</i> McLean, 1988	Smooth	None	3 pairs	hist	ZSM	Not depicted
Lepetodrilidae	<i>Clypeosectus curvus</i> juv. McLean, 1988	Smooth	None	1 pair (juv.)	hist	ZSM	1A
Scissurellidae	<i>Scissurella jucunda</i> Smith, 1890	Papillate	1 pair papillate	1 pair with few papillae	hist, 3D	ZSM	1G, 7A–C
Scissurellidae	<i>Scissurella</i> sp. (Santos)	Papillate	1 pair papillate	1 pair with few papillae	SEM	SMNH	1G, 7D–F
Scissurellidae	<i>Larochea miranda</i> Finlay, 1927	Papillate	2 pairs papillate	1 pair	hist	ZSM	Not depicted
Seguenzioidea (inc. sedis)	<i>Ventsia tricarinata</i> Warén & Bouchet, 1993	Papillate	1 pair papillate	1 pair	hist, 3D, SEM	MNHN 20948	8A–F
Seguenzioidea (inc. sedis)	<i>Putilla porcellana</i> (Tate & May, 1900)	Papillate	4 pairs papillae	1 pair	hist, 3D, SEM	SMNH	Not depicted
Skeneidae	<i>Skenea serpuloides</i> (Montagu, 1808)	Papillate	3 pairs papillate	1 pair attached to first epipodial tentacle	hist, 3D	SMNH, ZSM	1H
Skeneidae	<i>Lissospira</i> sp.	Papillate	4 pairs papillae	1 pair attached to third epipodial tentacle	SEM	SMNH	Not depicted

Abbreviations: hist, histological sections; 3D, 3D reconstructions; SEM, scanning electron microscopy. Institutional abbreviations: MNHN, Muséum National d'Histoire Naturelle, Paris; SMNH, Swedish Museum of Natural History, Stockholm; ZSM, Bavarian Zoological State Collection, Munich.

in a graded acetone series; embedding in epoxy resin, Spurr's resin or Histo-resin (BiosystemsSwitzerland AG); serial sectioning with a RMC Ultra MT-7000 with a glass or diamond knife (thickness 1.5 or 5 µm; Ruthensteiner, 2008); staining with methylene blue after Richardson, Jarett & Finke (1960), with 'Kernechtrot' (Mulisch & Welsch, 2010) or a mixture of both; and finally sealing with DPX (Agar Scientific, Essex) or cedar oil.

The histological sections were photographed with a digital camera (Olympus DP25) on an Olympus CX41 light microscope (objectives Olympus Plan N 4x, Plan CN 10x, Plan CN 20x, Plan CN 40x). Using these digital images, 3D reconstructions were compiled and selected perspective views displayed with the AMIRA software Resolve RT v. 4.2 (TFG Template Graphics Software, Inc., USA) according to Ruthensteiner (2008).

In the descriptions below, the following abbreviations are used: BL, body length; D, diameter; L, length.

RESULTS

All measurements are approximate values with a tolerance of less than 5% and most are given to the nearest 10 µm. Shrinkage caused by chemical fixation and sectioning was disregarded. An overview of the tentacle arrangements of the taxa investigated are given in Figure 1, while authorities of names and their higher classification are given in Table 1.

Cocculina sp. (Figs 1A, 2A–C)

BL 880 µm. The cephalic tentacles are very short and devoid of sensory papillae; there are no epipodial tentacles. A single pair of simple ESOs, each with a ciliated depression at the tip, is found in a posterior position (L 100 µm, D 40 µm). Large sensory papillae ('macro-papillae': D 20 µm) occur at the edge of the mantle skirt.

Teuthirostria cancellata (Fig. 2D)

BL < 700 µm. There are no sensory papillae or epipodial tentacles. There is a single pair of elongated, simple ESOs (L 350 µm, D 90 µm) in a posterior position, with ciliated tips.

Pelto-spira operculata (Figs 1C, 3A–B)

BL 3.4 mm. The cephalic tentacles are quite broad (L 580 µm, D 400 µm) and devoid of sensory papillae. Epipodial tentacles are lacking. Many knob-like, simple ESOs are placed all around the epipodial ridge except for the frontal part. There are more than 30 on either side, with smaller and larger ones mixed, but the smaller ones are more ventral and the larger ones more dorsal (L/D of three ESOs: 50/90 µm, 70/100 µm, 75/120 µm). The ciliated groove at the tip of the ESOs is irregularly stellate.

Pelto-spira smaragdina (Figs 1C, 3C, D)

BL 3.5 mm (juvenile; reaches maximum L of 12 mm). The cephalic tentacles are quite broad (L 730 µm, D 370 µm) and lack sensory papillae. There are no epipodial tentacles. About ten knob-like, simple ESOs on either side are situated on the posterior part of the epipodium (see also Warén & Bouchet, 2001: fig. 26A, B). The size of the ESOs is variable (L 110–200 µm, D 70–180 µm), the largest ones being situated at the posterior end, while those towards the anterior end are smaller. Each ESO bears a ciliated groove of oval shape at the tip.

Cyathermia naticoides (Fig. 3E, F)

BL 2.5 mm. The cephalic tentacles are long (L 930 µm, D 230 µm) and lack sensory papillae. Epipodial tentacles are absent. Two pairs of elongated, simple ESOs (L/D 160–200/110 µm) are

situated in a posterior position below the operculum. The groove at the tip of each ESO is elongate, of oval shape and densely ciliated.

Diodora sp. (Fig. 1B, C, 4A–I)

This brooding species is probably undescribed; the same species was studied by Künz & Haszprunar (2001). Accordingly, a DNA-barcode (COI) is given: GGTTGGTTGGGACGAGGCTAAGGTTACTGATTCGGGCTGAATTGGGTCAGCCCCGGGGCTTTATTAGGGGATGACCAGTTATATAATGTTGTTGTGACTGCGCATGCCTTTGTGATGATTTTTTTTCTTGTAATGCC TATGATGATCGGGGGGTTGGTAATTGGTTAGTGGCCGCTAATGTTGGGTGCTCCTGATATAGCATTTCCTCGCAC TGAATAACATGAGATTTTGGTTGTTACCATTTTTCTTTGG TTTTGCTGTTGATTTCTGCGGCAGTTGAAGGGGGGGCTGGGACTGGTTGGACCGTCTACCCCCATTGGCGGGG AATTTGGCTCATGCTGGTCCGTCTGTTGATCTAACTATTTTTTCTTTACATTTTGGCAGGTGATCTTCTATTTTTGGTGCTGTAATTTTATTACTACTGTGGTTAACATGCGGTGAGATGGTATACGCCCTGGAGCGTATTCCTTTATTTGTGTGATCTGTAAGTACAGCTATTTTATTGTTGTT

A BLAST search of the GenBank database revealed *Diodora cayenensis* as most similar (84.42%), but they are certainly not conspecific.

BL up to 5 mm. The cephalic tentacles (L 140 µm; D 40 µm) of an early juvenile (BL max. 0.5 mm) bear a few sensory papillae on the most distal part (Fig. 4A–C). Such visible papillae exist only in juveniles, whereas larger specimens (BL > 2 mm) have smooth tentacles. Epipodial tentacles are absent. Early juveniles show a single pair of simple ESOs (L 45 µm, D 30 µm), whereas subadults (BL 3 mm) show several ESOs along the epipodial ridge, but these are fewer in number and more distantly spaced than in *Pelto-spiridae* (Fig. 4D–F). The sensory epithelium is situated subterminally (Fig. 4G). TEM studies on a subadult specimen (Fig. 4H, I) revealed sensory cells with collar receptors very similar to the conditions described by Crisp (1981) and Herbert (1984) for trochid ESOs.

Kaiparapelta sp. 1 (Figs 1F, 5A–C)

BL 2 mm. The cephalic tentacles are short and sturdy (L 370 µm, D 160 µm) and bear sensory papillae (see Haszprunar, Graf & HEB, 2014: fig. 9A), whereas the epipodial appendages are smooth. There is an epipodial fold at half the height of the pallial cavity (see Haszprunar et al., 2014: figs 4A, 5A). A 'bifid tentacle' is situated at the posterior third of the epipodium, consisting of a short trunk (L 280 µm, D 320 µm) and two tentacles: the outer one is an ESO (L 140 µm, D 95 µm) with a swollen tip, the other (inner branch) is a slender, tapered tentacle without sensory papillae (L 250 µm, D 60 µm) (Fig. 5B, C).

Kaiparapelta sp. 2 (Figs 1F, 5D–F)

Similar to *Kaiparapelta* sp. 1, but smaller; BL 1.5 mm. The trunk of the bifid tentacles is longer and more slender (L 230 µm, D 120 µm) and the ESO (L 160 µm, D 70 µm) and epipodial tentacle (L 160 µm, D 80 µm) are smaller.

Lepetodrilus sp. aff. *pustulosus* (Figs 1E, 5G–L)

BL 4.6 mm. The cephalic tentacles are very slender (L 1.1 mm, D 220 µm) and lack sensory papillae, but show distinct ciliated tufts (see also Fretter, 1988: pl 1, fig. 26). In contrast, the mantle skirt bears a dense line of large papillae (D ca 30 × 40 µm) (Fretter, 1988: pl 1, figs 21, 23; Fig. 5K), each with a ciliated tip. In addition, a single, significantly larger mantle tentacle (D 60 µm), again with a ciliated tip, is situated at the anterior right end of the mantle skirt, slightly outside the row of papillae (Fig. 5K, L). Epipodial tentacles are absent, but there are three pairs of slightly differently shaped,

