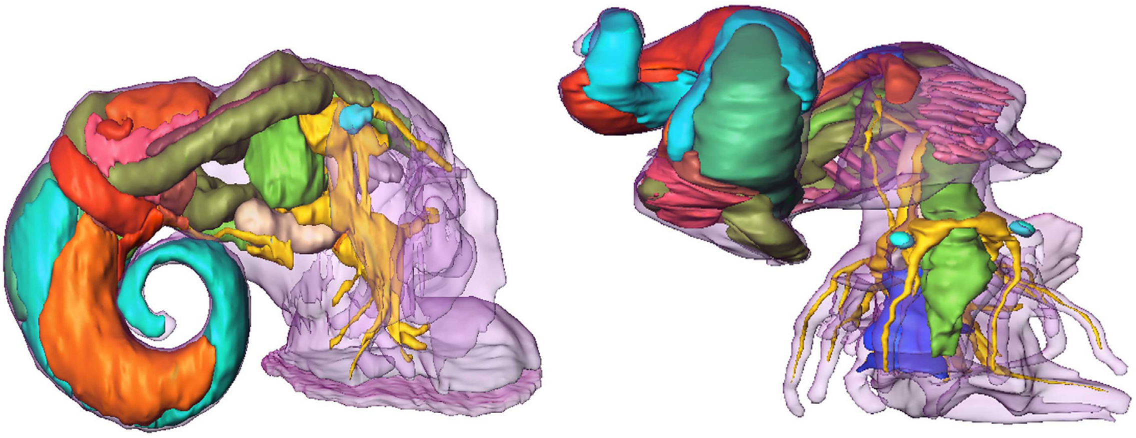
Comparative 3D microanatomy and systematics of skeneimorph gastropods, with a survey on epipodial tentacles in lower gastropods



Dissertation

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vorgelegt von
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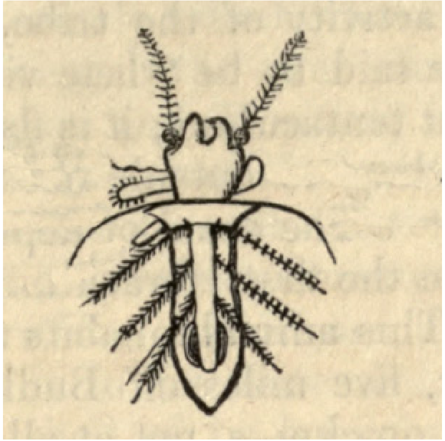
“Als ich vor zwei Jahren die Absicht fasste, die Anatomie der Prosobranchier kennen zu lernen, war mir nur zu wenig bewusst, welch’ unbekannte Länder vor mir lägen, welche Ausdauer es erfordern würde, eine auch nur vorläufige Orientirung über diese Thiere zu erhalten.”
Belá Haller 1884

Skenea serpuloides, first figure of the shell
George Montagu 1808



Skenea serpuloides, first figure of the soft body,
William Clark 1851b

“ ‘Skeneidae’ are probably the most infamous case of a polyphyletic family in Vetigastropoda.”
Yasunori Kano, Eri Chikyu & Anders Warén 2009

Cover picture

Left side: Lateral view of the 3D reconstruction of *Skenea serpuloides* (Montagu, 1808) with all inner organs, body surface transparent.

Right side: Frontal view of the 3D reconstruction of *Wanganella fissura* Laseron, 1954 with all inner organs, body surface transparent.

Contents

1 Summary

Traditionally the family Skeneidae (Vetigastropoda: Trochoidea) comprehends around 200 species of very small gastropods with a coiled and mostly colourless shell of a diameter smaller than 5 mm, lacking nacre, and with a rhipidoglossate radula. It has become obvious that these few characters do not prove a phylogenetic relation and this taxon has been suspected for quite some time to be a polyphyletic assemblage. Using recent methodological techniques including serial semi-thin sectioning combined with computer-aided 3D reconstructions (Amira®) the internal anatomy can be examined and illustrated. Detected new characters shed some light on the morphology and phylogeny of Skeneidae.

Within this study the polyphyly of skeneimorph gastropods could be proved. [1] The internal anatomy of the type species *Skenea serpuloides* (Montagu, 1808) was described. Together with the data of closely related species like other *Skenea* and *Dillwynella* species, Skeneidae sensu stricto (Skeneinae) could be accurately defined by having a propodial penis and being true hermaphrodites. However, the skeneid genera *Lodderena*, *Bruceiella* and *Leucorhynchia* lack such a penis and showed a different reproduction system. [2] Other species originally described as Skeneidae turned out not only to be excluded from this family but even belong to other vetigastropod superfamilies like Seguenzioidea or other gastropod clades like Neomphalina or Heterobranchia. With the anatomy of the seguenzioid *Ventsia tricarinata* Warén & Bouchet, 1993 the first complete morphological description of a member of this superfamily is provided. [3] The "dwarf body size" between 1 mm and a maximum of up to 5 mm constrains especially the reproductive system (like penis, seminal receptacle and true hermaphrodism). The rhipidoglossate radula is found in different juvenile trochoids and therefore progenesis in a juvenile ancestor of Skeneidae seems to be likely. [4] Analysing members of several vetigastropod superfamilies it has become obvious that the recent understanding of the evolution of the tentacles within lower gastropods, including the clades Patellogastropoda, Neomphalina, Cocculiniformia and Vetigastropoda, is incomplete and partly erroneous. The inclusion of an intensive literature review about epipodial appendages in lower gastropods allowed defining the different appendages correctly. SEM pictures, histological sections and 3D reconstructions of most of the groups were prepared to give a comprehensive overview of the epipodial appendages found in the lower gastropods. A new type of epipodial sense organ (ESO) was found in the Scissurellidae. It could be demonstrated that a particularly important systematic character, the ESO, is not restricted to the Vetigastropoda as usually stated, but does occur much more frequently as thought. A lot of structures originally described as epipodial tentacles are indeed ESOs. Therefore the evolution and distribution of the ESOs and also of the common epipodial tentacles has to be reinterpreted and also influences our view of general gastropod systematics. This new definition of epipodial appendages perfectly agrees with and thus supports the recent molecular phylogenetic approaches.

Zusammenfassung

Traditionell umfasst die Familie Skeneidae (Vetigastropoda: Trochoidea) ca. 200 Schneckenarten, die sich durch eine sehr kleine und meist farblose Schale mit einem Schalendurchmesser von weniger als 5 mm, das Fehlen der Perlmuttschicht und eine rhipidoglossate Radula auszeichnen. Es zeigte sich, dass diese wenigen Merkmale nicht ausreichen, um engere verwandtschaftliche Beziehungen zu rechtfertigen, und schon seit geraumer Zeit wird angenommen, dass dieses Taxon eine polyphyletische Ansammlung kleiner Schnecken ist. Verbesserte Verfahren, wie serielle Semi-Dünnschnitte, kombiniert mit computergestützter 3D-Rekonstruktion (Amira®), ermöglichten die Untersuchung und Darstellung der inneren Anatomie. Dadurch war es möglich, neue Merkmale zu beschreiben und die Morphologie und Phylogenie der Skeneidae im neuen Licht zu betrachten.

Im Rahmen dieser Studie konnte die Polyphylie skeneimorpher Gastropoden nachgewiesen werden. [1] Die Anatomie der Typusart *Skenea serpuloides* (Montagu, 1808) wurde zum ersten Mal beschrieben. Zusammen mit Daten von eng verwandten Arten der Gattungen *Skenea* und *Dillwynella* konnten die Skeneidae sensu stricto (Skeneinae) eindeutig durch das Vorhandensein eines propodialen Penis und echten Hermaphroditismus definiert werden. Die ebenfalls als Skeneidae beschriebenen Gattungen *Lodderena*, *Bruceiella* und *Leucorhynchia* haben aber keinen derartigen Penis und zeigten sehr unterschiedliche Ausformungen der Reproduktionsorgane. [2] Andere, ursprünglich als Skeneidae beschriebene Arten sind definitiv anderen vetigastropoden Superfamilien (Scissurelloidea und Seguenzioidea) bzw. Großgruppen der Gastropoda (Neomphalina und Heterobranchia) zuzuordnen. Die Beschreibung der Anatomie von *Ventsia tricarinata* Warén & Bouchet, 1993 ist die erste vollständige für einen Vertreter der gesamten Superfamilie Seguenzioidea. [3] Die extrem kleinen Schalendurchmesser (1-5 mm) dieser Schnecken bedingen spezielle Anpassungen und vor allem die Geschlechtsorgane sind durch die Verzwergung beeinflusst (z.B. Penis, Receptaculum seminis und echter Hermaphroditismus). Eine rhipidoglossate Radula wurde in verschiedenen, juvenilen trochoiden Schneckenarten gefunden und weist auf eine mögliche Progenesis in einem juvenilen Vorfahren der Skeneidae hin. [4] Bei der Untersuchung von Mitgliedern diverser Superfamilien der Vetigastropoden hat sich herausgestellt, dass unser momentanes Verständnis über die Evolution von Tentakeln in basalen Gastropoden (Patellogastropoda, Neomphalina, Cocculiniformia und Vetigastropoda) unvollständig und teilweise fehlerhaft ist. Eine ausführliche Literaturrecherche über epipodiale Anhänge in basalen Gastropoden hat es ermöglicht die verschiedenen Arten von Anhängen korrekt zu definieren. REM-Bilder, histologische Schnitte und 3D-Rekonstruktionen von den meisten dieser Gruppen wurden angefertigt, um einen umfangreichen Überblick über die in basalen Gastropoden gefundenen epipodialen Anhänge zu geben. In den Scissurelliden wurde ein neuer Typ von epipodialen Sinnesorganen (ESOs) gefunden. Es konnte gezeigt werden, dass das für die Systematik der Vetigastropoda bedeutende Merkmal der ESOs nicht, wie ursprünglich angenommen, auf Vetigastropoden beschränkt ist, sondern wesentlich öfter als gedacht vorkommt. Aus diesem Grund ist eine Neuinterpretation der Evolution und Verbreitung der ESOs, als auch der epipodialen Tentakel nötig und beeinflusst somit unsere aktuelle Sicht der allgemeinen Gastropodensystematik. Diese neue Interpretation des Vorkommens von epipodialen Anhängen deckt sich hervorragend mit den neuen molekularen Ergebnissen zur Phylogenie der Gastropoden.

2 General introduction

Gastropod and vetigastropod systematics

Gastropoda is with at least 62,000 described species (Lindberg et al. 2004) and estimations of up to 150,000 species (Lindberg et al. 2004; Aktipis et al. 2008) one of the largest animal classes. The relations of the major groups of this taxon are studied intensively, but changes occur continuously on all levels (Fig. 2.1). Grouped before in two, three or five higher taxa (Milne-Edwards 1848; Thiele 1929-1931; Salvini-Plawen & Haszprunar 1987; Ponder & Lindberg 1997), the division of Gastropoda in seven clades is broadly accepted nowadays: Patellogastropoda, Cocculiniformia, Neomphalina, Vetigastropoda, Neritimorpha, Caenogastropoda and Heterobranchia. However, discussions on this division continue, and textbooks often use one of the older gastropod systems until recently as outlined by Gofas (2012). Especially the position of Neomphalina as a separate clade (e.g. Heß et al. 2008; Appeltans et al. 2012) or part of the Vetigastropoda (e.g. Bouchet et al. 2005; Geiger et al. 2008) is matter of a lively debate and unsolved yet.

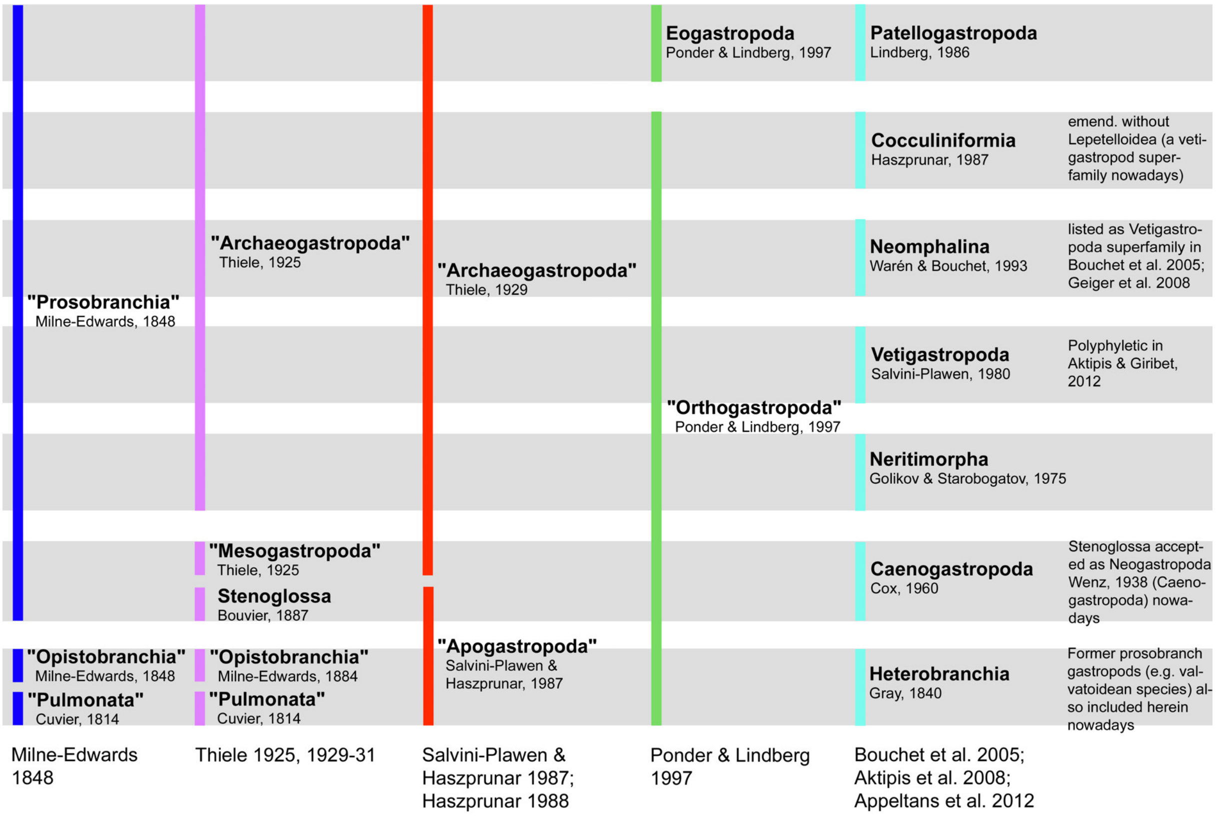


Figure 2.1 Simplified overview of the major taxonomic changes of the gastropod clades in different phylogenetic views.

Patellogastropoda Lindberg, 1986

- Eoacmaeoidea Nakano & Ozawa, 2007
  - Eoacmaeidae Nakano & Ozawa, 2007
- Lottioidea Gray, 1840
  - Acmaeidae Forbes, 1850
  - Lepetidae Gray, 1850
  - Lottiidae Gray, 1840
  - Nacellidae Thiele, 1891
  - Neolepetopsidae McLean, 1990
  - Pectinodontidae Pilsbry, 1891
- Patelloidea Rafinesque, 1815
  - Patellidae Rafinesque, 1815

Cocculiniformia Haszprunar, 1987

- Cocculinoidea Dall, 1882
  - Bathysciadiidae Dautzenberg & Fischer, 1900
  - Cocculinidae Dall, 1882

Neomphalina Warén & Bouchet, 1993

- Neomphaloidea McLean, 1981
  - Melanodrymiidae Salvini-Plawen & Steiner, 1995
  - Neomphalidae McLean, 1981
  - Peltospiridae McLean, 1989

Vetigastropoda Salvini-Plawen, 1980

- Angarioidea Gray, 1857
  - Angariidae Gray, 1857
  - Areneidae Adams, 1854
- Fissurelloidea Fleming, 1822
  - Fissurellidae Fleming, 1822
- Haliotoidea Rafinesque, 1815
  - Haliotidae Rafinesque, 1815
- Lepetelloidea Dall, 1882
  - Addisoniidae Dall, 1882
  - Bathyphytophilidae Moskalev, 1978
  - Cocculinellidae Moskalev, 1971
  - Lepetellidae Dall, 1882
  - Osteopeltidae Marshall, 1987
  - Pseudococculinidae Hickman, 1983
  - Pyropeltidae McLean & Haszprunar, 1987
- Lepetodriloidea McLean, 1988
  - Lepetodrilidae McLean, 1988
  - Sutilizonidae McLean, 1989
- Phasianelloidea Swainson, 1840
  - Colloniidae Cossmann, 1917
  - Phasianellidae Swainson, 1840
- Pleurotomarioidea Swainson, 1840
  - Pleurotomariidae Swainson, 1840
- Scissurelloidea Gray, 1847
  - Anatomidae McLean, 1989
  - Depressizonidae Geiger, 2003
  - Larocheidae Finlay, 1927
  - Scissurellidae Gray, 1847
- Seguenzioidea Verrill, 1884
  - Calliotropidae Hickman & McLean, 1990
  - Cataegidae McLean & Quinn, 1987
  - Chilodontidae Wenz, 1938
  - Choristellidae Warén & Bouchet, 1979
  - Seguenziidae Verrill, 1884
  - “skeneimorph Seguenzioidea” (e.g. *Ventsia*)
- Trochoidea Rafinesque, 1815
  - Calliostomatidae Thiele, 1924
  - Cyclostrematidae Fischer, 1885
  - Liotiidae Gray, 1850
  - Margaritidae Stoliczka, 1868
  - Skeneidae Clark, 1851
  - Solariellidae Powell, 1951
  - Tegulidae Kuroda, Habe & Oyama, 1971
  - Trochidae Rafinesque, 1815
  - Turbinidae Rafinesque, 1815

Neritimorpha Golikov & Starobogatov, 1975

- Helicinoidea Férussac, 1822
  - Helicinidae Férussac, 1822
  - Neritiliidae Schepman, 1908
  - Proserpinellidae Baker, 1923
  - Proserpinidae Gray, 1847
- Hydrocenoidea Troschel, 1857
  - Hydrocenidae Troschel, 1857
- Neritoidea Rafinesque, 1815
  - Neritidae Rafinesque, 1815
  - Phenacolepadidae Pilsbry, 1895
- Neritopsoidea Gray, 1847
  - Globocornidae Espinosa & Ortea, 2010
  - Neritopsidae Gray, 1847
  - Titiscaniidae Bergh, 1890

Figure 2.2 Accepted families and superfamilies of the gastropod clades Patellogastropoda, Cocculiniformia, Neomphalina, Vetigastropoda and Neritimorpha (formerly ‘Archaeogastropoda’) (according to Appeltans et al. 2012, Gofas 2012, Williams 2012; personal communication Y. Kano).

Among the four rhipidoglossate taxa (Cocculiniformia, Neomphalina, Vetigastropoda and Neritimorpha) the Neritimorpha alone have retained their status since the classic system of Thiele (1925, 1929-31 as Neritacea). Cocculiniformia comprehends in the recent emended view only two families of deep water limpets (Fig. 2.2), and the family Cocculinidae is long known (Dall 1882). Lepetelloidea, originally placed beyond the Cocculiniformia (Haszprunar 1987), is accepted as a vetigastropod superfamily nowadays (Bouchet et al. 2005).

Neomphalina were explored together with the hydrothermal vents in the last quarter of the 20th century and are restricted to sunken wood or hydrothermal vents (e.g. McLean 1981, 1985, 1990; Fretter 1989; Haszprunar 1989b; Warén & Bouchet 1989, 1993, 2001, 2009; Heß et al. 2008). Both limpet-like and coiled species are described in three families (Fig. 2.2). The presence of ctenidial bursicles in Vetigastropoda and certain Neomphalina (Haszprunar 1988; Ponder & Lindberg 1997; Sasaki 1998; Geiger et al. 2008; Heß et al. 2008) boosted the discussions around the status of Neomphalina as part of the Vetigastropoda (Bouchet et al. 2005; Geiger et al. 2008) or as an own gastropod clade again (Sasaki 1998; Heß et al. 2008; Kano 2008).

Since the clade Vetigastropoda was founded by Salvini-Plawen (1980) it was part of general discussions, reconsiderations and had a permanent ingress of taxa e.g. Seguenzioidea (Salvini-Plawen & Haszprunar 1987; Haszprunar 1988; Haszprunar 1993; Ponder & Lindberg 1997). Figure 2.2 gives an overview of the accepted vetigastropod families and superfamilies according to Appeltans et al. (2012). Vetigastropoda is accepted to be monophyletic by most authors (Ponder & Lindberg 1997; Sasaki 1998; Geiger & Thacker 2005; Kano 2008; Williams et al. 2008). However, in the molecular investigations of Aktipis & Giribet (2010, 2012) with a very large outgroup sampling Vetigastropoda not always turned out to be monophyletic. Pleurotomarioidea grouped outside the Vetigastropoda and Lepetelloidea was a sister group to the Patellogastropoda. This underlines the complex systematic problems of this gastropod clade. Discussion and changes continue on all levels of Vetigastropoda. The former superfamilies Trochoidea and Turbinoidea (Bouchet et al. 2005) were united to Trochoidea, while Phasianelloidea and Angarioidea have superfamily status now (Williams & Ozawa 2006; Williams et al. 2008; Williams 2012). A turnover exists also between the superfamilies: both the former scissurelloid family Sutilizonidae and the fissurelloid family Clypeosectidae (Haszprunar 1989a; McLean 1989) are nowadays assorted to the superfamily Lepetodriloidea (Warén & Bouchet 2001).

All Vetigastropoda are strictly marine and shelled, including a lot of well known members like top snails, turban snails, keyhole limpets, abalones or the large slit snails. Many superfamilies have a fossil record dating back deep into the Palaeozoic, so much time for evolution inside these taxa was available (Geiger et al. 2008). This concurs with the fact, that apomorphies on all levels are rather rare. There are often good characters to define a group but always with exceptions. So for example the characters “epipodial sense organs (ESOs)” and “sensory papillae” occur in many superfamilies, but are reported to lack in Pleurotomarioidea and Lepetelloidea (Haszprunar 1988, 1993; Ponder & Lindberg 1997; Sasaki 1998).

Because the vetigastropod shell shows many characteristics (often confirmed with radula details), species description based only on shell (and radula) are enabled. The soft bodies were often not examined and the data sets including gross anatomy and internal morphology are very poor and lack for many groups. Many species are only known from the shell and even some species and higher taxa described recently are based on shell features exclusively (e.g. Geiger 2009).

Skeneimorph gastropods

Skeneidae is a trochoid family (Fig. 2.2) including small marine gastropods from the shallow water down to bathyal depth all over the world. Kano et al. (2009) summed it up most appropriately as: “‘Skeneidae’ are probably the most infamous case of a polyphyletic family in Vetigastropoda”.

The type species, *Skenea serpuloides* (Montagu, 1808), was originally described as *Helix serpuloides*, assorted to a genus of terrestrial pulmonate gastropods by Montagu (1808). Fleming (1825) erected the genus name *Skenea* and Clark (1851a, b) finally named the family Skeneidae and designated *S. serpuloides* as type species. Both the status as the family Skeneidae (e.g. Clark 1851a, b; Wenz 1938; McLean in Keen 1971; Fretter & Graham 1977; Marshall 1988; Hickman & McLean 1990; Warén 1991, 1992, 1993; Warén & Bouchet 1993, 2001; Williams & Ozawa 2006; Williams 2012) or as the subfamily Skeneinae (Thiele 1929-31; Bouchet et al. 2005; Williams et al. 2008) was used over time. Recent molecular studies (Williams & Ozawa 2008; Williams 2012) involved the acceptation of Skeneidae as a family in the Trochoidea (Fig. 2.2). Since that point many small species were described as Skeneidae, but besides *Skenea* also other generic names like *Delphinula* and *Cyclostrema* were used without a clear differentiation to the type genus. Already Iredale (1915) tried to clear those “misused generic names”. This was continued by Höisæter (1968), who sorted 13 “*Cyclostrema*” species into the Skeneidae genera *Dikoleps* and *Skenea*. However, much more species were added to the Skeneidae, especially new ones found at hydrothermal vents and sunken wood associations (e.g. Marshall 1988; Warén & Bouchet 1993, 2001; Hasegawa 1997). The taxon Skeneidae was defined by few characters of the shell and the radula. McLean (in Keen 1971) described as characters for Skeneidae a rhipidoglossate radula, lack of nacre, and a multispiral operculum, besides the small size of those snails (Fig. 2.3). By time Skeneidae reached around hundreds of described and more undescribed species in around 80 genera (Marshall 1988; Kano et al. 2009). The few characters defining Skeneidae have been recognised to be an analog development and Hickman & McLean (1990) reported the status for Skeneidae as “highly provisional”. Several authors accepted this taxon as polyphyletic (Marshall 1988; Marshall in Hickman & McLean 1990; Warén 1992; Warén & Bouchet 1993; Hickman 1998), culminating in the citation of Kano et al. (2009) mentioned above. To accomplish this changed situation authors tended to call these gastropods “skeneimorph” (Warén 1992; Kano 2008) or “skeneiform” (Hickman 1998). This view is followed herein calling skeneimorph such microgastropods sharing the characters described above and reserve Skeneidae for such species being closer related to the type genus *Skenea serpuloides*. Skeneimorph gastropods are widely distributed on European coasts up to the North Atlantic, but also in other marine areas and so they were often reported in faunal investigations (e.g. Fretter & Graham 1977; Ponder 1990; Rubio-Salazar 1990; Warén 1991, 1992, 1993; Engl 1996, 2001; La Perna 1998: Rubio et al. 1998, 2004; Hoffman et al. 2008). Descriptions and pictures of the shell and radula of Skeneidae were published regularly, but even the external soft body was investigated in less than 1/3 of the described species (Paper 4, Tab. 3). Still some species are described exclusively by shell characters (e.g. Moolenbeek 1996). Data about the

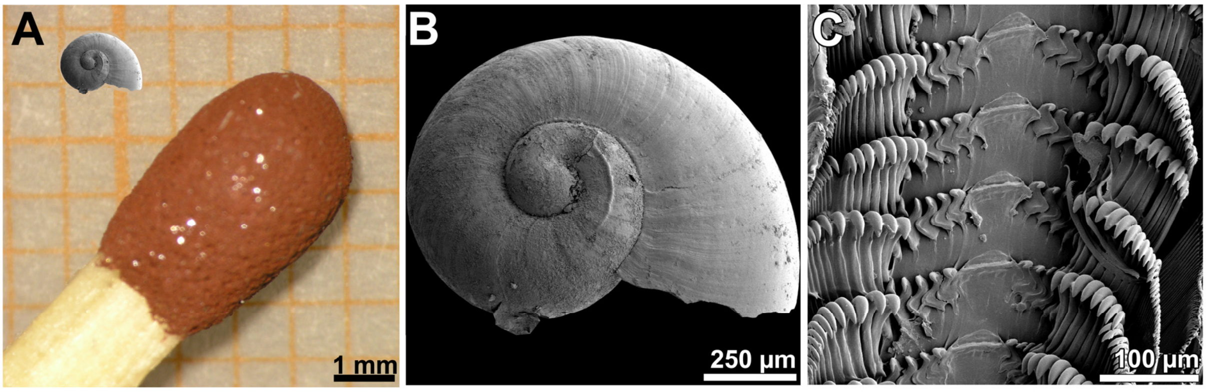


Figure 2.3 Overview of the historic main characters of Skeneidae shown on *Dillwynella voightae*.
A: Small size, SEM picture of the shell compared to the head of a match; **B:** Helicoid (skeneimorph) shell, SEM picture of the shell; **C:** Rhipidoglossate radula (large, solid central tooth in the middle; flanked by several, here 5, smaller lateral teeth; followed by many marginal teeth on the both sides), SEM picture of the radula.

inner anatomy of Skeneidae are missing entirely besides some comments on the ctenidium. In Warén's reviews (1991, 1992, 1993, 1996) about skeneimorph microgastropods many figures and descriptions of the external soft body were published for the first time. Warén found out that certain Skeneidae genera share an outgrowth formed by the right anterior edge of the propodium (thus pedally innervated) with a sperm channel in the center and named this copulatory organ propodial penis (*Skenea*, *Dikoleps*, *Protolira*, *Lissospira*, *Parviturbo*). He proposed this as a significant character for the species closely related to *Skenea*. However, some genera lacking such a penis were still included in the Skeneidae (e.g. *Bruceiella*, *Cirsionella*, *Leucorhynchia*). Later he tended (Warén & Bouchet 1993; Warén pers. com.) to use Skeneidae as a provisional storing place for new species with a skeneimorph shell, although he was aware they are not closely related to *Skenea*. This should make it easier to find them later for review, when new data allow a better classification (see e.g. *Ventsia*: Paper 3 herein).

As described above the species often have a wide distribution, though they are also quite rare and a huge amount of sediment has to be searched for a single specimen. The same problems occur for those deepwater species only known from the type locality. This material is often fixed with formalin and hence insufficient both, for molecular and for ultrastructural methods. Molecular data are so far restricted to two genera with a propodial penis, *Protolira* and *Dillwynella* (Williams & Ozawa 2006; Kano 2008; Aktipis & Giribet 2012; Williams 2012), but no data exist for *Skenea*, *Dikoleps* or *Lissospira*.

Finally, it has become obvious, that a revision and clear definition of Skeneidae is urgently needed and especially more data about the internal anatomy must be available.

Aims of the study

As the taxon Skeneidae is suspected to be a polyphyletic assemblage by several authors (see above), the aim of this study was to clear up this mess as good as possible. The decision to use morphological rather than molecular methods was caused by several factors. Most skeneimorph gastropods are very tiny with a shell diameter between 1 to 2 mm. Recent methodological progress with plastic embedding serial semi thin sectioning (slice thickness 0.75 to 2 µm), computer aided 3D reconstructions using AMIRA 4.1.2 (Mercury systems) and embedding of 3D PDF-models (Adobe Acrobat Pro Extended; Right Hemisphere: Deep Exploration) in the publications allowed investigating and displaying the complex soft bodies of these microgastropods (Ruthensteiner 2008; Ruthensteiner & Heß 2008; Ruthensteiner et al. 2010). International working groups around Dr. Kano (University of Tokyo, Japan), Dr. Williams (NHM, London) and Dr. Giribet (Harward University, Boston) are currently investigating molecular data to clear up vetigastropod phylogeny. Although molecular data are very useful to clear up phylogenetic relations, morphological methods link these information to the phaenotypic adaptation. Furthermore a morphological approach not only enables to analyse systematic relations, but also to examine the ecomorphological adaptation to the extreme small size of these snails.

Technical problems occurred when *Protolira valvatoides* Warén & Bouchet, 1993 was examined, a species very likely closely related to *Skenea* (Warén & Bouchet 1993; personal communication A. Warén). These small snails have a huge amount of small stony particles placed in the mantle cavity and around the external head-foot area. These particles could not be removed mechanically or using chemical solvents. As the particles would immediately destroy any type of glass or diamond knife, non-invasive methods, namely microCT and synchrotron scans were applied to test if the quality and resolution gained with such methods is suitable for 3D reconstructions of microgastropods. These results were compared to reconstructions carried out on sectioned specimens (see Figs. 4.4, 4.5).

The external features of the soft body were examined using critical point drying and SEM examinations. These methods were also applied to examine the hard structures like shell, radula, operculum and jaws if they were not already figured in the literature. The internal anatomy and histology need more difficult and time consuming methods and techniques as described above.

A couple of Diploma theses carried out in the Systematic Zoology group at the LMU supervised by Prof. Dr. Haszprunar (Brückner 2003; Beck 2006; Kunze 2007; Speimann 2007) dealing with microgastropods originally described as Skeneidae yielded surprising results: all species examined there, besides *Skenea serpuloides*, turned out to be not only no Skeneidae, but had to be placed into other vetigastropod superfamilies or even other gastropod clades like Neomphalina or Heterobranchia. So the first part of the study should be to exclude such species which are no trochoids and so definitely no Skeneidae.

As Warén proposed a propodial penis as diagnostic character for certain Skeneidae species this character should be tested. Also the anatomy of certain related and penisless, but as Skeneidae classified, species had to be investigated to prove their particular relation to *Skenea* and the Skeneidae. The material of *Dillwynella* loaned from the Field Museum Chicago was in a very good condition and turned out to be a new species. As *Dillwynella* was suspected to be closely related to *Skenea* a description of the species was needed.

Performing the first morphological comparisons it had become obvious that data were scarce for most of the groups investigated. The anatomical description of *Ventsia tricarinata* Warén & Bouchet, 1993 is the first complete one of a Seguenzioidea member. Working with skeneimorph gastropods included the morphological data and the literature investigation of many vetigastropod superfamilies and the Neomphalina. It turned out that the datasets are very scarce and often lack relevant data like detailed descriptions of the relation of heart and rectum, the reproductive system or the setting of the tentacles. Especially the latter is a very important character and as it can be examined using SEM it is rather easy to obtain.

The epipodial sense organs (ESOs) are a specific type of tentacles regarded to be an apomorphy for the Vetigastropoda (Haszprunar 1988; Ponder & Lindberg 1997, Sasaki 1998), although it is not found in the Pleurotomarioidea, except one interpretation by Sasaki (1998). For all other gastropod clades it was previously reported to be lacking. In Trochoidea, Angarioidea, and Phasianelloidea it is combined with a common epipodial tentacle and so an important character (Crisp 1981), while it is a separate tentacle in the other vetigastropod taxa. When I examined the ESOs of various Vetigastropoda and compared the findings with literature data, it became clear that in the past ESOs and also the other tentacle features were not described continuously or were overlooked in several occasions. Furthermore, the comparison of the ESOs of Vetigastropoda and the epipodial tentacles in Neomphalina resulted in certain morphological similarities. As the systematic relation of Vetigastropoda and Neomphalina is still discussed and ESOs are enlisted as apomorphy for the first taxon, a clear definition appeared to be important. Gastropoda are widely distributed, well known and studied for a long time. This caused a number of different expressions used for the same structure over time. So, for example, ESOs are known as “tentacle sensory structure” since the late 19th century (Boutan 1885), mentioned as “organs sensoriels lateraux” by Robert (1903), but are also described as “setose tentacles, ‘seta’-like projections, tentacles with (sensory) papillae, papillate tentacles” (e.g. Flemming 1884; Fretter & Graham 1977; Warén & Bouchet 1993; Fretter et al. 1998; Okutani et al. 2000; Geiger 2003). Hence a revision of the tentacles in lower gastropods in comparison with these new data was urgently needed and became of further interest of this work.

The following points turned out as the main aims of this study:

- Description of the morphology of *Skenea serpuloides* and definition of Skeneidae
- Morphological analysis of other skeneimorph gastropods and their systematic position
- Ecomorphology of dwarfing in microgastropods
- Morphology and revision of the tentacles of lower gastropods.

The papers in chapter 2 were arranged in order of publication date and contain following aspects:

Paper 1 is an overview of the morphology of *Skenea serpuloides* and five other skeneimorph gastropods with a highlight on the non-trochoid skeneimorph gastropods. Paper 2 contains the species description of the new Skeneidae species *Dillwynella voightae* Kunze, 2011. Because the data of *Ventsia tricarinata* is the first comprehensive description of a member of the superfamily Seguenzioidea, an own paper (Paper 3) with references to this group seems appropriate. Paper 4 comprises a detailed anatomical description of *Skenea serpuloides*, type species of Skeneidae, compared with the data of two Skeneinae species sharing a propodial penis, two further Skeneidae species lacking a penis and a liotiid species (Phasianelloidea). Paper 5 finally is dedicated to the appendages of basal gastropods with special reference to the epipodial sense organs.

3 Publications

Paper 1

Skeneimorph gastropods in Neomphalina and Vetigastropoda – a preliminary report

Kunze T, Heß M, Brückner M, Beck F & Haszprunar G (2008). *Zoosymposia* 1: 119-131

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Paper 2

Dillwynella voightae **new species, a new skeneimorph gastropod (Turbinidae) from the western Atlantic and a new record of** ***Dillwynella modesta*** **(Dall, 1889)**

Kunze T (2011). *The Nautilus* 125: 36-40

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Paper 3

3D-interactive microanatomy of ***Ventsia tricarinata*** **Warén & Bouchet, 1993 from Pacific hydrothermal vents (Vetigastropoda: Seguenzioidea)**

Kunze T, Heß M & Haszprunar G. *Journal of Molluscan Studies*: in review

Paper 4

What is a Skeneidae (Mollusca, Vetigastropoda)? 3D-interactive anatomy of the type species, ***Skenea serpuloides*** **(Montagu, 1808), with comments on dwarfing**

Kunze T, Heß M & Haszprunar G. *Frontiers in Zoology*: in preparation

Paper 5

Epipodial appendages in basal gastropods (Mollusca): new insights, homology assumptions, and evolutionary scenarios

Kunze T, Heß M, Warén A & Haszprunar G. *Zoologica Scripta*: in preparation

Paper 1

Skeneimorph gastropods in Neomphalina and Vetigastropoda – a preliminary report

Thomas Kunze, Martin Heß, Martin Brückner, Friederike Beck & Gerhard Haszprunar

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Skeneimorph gastropods in Neomphalina and Vetigastropoda — A preliminary report

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Abstract

Until recently the systematics of the Skeneidae (type species *Skenea serpuloides* Montagu, 1808) has been solely based on shell characters, radula details and external morphology. However, methodological progress (*e.g.* SEM) and preliminary anatomical data suggest that this vetigastropod group represents a polyphyletic, “skeneimorph” assemblage. Serial semithin sectioning combined with computer-aided 3D-reconstruction permits the detailed anatomical investigation of such small (1–3 mm), helicoid gastropods.

The taxa for which micro-anatomical data are available include six skeneimorph species from six genera: (1) True Skeneidae, exemplified by the type species, *Skenea serpuloides* (Montagu, 1808), doubtlessly belongs to Vetigastropoda and probably rests within the Trochoidea/Turbinoidea. Apomorphies of *Skenea* and related genera include a penis formed by the right propodium. (2) *Bathyxylophila excelsa* Marshall, 1988, *Ventsia tricarinata* Warén & Bouchet, 1993 and an undetermined “skeneimorph vetigastropod” have papillate cephalic and epipodial tentacles, a single monopectinate ctenidium with skeletal rods and bursicles, a papillary left and a right excretory organ, and statocysts with several statoconia. All these characters are indicative for a position of these species inside Vetigastropoda. Distinct appearance of epipodial tentacles and the lack of a combined epipodial sense organ argue against an inclusion into Trochoidea/Turbinoidea and thus Skeneidae s.s. (being defined by the characteristics of *Skenea serpuloides)*. At present, these species cannot be classified in any known vetigastropod subclade. (3) *Leptogyra constricta* Marshall, 1988 and *Leptogyropsis kalinovoae* Marshall, 1988 both are characterized by smooth cephalic and epipodial tentacles, a single, left excretory organ and statocysts with one statolith. These anatomical data strongly suggest a systematic position in the likewise rhipidoglossate Neomphalina, which might be considered as an independent rhipidoglossate clade outside the Vetigastropoda.

Although we are still at the very beginning in our investigation of skeneimorph anatomies, it is clear that this polyphyletic assemblage needs to receive much more attention for a complete understanding of vetigastropod and neomphalinan phylogeny.