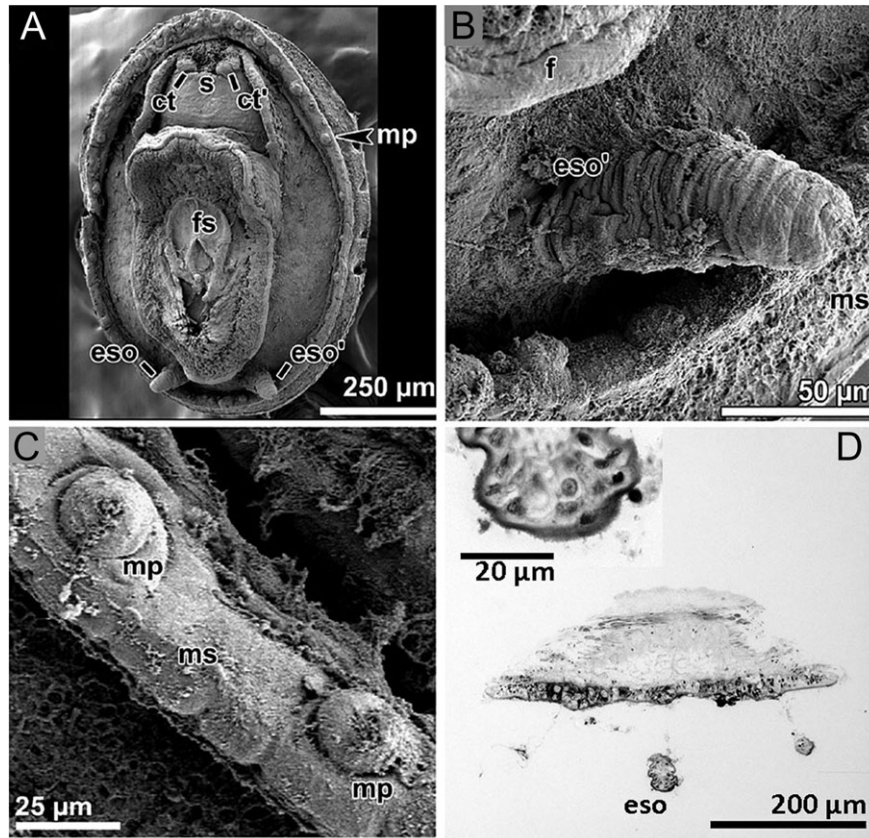


Figure 2. Tentacle conditions in Cocculinidae (Cocculiniformia). **A–C.** SEM images of *Cocculina* sp. **A.** Ventral view of soft body. **B.** Left ESO. **C.** Mantle edge with papillae. **D.** Histological cross section of the most posterior body and the two ESOs of *Teuthrostria cancellata*; insert: ESO with ciliated cells. Abbreviations: ct/ct', right/left cephalic tentacle; eso/eso', right/left epipodial sense organ; f, foot; fs, foot sole; mp, macro-papillae; ms, mantle skirt; s, snout.

simple ESOs (Fig. 5G; see also Fretter, 1988: fig. 3b): (1) the anterior edge of the epipodium on both sides is drawn out to form an ESO (L 200 µm, D 60 µm) with an indistinct, pointed, ciliated groove; (2 and 3) two further pairs of ESOs are situated along the most posterior quarter of epipodium (Fig. 5I, J); (2) the middle one is broader and shows a large, ciliated groove of oval shape (L 80 µm, D 125 µm); (3) the most posterior ESO is slender (L 140 µm, D 60 µm) and has a small ciliated groove at the tip.

Leptodrilus fucensis

BL 8.5 mm. As in the former species, but the mantle skirt is smooth and the three pairs of ESOs (L 30 µm, D 20 µm) are smaller.

Clypeosectus curvus (Fig. 1A)

BL 4.3 mm. The cephalic tentacles of juvenile specimens lack papillae and epipodial tentacles are absent. There is a single pair of simple ESOs (L 230 µm, D 90 µm) with a thick, ciliated epithelium at the tip, being supplied by a nerve.

Scissurella jucunda/*Scissurella* sp. (Figs 1G, 6A–F)

BL 0.8/1.2 mm. The cephalic tentacles are short and slender (L 240 µm, D 50 µm/L 550 µm, D 120 µm). Both cephalic and epipodial tentacles are densely covered with sensory papillae as is a small tentacle at the mantle slit. There is only one pair of epipodial tentacles (L 120 µm, D 25 µm/L 150 µm, D 40 µm), situated posteriorly below the operculum (Fig. 6A, D). The single pair of simple ESOs is placed slightly more anteriorly, still under the operculum.

Each ESO is quite long (L 160 µm, D 30 µm/L 120 µm, D 40 µm) and the stubby tip shows a thick sensory epithelium with long cilia (Fig. 6C). Unusually, several sensory papillae are situated around the edge of the tip (Fig. 6C, E, F), while very few papillae are further found more proximally. Because of the overall structure and the stubby and ciliated (*vs* tapered) tip we consider this appendage as an ESO despite the presence of papillae.

Larochia miranda

BL 900 µm. The cephalic tentacles are short (L 230 µm, D 80 µm) and papillate. There are three pairs of epipodial appendages: the first and third are papillate epipodial tentacles (L 230 µm, D 50 µm), the second one lacks papillae and is most likely a pair of simple ESOs, although the sensory epithelium at the tip is not clearly visible.

Ventsia tricarinata (Figs 1D, 6G–L; see also Kunze, Heß & Haszprunar, 2016)

The body is almost completely retracted (D 1.15 mm), nevertheless the cephalic tentacles are quite long (L 600 µm, D 100 µm). Cephalic and epipodial tentacles have densely arranged sensory papillae, which are quite large. There is a single pair of long (L 300 µm, D 90 µm) epipodial tentacles and a single pair of simple ESOs (L 80 µm, D 100 µm) (Fig. 6G, J, K). The latter lies anterior to the epipodial tentacle and has a thick sensory epithelium with many cilia at the tip (Fig. 6I, L).

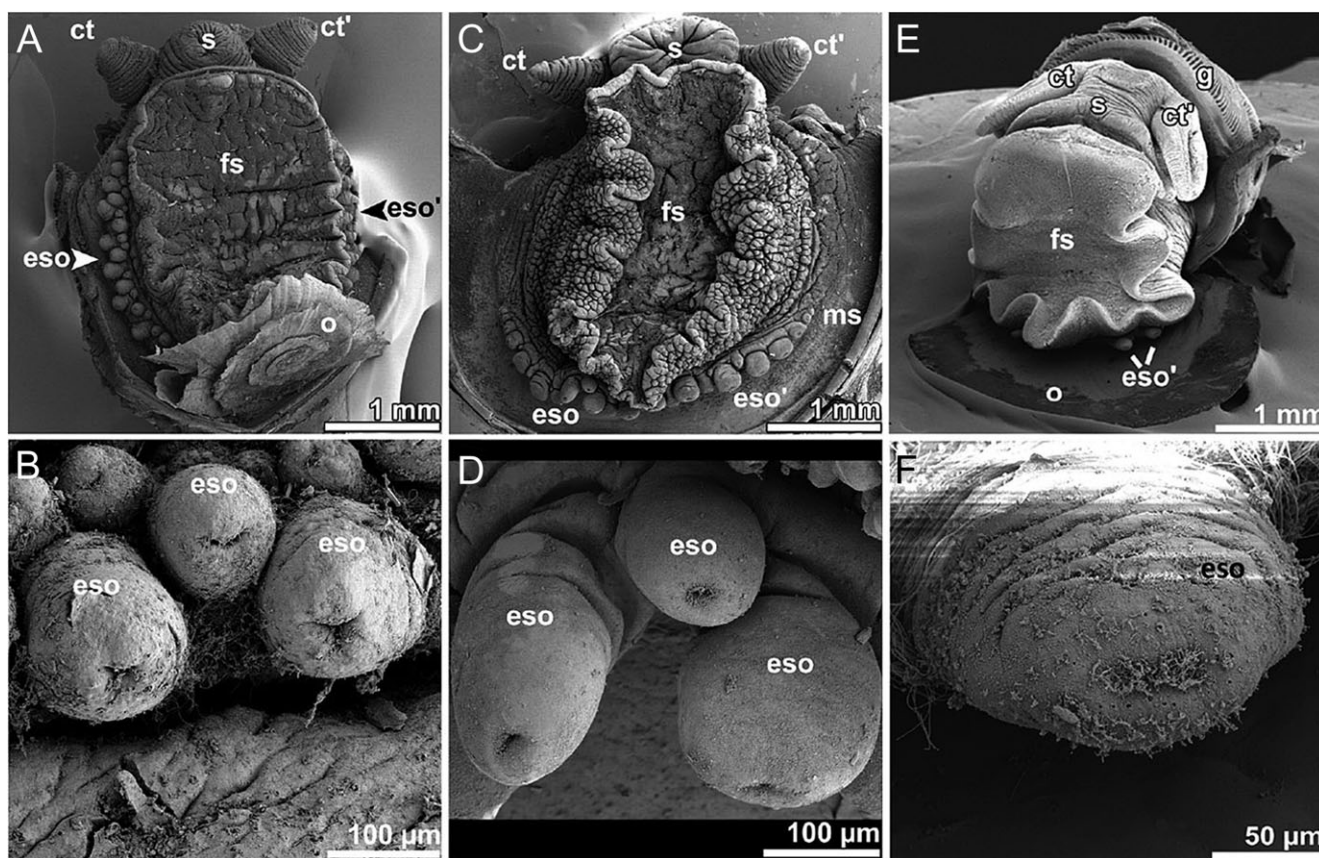


Figure 3. Tentacle conditions in Neomphalidae and Peltospiridae (Neomphalina). **A, B.** SEM images of *Peltoispira operculata*. **A.** Ventral view of body. **B.** ESO. **C, D.** SEM images of *P. smaragdina*. **C.** Ventral view of body. **D.** ESOS. **E, F.** SEM images of *Cyathiermia naticoides*. **E.** Ventral view of body. **F.** ESO. Abbreviations: ct/ct', right/left cephalic tentacle; eso/eso', right/left epipodial sense organ(s); f, foot; fs, foot sole; g, gill; ms, mantle skirt; o, operculum; s, snout.

Similar conditions (four pairs of papillate epipodial tentacles, one pair of nonpapillate ESOs) have been observed by SEM and histological sectioning for *Putilla porcellana* (TK, personal observation).

Skenea serpuloides (Fig. 1H; see also Rubio & Rolán, 2013; Haszprunar et al., 2016)

The body is completely retracted (D 670 µm). Cephalic (L 200 µm, D 70 µm) and epipodial tentacles show sensory papillae. There are three pairs of epipodial tentacles (L 90–140 µm, D 25–50 µm), the most anterior one situated in front of the operculum, the others behind the operculum. A short ESO (L 45 µm, D 45 µm), which lacks papillae and shows a thick, ciliated sensory epithelium at the tip, is attached to the base of the most anterior epipodial tentacle, i.e. a compound ESO.

We add here some SEM-data on a further skeneid, *Lissospira* sp., which shows four pairs of papillate epipodial tentacles and one pair of ESOs that are attached to the ventral base of the third epipodial tentacle.

LITERATURE REVIEW

In the following paragraphs, we collate and compare our findings with data on epipodial and cephalic appendages found in the literature. As will be outlined, epipodial conditions vary significantly among basal gastropod clades (Fig. 1; Supplementary Material Tables S1–8).