Keywords: Skeneidae, microanatomy, micrograstropods, 3D-reconstruction, hydrothermal vents, sunken wood

Introduction

Since the erection of the taxon Skeneidae Clarke, 1858 numerous species have been formally described in this family, which usually is referred to Trochoidea within Vetigastropoda (*e.g.*, Hickman & McLean 1990). With the exploration of the deep sea inhabitants, especially sunken wood associations and the hydrothermal vent fauna, a series of new genera were added to this family in recent decades

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(Marshall 1988; Warén & Bouchet 1993, 2001; Hasegawa 1997). Nearly all these taxa were based on shell morphology, radula characters, and external morphology nowadays usually examined by SEM. It is obvious that this limited character set is not sufficient to clarify phylogenetic relationships, since parallelism is common (*e.g.*, in the radulae of Trochoidea/Turbinoidea; cf. Warén 1990). Accordingly, several authors refer to "skeneimorph" gastropods to express their doubts concerning the monophyly of the species usually listed as Skeneidae (Marshall 1988; Warén 1992). Traditionally Skeneidae s.l. are defined as: small vetigastropods, slitless, lacking nacre, single left gill, monotocardian heart, copulatory organ present. Until recently, the lack of data on additional characters (morphological and molecular ones) made it difficult to solve this systematic puzzle.

Recent molecular studies on vetigastropods (McArthur & Koop 1999; Schwarzpaul & Beck 2002; McArthur & Harasewych 2003; Geiger & Thacker 2005; Yoon & Kim 2005; Williams & Ozawa 2006; Kano 2008) strongly suggest the necessity of major revision in the vetigastropod systematics/classification, but still are too inconsistent among each other as are morphological trees (Geiger *et al.* 2008). In addition, we do not only want to resolve relationships but also to clarify evolutionary patterns of these small gastropods, with the mechanisms of miniaturization as an example. Indeed, phenotypic studies not only add new lines of evidence to clarify relationships, but also identify functional and ecological features, *e.g.*, changes in the reproductive biology or of feeding niches.

Substantial methodological advances based on serial semithin section and computer-aided 3D-reconstruction techniques provide significant new insights for a new understanding of systematics and biology of skeneimorph microgastropods. Three diploma theses carried out in our workgroup deal with the anatomy of six "skeneimorph" species (Brückner 2003; Beck 2006; Kunze 2007). This paper summarizes the results: of all the examined species only *Skenea serpuloides* will remain in Skeneidae, the other species are all excluded from Trochoidea/Turbinoidea, partly even from Vetigastropoda.

Material and methods

Institutional abbreviations

MNHN	Muséum Nationale d'Histoire Naturelle, Paris, France.
NMNZ	National Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.
SMNH	Swedish Museum of Natural History, Stockholm, Sweden.
ZSM	Zoologische Staatssammlung, München, Germany.

Species examined (alphabetic order)

Bathyxylophila excelsa Marshall, 1988: North-Eastern Chatham Rise, New Zealand (42°43.9'S, 176°08'E), depth 800–810 m, found on sunken wood. Paratypes NMNZ BS925/M74982, section series ZSM Mol 20080360, 20080361, 20080362.

Leptogyra constricta Marshall, 1988: Near White Island, New Zealand (37°23.7'S, 177°39.5'E), depth 1,074–1,100 m, found on sunken wood. Paratypes NMNZ BS924/M74999, section series ZSM Mol 20080045.

Leptogyropsis kalinovoae Marshall, 1988: North-Eastern Chatham Island, New Zealand (42°47.1'S, 175°45.6'W), depth 1,174–1,180 m sunken wood. Paralectotypes NMNZ BS931/M74292, section series ZSM Mol 20080049, 20080050.

Skenea serpuloides (Montagu, 1808): Collected off Roscoff, Bretagne, France (on the surface of "amphioxus-sand": 48°43.532'N, 3°50.712'W, 20–25 m). Leg. et det. Anders Warén (Naturhistoriska Riksmuseet, Stockholm). Section series SMNH 98643, 98644, 98645, 98646.

"Skeneimorph vetigastropod": Found in the sand of a tropic sea-water aquarium, probably introduced with imported corals. Leg. Brückner and Haszprunar. Section series ZSM Mol 20080369, 20080370, 20080371.

Ventsia tricarinata Warén & Bouchet, 1993: Hine-Huna, Lau Basin, Fiji (22°32'S, 176°43'W), depth 1,900 m, found at hydrothermal vents. Paratypes MNHN Moll 20947, paratypes section series MNHN Moll 20948, 20949, 20950, 20951.

Methods applied

The specimens of *Skenea serpuloides* was fixed in formalin and stored in 70% ethanol. The shells were decalcified with Bouin`s fluid (picric acid, formaldehyde, and acetic acid) and the soft parts were embedded in araldite resin. Specimens of the "skeneimorph gastropod" were fixed directly in Bouin's fluid, washed with ethanol and embedded in araldite resin. The other species were directly fixed and stored in 70% Ethanol. After decalcification the soft parts were embedded in epoxy resin after Spurr (1969). Semi-thin section series were performed with a histo-jumbo diamond or glass knifes, stained with a 1:1 mixture of Methylene blue and Azur II and heated for approximately 10 seconds at 80C° (Richardson *et al.* 1960). *Skenea serpuloides* and the "skeneimorph gastropod" were sealed with araldite resin. The other species were sealed with DPX (Agar Scietntic, Essex).

For computer-aided 3D-reconstruction, digital photos of the sections were taken using a lightmicroscope and a digital camera (both Olympus). The digital images were pre-processed in *Adobe Photoshop*, then imported in *AMIRA Resolve RT* (Mercury Computer Systems Inc., Chelmsford, MA, USA), aligned, segmented manually, 3D-rendered, and morphometric data were calculated. For methodological details see Ruthensteiner (2008). *Skenea serpuloides* and the "skeneimorph vetigastropod" were sectioned as mentioned above but the reconstructions were made by hand on scale paper.

For the scanning electron microscopy (SEM) specimens of the "skeneimorph gastropod" were macerated for one hour with a 12.5% potassic-hyperchloride solution for radula preperation. Shell and radula were dried for several days at 40C°. Then they were sputtered with gold for 150 seconds (Polaron) and examined with a scanning electron microscope (LEO 1430VP).

Results

The specimens examined of *Bathyxylophila excelsa*, *Leptogyra constricta*, *Leptogyropsis kalinovoae* and *Ventsia tricarinata* are para- or paralectotypes. For shell and radula patterns we refer to Marshall (1988: 958, 963, 975) and Warén & Bouchet (1993: 29–31). The examined specimens of *Skenea serpuloides* were collected and determined by A. Warén (*cf.* Warén 1991: 57, 66). Radula and shell of the "skeneimorph gastropod" are described below and shown in Figure 3.

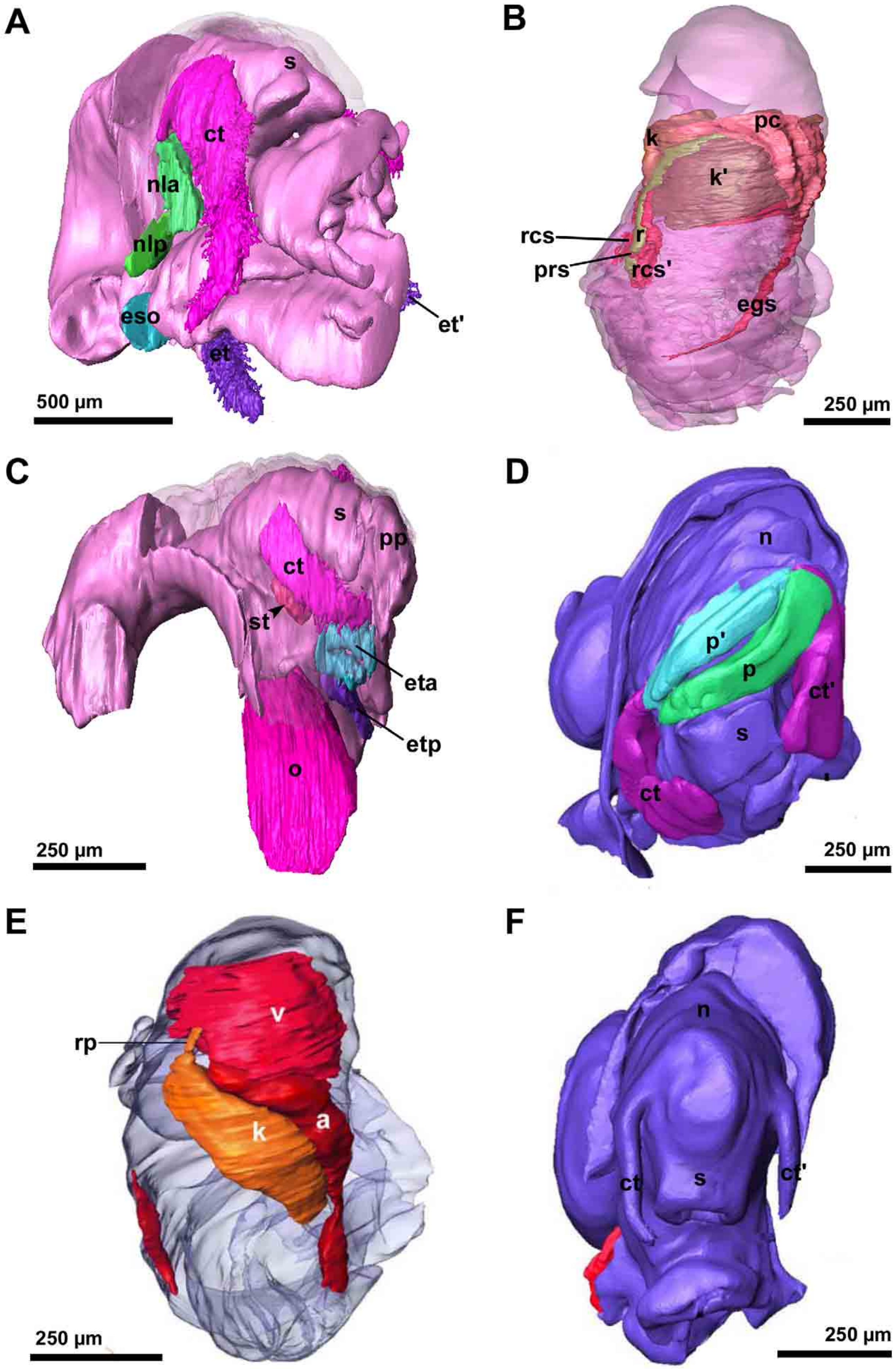
***Skenea serpuloides* (Montagu, 1808).** *Skenea serpuloides* has one pair of papillate cephalic tentacles and a single pair of papillate epipodial tentacles combined with an epipodial sense organ (ESO) at their bases (Fig. 2B). There are two smooth additional, unpaired appendices. One is some sort of single tentacle and the other one is a propodial penis (Fig. 2C). In the mantle cavity a monopectinate ctenidium can be found, bearing skeletal rods and bursicles. The monotocardian heart lies more on the right side. Due to the poor fixation the relationship between heart and intestine could not be established. Both kidneys are connected with the pericardium via a renopericardial duct. This hermaphroditic species has a highly specialised genital system consisting of separated testis and ovary, both opening separately via a small porus into the right kidney. The large, yolky eggs have a thick vitelline coat (Fig. 2D). The separated receptaculum seminis shows a spermatolytic portion. The radula is rhipidoglossate. The stomach bears a gastric shield and has a single opening into the midgut gland. The intestine has two loops. The nervous system is hypoathroid and streptoneurous; paired statocysts with several statoconia are attached to the pedal ganglia. The eyes are retinal cups with pigmentation. Due to the formalin fixation the eyes lost their pigmentation and on the section series the pigmentation is not visible (Warén pers. com.), but it is visible in the living animals.

Bathyxylophila excelsa **Marshall, 1988.** *Bathyxylophila excelsa* has one pair of papillate cephalic and epipodial tentacles each (Fig. 1C). The monopectinate ctenidium consists of short leaflets with skeletal rods and bursicles. The monotocardian heart does not encircle the rectum, a papillate left kidney and a right kidney are present. All specimens examined were females. The genital apparatus includes an ovary and an ovary duct, which form, together with a channel from the right kidney, a urinogenital duct. The big yolky eggs are covered by a thick vitelline layer. The receptaculum seminis lies separately on the left side of the mantle cavity. The alimentary tract shows a rhipidoglossate radula, a pair of radular cartilages, an oesophagus without papillae, a stomach with a gastric shield and two intestinal loops. The nervous system is hypoathroid and streptoneurous, a pair of statocysts with several statoconia is present. Eyes are lacking. Due to insufficient fixation (originally the specimens were frozen), histological details could not be sufficiently resolved.

”Skeneimorph vetigastropod”. Four pairs of papillate tentacles are present, one cephalic and three epipodial ones. A pair of smooth tentacles, each with an epipodial sense organ at its tip is not fused with the papillate epipodial tentacles. The single, monopectinate gill contains bursicles and skeletal rods. The monotocardian heart lies more on the right side in the mantle cavity, with the ventricle encircling the rectum. Both the small left and the larger right kidney have a nephroporus to the mantle cavity. We could only find the renopericardial duct of the right kidney. The “skeneimorph vetigastropod” is a simultaneous hermaphrodite with a true hermaphroditic gland (including sperm/sperma-

→

Figure 1 (next page)**.** 3D-reconstructions. **A.** *Ventsia tricarinata* (female), view to the right side (mantle roof transparent). **B.** *Ventsia tricarinata* (female), dorsal view (soft parts transparent). **C.** *Bathyxylophila excelsa* (female), view from the right side (mantle roof transparent). **D.** *Leptogyra constricta* (hermaphrodite), frontal view (mantle roof removed) **E.** *Leptogyra constricta*, dorsal view (soft parts transparent). **F.** *Leptogyropsis kalinovoae* (female), frontal view (mantle roof removed). a: auricle, ct/ct’: right/left cephalic tentacle, egs: efferent gill sinus, eso: right epipodial sense organ, et/et’: right/left epipodial tentacle, eta: right anterior epipodial tentacle, etp: right posterior epipodial tentacle, k/k’: right/left kidney, n: neck, nla: anterior neck lobe, nlp: posterior neck lobe, o: operculum, p/p’: penis/”accessory” penis, pc: pericardium, pp: propodium, prs: perirectal sinus, r: rectum, rcs/rcs’: right/left rectal sinus, rp: renopericardial duct s: snout, st: right suboptic tentacle, v: ventricle.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tozoa and yolky eggs in all stages of gametogenesis), which opens into the right kidney. The eggs have yolky drops and a thin vitelline layer. The alimentary tract consists of a rhipidoglossate radula (Fig. 3A,B), an oesophagus without papillae, a stomach bearing a gastric shield, an unpaired midgut gland and an intestine with several loops. The nervous system is hypoathroid and streptoneurous, a pair of statocysts having several statoconia. The eyes are closed and pigmented, but have no lens.

Ventsia tricarinata **Warén & Bouchet, 1993.** *Ventsia tricarinata* has a single pair of papillate cephalic and epipodial tentacles each. An additional pair of epipodial sense organs is not combined with the epipodial tentacles (Fig. 1A). The monopectinate ctenidium is located in the left part of the mantle cavity. The gill leaflets contain bursicles and skeletal rods (Fig. 2E). The ventricle encircles the rectum. The left kidney is papillate and connected by a sphincter-closed opening to the mantle cavity (Fig. 1B). The right kidney is much larger, has a spacious lumen and releases the gametes. Only the left renopericardial duct was found. *Ventsia tricarinata* is gonochoristic: The female genital apparatus consists of an ovary, an oviduct and a receptaculum seminis. The large, yolky eggs are covered by a thin vitelline layer. Together with the right kidney channel, the oviduct forms an urinogenital duct, which opens into the right mantle cavity. The separated receptaculum seminis is located on the left side of the mantle cavity (Fig. 2F). Males have a lobate testis. Due to the poor fixation further details of the male reproductions system could not be established. The alimentary tract consists of a rhipidoglossate radula, one pair of radular cartilages, a papillate anterior oesophagus, a straight posterior oesophagus, a stomach with a gastric shield and an intestine with two loops. The nervous system is hypoathroid and streptoneurous, paired statocysts with several statoconia are attached to the pedal ganglia (Fig. 2G). Eyes are lacking.

Leptogyra constricta **Marshall, 1988.** The snout of *L. constricta* is blunt, the round propodium shows short lateral outgrowths. There are four head appendages (one pair of smooth cephalic tentacles, a penis and an accessory penis) and several smooth epipodial tentacles (Fig. 1D). The single bipectinate ctenidium lacks skeletal rods. Due to the poor state of preservation the presence of bursicles can neither be confirmed nor rejected [in *Leptogyra patula* Marshall, 1988 bursicles are present (Heß *et al.* in press)]. In the left part of the mantle cavity the single (left) kidney is situated in front of the monotocardian heart (Fig. 1E) with the pericardium encircling the rectum. The hermaphroditic genital system consists of separated testis and ovary, a common gonoduct and a separated receptaculum seminis. Even ripe, yolky eggs lack a vitelline layer. The alimentary tract has a rhipidoglossate radula, one pair of radular cartilages, jaws, one pair of distinct salivary glands, an oesophagus showing longitudinal twisting by torsion, a stomach with a gastric shield, two midgut glands and an intestine

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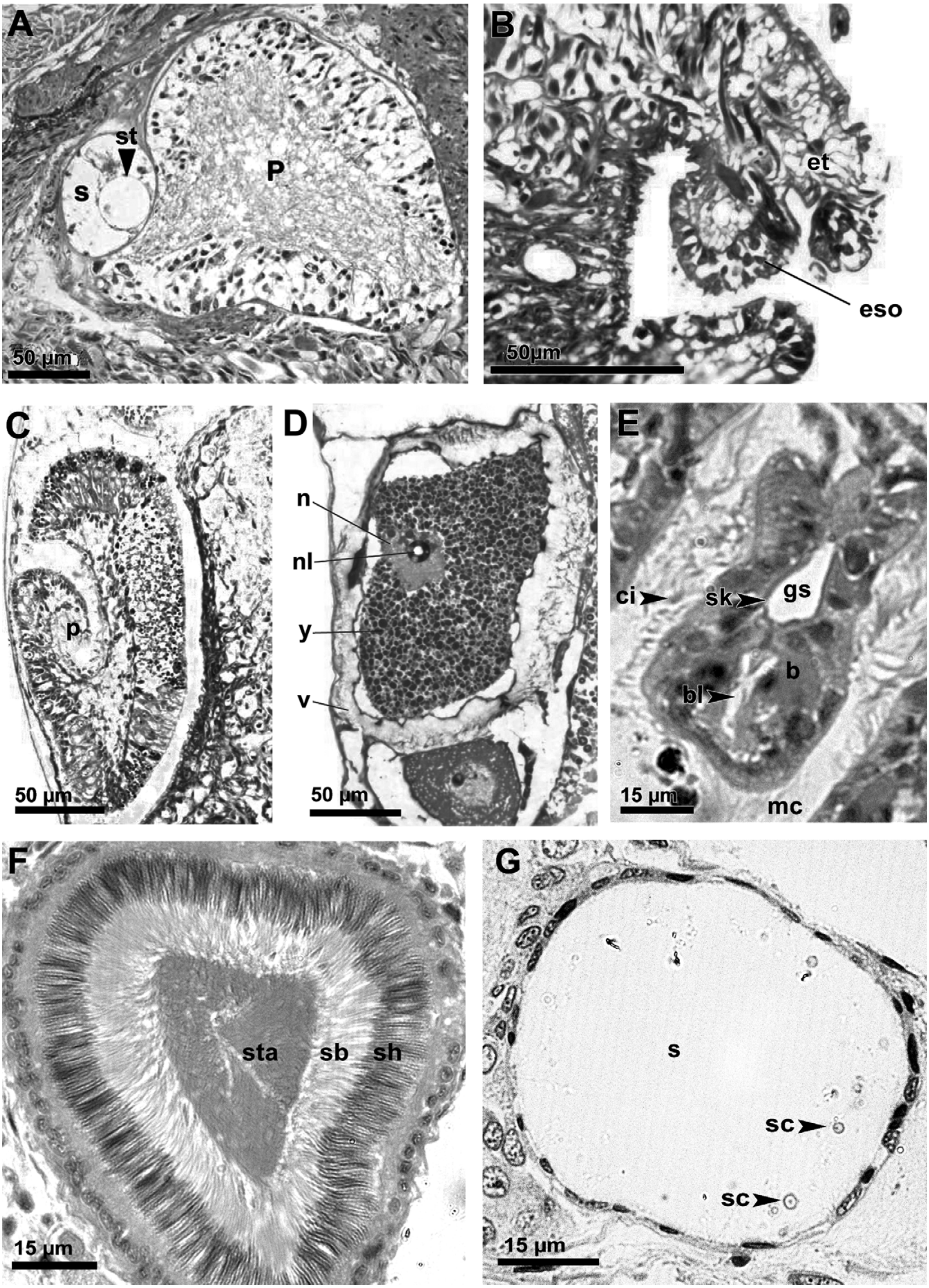
Figure 2 (next page)**.** Histological sections (all cross sections). **A.** *Leptogyropsis kalinovoae* (female), statocyst with single statolith. **B.** *Skenea serpuloides* (hermaphrodite), epipodial sense organ at the ventral basis of epipodial tentacle, **C.** *Skenea serpuloides*, propodial penis. **D.** *Skenea serpuloides*, egg with vitelline layer. **E.** *Ventsia tricarinata* (female), bursicle with skeletal rods. **F.** *Ventsia tricarinata* (female), receptaculum seminis. **G.** *Ventsia tricarinata* (female), statocyst with several statoconia. b: bursicle. bl: bursicle lumen. ci: cilia. eso: epipodial sense organ. et: epipodial tentacle. gs: gill sinus. mc: mantle cavity. n: nucleus. nl: nucleolus. P: pedal ganglia. p: penis. s: statocyst. sb: sperm bodies. sc: statoconia. sh: sperm heads. sk: skeletal rods. st: statolith. sta: sperm tails. v: vitelline layer. y: yolk.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with two loops, the rectum opening into the right part of the mantle cavity. The nervous system is hypoathroid and streptoneurous. The paired statocysts with a single statolith each are attached to the pedal ganglia. There are no eyes.

Leptogyropsis kalinovoae **Marshall, 1988.** This species resembles *L. constricta* in most anatomical characters (Figs 1F, 2A). The two species differ as follows: The bipectinate ctenidium contains skeletal rods, but no bursicles. The heart is bypassed by the rectum. Females of *L. kalinovoae* have an ovary, a simple oviduct, and a separated receptaculum seminis. The male gonoduct is highly glandular and hypertrophied. The radular cartilages are asymmetrically orientated, the oesophagus is papillate, and there is only a single midgut gland. *Leptogyropsis kalinovoae* has a pair of large, but pigmentless eyes.

Discussion

The new data about the soft part microanatomy of the six representatives investigated so far require a fundamental reconsideration of their current taxonomic classification.

Vetigastropoda have been characterized by the following anatomical characters: papillate cephalic and epipodial tentacles (few exceptions), an epipodial sense organ (few exceptions), two kidneys, eggs with vitelline layer, and statocysts with several statoconia (Salvini-Plawen 1980; Haszprunar

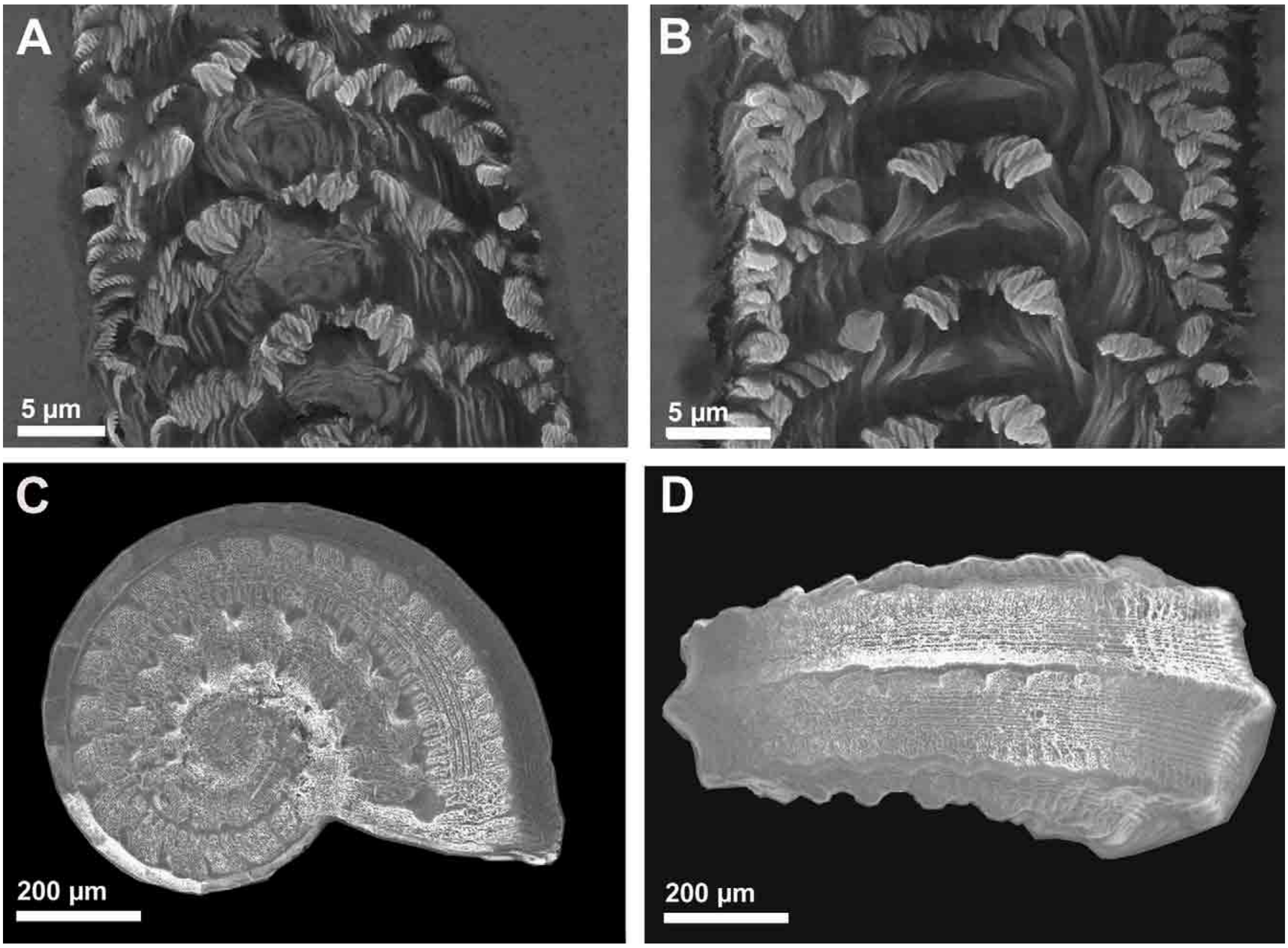

Figure 3. SEM pictures of "skeneimorph gastropod". **A–B.** radula. **C–D.** shell.

1988, 1993; Ponder & Lindberg 1996). With few exceptions bursicles are present, the radula is rhipidoglossate/hystrichioglossate, mantle organs may be paired (Table 1). The occurrence of these features in *B. excelsa*, *S. serpuloides,* the "skeneimorph gastropod" and *V. tricarinata* strongly suggest a position of these four species inside Vetigastropoda. Contrary to Hickman & McLean (1990) we confirm ctenidial bursicles in *S. serpuloides* and thus for Skeneidae.

Among the species investigated here only *S. serpuloides* shows characters that are regarded as apomorphies of the Trochoidea/Turbinoidea: i.e., combined epipodial sense organs (Crisp 1981). *Skenea serpuloides* is the type species of Skeneidae, thus defines the family. Accordingly and in agreement with Warén (1992), at the current state of knowledge we characterize the family by the apomorphic (but homoplastic) monopectinate ctenidium, a heart lying more on the right side of the mantle cavity, a hermaphroditic genital system with a separated receptaculum at the left side of mantle cavity, and (unique and possibly diagnostic) a penis on the right propodium, the latter character is shared by a (limited) number of other skeneimorph genera, which are therefore considered true skeneids [*e.g.*, *Dikoleps* (Warén 1992; Brückner 2003), *Lissospira* (Warén pers. com.), *Protolira* (Warén 1992), and *Skeneoides* (Warén 1992). This also supports the integration of Skeneidae within Trochoidea/Turbinoidea, although the monophyly of the latter has become highly doubtful (Williams & Ozawa 2006; Kano 2008). On the other hand, the lack of a combined epipodial sense organ and otherwise structured copulatory organs argue strictly against an inclusion of *B. excelsa*, the "skeneimorph vetigastropod" and *V. tricarinata* in Skeneidae s.s. and even Trochoidea/Turbinoidea.

Ventsia tricarinata shows a unique mixture of plesiomorphic (*e.g*., subradular organ) and apomorphic (*e.g*., presence of a receptaculum seminis) characters. The peculiar structure of the receptaculum seminis (Fig. 2F) suggests a position within Seguenzioidea (Sasaki pers. comm.), being supported by recent molecular analyses (Kano 2008). Already Warén & Bouchet (1993) assumed a relationship of *Ventsia* and the seguenzoid group Calliotropiinae. However, the definition and content of Seguenzioidea, is still far from being clear and requires anatomical and molecular data from many additional taxa.

The shell of the "skeneimorph vetigastropod" is very similar to the East Pacific species *Cyclostremiscus emeryi* (Ladd, 1966) (SEM pictures in Okutani 2000). Both species are definitely not part of Vitrinellidae (Caenogastropoda), in which *Cyclostremiscus* is classified (Warén pers. com.) [type species by Pilsbry & Olsson (1945) *Cyclostremiscus panamensis* (Adams, 1859), formerly *Vitrinella panamensis*]. Some shell characters seem to be turbinoid, which do not agree with the lack of a combined ESO in the examined specimens of the "skeneimorph vetigastropod". Due to the lack of clear synapomorphies with any existing vetigastropod clade the "skeneimorph vetigastropod" seems best to be classified as Vetigastropoda incertae sedis, until more comparative data are available. Also the genus *Cyclostremiscus*, which is similarly to Skeneidae a "lumping pot" for small round snails, awaits a much-needed revision.

The missing male specimens and the poor state of preservation of the examined specimens of *B. excelsa* led to a still incomplete morphological data set. So far the morphological data only confirm the vetigastropod nature of this species. However, molecular data suggest a position near *Anatoma* (Scissurellidae s.l.) (Kano, 2008). If so, *Bathyxylophila* would represent another slit-less species in the Scissurellidae s.l. as is the case with *Coronadoa* (Scissurellidae s.s.), *Larochea* and *Trogloconcha (Larocheidae)* (Marshall 1993; Kase & Kano 2002; Geiger 2003). However, although the shell is slit-less, it shows two small indentations (Warén pers. com.). Marshall (1988) has already diagnosed

Table 1. Comparison of relevant morphological characters among the examined species, Vetigastropoda and Neomphalina (for more details see Sasaki 1998). ?: Due to the poor state of preservation the character cannot be described in this species.*: ESO (epipodial sense organ); a) ESO not combined: ESO on the tip of a smooth tentacle; b) combined ESO: ESO on the basis of a papillate tentacle (see also Crisp 1981).

Vetigastropoda	Neomphalina	*Skenea serpuloides* (Montagu, 1808)	*Bathyxylophila excelsa* Marshall, 1988
papillate tentacles (few exceptions)	non-papillate tentacles	papillate tentacles	papillate tentacles
variable ESO*	no ESO*	combinded ESO*	?
two or only left ctenidium	left ctenidium	left ctenidium	left ctenidium
bursicles (few exceptions)	bursicles (few exceptions)	bursicles	bursicles
skeletal rods present (few exceptions)	skeletal rods variable	skeletal rods	skeletal rods
two or left auricle	left auricle	left auricle	left auricle
two kidneys (no exception)	left kidney	two kidneys	two kidneys
mostly separated	separated (so far known)	hermaphrodite	sexes separated
eggs with vitelline layer (no exceptions)	no vitelline layer	thick vitelline layer	thick vitelline layer
two or one pair of radula cartilages	one pair of radula cartilages	one pair of radula cartilages	one pair of radula cartilages
heart encircling the rectum (exceptions)	rectum passes heart	?	rectum passes heart
nerve ring hypoathroid	nerve ring hypoathroid	nerve ring hypoathroid	nerve ring hypoathroid
statocysts with statoconia	statocysts with statolith	statocysts with statoconia	statocysts with statoconia

"skeneimorph gastropod"	*Ventsia tricarinata* Warén & Bouchet, 1993	*Leptogyra constricta* Marshall, 1988	*Leptogyropsis kalinovoae* Marshall, 1988
papillate tentacles	papillate tentacles	non-papillate tentacles	non-papillate tentacles
ESO not combined*	ESO not combined*	no ESO*	no ESO*
left ctenidium	left ctenidium	left ctenidium	left ctenidium
bursicles	bursicles	? (present in *L. patula* Marshall, 1988)	no bursicles
skeletal rods	skeletal rods	no skeletal rods	skeletal rods
left auricle	left auricle	left auricle	left auricle
two kidneys	two kidneys	left kidney	left kidney
hermaphrodite	sexes separated	hermaphrodite	sexes are separated
thin vitelline layer	thin vitelline layer	no vitelline layer	no vitelline layer
one pair of radula cartilages	one pair of radula cartilages	one pair of radula cartilages	one pair of radula cartilages
heart encircling the rectum	heart encircling the rectum	rectum passes heart	rectum passes heart
nerve ring hypoathroid	nerve ring hypoathroid	nerve ring hypoathroid	nerve ring hypoathroid
statocysts with statoconia	statocysts with statoconia	statocysts with statolith	statocysts with statolith

similarities in shape, size and teleoconch shape between *Larochea* (type species *Larochea miranda* Finlay, 1927) and *Bathyxylophila*. However, both monophyly and content of Scissurellidae s.l. is debateable (Geiger & Thacker 2005; Geiger *et al.* 2008).

Leptogyra constricta and *Leptogyropsis kalinovoae* share smooth cephalic and epipodial tentacles, a single, left excretory organ, a monotocardian heart, and statocysts with only one statolith each. This combination of characters suggests neomphalinan affinities, in particular to the genus *Melanodrymia* Hickman, 1984 (shell, radula, external morphology: Hickman 1984; Warén & Bouchet 1989; soft parts: Haszprunar 1989). The anatomical data combined with shell characters (Heß *et al.* 2008) underline a position inside Neomphalina, being also recently confirmed by molecular data (Kano 2008). Accordingly, both genera probably represent basal Neomphalina, which are not yet adapted to the hydrothermal vent habitat.

Yet, it is not clear if Neomphalina presents an early offshoot of Vetigastropoda or is more closely related to other gastropod clades. All similarities between Neomphalina and Vetigastropoda (Table 1) are plesiomorphic characters, with one exception: both taxa share ctenidial bursicles, which might serve with their highly complicated structure and specific position, as a synapomorphy (Szal 1971; Haszprunar 1987). However, absence (i.e. secondary loss) of bursicles occurs in a few vetigastropod groups (Pleurotomariidae, certain Lepetelloidea) and many Neomphalina. Accordingly, bursicles could have been present in a stem rhipidoglossate gastropod, and subsequently lost in all lineages except stem-Vetigastropoda and stem-Neomphalina, with subsequent losses within the latter two clades. So it is unclear at present, whether this feature represents a synapomorphic or symplesiomorphic character of a common clade or a parallelism of a grade. Moreover, the Neomphalina share a number of derived characters with Cocculinida, Neritimorpha, Caenogastropoda and Heterobranchia, such as the loss of the right kidney and the occurrence of glandular gonoducts. However, parallelism cannot be excluded (Haszprunar 1988; Ponder & Lindberg 1997; Sasaki 1998). Also molecular data cannot solve this problem at the moment (Kano 2008). All these together support Neomphalina as a group with affinities both to the Vetigastropoda and the remaining Orthogastropoda, perhaps representing a separate primary clade of rhipidoglossate gastropods.

Two further examples for taxa originally placed in the Skeneidae are the genus *Hyalogyrina* Marshall, 1988, and *Xenoskenea pellucida* (Monterosato, 1874), with *Skenea pellucida* as the original combination (Warén *et al.* 1993), which already have been transferred to the heterobranch Valvatoidea (Warén *et al*. 1993; Warén & Bouchet 1993). The corresponding microanatomical data have confirmed this placement (Speimann *et al*. 2007).

All these findings demonstrate that we have only scratched the surface of the polyphyletic assemblage "skeneimorph microgastropods"—close to 70 genera remain to be studied. Even species originally placed in the type genus *Skenea* are now placed in very distant clades, accordingly we expect major rearrangements. The combined evaluation of phenotypic and genotypic data will probably strongly modify our current understanding of vetigastropod and neomphalinan relationships. In addition, the microanatomical studies will also enhance our understanding about the biological constraints (*e.g.*, in reproduction) on these "microgastropods".

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Paper 2

Dillwynella voightae new species, a new skeneimorph gastropod (Turbinidae) from the western Atlantic and a new record of *Dillwynella modesta* (Dall, 1889)

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Dillwynella voightae new species, a new skeneimorph gastropod (Turbinidae) from the western Atlantic and a new record of *Dillwynella modesta* (Dall, 1889)

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ABSTRACT

Dillwynella is a marine gastropod genus found on natural wood falls and sunken algal holdfasts in the Caribbean Sea and the Pacific Ocean. *Dillwynella voightae* new species from the Gulf of Mexico was the second species found in the Atlantic. Previously known only from two localities in the Caribbean Sea, *D. modesta* (Dall, 1889) has now been recorded at a third site, off southeastern Brazil.

Additional keywords: Bathyal, deep sea, Skeneidae, wood fall

INTRODUCTION

Dillwynella modesta (Dall, 1889) was originally described as *Teinostoma* (*Dillwynella*) *modesta* (Dall, 1889a), in the family Trochidae. Later in the same year, Dall changed the status of *Dillwynella* to a full genus within the Trochidae (Dall, 1889b). The species was described from off St. Lucia (13°51.30′ N, 61°03.45′ W; Smith, 1889: 968), on coarse sand at a depth of 413 meters (Dall, 1889a). Marshall (1988) mentioned that at the same station the wood ingesting limpet *Pectinodonta arcuata* Dall, 1882 was also found, therefore both species may have lived originally on wood (Marshall, 1988). A second record of 5 specimens of *D. modesta* from off the coast of Georgia, USA (Dall, 1927) was given, but the specimens are mostly immature (Dall, 1927) and, according to Warén (pers. com.), in a very bad condition. Nowadays, the genus *Dillwynella* is referred to the subfamily Skeneinae, family Turbinidae (Marshall, 1988; Bouchet & Rocroi, 2005). Williams and Ozawa (2006) placed the Turbinidae inside the vetigastropod superfamily Trochoidea. This is the third record of *D. modesta* since the type lot was recorded. It is the first time that this species has been found south of the Caribbean Sea.