Patellogastropoda (Supplementary Material Table S1)

All Patellogastropoda show smooth cephalic tentacles (Künz & Haszprunar, 2001) and adults entirely lack epipodial appendages. However, Anderson (1965: fig. 8) figured a 10-d old, newly settled larva of the lottiid *Notoacmea petterdi* with a pair of small appendages slightly in front of the operculum (Fig. 1A). This structure is difficult to see when the body is transparent and thus was probably overlooked by Smith (1935), Dodd (1957), Kay & Emlet (2002), Kristof et al. (2016) and others, but has been confirmed by Wanninger et al. (1999: fig. 3D 'et') in postmetamorphic early juveniles of the patellid *Patella caerulea*. These paired appendages with ciliated tips show striking similarities in position and structure with the early juveniles of *Scissurella*, *Diodora* and *Haliotis* (see below) and thus we regard them as simple ESOs too.

Cocculiniformia (Supplementary Material Table S1)

Haszprunar (1988c) included the Lepetelloidea in Cocculiniformia, but the former are now reasonably considered to be a vetigastropod clade (e.g. Ponder & Lindberg, 1997; see below). Thus, Cocculiniformia currently comprise only Cocculinidae and Bathysciadiidae. Sensory papillae have never been reported in any tentacle of Cocculiniformia. Epipodial conditions similar to those reported herein for *Teuthirostria cancellata* (Fig. 2D) have been described using SEM, e.g. for *Cocculina rathbuni* by McLean & Harasewych (1995). Strong, Harasewych & Haszprunar (2003) have already homologized the cocculiniform epipodial appendages (see below) with ESOs rather than with the true epipodial tentacles of vetigastropods.

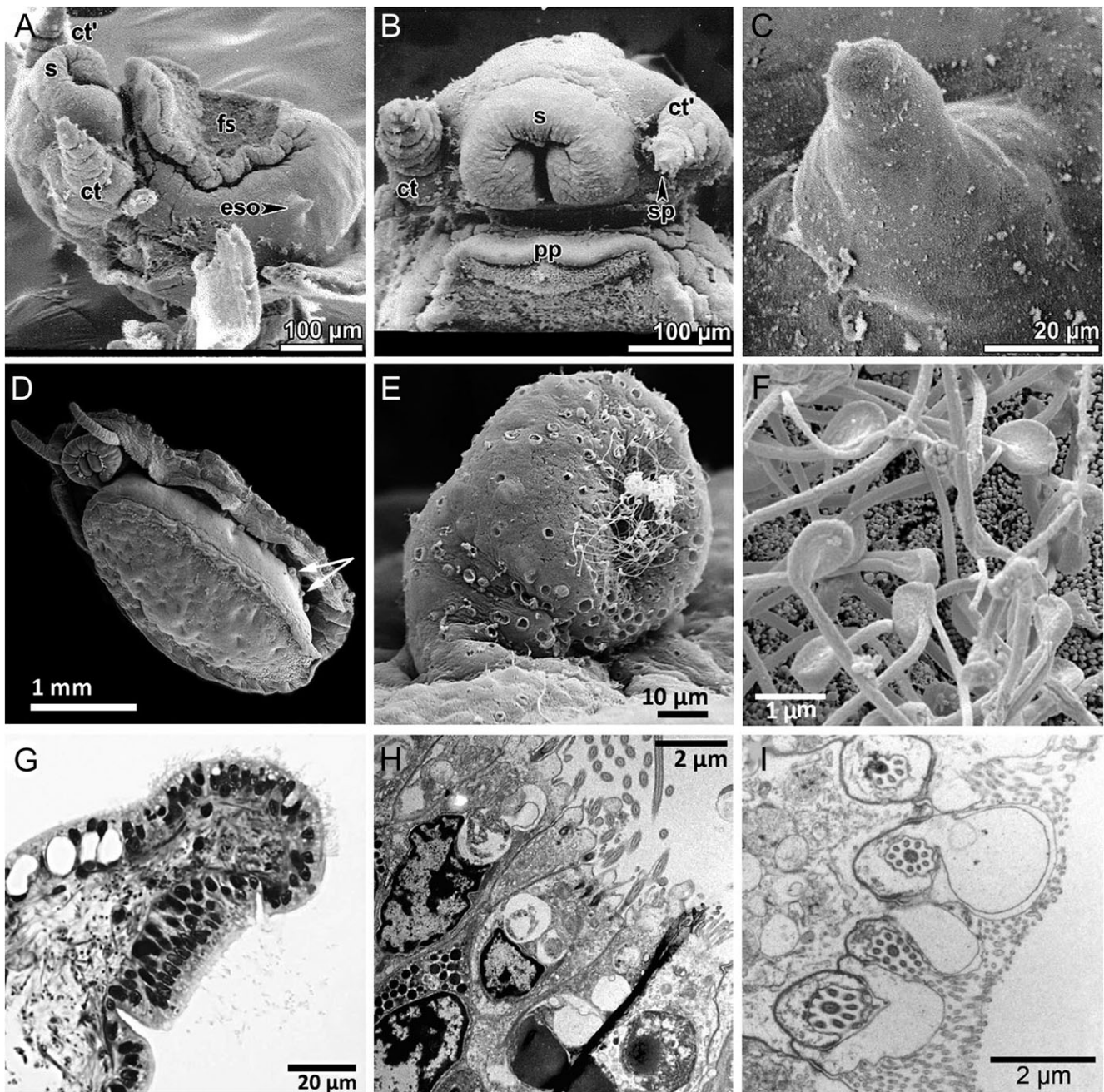


Figure 4. Tentacle conditions in brooding *Diodora* sp. (Vetigastropoda: Fissurellidae). **A–C.** SEM images of juvenile. **A.** Ventrolateral view from right side. **B.** Ventral view of head. **C.** ESO. **D–F.** SEM images of subadult. **D.** Whole body showing a row of ESOs in left subpallial cavity. **E.** ESO with ciliated depression. **F.** Paddle cilia (artifact) of sensory cilia of ESO. **G.** Longitudinal semithin section of ESO of subadult. **H.** TEM image of back side of ESO showing gland cells with electron-dense vacuoles and ciliated cells with large vacuoles. **I.** TEM photo of sensory epithelium (oblique plane) showing several collar receptors. Abbreviations: ct/ct', right/left cephalic tentacle; eso/eso', right/left epipodial sense organ; f, foot sole; pp, propodium; s, snout; sp, sensory papillae.

A single pair of simple ESOs at the posterior end of the epipodium have been positively reported for: *Cocculina craigmithi*, *Cocculina emsoni*, *Cocculina fenestrata*, *Cocculina messingi*, *Cocculina nipponica*, *Cocculina rathbuni*, *Cococrater portoricensis*, *Fedikovella beanii*, *Fedikovella caymanensis*, *Macleaniella moskalevi* and *Teuthirostria cancellata* (Marshall, 1986; Haszprunar, 1987; McLean, 1992b; McLean & Harasewych, 1995; Sasaki, 1998; Leal & Harasewych, 1999; Strong & Harasewych, 1999; Ardila & Harasewych, 2005; Fig. 1A). In contrast, several authors have confirmed the absence of epipodial appendages in the cocculinid genus *Coccopigyra* (Marshall, 1986; Haszprunar, 1987; Dantart & Luque, 1994b; McLean & Harasewych, 1995; Strong *et al.*, 2003).

Thiele (1908) did not mention any epipodial tentacles for *Bathypelta pacifica*. Hartmann, Heß & Haszprunar (2011: 263) positively confirmed this lack for several representatives of *Bathysciadium* and *Bathyaltum*, but “*Bathypelta pacifica* alone shows an epipodial ridge, which surrounds the posterior half of the body, and a pair of prominent epipodial lappets [simple ESOs] near the posterior end of the animal”.

According to the phylogeny of Cocculiniformia provided by Strong *et al.* (2003), the loss of ESOs occurred most likely independently in *Coccopigyra* and within the Bathysciadiidae.

In conclusion, we re-diagnose the Cocculiniformia as follows: cephalic tentacles never with sensory papillae; no epipodial

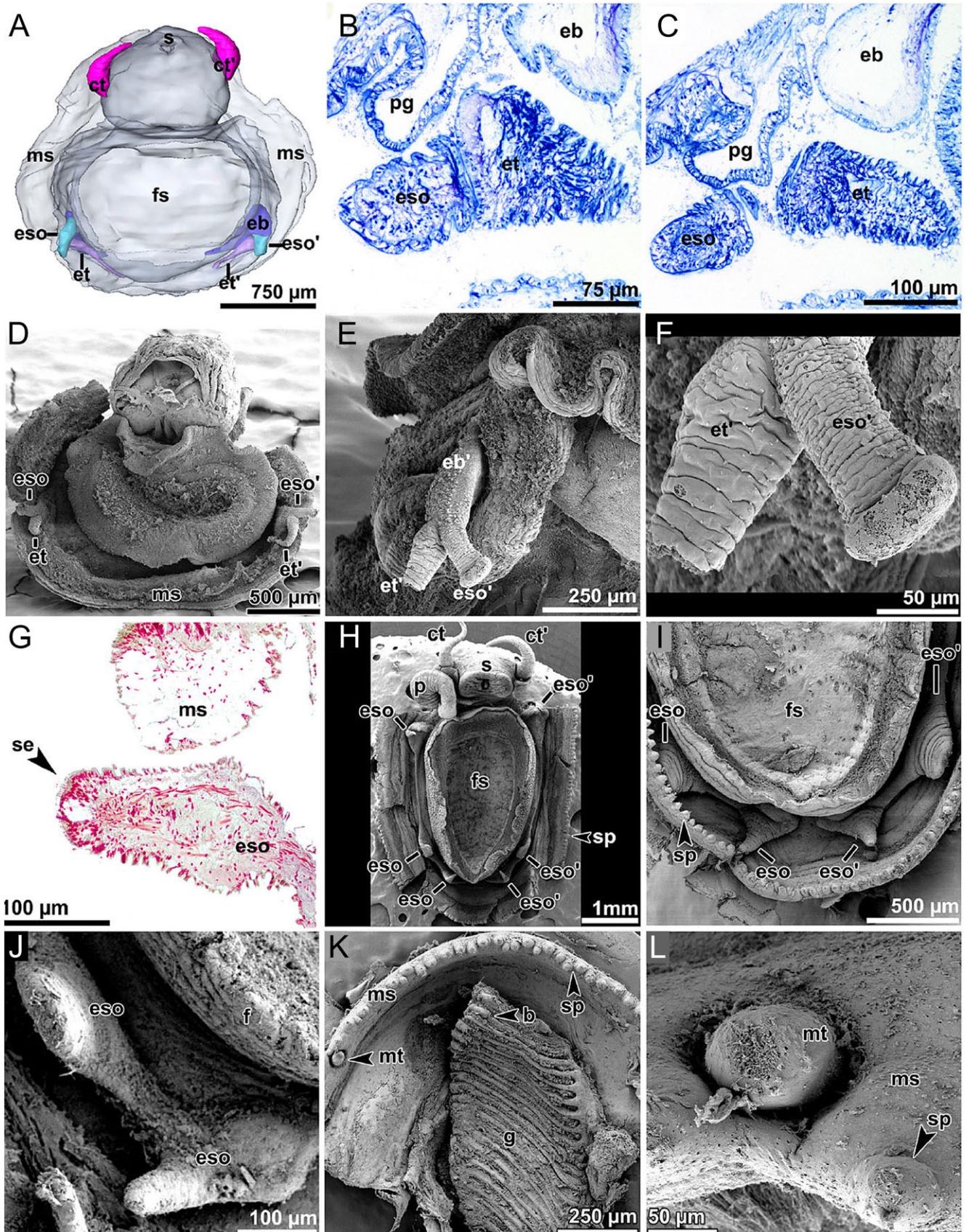


Figure 5. A–F. Tentacle conditions in *Kaiaparapelta* (Vetigastropoda: Lepetelloidea). **A.** 3D reconstruction of *Kaiaparapelta* sp. 1, ventral view, body transparent. **B., C.** Sequential histological sections of the right ESO and tentacle. **D–F.** SEM images of *Kaiaparapelta* sp. 2. **D.** Ventral view. **E., F.** Epipodium with two different tentacles. **G–L.** Tentacle conditions in *Lepetodrilus* aff. *pustulosus* (Vetigastropoda: Lepetodriiloidea). **G.** Longitudinal histological section of

tentacles; if ESOs present (Cocculinidae except *Coccolpiga*; *B. pacifica*) then a single pair, posteriorly placed, of simple type.