Marshall (1988) described *Dillwynella lignicola*, *Dillwynella haptricola,* and *Dillwynella ingens* from the New Zealand region. Hasegawa (1997) added the following four species from the Suruga Bay to this genus: *Dillwynella vitrea*, *Dillwynella planorbis*, *Dillwynella fallax* and *Dillwynella sheisinmaruae*. Macrophotographs of the species described by Hasegawa are illustrated in Okutani (2000: 84–85). All these species of *Dillwynella* were associated with sunken wood, except *Dillwynella haptricola* Marshall, 1988, which lives on sunken algal holdfast (Marshall, 1988) in depths of 529–1200 m.

Ganesa panamensis Dall, 1902 may be a ninth species included in the genus *Dillwynella*. It was found in the Gulf of Panama at a depth of 1865 meters in mud and has never been found outside this type locality. In his description and figure five years later, Dall (1902; 1908) recorded the genus with a question mark and stated his uncertainty about the status of *Ganesa*. The shell figured (Dall, 1902: pl. 19, fig. 4) resembles that of a *Dillwynella* species. If it were to be reclassified within *Dillwynella*, not only it would be the first species of this genus found in the eastern Pacific, but would also be the deepest occurring one.

Dillwynella voightae new species is the second species of this genus described from the Atlantic region.

MATERIALS AND METHODS

The specimens were fixed in formaldehyde and preserved in ethanol. Pictures of the shells with soft parts in ethanol and of the dried shell were taken with a macro objective and digital camera. After drying of the specimen, the body was pushed into the shell gently, with a needle, to disconnect the columellar muscle. Afterward, the shell with the soft parts was rehydrated in a solution of water and very little dishwashing liquid. With a hooked needle, the body was then pulled out of the shell (Geiger et al., 2007). For the scanning electron microscope (SEM), the rehydrated soft parts were critical-point dried. To facilitate acquisition of more information on the soft parts, the mantle roof was removed after the first SEM session and mounted separately. Both the soft parts (without the mantle roof) and the mantle roof itself were examined again under SEM. After image-acquisition of the body under SEM, the head-food was dissolved in KOH and the radula cleaned and mounted for SEM. For the SEM of the shell (paratype), the operculum and the radula were air dried. All SEM specimens were coated twice with gold from different orientation, for 180 seconds.

Institutional abbreviations used are: FMNH: The Field Museum of National History, Chicago, USA; MNHN: Muséum National d'Histoire Naturelle, Paris, France; and USNM: National Museum of Natural History, Washington, DC, USA.

SYSTEMATICS

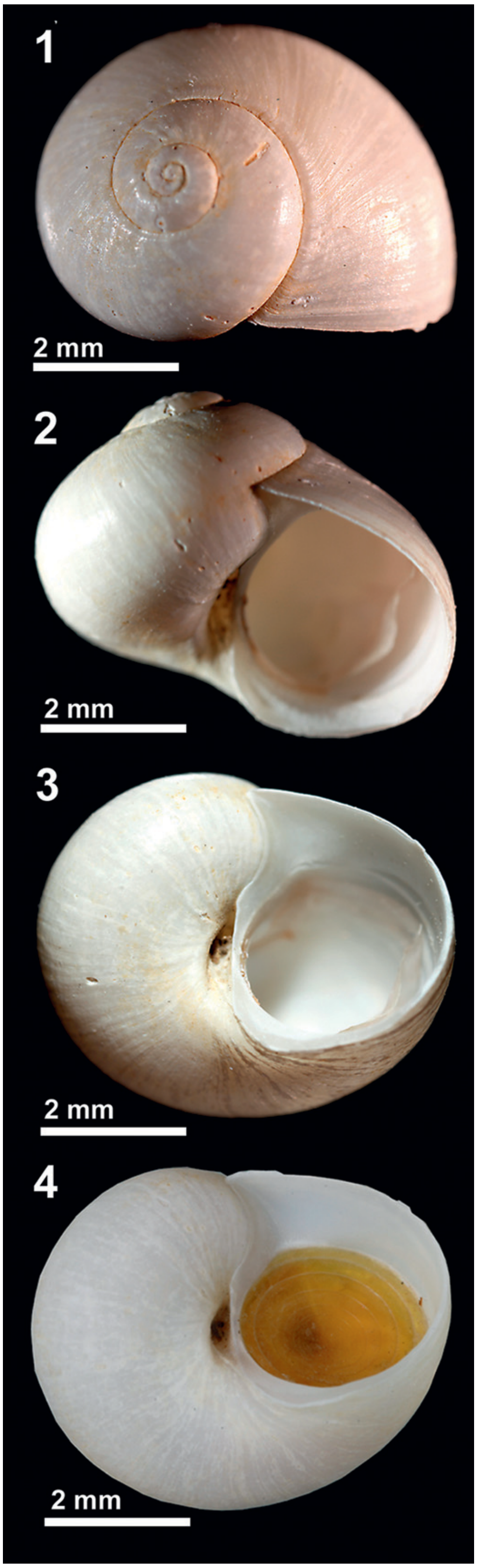
Family Turbinidae Rafinesque, 1815
Subfamily Skeneinae Clark, 1851
Genus *Dillwynella* Dall, 1889

Type Species: *Dillwynella modesta* (Dall, 1889) (by subsequent lectotype designation of Marshall, 1988)

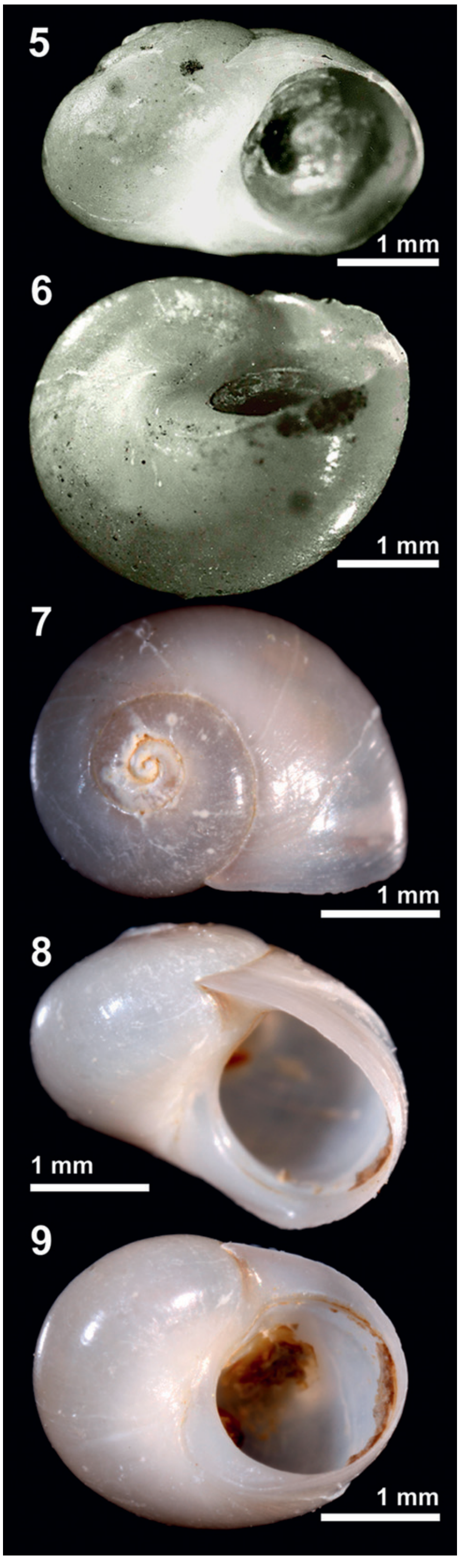
Dillwynella voightae new species
(Figures 1–4, 10–20)

Description: Protoconch (paratype, Figures 10–11): Most specimens badly corroded. Pictures of protoconch (Figure 11) are taken from a juvenile specimen (shell diameter = 1.5 mm). Protoconch 390 µm maximum diameter, 0.5 whorls, covered by a thick deposit, hiding all structures. Teleoconch (holotype, Figures 1–4): Adult shell with 2.7 whorls, large (diameter 5.8 mm, height 4.8 mm), rather thin and fine, color pure white. Teleoconch smooth, except for growth lines, which are prosocline and cover entire teleoconch. Suture distinct and narrow, getting a little deeper on first half whorl. First quarter of apical teleoconch whorl with a median, strong, spiral rib starting quite strong at the border of protoconch and teleoconch, fading out and disappearing (Figure 11). Umbilicus a narrow chink, demarcated by inner lip, distinct, elongated, oval, and deep. Aperture moderately D-shaped. Parietal callus thin. Lower part of the outer lip broad. Parietal glaze thin.

Operculum (Holotype, Figures 4, 12): Diameter 2.8 mm, multispiral, moderately thick, short growth edge; yellow, partly brownish, translucent at outer edge.



Figures 1–4. *Dillwynella voightae* new species (holotype, FMNH 312467, Gulf of Mexico, 5.8 mm width).



Figures 5–9. *Dillwynella modesta* (Dall, 1889). **5–6.** Lectotype (USNM 859220, off St. Lucia, 3.9 mm width). Photos by A. Warén. **7–9.** MNHN unnumbered, off southeastern Brazil, 3.1 mm width).

Radula (Holotype, Figures 16–18): Formula n-5-1-5-n, length 3.5 mm, width 300 µm. Central tooth large, with broad and smooth cutting edges, shaft reduced to a low ridge, not hooked at tip. Lateral teeth longer than broad, outer teeth getting larger, S-shaped, tip strongly hooked, cutting area long and smooth. Marginal teeth slender, elongated and simple, with smooth edge, strongly hooked at tip. Third to fourth marginal teeth longest, getting shorter and narrower laterally. Jaws present, with prismatic elements, thin (Figure 20).

Gross Anatomy (Holotype, Figure 13–15): Body flesh-colored; snout broad and flat; cephalic tentacles broad at basis, getting long and slender at tip, with sensory papillae. Large, V-shaped propodium. [Due to drying and rehydration of soft parts, small structures like eyestalks and suboptic tentacles were stuck together and could not be seen.] Four epipodial tentacles on each side of mesopodium. Three epipodial tentacles, relatively short, conical shaped with laterally placed sensory papillae. First one has attached a small accessory tentacle, which is smooth and small, without sensory papillae (epipodial sense organ). Large number of sensory papillae present on mantle edge and mantle roof. [Attempts to separate the mantle roof from the soft parts caused exposure of gut contents, which consisted of wood fibers (Figure 19).

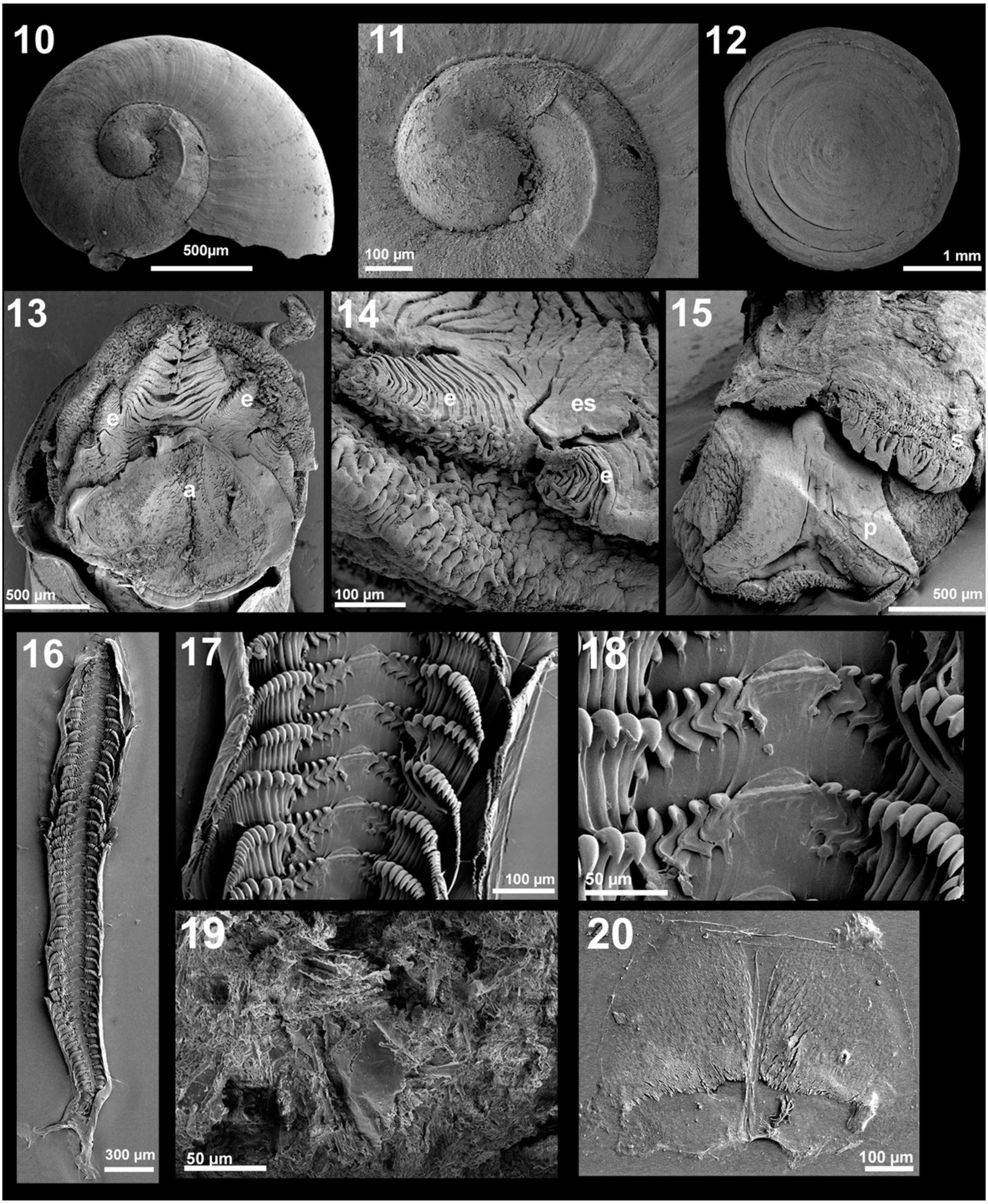
Type Material: Holotype: A dried shell, FMNH 312467 (Figures 1–4, 12–20). Paratypes: 16 specimens in ethanol, FMNH 312220, 1 juvenile shell dried, used for SEM pictures of the protoconch, FMNH 312468 (Figures 10–11).

Type Locality: North Atlantic, Gulf of Mexico, Louisiana, U.S.A. (27°44.09′ N, 91°14.49′ W), natural wood fall, 610 m depth. The sample was taken by the grab of the DSV Johnson-Sea Link I (operating from R/V Seward Johnson), 19 Aug. 2006.

Material Preservation: The specimens were fixed in formalin and stored afterward in 70% ethanol.

Etymology: Named after Dr. Janet R. Voight, Field Museum of Natural History, who collected the specimens.

Comparative Remarks: *Dillwynella voightae* new species is the largest described species of this genus. The teleoconch resembles *Dillwynella vitrea* Hasegawa, 1997, *D. haptricola* Marshall, 1988, and *D. modesta* (Dall, 1889). These four species have a distinct, median strong spiral rib on the beginning of the protoconch and have no ribs in the area around the umbilicus. *Dillwynella vitrea*, *D. haptricola,* and *D. voightae* differ by the shape of their umbilicus. *Dillwynella vitrea* has a distinct big umbilicus, whereas *D. voightae* shows a narrow chink, and *D. haptricola* a small chink almost closed by its thin inner lip. *Dillwynella modesta* (Figures 5–9; SEM images: Marshall, 1988: fig. 2: D–E) differs by lacking an umbilicus.



Figures 10–20. *Dillwynella voightae* new species. **10–11.** Juvenile specimen shell (paratype, FMNH 312220, shell 2.9 mm width). **10.** Shell. **11.** Protoconch of juvenile specimen shell. **12–20.** Holotype (FMNH 312467, 5.8 mm width). **12.** Operculum. **13.** Ventral view of foot. **14.** Epipodial tentacles and epipodial sense organs. **15.** Lateral view of soft parts with propodium and snout. **16–18.** Radula. **19.** Gut content. **20.** Jaw. Abbreviations: **a,** attachment area of the operculum; **e,** epipodial tentacle; **es,** epipodial sense organ; **s,** snout; **p,** propodium.

Distribution: Known only from type locality.

Remarks: The wood fibers in the gut show that *D. voightae* feeds directly on wood and grazes not only on the bacteria film.

Dillwynella modesta (Dall, 1889)

Type Material: Lectotype: A dried shell, USNM 859220 (Marshall, 1988; originally syntype USNM 95077, after Dall, 1889a), illustrated in Dall (1889a), macrophotographs (Figures 5–6). Paralectotype: A dried shell, USNM 95077; SEM pictures in Marshall (1988: 958, 993).

Type Locality: St. Lucia at Blake Station 205 coarse sand in 413 meters depth.

Material Examined: Two dry specimens, one empty shell, and one shell with soft parts, MNHN (Figures 7–9), off southeastern Brazil (23°47′ S, 42°10′ W), N.O. Marion Dufresne, Cruise MD 55, Bouchet, Leal, and Métivier coll. May 1987, sta. CB105, 610 m depth.

Distribution: Western Atlantic from Gulf of Mexico to Brazil, but only known from three localities.

Remarks: The specimens of *Dillwynella modesta* found off Brazil (Figures 7–9) are quite similar to the types. This is the second finding of this species and shows its wide distribution. Unfortunately, there are no data available for the substrate of the specimens.

DISCUSSION

The presence of an epipodial sense organ at the base of the papillate epipodial tentacles, described by Crisp (1981) and histology shown for microgastropods in Kunze et al. (2008), underlines the position of this genus in the Trochoidea/Turbinoidea (Bouchet and Rocroi, 2005). To solve its precise position in this group and confirm the position in the Skeneinae more information like microanatomy or sequencing are needed. The new record of *Dillwynella modesta* shows its wide occurrence in the western Atlantic. It also demonstrates how rare and incomplete the records of sunken wood species are in this area.

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Paper 3

3D-interactive microanatomy of *Ventsia tricarinata* Warén & Bouchet, 1993 from Pacific hydrothermal vents (Vetigastropoda: Seguenzioidea)

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Journal of Molluscan Studies: in review

3D-INTERACTIVE MICROANATOMY OF *VENTSIA TRICARINATA* WARÉN & BOUCHET, 1993 FROM PACIFIC HYDROTHERMAL VENTS (VETIGASTROPODA: SEGUENZIOIDEA)

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ABSTRACT

The microanatomy of *Ventsia tricarinata* Warén & Bouchet, 1993, a small coiled 'skeneimorph' gastropod from Pacific hydrothermal vents, is described based on computer-aided reconstructions of semi-thin section series and visualized by interactive 3D modeling. This is the most complete account of the anatomy of a seguenzioid presented to date. This species was placed originally in the Skeneidae (Trochoidea), but molecular data subsequently suggested a basal seguenzioidean position. The latter hypothesis is supported herein by morphological data, in particular by the conditions of the epipodium (separated epipodial sense organ) and the type of seminal receptacle with concentric arrangement of sperm.

INTRODUCTION

The superfamily Seguenzioidea has been placed either as a separate 'archaeogastropod' clade (e.g., Jeffreys, 1876; Golikov & Starobogatov, 1975; Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988) or within the Vetigastropoda (e.g., Seguenza, 1876; Quinn, 1983b; Ponder & Lindberg, 1997; Sasaki, 1998; for historical reviews of this controversy see Quinn, 1983b and Kano, 2008). Whereas the vetigastropod nature of Seguenzioidea is currently accepted (e.g., Bouchet *et al.*, 2005; Geiger *et al.*, 2008; Aktipis *et al.*, 2008; Aktipis & Giribet, 2010), the internal systematics and content of the group are far from settled because of the poor knowledge of seguenzioid taxa and potential vetigastropod outgroups. Most studies on seguenzioid species have dealt only with the shell, operculum, radula and few characters of the head-foot (e.g., Watson, 1879; Quinn, 1983b, 1987, 1991; Marshall, 1983, 1988a, b, 1991; Warén & Bouchet, 1993; Poppe *et al.*, 2006; Zelaya *et al.*, 2006). Kano *et al.* (2009) provided a thorough overview of shell, external morphology and molecular data of all known species in the genus *Adeuomphalus*, but the internal anatomy was not covered. So they reported for example papillate cephalic tentacles, papillate epipodial tentacles and smooth ESOs for *Adeuomphalus collinsi* Kano, Chikyu & Warén, 2009 and *A. trochanter* Warén & Bouchet, 2001. Knudsen (1964) described details of the head-foot of *Guttula galatheae* Knudsen, 1964. McLean (in Quinn 1983b) also provided some comments on the morphology of the external head-foot of *Seguenzia megaloconcha* Rokop, 1972. Quinn (1983b) briefly described the external anatomy and some anatomical characters of *Seguenzia* cf. *eritima* Verrill, 1884, but did not provide information on renopericardial ducts or internal reproductive organs. Quinn (1983b) also failed to find the right kidney, although this is present in all Vetigastropoda so far studied, and a hypobranchial gland and an osphradium were not observed.

In his morphological analyses Haszprunar (1988, 1993) refers to personal observations of sections of *Carenzia carinata* (Jeffreys, 1876) and provided a sketch of an aspect of its anatomy (Haszprunar, 1988: fig. 2Q). Sasaki (1998) used sections of *Seguenzia* sp. for his description but only selected characters useful for his phylogenetic analysis are mentioned by him. Thus, until now a comprehensive description of the anatomy of any seguenzioid species is lacking.

To summarise, we have limited anatomical data of only two seguenziid genera, *Seguenzia* and *Carenzia*. However, many details like renopericardial ducts are entirely missing and phylogenetically important features including the state of the bursicles (Haszprunar, 1988; Sasaki, 1998; Geiger *et al.*, 2008) are not unequivocally reported.

Recently, a number of small, ‘skeneimorph’ gastropods have been investigated by means of semithin serial sectioning and computer-aided 3D reconstruction of the anatomy. Two groups have been shown to be placed outside the trochoid-skeneimorph assemblage: *Leptogyra, Leptogyropsis,* and *Xyleptogyra* are to be classified close to *Melanodrymia* within the Neomphalina (Heß *et al.*, 2008; Kunze *et al.*, 2008), whereas *Hyalogyrina, Hyalogyra,* and *Xenoskenea* belong (as Hyalogyrinidae) to the ectobranch Heterobranchia (Warén *et al.*, 1993;

Speimann *et al.*, 2007; Kunze *et al.*, 2008; Haszprunar *et al.*, 2011). To characterise the nominal family, Skeneidae, microanatomical studies on the type species, *Skenea serpuloides* (Montagu, 1808), are in progress. Within this paper we present a detailed 3D-anatomical data set of a 'skeneimorph' seguenzioid vetigastropod in order to confirm Kano's (2008) conclusions concerning a seguenzioid nature of *Ventsia tricarinata* Warén & Bouchet, 1993 based on molecular sequence data and in so doing complement and refine the existing data on the superfamily.

MATERIAL AND METHODS

Paratypes of *Ventsia tricarinata* from hydrothermal vents at Hine-Hina site, Lau Basin, Fiji (22°32'S, 176°43'W, 1,900 m depth) were examined for the internal anatomy and histology (MNHN Moll 20947; section series 20948, 20949, 20950, 20951). Figures in this paper are taken from following specimens: 3D reconstructions and histology of female specimen: MNHN Moll 20949; Histology of male specimen: MNHN Moll 20948. Non-type material used for SEM observation also originated from Hine-Hina (1,847 m depth, ROV Jason 2, Dive 145; SMNH 78573). For details of the habitat, see Jones & Bright (1985) and Warén & Bouchet (1993).

The shell was decalcified with Bouin's fluid (saturated picric acid, glacial acetic acid and 37% formaldehyde in a mix ratio of 15:1:5) and the remaining soft body rinsed in 70% ethanol with a drop of ammonia. After dehydration in an ethanol series the specimens were embedded in epoxy resin after Spurr (1969). Semi-thin section series were cut with diamond knife (Diatom) or glass knife with the glue-method according to Ruthensteiner (2008), stained with a 1:1 mixture of methylene blue and toluidine blue, heated for approx. 10 s at 80 C°

Table 1. Overview of section series of *Ventsia tricarinata* Warén & Bouchet, 1993, with type of knife and sealing reagent used.

MNHN inventory number	Sex	Type of knife	Slice-thickness	Sealing detergent
Moll 20948	Male	Glas	2 µm	Cedar oil
Moll 20949	Female	Diamond	1.5 µm	DPX*
Moll 20950	Female	Diamond	1.5 µm	DPX*
Moll 20951	Female	Glas	2 µm	Cedar oil

*DPX Mounting Medium (Agar Scientific, Essex).

(Richardson *et al.*, 1960; Ruthensteiner, 2008) and sealed with DPX (Agar Scientific, Essex) or cedar oil (Table 1).

The sections were photographed with a digital camera (Olympus Camedia C-5060) mounted on a light microscope (Olympus CX 41, objective Plan C 10x). The digital images were pre-processed in Adobe Photoshop: RGB-images set to greyscale, contrast and brightness adjusted and size reduced by resampling. Thereafter the images were imported in AMIRA Resolve RT 4.2 (TFG Template Graphics Software, Inc., USA). In AMIRA the 3D reconstructions were performed after manual segmentation (Ruthensteiner, 2008), snapshots of the surface-model were taken and morphometric measurements were performed. Morphometric values are given on an information basis about size dimensions of the species, as such values depend on the size and the retraction grade of the specimen. The 3D-PDF was created with Adobe Acrobat 3D according to Ruthensteiner & Heß (2008).

RESULTS

All measurements are approximate values (variance of 2%) without mentioning “approx.” before each value in the text. Most of the anatomical descriptions and measurements were made on the section series of an adult female specimen (MNHN Moll 20948). In cases where other section series were used, it is mentioned as such in the text (e.g. male one, other female series).

External morphology

SEM pictures of the body, head-foot and tentacles are shown in Figure 1A–D. The retracted body removed from the shell has a diameter of 1,150 µm and a maximum width of 600 µm (Fig. 2A). The visceral mass consists of one whorl (580 µm in height) and loops on the right side of the mesopodium.

The snout is conical and ends blunt with the mouth opening lying terminal-ventral (Figs 1A, 2C, D). The snout is flattened with a pair of terminal-lateral bulges of 80 µm in length. There is a single pair of cephalic tentacles (Figs 1A–D, 2A, C, D, 3C). They are long (600 µm) and slender, smooth on the dorsal side but elsewhere covered densely with sensory papillae. Due to the poor state of histological preservation inside the tentacles only the black stained nuclei of the diagonal and longitudinal muscles are visible. At the base of each tentacle the tentacle nerve is thickened where it emerges from the cerebral ganglion. The neck forms two neck lobes on the right (Figs 1D, 2C). The anterior lobe is larger (250 µm in length and 90 µm in width). It is formed roughly rectangular, thickened on the distal end with small appendices. The posterior neck lobe is smaller and oval. Light microscopy could not reveal the innervations of the neck lobes. The longitudinal muscles are found directly beneath the epithelium. Both lobes are densely ciliated.

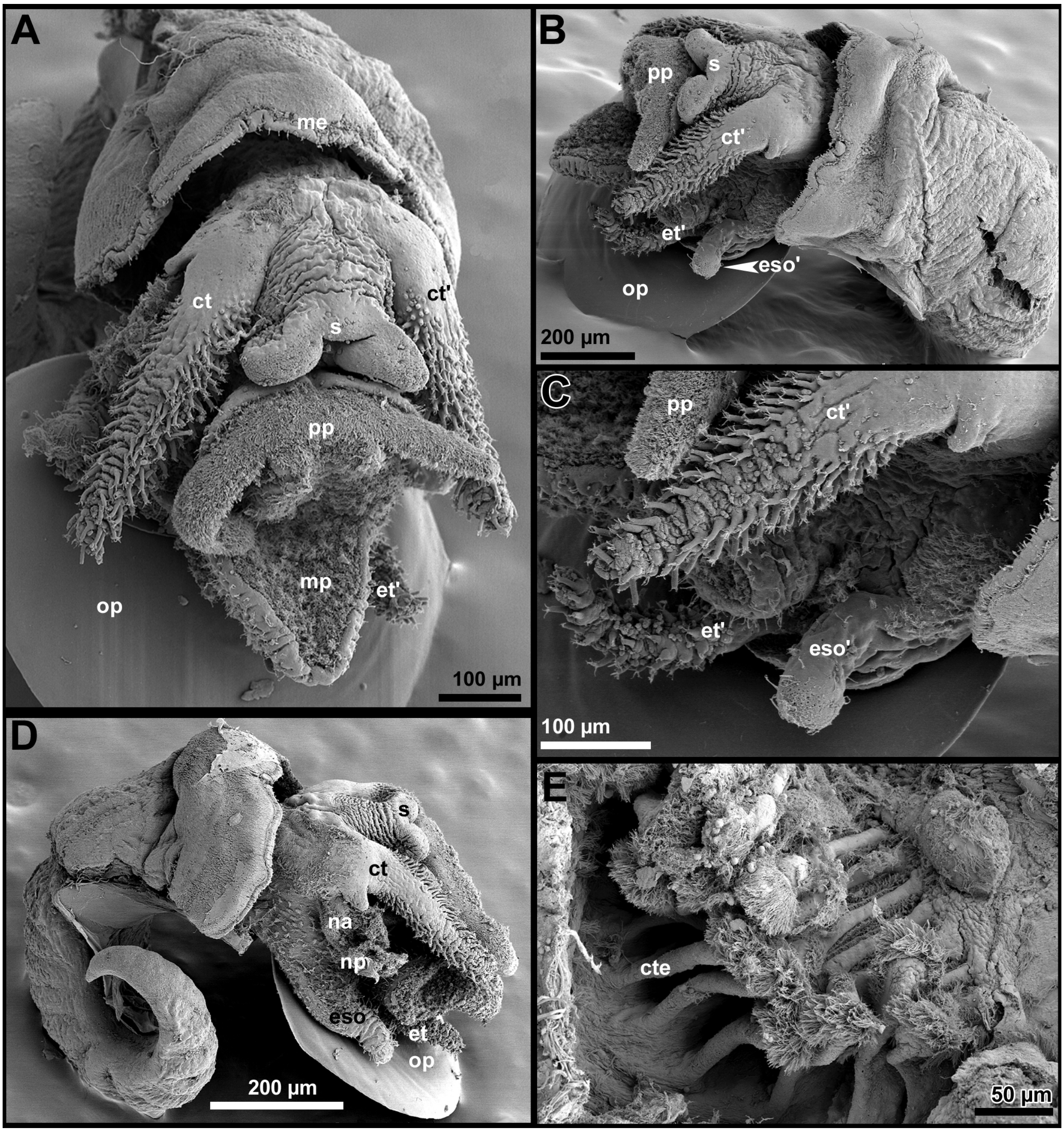

Figure 1. SEM pictures of the body of *Ventsia tricarinata*.

A. Frontal view of body and operculum. **B.** Left side of body with operculum. **C.** Tentacles of the left body side. **D.** Right side view of body with operculum. **E.** Ventral view of mantle roof with gill (removed from the body) (SEM images by A. Warén). Abbreviations: ct/ct', right/left cephalic tentacle; cte, ctenidium; eso/eso', right/left epipodial sense organ; et/et', right/left epipodial tentacle; me, mantle edge; mp, mesopodium; na, anterior neck lobe; np, posterior neck lobe; op, operculum; pp, propodium; s, snout.

Two pairs of epipodial tentacles, formed by the foot, are located beneath the operculum. The anterior pair lies left and right just in front of the operculum, being small, compact cylindrical and not covered by sensory papillae (80 µm in length and 120 µm in diameter). These tentacles are 'epipodial sense organs' (ESO), characterised by a thickened sensory epithelium on the tips (Figs 1B–D, 2C, D, 3C, E). The posterior pair of 'true' epipodial tentacles is located below the posterior part of the operculum. It is much longer (290 µm in length and 85 µm in width) and densely covered by sensory papillae (Figs 1B–D, 2C, D, 3B). The operculum is round-oval (600 x 750 µm) and multispiral with a central nucleus. It is located on the dorsal-posterior part of the metapodium.

Due to retraction the foot is folded double in the representative female specimen. The anterior pedal gland (Figs 2B, 3C) lies in the dorsal part of the propodium. It consists of loosely arranged cells, dark stained, with small vacuoles. The pedal gland opens via a channel at the anterior tip of the propodium. The sole is ciliated and contains many gland cells and there are many large, grey stained, sub-epithelial sole gland cells that open individually to the

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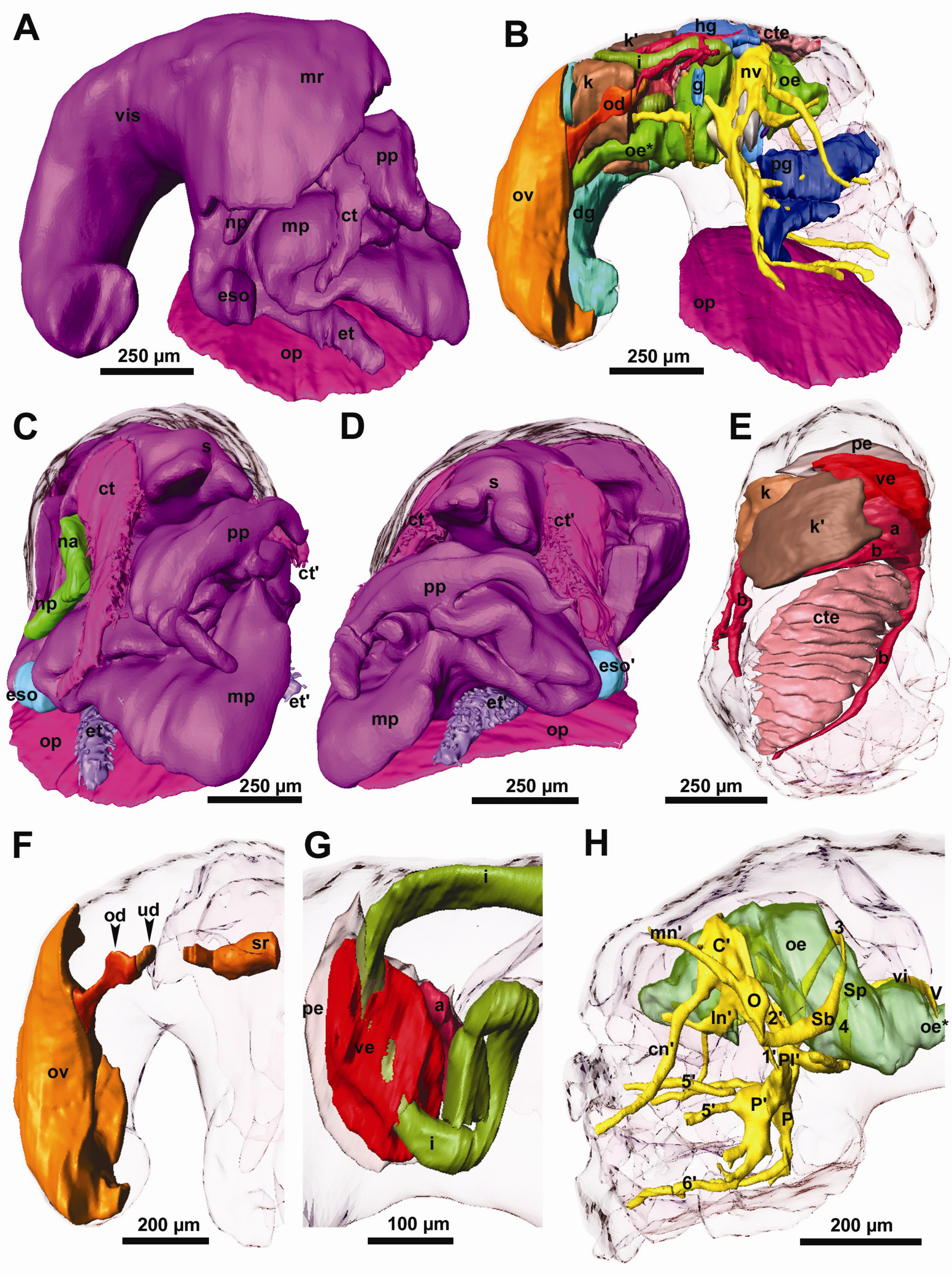
Figure 2. 3D reconstructions of the body of a female specimen of *Ventsia tricarinata* (end of the visceral mass was broken off during embedding).

A. Right side view of body. **B.** Right side view of animal with all inner organs, body surface transparent. **C.** Latero-frontal view of the right side, mantle roof transparent, tentacles coloured. **D.** Latero-frontal view of the left side, mantle roof transparent, tentacles coloured. **E.** Dorsal view of ctenidium, vascular and excretory system, body surface transparent. **F.** Right side view of the reproduction system, body surface transparent. **G.** Ventral view of the heart and the intestine, pericardium and body surface transparent. **H.** Left side view of the nervous system, oesophagus and body surface transparent. Abbreviations: a, auricle; b, blood vessels; C', left cerebral ganglion; cn', left cephalic tentacle nerve; ct/ct', right/left cephalic tentacle; cte, ctenidium; dg, digestive gland; eso/eso', right/left epipodial sense organ; et/et', right/left epipodial tentacle; g, gland at mantle edge; hg, hypobranchial gland; i, intestine; k/k', right/left kidney; ln', left labial nerve; mn', left mantle nerve; mp, mesopodium; mr, mantle roof; na, anterior neck lobe; np, posterior neck lobe; nv, nervous system; O, osphradial ganglion; od, oviduct; oe/oe*, anterior/posterior oesophagus; op, operculum; ov, ovary; P/P', right/left pedal ganglion; pe, pericardium; pg, anterior pedal gland; Pl', left pleural ganglion; pp, propodium; s, snout; Sb, suboesophageal ganglion; Sp, supraoesophageal ganglion; sr, seminal receptacle; ud, urogenital duct; V, visceral ganglion; ve, ventricle; vi, visceral loop; vis, visceropallium; 1', left cerebro-pedal connective; 2', left cerebro-pleural connective; 3, pleuro-suboesophageal connective; 4, pleuro-supraoesophageal connective; 5', left anterior pedal nerves; 6', left posterior pedal nerves.

The **interactive 3D model** of *Ventsia tricarinata* can be accessed by clicking into Fig. 2 (Adobe Reader Version 7 or higher required). Rotate model by dragging with left mouse button pressed, shift model: same action + ctrl, zoom: use mouse wheel (or change default action for left mouse button). Select or deselect (or change transparency of) components in the model tree, switch between prefab views or change surface visualization (e.g. lightning, render mode, crop etc.).

foot sole. The foot mass includes muscle fibres, colloblasts and blood sinuses, as well as small, round, finely granulated cells (rhogocytes).

The attachment points of the two shell muscles and the shell are located in the transition area between the cephalopodium and visceropallium. In the anterior part of the foot



the fibres of both muscles are intertwined. The left one is attached to the shell on the level of the seminal receptacle and ends posteriorly at the level of the ventricle. The right shell muscle reaches much more posteriorly to the edge of the right kidney. Its adhesion zone is found at the level of the middle part of the oesophagus.