Neritimorpha (Supplementary Material Table S1)

Neritimorph gastropods have smooth cephalic tentacles. However, TEM studies have revealed that the ciliated tufts of these tentacles show remarkable similarities with the papillae of Vetigastropoda (see below) in that the distal portions of the sensory cells envelope each other (Künz & Haszprunar, 2001).

Nearly all neritimorphs entirely lack epipodial appendages. The only notable exceptions are the genera *Shinkailepas* and *Olgasolaris*, both inhabiting hydrothermal vents. In both genera several (14 to 30) ‘epipodial papillae’ occur in a posterior position (Beck, 1992b: pl. 4: fig. 4, pl. 5: fig. 3; Sasaki, Okutani & Fujikura, 2006: fig. 2). Histological and SEM photos of these papillae were provided by Sasaki *et al.* (2006: figs 3C, 4C) and suggest an interpretation as simple ESOs, although this needs confirmation by TEM studies.

Among the detailed studies on neritid ontogeny, only that by Page & Ferguson (2013: fig. 6F) has mentioned the existence of one pair of posteriorly situated ‘epipodial bulges’ in a late larva of *Nerita melanotragus*, being more a fold than a tentacular structure. Accordingly, the interpretation of this structure remains equivocal and requires more detailed studies.

Neomphalina (Supplementary Material Table S1)

Neomphalina are currently considered as a major clade of rhipidoglossate gastropods distinct from the Vetigastropoda (e.g. Sasaki, 1998; Heß *et al.*, 2008; Aktipis & Giribet, 2012; Kano & Warén, 2013).

The absence of sensory papillae on the tentacles has been reported for all families of the Neomphalina (Haszprunar, 1989; Ponder & Lindberg, 1997; Sasaki, 1998; Warén & Bouchet, 2001; Heß *et al.*, 2008). Up to now all authors have described ‘epipodial tentacles’, but their structure with concave ciliated depression at the tip (Fig. 3D, F) suggests identity with simple ESOs, although TEM data are needed to confirm the presence of collar receptors.

ESO of Neomphalina vary even with individuals: they may differ in size as in *Lirapex humata*, in the numbers on either side as in *Neomphalus fretterae*, are irregularly shaped in *Peltoispira smaragdina*, or may decrease in size from posterior to anterior as e.g. in *P. smaragdina* (Fretter, 1989; Warén & Bouchet, 1989, 2001; Fig. 3C, D).

Among Melanodrymiidae the number of ESOs is generally low: *Leptogyra* and *Leptogyropsis* species have two pairs (Marshall, 1988b; Heß *et al.*, 2008), while *Melanodrymia aurantiaca* bears four to five quite short pairs (Haszprunar, 1989; Warén & Bouchet, 2001). A single pair of ESOs was described and depicted in the small (2.6 mm) *Retiskenea cf. diploura* by Warén & Bouchet (2001: fig. 25). The inclusion of *Retiskenea* within Neomphalina can be confirmed by preliminary studies of a series of sections of *R. diploura* from the Japan Trench (GH, personal observation).

Nearly all Peltospiridae have many (up to 100) ESOs around the epipodium, often densely packed and mostly stubby (Figs 1C, 3A). The only exception is the ‘scaly foot gastropod’, *Chrysomallon squamiferum*, where the whole epipodium is covered by large scales of iron sulphide (pyrite) and is thus devoid of any tentacles, without doubt a secondary, highly derived condition (Chen *et al.*, 2015a, b). The number of ESOs in the Peltospiridae ranges from few pairs to more than 100 in *Echinopelta fistulosa* (Fretter, 1989), but there is no clear correlation with the size of the animals.

In general, the number of ESOs in Neomphalina is lower than in the Peltospiridae, but this fact may be correlated with the smaller size of most of the species: four pairs in *Cyathermia naticoides* and in *Solutigra reticulata*; six pairs in *Lacunoides exquisitus*; five to six pairs in *L. vitreus*; six to 11 ESOs along the right and five to six along the left side in *N. fretterae*; some more in *Symmetromphalus regularis*; about ten pairs in *S. hageni* (McLean, 1981, 1990; Warén & Bouchet, 1989; Beck, 1992a; Warén & Bouchet, 2001: fig. 3E, F; Goffredi, 2010: fig. 2B–D).

In conclusion, we redefine the conditions of Neomphalina as follows: cephalic tentacles without sensory papillae; no true epipodial tentacles; from one pair up to more than 100 ESOs; simple type.

Vetigastropoda: Pleurotomarioidea

All recent molecular phylogenies place Pleurotomariidae as the earliest vetigastropod offshoot (Harasewych, 2002; Williams, Karube & Ozawa, 2008; Aktipis & Giribet, 2010, 2012; Zapata *et al.*, 2014). Indeed, aside from a highly specialized (hystriochoglossate) radula type, the external features of Pleurotomariidae are also quite exceptional among the Vetigastropoda: nearly all authors have reported the entire absence of distinct epipodial appendages and their cephalic tentacles are devoid of sensory papillae (Dall, 1889; Woodward, 1901; Fretter, 1964, 1966; Tan, 1974). However, there are papillae on the pleurotomariid mantle skirt (Fretter, 1964, 1966; Harasewych & Askew, 1993). Due to the entire lack of data concerning early juvenile pleurotomariids it is not possible to exclude the possibility that papillae on the cephalic tentacles do occur during development, as in Fissurellidae (see below).

Whereas most authors have claimed an epipodial fold (e.g. Voltzow, Morris & Linsley, 2004), Sasaki (1998: fig. 27C) observed a row of knob-like structures located at the ventral margin of the epipodial flaps of *Mikadotrochus beyrichii* and considered them ‘presumably’ as ESOs. However, he coded both epipodial tentacles and ESOs as present in Pleurotomariidae in his phylogenetic analysis. In contrast, we think that the tentacle structure suggests an ESO, so Pleurotomariidae might have several simple ESOs, but no true epipodial tentacles. Needless to say, detailed histological or preferably TEM studies are necessary to clarify the matter.

Vetigastropoda: Lepetelloidea (Supplementary Material Table S2)

Formerly classified as Cocculiniformia, all recent authors agree upon the vetigastropod nature of Lepetelloidea. The superfamily traditionally consists of eight to ten families, the majority of which comprise only one to four genera (Haszprunar, 1998; Bouchet *et al.*, 2005). In contrast, Lepetellidae, Pseudococculinidae and Caymanabyssiidae (sensu Kano *et al.*, 2016) include several genera. However, recent preliminary molecular data (Kano *et al.*, 2013, 2016) suggest fewer primary clades. Sensory papillae on cephalic tentacles and mantle margin are regularly found in the Pseudococculinidae and Caymanabyssiidae, often also in Lepetellidae and occasionally also in adults (no data on juveniles) of all other nominal families (Supplementary Material Table S2). Usually epipodial appendages (if present) lack papillae and their histology suggests that they are in fact simple ESOs. The highly specialized genera *Addisonia* and *Cocculinella* entirely lack epipodial appendages, while within other families the presence and number of epipodial appendages is variable (Supplementary Material Table S2).

anterior right ESO. **H–L.** SEM images. **H.** Ventral view of soft body. **I.** Ventral view of posterior body with mantle skirt and ESOs. **J.** Right posterior ESOs. **K.** Ventral view of mantle skirt with gill; rest of body removed. **L.** Mantle skirt with tentacle and sensory papillae. Abbreviations: b, bursicle; ct/ct’, right/left cephalic tentacle; eb/eb’, right/left body of epipodial tentacles; eso/eso’, right/left epipodial sense organ; et/et’, right/left epipodial tentacle; fs, foot sole; g, gill; ms, mantle skirt; mt, mantle tentacle; p, penis; pg/pg’, right/left pedal gland; s, snout; se, sensory epithelium.