Mantle cavity

The mantle cavity is 640 µm deep and takes less than a half whorl of the body. In the anterior part the mantle roof is thin and thickens posteriorly around the embedded organs. The mantle is thickened terminally on both sides at the mantle margin, bearing blood spaces and many muscle cells. The single, left ctenidium, the osphradium, and the seminal receptacle are located in the left mantle roof. The right portion of the mantle cavity bears the hypobranchial gland and rectum and shows the urogenital and anal opening. The heart and both kidneys are situated at the middle of the posterior end of the mantle cavity. There is a mantle gland on both sides of the anterior adhesion part of the mantle roof and visceropallium. This gland has two types of mucous cells, one large (25 µm in height) and non-staining, the other are smaller and filled with greyish granules. The anterior edge of the mantle bears the periostracal groove and it is slightly bent outward. The whole mantle margin lacks sensory papillae, but its inner side shows large glandular cells.

The single, left osphradium is found in the very left part of the mantle cavity, between the left mantle gland and the ctenidium and proximal of the osphradial ganglion. The single, left monopectinate ctenidium occupies the left part of the mantle cavity. The ctenidial axis is fused with the mantle roof. The complete gill (480 µm in length and 240 µm in maximum width) consists of 14 lamellae (Figs 1E, 2E, 3G). The first anterior two gill lamellae are small and located median on the mantle roof. The posterior ones are much larger (up to 200 µm in length) and claviform in cross section. The distal, efferent parts of the lamellae are covered with cilia and have bursicles and skeletal rods (see below for details). The single hypobranchial gland (230 µm in length and 35 µm in height) is embedded in the mantle roof between the gill and rectum. The cells are uniformly shaped, stain grey and with fine grained contents. The gland is not divided into histologically different parts.

Both the left and the right kidney opens into the mantle cavity (see excretory system). The rectum runs through the right side of the mantle roof and opens into the right side of the mantle cavity. From the opening of the seminal receptacle on the left side (see genital system) a ciliary band (120 µm in length) origins and runs along the bottom of the mantle cavity until it ends median of the mantle cavity.

Vascular and excretory system

The monotocardian heart starts on the left posterior part of the mantle cavity and reaches back to the stomach. The heart consists of a pericardium, a single (left) auricle and the ventricle. The pericardium is 390 µm in length and boomerang-shaped. It is connected to the left kidney by a partly ciliated renopericardial duct (150 µm in length and 10 µm in diameter). There is no connection from the pericardium to the right kidney. The auricle is located in front of the ventricle, the latter is encircling the intestine (Fig. 2G). Pericardial vesicles (probably podocytes) are located in the walls of the auricle in high numbers and there are a few on the ventricle.

Due to the poor state of preservation and the minute size of the specimens, only the course of main blood sinuses could be reconstructed: (1) There is a sinus on both sides of the rectum; the left sinus (280 µm in length and up to 65 µm in diameter) is much larger than the right one (205 µm and 25 µm, respectively), and both are connected by a perirectal sinus. The right sinus is connected with the foot via the right side of the mantle. (2) The blood flows from the left sinus over the thin afferent gill sinus into the gill lamella. (3) The efferent gill sinus (570 µm in length and 40 µm in width) runs along the left side of the mantle roof to the auricle.

On the left mantle roof the left kidney is connected by an efferent sinus to the auricle. The anterior aorta (230 µm in length) emerges from the ventricle. The aorta lies on the left side of the body and dorsal to the seminal receptacle, branches into a couple of blood vessels and could not be traced beyond that point. A horizontal sinus is found ventral to the operculum over the whole width of the foot (350 µm in length). It is connected with the sinus of the mantle margin.

The left kidney (230 µm in length, 350 µm in width and 150 µm in thickness) is located posterior to the ctenidium and crosses the mantle cavity on the mantle roof (Fig. 2E). This kidney is structured like a papillate sac with many blood lacunae (Fig. 3J) and opens to the mantle cavity on the ventral side; the aperture is equipped by a sphincter muscle. The opening is located in the middle of the mantle roof, a little posterior to the level of the urogenital opening. The much larger and voluminous right kidney lies behind the mantle cavity between the oesophagus, stomach and heart, forming three main lobes (300 µm in diameter and 175 µm in length; Figs 2B, E, 3J). The cells of its uniform epithelium have large vacuoles. A small compressed tube origins from the right kidney and fuses with the oviduct to form a common urogenital duct. This duct runs about 50 µm anteriorly and provides passage of the excretory products from the right kidney and the eggs. The urogenital duct then enlarges and opens out (without a sphincter) into the right side of the mantle cavity. Distally the urogenital duct aperture is densely covered with cilia.

Genital system

Ventsia tricarinata is a gonochoristic species. The female genital system consists of an ovary, an oviduct and a seminal receptacle (Fig. 2F). Together with the digestive gland the large, homogeneous ovary fills the first half whorl of the broken visceral mass. The eggs show various developmental stages. The mature eggs are yolky and roundish with a diameter of about 130 µm, being covered by a thin vitelline layer (Fig. 3K). Measurements of three ripe eggs results in the following averaged volume fractions: yolky cytoplasm 92.8%, nucleus 6.7%, nucleolus 0.4%. The oviduct (220 µm in length) originates on the right side of the ovary and merges with the right renal duct to form the urogenital duct (see above). Its epithelium is non-glandular and lacks cilia, and its lumen was empty.

The cylindrical seminal receptacle (230 µm in length and 100 µm in diameter) is located at the left posterior corner of the mantle cavity (Figs 2F, 3H, I) and opens at its posterior end into the mantle cavity (Fig. 2F). The inner surface of the opening is covered with long cilia. The seminal receptacle of the investigated female specimen is filled with sperm. The anterior located sperm form an unorientated mass (Fig. 3H). Posteriorly the sperm become more orientated so that most posteriorly their tails point to the centre of the receptacle lumen while the sperm heads point outwards and attach the epithelial cells of the seminal receptacle (Fig. 3I).

The only male specimen sectioned is partly fragmented and poorly fixed. Therefore

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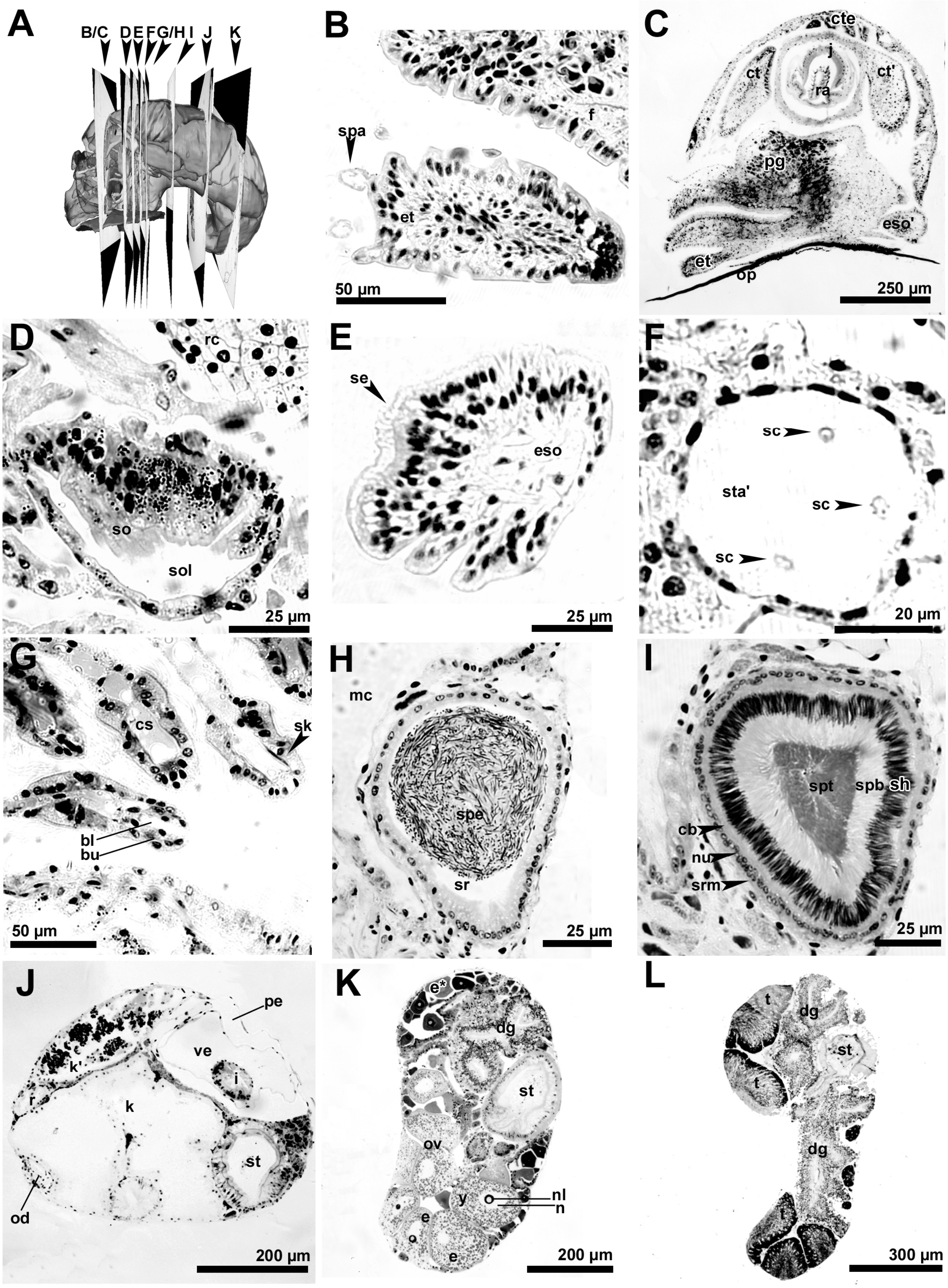
Figure 3. Histological details of *Ventsia tricarinata*.

A–K. Female specimen. **L.** Male specimen. **A.** Overview: 3D reconstruction with the orientation of the sections. **B.** Left epipodial tentacle with sensory papillae. **C.** Transverse section of the anterior body. **D.** Subradular organ. **E.** Right epipodial sense organ. **F.** Left statocyst with several statoconia. **G.** Apical tips of ctenidium leaflets. **H.** Anterior part of the seminal receptacle with dissolving sperms. **I.** Posterior part of the seminal receptacle. **J.** Transverse section of the body with ventricle encircling the intestine. **K.** Transverse section of the posterior body with ovary. **L.** Transverse section of a male specimen with testis. Abbreviations: bl, bursicle lumen; bu, bursicle; cb, cell bodies; cs, ctenidium sinus; ct/ct', right/left cephalic tentacle; cte, ctenidium; dg, digestive gland; e/e*, ripe/unripe eggs; eso/eso', right/left epipodial sense organ; et, right epipodial tentacle; f, foot; i, intestine; j, jaws; k/k', right/left kidney; mc, mantle cavity; n, nucleus; nl, nucleolus; nu, nuclei; od, oviduct; op, operculum; ov, ovary; pe, pericardium; pg, anterior pedal gland; ra, radula; rc, radular cartilage; sc, statoconia, se, sensory epithelium; sh, sperm heads; sk, skeletal rods; so, subradular organ; sol, lumen of subradular organ; spa, sensory papillae; spb, sperm bodies; spe, sperms; spt, sperm tails; sr, seminal receptacle; srm, muscle of seminal receptacle; st, stomach; sta', left statocyst; t, testis; ve, ventricle; y, yolk.

only a few characters of the male genital system can be described. The testis forms about 6–8 lobes and is found at the same relative position as the ovary in females (Fig. 3L). It could not be clarified, whether or not there is a penis formed by the anterior neck lobe and whether the proximal vas deferens also acts as a seminal vesicle.



Alimentary tract

The mouth opens anteriorly between terminal-lateral bulges of the snout and passes into the T-shaped oral tube (40 µm in length). This tube enlarges towards the buccal cavity, which has a pair of jaws and the radula. The jaws are located dorsally, are thin (10 µm), consist of densely packed prismatic elements and show a tooth like structure at the ventral rims.

Description and SEM photos of the rhipidoglossate radula are presented in Warén & Bouchet (1993). The s-shaped radula (260 µm in length) lies posterio-dorsal to the jaws. The radular diverticulum is short (100 µm), not bilobed, and with small dark-staining cells at the end. A short radular caecum is present. There is a single pair of radular cartilages (180 µm in height), which are in contact with several cross striated, buccal muscles (details of musculature not determined). The cartilage cells are small (8 µm in diameter) with small nuclei (4 µm in diameter) and large vacuoles. The subradular organ (Fig. 3D) is placed below the radula and radular cartilages (see below for details).

The buccal cavity narrows at the level of the radular cartilages and is followed by the pharynx. The pharynx is an upside-down Y in shape, with a densely ciliated dorsal food-channel. Its anterior end forms a short pouch. A single pair of salivary glands (120 µm in length and 60 µm in diameter) opens directly to the pharynx without any channel. The salivary glands are pouch-like and have a small lumen. The pharynx is slightly twisted clockwise (10°). After 100 µm the pharynx is continued by the voluminous anterior oesophagus, the epithelium of which is densely ciliated. The oesophagus here has short lateral pouches with papillae (mainly in the left part). The dorsal food channel disappears at the level of torsion at a dorsal-left position. The oesophagus abruptly narrows at the level of the auricle and makes a small loop to the left side. The posterior oesophagus leads straight backwards 330 µm; it is quite thin (60 µm in diameter) with a cross-shaped lumen in cross-section. At its beginning the wall of the posterior oesophagus contains high-prismatic, vacuole rich cells, and storage cells with concentrically layered, black to brown coloured granules are interspersed. The posterior oesophagus opens into the stomach on the right side between the openings of the digestive glands.

The stomach (365 µm in length and 170 µm in frontal width) abruptly enlarges up to a width of 360 µm in the posterior third, where the oesophagus enters. The glandular epithelium of the stomach wall consists of high prismatic cells (25 µm in height) with basally located nuclei. The basal part of the cytoplasm is clear; the apical one is rich in vacuoles and densely ciliated. The basal bodies of the cilia generate a uniform, dark line. The small gastric shield (140 µm in length and 65 µm in width) is oval in shape, and located on the dorsal side of the stomach, opposite to the short and broad style sac. In the area of the oesophagus opening the epithelial cells are small but with large vacuoles.

The two digestive glands form lobes, each with its own lumen. The epithelium consists of small gland cells with a compact microvillous border on the apical surface. Each digestive gland opens separately into the stomach; the left one postero-dorsal of the oesophagus, the right one postero-ventral.

The intestine (670 µm in length) originates from the elongated anterior part of the stomach, makes a large, counter-clockwise loop and continues as the rectum, which is encircled by the ventricle (Fig. 3J). The intestinal epithelium forms a deep, longitudinal groove, otherwise the cells are high prismatic (17 µm in height) with basal, centrally situated nuclei (5 µm in diameter). Following the loop the rectum (650 µm in length) runs straight through the mantle roof and opens anteriorly into the mantle cavity. The intestine and rectum are densely ciliated throughout.

Nervous system

The central nervous system is concentrated in the cephalopodium. It consists of four pairs of ganglia (cerebral, buccal, pleural and pedal ganglia) and four unpaired ganglia (osphradial, suboesophageal, supraoesophageal and visceral ganglion) (Fig. 2H). Especially the nervous system is affected by a quite poor state of preservation, hence a couple of small nerves (e.g. in the foot and neck lobes) are not visible.

The cerebral ganglia (70 µm x 20 µm x 170 µm) lie on the side of the pharynx at the level of the radular cartilage. They are connected by the cerebral commissure (length 170 µm) above the dorsal food channel of the pharynx. The paired buccal ganglia are located postero-lateral of the food channel. The buccal commissure runs in a small ventral loop below the posterior part of the pharynx. These ganglia are connected with the cerebral ganglia by short and thin cerebro-buccal connectives. At the anterio-ventral part of the cerebral ganglia the labial nerves emerge. The nerves of the cephalic tentacles are quite thick (20 µm), thicken at their bases and enter the cerebral ganglia laterally. The cerebropleural and cerebropedal connectives emerge from the ventral side of the cerebral ganglia. The pedal ganglia are very elongate (180 µm in height and 60 µm in length) and connected ventrally by the short, thick pedal commissure (70 µm in length and 20 µm in diameter). Posterio-dorsal of the pedal ganglia the statocysts are attached (see below). Nerves from the pedal ganglia supply the foot and the epipodial tentacles. The pleural ganglia (length 120 µm, diameter 25 µm) are connected with the pedal ganglia by the short, thick pleuro-pedal connective (hypoathroid condition).

The visceral loop is streptoneurous. The pleural-supraoesophageal connective (420 µm in length) runs from the right pleural ganglion over the oesophagus to the supraoesophageal ganglion on the left side. From here another connective leads to the osphradial ganglion and further upwards until it reaches the ctenidium. The connective from left pleural ganglion to the suboesophageal ganglion runs on the right side below the oesophagus. A small nerve runs from the suboesophageal ganglion into the shell muscle. Both oesophageal ganglia are connected by very thin connectives (reconstruction succeeded only in parts) with the small and inconspicuous visceral ganglion on its posterior end.

Sense organs

The cephalic tentacles and the posterior pair of epipodial tentacles are covered densely by sensory papillae, which are similar to a palm tree with a length of 15 µm (Fig. 1C). In contrast, the anterior pair of epipodial tentacles is smooth and equipped with a sensory epithelium (Fig. 3E; see above). Eyes are entirely lacking. The efferent edges of the gill lamellae have bursicles (Fig. 3G), located ventrally of the gill vessels covered by skeletal rods. The lobate lumen of each bursicle is found approximately in its centre. The ciliated osphradium lies flat on the mantle roof (70 µm in length and 10 µm in height). The nodular statocysts are located side by side, postero-laterally of the pedal cords. Each statocyst contains several statoconia (Fig. 3F). The subradular organ is located below the radula (Fig. 3D). Its dorsal cells have strongly stained nuclei and are filled with dark coloured granules. Several channels radiate from the ventral lumen of the organ into the dorsal cell layers.

DISCUSSION

Comparative character analysis

The presence of oral bulges, right-side neck lobes and in particular of papillate cephalic and epipodial tentacles and epipodial sense organs (ESOs) are typical of vetigastropods (Table 2). Separated epipodial sense organs, which are placed on smooth stalks proper, are also found in other seguenzioid genera (Tables 2, 3) like *Adeuomphalu*s (Kano *et al.*, 2009), *Xyloskenea* (Marshall, 1988b; Kano *et al.*, 2009) and *Carenzia* (G.H. & T.K., personal observation). They are also found in other vetigastropod clades such as Scissurellidae (T.K., personal observation) and Lepetodrilidae (Haszprunar, 1989a). The alternative type is the combined one, where the

ESO is attached to an epipodial tentacle with sensory papillae as found in the Angarioidea, Haliotoidea, Phasianelloidea and Trochoidea (e.g., Crofts, 1929; Crisp, 1981; Kunze *et al.*, 2008). Two projections on the right side beyond the cephalic tentacle (Fig. 2C: anterior and posterior right neck lobe) were also found in several other seguenzioid species (Kano, 2008: fig, 4) and described there as subocular penduncles, but this character was regarded to be a plesiomorphic condition (Kano, 2008).

Two shell muscles are a plesiomorphic character state in gastropods and characteristic for Patellogastropoda, Cocculinida, most Neritimorpha and many, but not all, Vetigastropoda (Haszprunar, 1985a, 1988; Ponder & Lindberg, 1997).

As outlined by Haszprunar (1988, 1993) and Ponder & Lindberg (1996, 1997) the loss of the right auricle or of the right ctenidium and the monopectinate (versus the plesiomorphic bipectinate) condition of the ctenidial leaflets occurred repeatedly in gastropod evolution and also several times within the Vetigastropoda (see also Hickman & McLean, 1990). Ctenidial bursicles are typical for Vetigastropoda, but also occur in certain species of the Neomphalina (e.g. *Melanodrymia aurantiaca* Hickman, 1984; cf. Haszprunar, 1989b). They have been reported previously in seguenzioids (Haszprunar, 1993; Ponder & Lindberg, 1997; Sasaki, 1998; Table 3), but we provide the first pictures of their morphology in the superfamily (Fig. 3G). Within the gill-leaflets there is no trace of symbiotic chemoautotrophic bacteria as found in some hot-vent gastropods (Sasaki *et al.*, 2010).