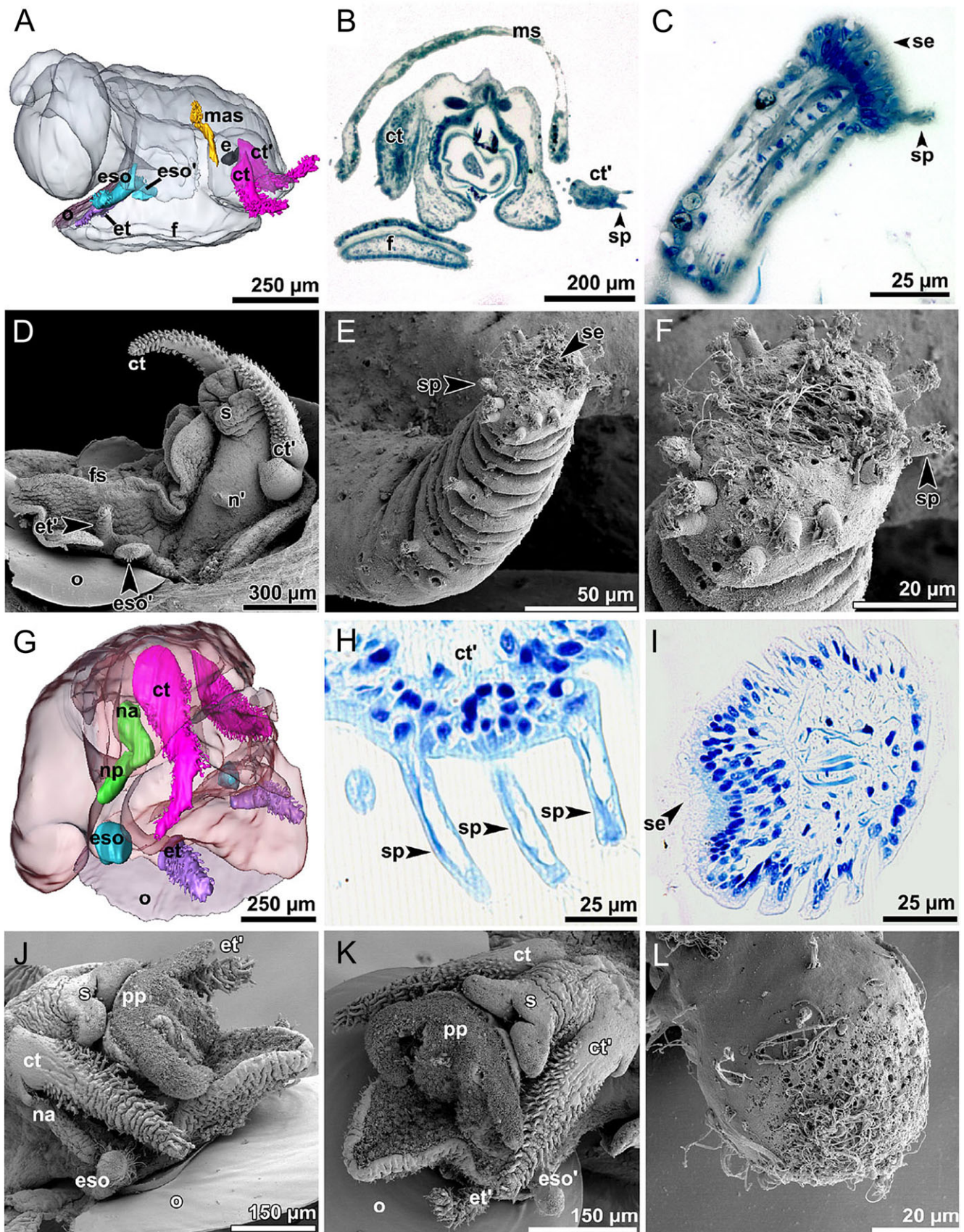


Figure 6. A–F. Tentacle conditions in *Scissurella* (*Vetigastropoda*: Scissurelloidea). **A.** 3D reconstructions of *Scissurella jucunda*, view from right, body transparent. **B, C.** Histological sections of *S. jucunda*. **B.** Cross section of head region. **C.** Longitudinal section of ESO. **D–F.** SEM images of *Scissurella* sp. **D.** Left lateral view of body. **E.** ESO. **F.** Tip of ESO. **G–L.** Tentacle conditions in *Ventsia tricarinata* (*Vetigastropoda*: Seguenzioidea). **G.** 3D reconstruction,

The helicoid Choristellidae [note: *Choristella* Bush, 1897, not *Choristella* Tillyard, 1917 = *Microcarista* Byers, 1974 (Insecta: Mecoptera)] are devoid of papillae and show several epipodial appendages. Detailed histological data on well preserved specimens are still lacking, so that it remains to be established whether these are epipodial tentacles or ESOs.

Within the Lepetellidae an unpaired median epipodial appendage at the posterior end of the epipodium has been reported in several *Lepetella* species. Histological examination of this 'epipodial appendage' has revealed absence of a specific innervation and a lack of a distal sensory epithelium. Accordingly, we do not consider this structure to be an ESO. However, other lepetellid species do have a single pair of ESOs or lack them entirely (Judge & Haszprunar, 2014: Table 1; Supplementary Material Table S2).

As recently outlined by Kano *et al.* (2016), a number of pseudococculinid and caymanabyssiid genera (*Bandabyssia*, *Caymanabyssia*, *Copulabyssia*, *Notocrater*, *Pseudococculina*) show a posteriorly situated pair of bifid epipodial appendages (Supplementary Material Table S2). SEM images of several genera and species enable a clear determination of the outer (ventral) ESO part and an inner (more dorsal), papillate epipodial tentacle. We have confirmed these conditions by histological examination of paratypes of *Bandabyssia costococoncentrica* (GH, personal observation).

Such bifid epipodial appendages are also present in *Kaiparapelta* species (Figs 1F, 4; Supplementary Material Table S2), a genus with strongly modified radula and anatomy (Haszprunar *et al.*, 2014). Again the outer branch is doubtless an ESO (lack of papillae, stout tip, distal thick sensory epithelium), whereas the inner branch is a true epipodial tentacle (papillate, tapered tip) as in the genera mentioned above. Both branches are set on a common base, which is more or less elongate.

Warén & Bouchet (2009: fig. 5F) depicted the epipodial conditions of the pseudococculinid-like *Tentaoculus granulatus* by SEM and confirmed the presence of a ciliated tuft at the ventral basis of an epipodial tentacle (i.e. suggesting a compound ESO), but again TEM data are needed to confirm collar receptors. A single, simple pair of posterior ESOs has also been described for several genera with a pseudococculinid-like radula (Supplementary Material Table S2: *Colobrachelus*, *Kurilabyssia*, *Mesopelex*, *Punctabyssia*, *Tentaoculus*, *Yaquinabyssia*). Whereas a bifid condition as described above can be reasonably excluded, the nature of this single pair of epipodial appendages as an epipodial tentacle or a compound ESO or a simple ESO tentacle remains obscure and requires further studies. This is also the case for the genus *Amphiplica*, although this was excluded by Kano *et al.* (2013, 2016) from Pseudococculinidae based on molecular data. Kano *et al.* (2013) also placed *Mesopelex*, *Punctabyssia*, *Kurilabyssia*, *Tentaoculus* and *Yaquinabyssia* outside the pseudococculinid/caymanabyssiid clade (the latter includes *Kaiparapelta*: all have a bifid epipodium). Accordingly, the bifid epipodial condition (e.g. figured by Warén, 2011: fig. 499A) appears as a good character to separate the latter clade from all other limpets with a retained (plesiomorphic) pseudococculinid-like radula (Kano *et al.*, 2016). We also recommend reevaluation of those species among these 'bifid' genera in which only a single pair of epipodial appendages has been reported (Supplementary Material Table S2).

A single pair of posteriorly placed ESOs is present in *Bathypheophilus*, *Osteopelta* and *Pyropelta* (GH, pers. obs.) and in the helicoid *Helicopelta* (this needs further study to be confirmed as an ESO). We doubt the original classification of *Helicopelta* among Addisoniidae, because the protoconch of *Helicopelta* is very different from that of *Addisonia* (Roldán & Luque, 1999, 2010); the latter was not yet

known when Marshall (1996) provided the first description. Indeed, molecular data place *Helicopelta* as sister taxon to all other Lepetelloidea or even outside the Lepetelloidea (Kano *et al.*, 2013, 2016).

Vetigastropoda: Fissurelloidea

We follow the phylogenies of Aktipis, Boehm & Giribet (2011) and Aktipis & Giribet (2012) and exclude Clypeosectidae (classified among Lepetodrilioidea, see below). Sensory papillae are lacking in all adults of the Fissurelloidea. However, as already shown by Boutan (1885: pl. 42, figs 1, 3) the cephalic tentacles of juvenile *Diodora* may have few sensory papillae at the tip (Fig. 4A, B).

Our results (Fig. 4H, I) revealed striking similarity with trochid ESOs (Crisp, 1981; Herbert, 1984): short appendage with stout tip, thick sensory and ciliated epithelium, and in particular the presence of densely arranged collar receptors. Accordingly, all 'epipodial tentacles' described for Fissurellidae are in fact simple ESOs (as already recognized by Brusca, Lindberg & Ponder, 2016: 462, fig. 13.5). Thus, the numerous ESOs in most Fissurellidae show a similar condition to that in Neomphalina (and possibly also in Pleurotomariidae, see above), being arranged in a more or less horseshoe-shaped formation around the foot (Fig. 1C). However, the sensory epithelium of the ESO is situated on the ventral side of each tentacle, not at the tip (e.g. Thiele, 1892: pl. 23: fig. 5; Fig. 4E, G). The number of ESOs ranges from a single pair up to 40 pairs in large representatives. ESOs may be all of equal size, or smaller and larger ones may alternate. Warén & Bouchet (2009: fig. 6H, I) depicted the ESO of *Puncturella similis* by SEM and confirmed the presence of a ciliated tip.

Both the juvenile *Diodora* of the present study and the juvenile described by Boutan (1885) have only a single pair of ESOs (Fig. 1B) and development starts with the most posterior one. The same condition is retained in a juvenile (1 mm) specimen of the very small (max. 2.6 mm) *Manganesepelta hessleri*, whereas *Cornisepta* species (max. 7 mm) bear two pairs of posteriorly placed ESOs (McLean & Geiger, 1998: 19, figs 11C, 12E, 14D). The small (max. 5 mm) *Profundisepta profundis* shows three pairs of ESOs, of which the most posterior is by far the largest (McLean & Geiger, 1998: 7, fig. 3E). This is similar to *Clathrosepta depressa* (13.1 mm) and *C. becki* (about 9 mm), which again have three pairs of ESOs, but of which only the most anterior one is small (McLean & Geiger, 1998: 12, fig. 6D, 7B).

Certain genera (*Manganesepelta*, *Clathrosepta*, *Fissurisepta*) additionally show a single, very slender, posterior 'foot-tentacle' of unknown histology and homology (McLean & Geiger, 1998: fig. 6D, E, 7B) similar to the condition in certain *Lepetella* species (see above). We agree with McLean & Geiger (1998) that this is probably an apomorphic character within Fissurellidae suggesting close relationship between these genera.

Vetigastropoda: Lepetodrilioidea (Supplementary Material Table S3)

We follow recent molecular studies (Kano, 2008; Aktipis & Giribet, 2010, 2012) and include here (1) the Lepetodrilidae with genera *Lepetodrilus*, *Gorgoleptis*, *Clypeosectus* and *Pseudorimula* (the latter two were formerly placed in Clypeosectidae within Fissurelloidea) and (2) the Sutlizionidae with the genera *Tennocinclis*, *Temozaga* and *Sutliziona* (formerly Scissurelloidea).

A lack of sensory papillae in all tentacles of Lepetodrilioidea has been described for all species that have been investigated in detail (Haszprunar, 1989; McLean, 1989; Sasaki, 1998; Geiger, 2012). In contrast, Ponder & Lindberg (1997) coded papillae as present

right lateral view, body transparent. **H, I.** Histological sections. **H.** Longitudinal section of anterior part of left cephalic tentacle. **I.** Cross section of left ESO. **J-L.** SEM images. **J.** Laterofrontal view from right side. **K.** Laterofrontal view from left side. **L.** Left ESO. Abbreviations: ct/ct', right/left cephalic tentacle; e/e', right/left eye; eso/eso', right/left epipodial sense organ; et/et', right/left epipodial tentacle; f, foot; fs, foot sole; mas, mantle slit; ms, mantle skirt; n', left neck lobe; na/np, anterior/posterior neck lobe; o, operculum; pp, propodium; s, snout; se, ciliated sensory epithelium; sp, sensory papillae.

in this superfamily, because Fretter (1988: fig. 26) described and figured a special kind of retractable ciliated tuft, which might represent a somewhat reduced (or heavily contracted, or both) papilla. The latter view is supported by the fact that the mantle margin of *Lepetodrilus* aff. *pustulosus* shows sensory papillae very similar to those of certain pseudococculinid limpets and thus probably of the vetigastropod type (Fig. 5L), confirming observations on *Lepetodrilus nux* by Sasaki (1998: fig. 65A). Studies on early juveniles and final confirmation by TEM (sensory cells enveloping each other; see Künz & Haszprunar, 2001) are still required, however.

According to McLean (1985a, 1988a, 1993), Fretter (1988) and Beck (1993), *Lepetodrilus* species are characterized by three blunt epipodial appendages (ESOs), one at the anterior end of the epipodium and two posterior ones, and we confirm this for *L. aff. pustulosus* (Fig. 5H–J). Also, Sasaki (1998) reported three pairs of ESOs in *L. nux*. In contrast, *Lepetodrilus shannonae* has only a single pair of posteriorly placed ESOs with additional lateral tentacles (Warén & Bouchet, 2009: fig. 6B, 7G).

There are five pairs of epipodial appendages in *Gorgoleptis* (McLean, 1985b, 1988a; Fretter, 1988: figs 16, 18—line drawings; Warén, Bouchet & Cosel, 2006: 86—photo): four of them are very long and slender, but the third one is thick and truncated. In *G. emarginatus* Fretter (1988: 59) described the conditions as follows: “Near the base of the first two appendages on the left and the first on the right there is a sense organ appearing as a hemispherical boss”. If this is correct, there would be three types in a single specimen, a simple ESO (appendage 3), pure epipodial tentacles (appendages 4 and 5) and compound ESOs (appendages 1 and 2). After examination of a specimen of the same species (AW, personal observation), the ESO on appendage 1 can be confirmed. However, it was not possible to discover whether the other tentacles also contain ESOs or are modified ESOs. Confirmation of this presumably unique condition at least by histology or preferably by TEM is badly needed.

Clypeosectus curvus and *C. delectus* have one anterior and two posterior, simple ESOs with the sensory epithelium located ventrally in the anterior ones, but at the tips in the posterior ones (McLean, 1989; Haszprunar, 1989). *Pseudorimula* shows the same condition, but the number of ESOs varies between species: two to four pairs in *P. marianae* (Haszprunar, 1989; McLean, 1989) and one to two pairs in *P. midatlantica* (McLean, 1992a).

Both *Lepetodrilus* and *Pseudorimula* develop a single pair of simple ESOs shortly after metamorphosis, followed by the other posterior epipodial appendages (AW, personal observation).

In both *Sutilizona* species that have been studied, *S. theca* and *S. pterodon*, a single pair of posteriorly placed, simple ESOs is present (Haszprunar, 1989; McLean, 1989; Warén & Bouchet, 2001; Geiger, 2012: fig. 1021C). *Temnocinclis euripes* has three differently shaped tentacles on the epipodium, but only the middle one is a simple ESO, while in *Temnozaga parilis* each of the three uniform appendages appears to be a simple ESO (McLean, 1989; Haszprunar, 1989; Marshall, 1993).

Vetigastropoda: Haliotoidea (Supplementary Material Table S4)

The superfamily Haliotoidea comprises only one family, with a single genus *Haliotis* including between 6 and 17 subgenera (Bouchet, 2011). The cephalic and mantle tentacles of *Haliotis*, and the very many and variable epipodial tentacles, are densely covered by sensory papillae and their fine structure has been repeatedly studied by TEM (Künz & Haszprunar, 2001; Li *et al.*, 2006; Molist, Nogal & Collado, 2016). As noted by Crofts (1929: 125), “the epipodium is more elaborate in *Haliotis* than in any mollusc”. Indeed, in addition to the papillate true epipodial tentacles, a second, apomorphic type of epipodial tentacle is found, which is short and dendritic as figured for instance in *H. diversicolor* by Na *et al.* (2006: pl. 1, figs 3, 7).

The compound ESOs of Haliotidae were first described and figured by Crofts (1929: 128) in *H. tuberculata* and termed ‘subtentacular sense organs’, positioned at the ventral base of the long and papillate epipodial tentacles. This agrees with the description provided by Sasaki (1998: 51) in *H. diversicolor* as follows: “Epipodial sense organs present only at bases of long tentacles, taking form of simple ciliated tufts”. Although Wanichanon *et al.* (2004) and Molist *et al.* (2016) did not mention any ESO in their specialized work about the epipodial tentacles of *H. asimina* and in *H. tuberculata* respectively, it is likely that such combined ESOs occur in all *Haliotis* species.

According to Crofts (1937) and Ino (1952), the epipodial tentacles develop from posterior to anterior. Several authors have reported a single pair of nonpapillate epipodial appendages with stout ciliated tips in the postmetamorphic early juveniles of *Haliotis* species (Fig. 1B; Supplementary Material Table S4), which very clearly can be identified as ESOs. It is interesting to note that a slightly older (28 d postsettlement) stage in *H. australis* still shows a separated ESO (nonpapillate, stout tip, smaller) in a lateral position between the second and third true (papillate, tapered) epipodial tentacle (Maxwell, 2015: fig. 29).

Vetigastropoda: Scissurelloidea (Supplementary Material Table S5)

We follow the systematic arrangement proposed by Geiger (2012), who accepted four families (Scissurellidae, Anatomidae, Larocheidae, Depressizonidae). Temnocinclinae and Sutilizoninae, formerly included in the Scissurelloidea because of their shell-slit (Haszprunar, 1989; McLean, 1989), are currently considered as the lepetodriloid family Sutilizonidae (Warén & Bouchet, 2001; Bouchet *et al.*, 2005; Geiger, 2012) and are thus reviewed above.

Recently, epipodial conditions in Scissurellidae and Anatomidae have been reviewed by Vafiadis & Hales (2015). Sensory papillae have been reported for cephalic and epipodial tentacles, and occasionally also for tentacles at the edge of the mantle slit, in both families.

Anatomidae generally have one pair of smooth suboptical (often called ‘subocular’) tentacles and three or four papillate epipodial tentacles, but only a single pair of ESOs, which is situated posterior to the first (of three pairs) or second (of four pairs) epipodial tentacles. Only Fretter & Graham (1976: 3) have reported two pairs of suboptic tentacles in *Anatoma crispata*; unfortunately this abnormal condition was not depicted.

Due to poor preservation of the specimens under study, the epipodial conditions in the Larocheidae (genera *Larochea* and *Trogloncha*) have still not been fully confirmed. As in most other vetigastropods, there is only one (smooth) suboptic tentacle on the right side. There are two pairs of papillate epipodial tentacles with a simple nonpapillate ESO posterior to the first pair. Better preserved specimens are badly needed to confirm this tentative diagnosis.

Concerning the Scissurellidae, the number of epipodial tentacles varies from one to three, but a clear correlation with size cannot be found. Most authors have reported paired (smooth) suboptic tentacles and a single pair of ESOs. *Scissurella costata* appears to be more variable, since Jeffreys (1865) depicted two pairs of suboptical tentacles and Vayssi re (1894) described two pairs of ESOs. All reports based on histology or SEM (for the genera *Incisura*, *Scissurella* and *Sinezona*) agree that the distal part of the ESOs also bear sensory papillae, though these are significantly fewer than on the other appendages (Fig. 1G). Although confirmation by TEM is still missing, the overall condition (shorter, stout tentacles with thick and ciliated epithelium at tip; Fig. 6A–C) strongly suggests a true ESO. Indeed, ‘ESOs with papillate tips’ appear to be a diagnostic character for Scissurellidae *sensu stricto* (Supplementary Material Table S5). Often the ESO shares a common base with the first epipodial tentacle, resulting in a condition similar to the compound type, but the ESO tentacle is typically much longer than in those.

Only two species of *Depressizona* are known and unfortunately soft bodies have not yet been collected.

Bathyxiphila excelsa was originally described as a skeneimorph species, but was transferred (but with weak support) to a position close to Anatomidae based on molecular data (Kano, 2008; Aktipis & Giribet, 2012) and thus probably represents another slit-less scissurelloid clade. Marshall (1988b) did not comment on papillae or ESOs for *B. excelsa*, *Bathyxiphila pusilla* or *Bathyxiphila iota*. Kunze *et al.* (2008) showed that *B. excelsa* has papillate cephalic and epipodial tentacles (a single pair); the stubby ‘anterior epipodial tentacle’ might be an ESO, but cannot be confirmed as such due to the poor conservation of the (frozen) specimen.

‘Trochacean’ Vetigastropoda

Epipodial conditions in those vetigastropods formerly united as ‘Trochacea’ by Thiele (1924, 1929) and Hickman & McLean (1990) vary considerably, and are in many taxa far from being understood. There is an increasing tendency to correlate the development of ESOs with the development of epipodial tentacles, but there are numerous exceptions to this rule. Thus, we present original data as far as possible in tabular format.

Vetigastropoda: Seguenzioidea (Supplementary Material Table S6)

We follow recent molecular studies (Kano, 2008; Kano, Chikyu & Warén, 2009; Aktipis & Giribet, 2010, 2012; Uribe *et al.*, 2016) in extending the content of this vetigastropod clade to include the families Calliotropidae, Cataegidae, Chilodontidae, Seguenziidae and more than 20 (mostly ‘skeneimorph’, i.e. small and probably progenetic) genera unassigned to a family (Gofas, 2011; Bouchet & Gofas, 2012; Supplementary Material Table S6).

The conditions of the epipodial appendages in the Calliotropidae are variable: Hickman & McLean (1990: 83–85, figs 45, 46) described and figured prominent epipodial tentacles in *Calliotropis* and *Bathybembix*, and a series of small, nonpapillate knobs in *Cidarina*; the latter may be interpreted as ESOs.

McLean & Quinn (1987) described small epipodial tentacles in *Cataegis* and Hickman & McLean (1990: 137) noted “the lack of specialization in epipodial characters”. Warén & Bouchet (1993: 19) described and depicted that “the crest of the [epipodial] ridge bears irregularly shaped and strongly contracted, wart-like tentacles”, which may be interpreted as ESOs. In the recently described *Kanoia myronfeinbergi*, Warén & Rouse (2016: 62) described and depicted by SEM “each side [of epipodium] with at least a dozen epipodial tentacles, each with a dorsal-basal epipodial sense organ”, a unique condition among vetigastropods.

In the Chilodontidae, Hickman & McLean (1990: 77–79) did not mention ESO conditions, but Herbert (2012: 394) reported that “Free-standing, mushroom-like epipodial sense organs such as occur in many trochiodean genera are not evident, even beneath neck lobes, but most of the larger epipodial tentacles have a basal swelling on the ventral side which probably represents an epipodial sense organ. Similar swellings are sometimes evident at the base of the larger neck lobe tentacles and *Damilia* possesses several distinct sense organs on the underside of its neck lobes”. Herbert (2012) also described the larger epipodial tentacles of several species (Supplementary Material Table S6) each with a basal ESO. Unfortunately, the only SEM photo of a chilodontid up to now, i.e. *Granata lyrata* by Kano (2008: 13, fig. 4A,B) does not show the ESOs. Duch (1969: fig. 2) depicted two pairs of very small, nonpapillate tentacles behind the large cephalic tentacles in a late veliger of the chilodontid *Euchelus gemmatus*, but the nature of these appendages remains obscure.

Seguenziidae have several papillate epipodial tentacles (Knudsen, 1964; Quinn, 1983; Marshall, 1988a; GH, personal observation), but up to now ESOs have not been unequivocally detected. Marshall (1988a: 246) reported for *Sericogyra perigenes*: “Left side

with a tight cluster of 10 epipodial tentacles, 3 larger, ciliated tentacles below them. Two large, tapered, ciliated epipodial tentacles set low on right side, another at end of thin opercular lobe,” and these ciliated tentacles can be reasonably interpreted as ESOs. Contrary to earlier statements (Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988c, 1993), a reinvestigation of histological section series of *Carenzia carinata* revealed several epipodial tentacles, but only a single pair of simple ESOs. The same is true for *Seguenzia* aff. *mirabilis* from the abyssal plain of the Kurile-Kamchatka Trench (GH, pers. obs.). Additional investigations on other genera are badly needed to confirm the latter condition as a general pattern in Seguenziidae.

All in all, the epipodial conditions in Seguenzioidea are quite diverse and the descriptions available are mostly insufficient or confusing (Supplementary Material Table S6), but the ESO is always represented by a single pair of short and knob-like tentacles, not combined with any other tentacular structure and devoid of sensory papillae (e.g. *Ventsia*: Figs 1D, 6G–L).

Vetigastropoda: Angarioidea

Formerly classified within Trochidae or Turbinidae, molecular data have clearly shown that Angariidae together with Areneidae [Note: formally established by McLean (2012), but used before, e.g. by Williams *et al.* (2008). The same name, Areneidae, has often been cited for a spider family, but is a misspelling of Araneidae Clerck, 1757, an available taxon though published prior to Linnaeus’ *Systema Naturae*; cf. ICZN (1999): Art. 3.1] form a separate clade of Vetigastropoda (e.g. Williams & Ozawa, 2006; Williams *et al.*, 2008, 2010; Williams, 2012; Uribe *et al.*, 2016).

Data on the epipodial conditions of Angarioidea are very limited: *Angaria delphinus* has sensory papillae on its cephalic and (quite small) epipodial tentacles (Hickman & McLean, 1990: fig. 13; Hickman, 1998: fig. 15.56B), but data on ESOs have not been provided and cannot be inferred from the published figures. A photograph of living *A. delphinus* by Merah (2009) shows four small and inconspicuous epipodial tentacles along the posterior part of the foot under the operculum, but again the presence of ESOs cannot be confirmed.

We could not find any publication with detailed data on the epipodial conditions of Areneidae.

Vetigastropoda: Phasianelloidea (Supplementary Material Table S7)

All recent molecular analyses show that Colloniidae and Phasianellidae, though quite different in their conchology and morphology, are sister taxa (Phasianelloidea) and quite distinct from other ‘trochacean’ Vetigastropoda.

Concerning Colloniinae, Hickman & McLean (1990: 47, figs 18A, 19D) described and depicted two separate ESOs in front of the epipodial tentacles, and also ESOs at the bases of these tentacles, in *Homalopoma luridum*. *Homalopoma* aff. *amussitatum* shows papillate cephalic and several epipodial tentacles, but only a single pair of ESOs (TK, pers. obs.). However, Dantart & Luque (1994a: 58, figs 9, 11, 12) described and depicted by SEM the epipodial conditions of *Homalopoma sanguineum* and reported four epipodial tentacles, each of which (with an ESO at its ventral base) appears to be of the compound type. Based on the description, SEM images and drawing of the colloniid *Anadema macandrewii* by McLean & Gofas (2008: 60), we regard the most anterior epipodial appendage (“hardly more than a rounded bulge”) as an additional, simple ESO.

Baxter & McLean (1984) and Hickman & McLean (1990: 43, fig. 15D) did not mention ESOs for the colloniid subfamily Moelleriinae and their SEM image of the epipodium of *Spiromoelleria quadrae* does not clear up the matter.

All Phasianellidae have papillate cephalic and two or three pairs of papillate epipodial tentacles. Details on ESOs are scarce. Vafiadis & Cram (2008) did not mention ESOs in their study on *Gabrielona*

species. However, Nangammbi (2010) provided detailed information on ESOs of several South African species (Supplementary Material Table S7) and, based on histological sections, we (GH, personal observation) can confirm this for *Tricolia pullus*.

According to Manly (1976), the postmetamorphic stages of *T. pullus* lack a posterior paired epipodial appendage as found in Scissurellidae, Haliotidae, Lepetodrilidae and Fissurellidae (see above).

Vetigastropoda: Trochoidea (Supplementary Material Table S8)

The current understanding of the superfamily Trochoidea (Williams & Ozawa, 2006; Kano, 2008; Williams *et al.*, 2008; Gofas, 2009 in WoRMS; Kano *et al.*, 2009; Aktipis & Giribet, 2010, 2012; Williams, 2012; Uribe *et al.*, 2016) includes (in alphabetical order) Calliostomatidae, Liotiidae, Margaritidae, Skeneidae, Solariellidae, Tegulidae, Trochidae and Turbinidae as extant families. Based on our recent studies on the type species of *Skenea*, *S. serpuloides*, and other skeneids (Haszprunar *et al.*, 2016) we confirm this assignment of Skeneidae to Trochoidea, whereas the status of Liotiidae (as a clade proper versus Liotiinae as a subfamily of Turbinidae) remains to be substantiated. Hickman (1996) provided a cladistic coding of epipodial characters among trochoidan vetigastropods. However, our review (Supplementary Material Table S8) shows that at least most (and probably all) taxa formerly coded as ‘ESOs absent’ in fact do have these sensory organs. Cephalic and epipodial tentacles are, with few exceptions, equipped with sensory papillae. So far as is known, ESOs are usually more or less associated with the epipodial tentacles, thus being of the compound type. However, there are frequently additional ESOs under the neck lobes. Moreover, losses or duplication of ESOs have occurred in many species and vary even between members of the same species or between left and right sides of the same specimen. A correlation in number and position of epipodial tentacles and ESOs is found in the larger species, while a reduction of the number of ESOs to a single pair is typically found in smaller, probably progenetic species like skeneids.

Several authors have explicitly claimed absence of ESOs in Calliostomatinae (Randles, 1904; Fretter & Graham, 1977; Cretella, Scillitani & Picariello, 1990), yet ESOs were described by Frank (1914), Ávila, Borges & de Frias Martins (2012) and Dornellas (2012). Detailed data on the epipodial conditions in the calliostomatid subfamily Thysanodontinae (Marshall, 1988c; Hickman & McLean, 1990: 140f) are still missing.

Margaritidae show the highest number (five to nine pairs) of epipodial tentacles of all Trochoidea and these are asymmetrically developed (six on the left, seven on the right side) in *Callogaza colmani*. ESOs are usually associated with the epipodial tentacles, but do also occur below the neck lobe.

As outlined elsewhere, Skeneidae are another clade of probably progenetic Trochoidea (Haszprunar *et al.*, 2016). Usually a single pair of ESOs is present (Fig. 1H), although some species of *Dikoleps* occasionally show a second ESO on the left side (Supplementary Material Table S8). Although the diagnostic propodeal penis of Skeneidae is lacking, we tentatively add here at least some species of *Iheyaspira* (Nye *et al.*, 2012; Haszprunar *et al.*, 2016), a genus that in its current usage is probably a polyphyletic assemblage (Chen *et al.*, 2015c).

Tegulidae generally show compound ESOs, but occasionally additional ESOs occur in *Tegula* species (McDonald & Maino, 1964; Collado, 2008). The notable exception is *Cittarium picta*, in which Graham (1965: 203) described and depicted a very different and unique condition: “Ventral to the epipodial fold, on each side, lies a row of epipodial tentacles; these are simple, rather short structures growing from slight depressions on the foot. There are no large oculiform sense organs associated with them as in many other trochids and in zeugobranchs. Most of the tentacles arise singly, but occasional pairs occur”. These very different epipodial conditions of Tegulidae and *Cittarium* add support for exclusion of

the latter from the Tegulidae based on molecular analyses by Williams (2012). On the other hand, *Tectus fenestratus*—placed in the same new clade as *Cittarium* in the same study—shows the regular tegulid pattern of the epipodium (Supplementary Material Table S8: clade NN).

Alcyna ocellata (Trochidae: Alcyninae) bears ESOs not, as usual, at the ventral base, but between the epipodial tentacles (Hickman & McLean, 1990: fig. 62B). Further species need to be studied to confirm this pattern as diagnostic for the subfamily or genus.

Among the trochid Cantharidinae several cases have been reported in which two ESOs are situated at the base of an epipodial tentacle (Supplementary Material Table S8). It is unclear whether this is a constant pattern among the respective species or an aberrant development in the studied specimens. In contrast, the trochid subfamilies Monodontinae, Stomatellinae, Trochinae and Umboniinae show the typical trochoid condition of the compound type of ESOs.

Hickman & McLean (1990: 57, fig. 24) described the epipodial tentacles of Turbininae as short and stubby, but did not mention ESOs. Though their sketches of relaxed specimens remain somewhat equivocal, it appears at least in certain species (Supplementary Material Table S8) that a compound ESO does occur at the ventral base of the first epipodial tentacle.

Robert (1902) described in detail the development of the epipodial appendages of six trochoidean species (genera *Calliostoma*, *Gibbula* and *Jujubinus*). Epipodial development generally proceeds from anterior to posterior with tentacles and associated ESOs (referred to as ‘organs sensorielles lateraux’). Unfortunately, Robert did not describe or depict an early postmetamorphic juvenile. In her thorough review on trochacean development, Hickman (1992: 262, fig. 2O) sketched a single pair of epipodial appendages (ESOs?) in a trochid of postmetamorphic stage and provided the equivocal comment that this stage “does not have the full complement of adult epipodial structures”. However, none of the original descriptions of postmetamorphic stages of trochoideans that we have checked show or describe any trace of a posteriorly placed epipodial or ESO appendage, as found in Scissurellidae, Haliotidae, Lepetodrilidae or Fissurellidae (see above). SEM studies on early juveniles are necessary to resolve these questions.

DISCUSSION

Limits of data

All sensory structures mentioned in this study, in particular papillae and ESOs, may easily be overlooked even when studied by SEM. Also, retraction of the animal into the shell often hinders a clear diagnosis of the small ESOs. Moreover, these structures often cannot be unequivocally diagnosed by histology in cases of poor fixation, suboptimal storage or other collection or preservation artefacts, which can result in a peeling of external epithelia.

Accordingly, literature data on ESOs are only relevant if presence of ESOs is explicitly stated or depicted and, even in these cases, there can be disagreements between authors.

Modularity of epipodial structures

Concerning epipodial appendages, there are three different modular structures (i.e. iterative homologues; cf. Haszprunar, 1992a; Klingenberg, 2014; Esteve-Altava, 2017), which may interact with each other in several ways:

- (1) Papillae with elongated tips and a ciliated crown are typically present in Vetigastropoda, although they have been reduced several times in evolution. Papillae occur not only on cephalic or epipodial tentacles, they are also common along the mantle edge and mantle slit, under the neck lobes,

- or may even be developed on ctenidial leaflets. They are characterized by a ciliated tip consisting of sensory cells which envelope each other. These enveloping cells, however, are also present in the ciliated tufts of the nonpapillate cephalic tentacles of Neritimorpha (Künz & Haszprunar, 2001).
- (2) ESOs are usually knob-like or short, hollow (i.e. with a large, central blood sinus), stout tentacles with a thick, ciliated epithelium at the tip; a few papillae occur on the tentacle only in Scissurellidae (see above). Up to now, TEM studies of ESOs in trochids have been restricted to a single species (Crisp, 1981; Herbert, 1984), showing many sensory cells with collar receptors which suggests a mechanoreceptive role for these organs (see review for Mollusca by Haszprunar, 1985). Herein, we confirm this character also for the Fissurellidae. Accordingly, this character probably is a plesiomorphic one at least for Vetigastropoda and probably for all Gastropoda, although the latter assumption still needs confirmation by TEM in other gastropod clades, namely Patellogastropoda and Neomphalina, but also in the remaining vetigastropod groups. Both loss and multiplication of ESOs have occurred repeatedly in early gastropod evolution.
 - (3) Despite the different innervation (cerebral *vs* pedal) of the true epipodial tentacles of Vetigastropoda and of cephalic tentacles, their identical structure (external appearance, papillae and a muscular hydrostate system; cf. Marshall, Hodgson & Trueman, 1989) suggests that these epipodial tentacles are iterative/serial (cf. Haszprunar, 1992a) homologues of cephalic tentacles. The same is probably true for certain caenogastropod taxa, e.g. the Litiopidae (Houbrick, 1987). In the Vetigastropoda this multiplication again occurred several times in evolution resulting in one (pseudococculinid–caymanabyssid clade of Kano *et al.*, 2016), very few ('Trochacea') or up to more than 100 epipodial tentacles (e.g. Haliotidae).

The correlation between ESOs and epipodial tentacles varies significantly among the Vetigastropoda (Fig. 1). In most groups a correlation of these two structures is not established, and even among the 'trochacean' groups the correlation remains weak: often there are differences in number and arrangement between individuals and between the left and the right side, and ESOs do occur without epipodial tentacles during ontogeny and in the adult condition. Nevertheless Sequenzioidea (except the cataegid *Kanoia*; see above) generally show simple ESOs, whereas Phasianelloidea and Trochoidea show compound ESOs. Unfortunately, detailed and unequivocal data on Angarioidea are currently not available.

Inference of gastropod ground pattern of epipodial conditions

There is a striking similarity in position and appearance of the single pair of blunt posterior epipodial appendages with ciliated tip in the early juveniles of Patellogastropoda (Patellidae and Lotidae confirmed), Vetigastropoda (Scissurellidae, Fissurellidae, Lepetodrilidae and Haliotidae confirmed; Seguenzioidea and Angarioidea doubtful; absent in Phasianelloidea and Trochoidea) and possibly also of Neritimorpha (Neritidae). Judging from the single pair of posterior tentacles in most Cocculiniformia and Lepetelloidea (except those with the 'bifid' condition, see above), we accept all these early tentacles as ESOs, but encourage confirmation by TEM studies and among the Neomphalina.

In particular the ontogenetic sequence suggests presence of a single and simple pair of ESOs in the gastropod stem species (hypothetical ancestral gastropod). This hypothesis was depicted 30 years ago by Haszprunar (1988b: fig. 4), but at that time ESOs were considered as 'epipodial tentacles'. It remains to be tested whether this was originally a late larval or early juvenile rather than an adult character. If, as certain palaeontological data suggest

(Chaffee & Lindberg, 1986; Nützel, 2014), the gastropod stem species was quite small (e.g. Haszprunar, 1992c), there may be only a small difference between these variants of the hypothesis.

Evolutionary scenarios

This original epipodial condition—just a single pair of simple ESOs—is still present and unchanged in most adult Cocculinidae and Lepetelloidea (Pseudococculinidae, Pyropeltidae) (Fig. 1A). This might be the retained plesiomorphic condition or might reflect paedomorphosis as in other characters (e.g. the pronounced asymmetry of the gills) of these taxa. If so, one might expect this condition also in early juveniles of other basal taxa (Neomphalina, Pleurotomariidae), which have not yet been studied.

Within Neomphalina and, in parallel, in Fissurellidae and Lepetodrilidae, multiplied ESOs form more or less a ring along the epipodial rim around the foot (Fig. 1C). In other vetigastropod taxa, ESOs also occur under the neck lobes or are more or less associated with true epipodial tentacles.

Künz & Haszprunar (2001) described by TEM the encircling ciliated receptor cells in the papillate cephalic tentacles of Vetigastropoda and in the nonpapillate ones of Neritimorpha (there are no TEM data on Neomphalina), whereas the ciliated sensory cells in the tentacles of Patellogastropoda show an entirely different fine structure. It requires a more robust phylogenetic tree of basal Gastropoda than those currently available, in order to determine which condition is plesiomorphic and which apomorphic for Gastropoda. If—contrary to current molecular trees (e.g. Williams, 2012; Zapata *et al.*, 2014)—the Patellogastropoda are still accepted as the earliest gastropod offshoot, this character might be regarded as a synapomorphy of Orthogastropoda (Haszprunar, 1988c; Ponder & Lindberg, 1997).

True papillae on tentacles and along the mantle margin are so far restricted to Vetigastropoda. Their absence in Pleurotomariidae (in all molecular phylogenies the first vetigastropod offshoot, but noting the lack of data on juveniles) might be primary or secondary. Secondary loss of papillae is likely in Lepetodrilidae (with papillae along the mantle skirt) and Fissurellidae (with papillae in juveniles).

It is likely that the multiplication of the cephalic tentacles as true epipodial tentacles (module 3, see above) occurred within Vetigastropoda rather than being present in the stem species of this clade. If so, Pleurotomarioidea, Lepetelloidea (with an independent 'bifid' condition in the pseudococculinid–caymanabyssid–*Kaiparapelta* clade; Kano *et al.*, 2016; Fig. 1F), Lepetodrilidae and Fissurellidae never had this condition and form a lower level, whereas Scissurelloidea, Haliotoidea and the 'trochacean' radiation (Seguenzioidea, Angarioidea, Phasianelloidea, Trochoidea) share (as a synapomorphy or by parallelism as in the Pseudococculinidae/Caymanabyssidae?) true epipodial tentacles. The latter condition has certainly been independently evolved in a few taxa of the caenogastropod Cerithioidea such as Bittiinae (Cerithiidae), Litiopidae and Plesiotrochidae (Healy & Wells, 1998).

As a last step in the evolution of epipodial structures we consider the arrangement of true epipodial tentacles and ESOs (i.e. compound ESOs) as found in Haliotoidea and the phasianelloidean and trochoidean radiation. Since we could not find the typical 'one pair ESO' stage in any of the numerous descriptions or figures of any 'trochacean' species, this might be a synapomorphic character of this radiation. A robust phylogenetic tree of Vetigastropoda (still needed) is a prerequisite to decide whether these modifications (i.e. occurrence of true epipodial tentacles; compound ESOs; loss of the early juvenile simple ESOs) occurred only once or several times during evolution.

On the function of the epipodium and ESOs

Accepting the epipodial tentacles as iterative/serial homologues of the cephalic tentacles also has implications for their inferred

function, which (according to their identical structure) is probably very much the same: there is little doubt that the cephalic and epipodial tentacles have mechano- and chemoreceptive functions. The first is obvious as required for exploring the surrounding environment of the animal, while the second may focus on the so-called ‘trail-following’ mechanism to meet conspecific mates, for homing or to communicate danger (e.g. Wells & Buckley, 1972; Liu, 2003; Ng *et al.*, 2013; Molist *et al.*, 2016; Gaskin & Collin, 2017).

However, it is much more difficult to discover a meaningful biological function of the ESOs. The presence of collar receptors strongly suggests a purely mechanoreceptive role of ESOs as served by these receptors in other molluscs (e.g. Crisp, 1981; Herbert, 1984; Haszprunar, 1985) and invertebrates. In particular, the so-called ‘lateral organs’ of polychaete Annelida show nearly identical fine structure (Purschke & Hausen, 2007). However, the various relative positions of ESOs do not support any clear and detailed hypothesis: a position anterior to and below the operculum may be useful to get information about the closure of the aperture—but many other operculate gastropods lack ESOs. A row of ESOs (e.g. Neomphalidae, Peltospiridae, Fissurellidae) might be useful to receive data about the ventilation and water currents of the subpallial cavity in limpets—but patello-gastropod limpets and many cocculiniform, lepetelloidean, neritimorph and caenogastropod limpets entirely lack ESOs. Also, the advantage of the compound type over the simple type of ESOs remains obscure. Once more we make a final plea for further studies on these so far largely neglected sense organs.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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