Two separate and differently structured kidneys are present only in Patellogastropoda and Vetigastropoda. Whereas the gametes are released via the right kidney in Patellogastropoda, most Vetigastropoda are characterised by a true gonoduct forming a common urogenital opening with the right kidney as found in *Ventsia tricarinata*, whereas the seguenziid *Carenzia carinata* (Jeffreys, 1877) has separate excretory and genital openings (Haszprunar, 1988).

Gonochoristic versus hermaphroditic gonads are of minor importance concerning the systematic placement in basal gastropod clades. However, the distinct vitelline layer of the yolky eggs is diagnostic for Vetigastropoda (including the Lepetelloidea; cf. Ponder & Lindberg, 1997). Small animals like *Ventsia tricarinata* can house only few eggs, accordingly internal or entaquatic fertilization is necessary to raise fertilization success. Therefore seminal receptacles and copulatory organs are commonly found in small, deep-water gastropod species (Kano, 2008). Unfortunately, the presence or absence of the penis could not be determined for *V. tricarinata* due to insufficient preservation of the single male available in the present study. Copulatory organs are reported for five species of Seguenzioidea (Table 3; see also Kano, 2008 and Kano *et al*., 2009 for review): *Bathymargarites* (Warén & Bouchet, 1989), *Carenzia* (G.H. & T.K., personal observation), *Guttula* (Knudsen, 1964), *Hadroconus* (Quinn, 1987) and *Seguenzia* (Quinn, 1983b), but only for *Carenzia* and *Seguenzia* a seminal receptacle has been described. However, the specific conditions of the separated seminal receptacle with its two regions and the concentric arrangement of the sperm cells in the posterior part (Fig. 3H, I; Table 2) have also been found in *Seguenzia* sp. (Sasaki, 1998; T. Sasaki, personal communication), *C. carinata* (G.H. & T.K., personal observation), and another skeneimorph

Table 2. Morphological and histological characters of *Ventsia tricarinata*, *Carenzia carinata* and *Seguenzia* spp.

	Ventsia tricarinata Warén & Bouchet, 1993	***Carenzia carinata*** (Jeffreys, 1877)	***Seguenzia* spp.**
Teleoconch	max. 2,5 mm	max. 4.2 mm	max. 4.5 mm[f]
Cephalic tentacles	with sensory papillae	with sensory papillae	with sensory papillae[c,d]
Epipodial tentacles	with sensory papillae	with sensory papillae	with sensory papillae[c,d]
ESO	single pair, smooth	single pair, smooth	present[b]
Anterior pedal gland	opening not cilliated	opening cilliated	present[b,d], opening?
Shell muscles	2	1[*]	1[*,b]
Ctenidium	monopectinate[*]	monopectinate[*]	monopectinate[*,c,d]
Skeletal rods	present	present	present[b,d]
Bursicles	present	present	present[b], (+)[d]
Right kidney	lobate, voluminous	lobate, voluminous	present[d]
Left kidney	papillary sack	papillary sack	present[d]
Genital system	gonochoristic	gonochoristic	? (gonochoristic?)[d]
Copulatory organ	?	penis[*]	penis[*,c]
Seminal receptacle	left mantle cavity[*]	left mantle cavity[*]	left mantle cavity[*,d]
Sperm arrangement	circular, heads outwards	circular, heads outwards	circular, heads outwards[d,e]
Eggs	yolky	yolky	yolky[d]
Vitelline layer	thin	thin	?
Alimentary system			
Jaws	rod-like	rod-like	rod-like[b,d]
Radula	rhipidoglossate, n+3+1+3+n[g]	no data[a]	5?-1-1-1-5?[d]
Radular cartilage	1 pair[*]	2 pairs	1 pair[d]
Oesophagus	papillate	papillate, narrow	?
Intestine	loops	loops, huge	few loops[d]
Rectum	no loops	several loops[*]	several loops[*,d]
Relation rectum/heart	heart encircling rectum	heart not encircling rectum	heart not encircling rectum[b,c]
Nervous system	pedal cords	pedal cords	pedal cords[b]
Statocysts	with statoconia	with statoconia	with statoconia[b]
Subradular organ	present	absent[*]	absent[b]

Citations: **a**, Marshall, 1983 (No radula data exist for *Carenzia carinata*, but there are some for the genus *Carenzia*: radula scheme (c.5+1+1+1+c.5), central tooth longer than broad); **b**, Ponder & Lindberg, 1997; **c**, Quinn, 1983b; **d**, Sasaki, 1998; **e**, T. Sasaki personal communication; **f**, Rosenberg, 2009; **g**, Warén & Bouchet, 1993. Abbreviations: *, apomorphic characters; ?, not stated in the literature or not detectable ; 1, The data for *Seguenzia* are a synopsis of all data available for this genus: Quinn (1983b) *Seguenzia* cf. *eritima*, Sasaki (1998) *Seguenzia* sp., Ponder & Lindberg (1997) *Seguenzia* sp., Rosenberg (2009) *Seguenzia eritima.*

seguenzioid, *Xyloskenea costulifera* Marshall, 1988 (G.H. & T.K., personal observation).

Teeth-like jaws consisting of prismatic elements, pouch-like salivary glands and a rhipidoglossate radula are characters typical for Vetigastropoda, but are also found in Neomphalina and in Hyalogyrinidae. Hyalogyrinids are basal Heterobranchia (e.g., Warén *et al.*, 1993; Speimann *et al.*, 2007) and are thus devoid of true cartilages (Katsuno & Sasaki, 2008; Haszprunar *et al.*, 2011) or a subradular sense organ (G.H., personal observation). *Ventsia tricarinata* has a radula similar to *Ventsia*, *Trenchia*, *Xyloskenea* and *Calliotropiiniae* (Warén & Bouchet, 1993; Kano, 2008; Kano *et al.*, 2009), but the similar radula type in some seguenziid gastropods was regarded together with shell characters as synplesiomorphic by Kano (2008). The posterior, broad and papillate oesophagus, stomach with the gastric shield, two digestive glands, looped intestine and rectum penetrating the heart in *V. tricarinata* reflect plesiomorphic gastropod conditions, whereas the longitudinal intestinal groove is typical for vetigastropods (Ponder & Lindberg, 1997).

As outlined by many authors (e.g., Haszprunar, 1988, 1993; Ponder & Lindberg, 1997, Sasaki, 1998), the hypoathroid and streptoneurous central nervous system is also a plesiomorphic gastropod feature, whereas the concentration of the pedal cords to true ganglia occurred several times in gastropod evolution. Deep-water gastropods often lack eyes (Sasaki *et al.*, 2010) as is the case in *V. tricarinata. Adeuomphalus* and *Xyloskenea* are further seguenzioid genera lacking pigmented eyes (Marshall, 1988b; Kano *et al.*, 2009). Statoconia are typical for all Vetigastropoda, but are also found in several other gastropod clades, e.g. Architectonicidae (Haszprunar, 1985b), Neritidae, Ampullariidae and Cerithiidae (Ponder & Lindberg, 1997).

Systematic placement of Ventsia tricarinata

The phylogenetic analyses of sequences of three genes (COI, 16S rDNA and Histone H3) provided evidence for a close relationship of *V. tricarinata* and *Xyloskenea* sp. (Kano, 2008; Kano *et al.*, 2009), as originally supposed by Warén and Bouchet (1993). These molecular data also suggest basal seguenzioid positions for *Ventsia* and *Adeuomphalus*, another skeneimorph genus being characterised by a strongly sculptured, planispiral shell. Aside from Seguenziidae, the current classification of Seguenzioidea also comprises *Spinicalliotropis* as well as the Cataegidae, Calliotropidae and Chilodontidae (Kano *et al.*, 2009), all formerly included in Trochoidea or even Trochidae (e.g., Hickman & McLean, 1990).

The vetigastropod nature of *V. tricarinata* is well supported by a large number of morphological characters: oral lappets, papillate cephalic and epipodial tentacles, ctenidium

Table 3. Overview of molecular and anatomical data available for Seguenzioidea genera.

Genus	Placed originally	Molecular data^{d,e}	Shell nacreous	External morphology		Anatomy	
				Tentacles, Neck lobes & Penis	ESO	Ctenidium	Inner organs
Seguenziidae							
Asthelys Quinn, 1987	Seguenziidae	n.r.	+^{h}	CT/ET, penis^{h}	n.r.	n.r.	n.r.
Bathymargarites Warén & Bouchet, 1989	Trochidae	+	+^{p}	CT/ET papillate, r/l neck lobe, penis^{p,q}	n.r.	bipectinate^{p}	rectum penetrates heart, testis, stomach, intestine^{p}
Carenzia Quinn, 1983	Seguenziidae	n.r.	+^{g,k}	CT/ET papillate, penis^{bt}	+^{t}	monopectinate, bursicles, skeletal rods^{t}	seminal receptacle, anatomy^{t}
Fluxinella Marshall, 1983	Seguenziidae	+	+^{g}	ET papillate^{n}	n.r.	n.r.	n.r.
Guttula Schepman, 1908	Trochidae	n.r.	+^{n}	CT and ET papillate^{n}, penis^{f}	n.r.	n.r.	anus^{f}, intestine^{n}
Hadroconus Quinn, 1987	Seguenziidae	+	+^{m}	CT papillate, ET, tentacle on mantle edge, penis^{m}	n.r.	n.r.	oesophagus, intestine^{m}
Halystes Marshall, 1988	Seguenziidae	n.r.	+^{h}	CT/ET, penis^{h}	n.r.	n.r.	n.r.
Seguenzia Jeffreys, 1876	Seguenziidae	+	+^{g}	CT/ET papillate, penis^{l,o}	+^{o}	monopectinate^{l,o}, skeletal rods, bursicles(?)^{o}	stomach, intestine^{l,o}, circulatory system, seminal receptacle^{o}
Sericogyra Marshall, 1988	Seguenziidae	n.r.	+^{h}	CT/ET papillate^{h}	n.r.	n.r.	n.r.
Calliotropidae							
Bathybembix Crosse, 1893	Trochidae	n.r.	+^{c}	CT/ET papillate, r/l neck lobe^{c}	n.r.	bipectinate, bursicles^{c}	n.r.
Calliotropis Seguenza, 1903	Trochidae	+	+^{d}	CT/ET papillate, r/l neck lobe^{c}	n.r.	bipectinate^{c}	n.r.
Ginebis Taki & Otuka, 1942	Trochidae	+	+^{f}	r/l neck lobe^{c}	n.r.	n.r.	n.r.
Turcica Adams & Adams, 1854	Trochidae	+	+^{t}	n.r.	n.r.	n.r.	n.r.
Cataegidae							
Cataegis McLean & Quinn, 1987	Trochidae	+	+^{j}	CT/ET^{j}, CT papillate, l/r neck lobe^{q}	n.r.	bipectinate^{j,q}, skeletal rods^{q}	kidneys, stomach, rectum hypobranchial gland^{q}

Table 3. Continued.

Genus	Placed originally	Molecular data[d,e]	Shell nacreous	External morphology		Anatomy	
				Tentacles, Neck lobes & Penis	ESO	Ctenidium	Inner organs
Chilodontidae							
Agathodonta Cossmann, 1918	Trochidae	+	+[c]	r/l neck lobe[c]	n.r.	bipectinate[c]	n.r.
Danilia Brusina, 1865	Trochidae	n.r.	+[c]	CT/ET, r/l neck lobe[a,c]	n.r.	bipectinate[c]	n.r.
Euchelus Phillipi, 1847	Trochidae	n.r.	+[c]	CT/ET papillate, r/l neck lobe[c]	n.r.	bipectinate[c]	n.r.
Granata Cotton, 1957	Trochidae	+	+[c]	CT/ET papillate, r/l neck lobe[c,d]	n.r.	bipectinate[c]	n.r.
Herpetopoma Pilsbry, 1890	Trochidae	+	+[c]	CT/ET papillate, r/l neck lobe[c]	n.r.	bipectinate[c]	n.r.
Hybochelus Pilsbry, 1890	Trochidae	n.r.	+[c]	r/l neck lobe[c]	n.r.	bipectinate[c]	n.r.
'Seguenzioid skeneimorphs'							
Adeuomphalus Seguenza, 1876	unassigned	+	-[e]	CT/ET papillate, r neck lobe[e]	+[e]	monopectinate[e]	n.r.
Akritogyra Warén, 1992	Skeneidae	n.r.	-[r]	CT/ET no papillae, r/l neck lobe[r,s]	n.r.	n.r.	n.r.
Anekes Bouchet & Warén, 1979	Skeneidae	n.r.	-[r]	CT/ET papillate, 1 pair ET smooth, r/l neck lobe[r]	n.r.	n.r.	n.r.
Granigyra Dall, 1889	Skeneidae	n.r.	-[s]	CT/ET no papillae, neck lobes[s]	n.r.	monopectinate[s]	pallial cavity, gonoduct, stomach, rectum[s]
Ventsia Warén & Bouchet, 1993	Skeneidae	+	-[q]	CT/ET papillate, 1 ET smooth, r neck lobe[q,t]	+[t]	monopectinate[q,t] skeletal rods, bursicles[t]	seminal receptacle, complete morphology[t]
Vetulonia Dall, 1913	Trochidae	n.r.	-[q]	CT/ET no papillae, r/l neck lobe[q]	n.r.	n.r.	n.r.
Xyloskenea Marshall, 1988	Skeneidae	+	-[i]	CT/ET[i]	+[t]	n.r.	n.r.
Incertae sedis							
Spinicalliotropis (Poppe et al., 2006)	Trochidae	+	n.r.	CT/ET[h]	n.r.	bipectinate[h]	n.r.

Citations: **a**, Beu & Climo, 1974; **b**, Haszprunar, 1988; **c**, Hickman & McLean, 1990; **d**, Kano, 2008; **e**, Kano *et al.*, 2009; **f**, Knudsen, 1964; **g**, Marshall, 1983; **h**, Marshall, 1988a; **i**, Marshall, 1988b; **j**, McLean & Quinn, 1987; **k**, Quinn, 1983a; **l**, Quinn,1983b; **m**, Quinn, 1987; **n**, Quinn, 1991; **o**, Sasaki, 1998; **p**, Warén & Bouchet, 1989; **q**, Warén & Bouchet, 1993; **r**, Warén, 1992; **s**, Warén, 1993; **t**, personal observation.

Abbreviations: CT, cephalic tentacles; ESO, epipodial sense organ; ET, epipodial tentacles; l, left; papillate, with sensory papillae; n.r., not reported in the literature – not known; r, right; +, present/available.

with skeletal rods and bursicles, two different kidneys, the left one as a papillary sac, the right one with an urogenital opening, the longitudinal grove in the intestine, a subradular organ and statoconia reflect vetigastropod conditions. In particular the eggs with vitelline layer are considered as diagnostic for Vetigastropoda. Because of the poor knowledge on the morphology of seguenzioid taxa, however, it is much more difficult to trace genuine seguenzioid characters in *V. tricarinata*. One major difference between Trochoidea and Seguenzioidea is found in the epipodial conditions. The presence of separate, papillate epipodial tentacles and smooth ESO-tentacles exclude *V. tricarinata* (and *Xyloskenea*) from the Trochoidea and thus also from the true Skeneidae, where combined epipodial tentacles are always present (Crisp, 1981; Kunze *et al.*, 2008). Up to now ESOs have been found in five seguenzioid genera (Tables 2, 3): *Adeuomphalus*, *Carenzia, Ventsia* and *Xyloskenea* all have separated ESOs (Kano *et al.*, 2009; G.H. and T.K. personal observation), while the type for *Seguenzia* has not been specified (Sasaki, 1998; Ponder & Lindberg, 1997). Skeneidae is additionally characterised by a propodial penis (Warén, 1992; Kunze *et al.*, 2008), which has not been found in any seguenzioid species (cf. Quinn, 1991). As outlined above, the specific conditions of the separated seminal receptacle might possibly represent a true synapomorphy of the whole Seguenzioidea. However, since data are available only from four genera (*Ventsia, Xyloskenea, Seguenzia* and *Carenzia*; a possible seminal receptacle has also been reported in *Spinicalliotropis*: Kano *et al.*, 2009), this hypothesis needs to be tested by investigating other species of the superfamily. Healy (1989) described the spermiogenesis of *Calliotropis glyptus* (Watson, 1879) and paid attention to the unusual embedding of the acrosomal apparatus in the sperm nucleus, whereas Trochidae (e.g., Azevedo *et al.*, 1985; Hodgson *et al.*, 1990), Skeneidae (Healy, 1990a), Haliotidae (e.g. Gwo *et al.*, 1997; Healy *et al.*, 1998; Singhakaev *et al.*, 2003), Scissurellidae (Healy, 1990b), Fissurellidae (Hodgson & Foster, 1992; Hodgson & Chia, 1993), Lepetodrilidae (Hodgson *et al.*, 1997) or Pleurotomariidae (Healy, 1988) do not show this character. Unfortunately, the fine structure of sperm has not been investigated for other seguenzioids. Accordingly, it is unclear (but intriguing) whether the embedded acrosome is a character of the genus alone, of all Calliotropidae or of the whole Seguenzioidea.

To summarise, although there is no clear phenotypic character unequivocally supporting the seguenzioid nature of *V. tricarinata*, there is not a single character contradicting this hypothesis. Compared with the seguenziid genera *Carenzia* and *Seguenzia*, *V. tricarinata* has retained several more plesiomorphies (see Table 2): two shell muscles (vs. one in *Carenzia* and *Seguenzia*), a clearly rhipidoglossate radula (vs. reduced marginals in *Carenzia* and *Seguenzia*), a radular caecum (lost in *Carenzia* and *Seguenzia*), a regular (though somewhat narrowed) anterior oesophagus with pouches (vestigial in *Carenzia*), a straight rectum (vs. coiled in *Carenzia* and *Seguenzia*) and a common (vs. separate in *Carenzia* and *Seguenzia*) opening of the gonoduct and right kidney. These conditions agree with a much more basal placement of *V. tricarinata* within the Seguenzioidea as revealed by molecular characters (Kano, 2008; Kano *et al.*, 2009). Furthermore, *Ventsia* has a ciliated opening of the pedal mantle gland (not ciliated in *Carenzia*, data lacking for *Seguenzia*) and a heart encircling the rectum as found also in the seguenziid genus *Bathymargarites* (Warén & Bouchet, 1989), while the heart is not encircling the rectum in *Carenzia* and *Seguenzia*.

Several other taxa of the 'skeneimorphs', which live on sunken wood, whale falls, hydrothermal vents or seeps, are nowadays excluded from the Trochoidea or even Vetigastropoda (Kunze *et al.*, 2008; Heß *et al.*, 2008; Kano, 2008; Kano *et al.*, 2009; Haszprunar *et al.*, 2011), suggesting that species from those habitats were often not real Skeneidae. The type species of the latter clade, *Skenea serpuloides* (Montagu, 1808), and other species of *Skenea* or *Dikoleps* live in sandy or muddy habitats or intertidal gravel (Ponder, 1990; Warén, 1991; T.K., personal observation). Thus, it might be useful to focus future studies on 'skeneimorphs' from the latter habitats.

The present study should only be regarded as a step towards a better knowledge of seguenzioid phenotypic characters. Many more taxa need to be studied by similar methodology and by molecular analysis to increase our understanding of seguenzioid phylogeny and the associated character evolution and to shed more light on the heterogeneous 'skeneimorph' assemblage.

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Paper 4

What is a Skeneidae (Mollusca, Vetigastropoda)? 3D-interactive anatomy of the type species, *Skenea serpuloides* (Montagu, 1808), with comments on dwarfing

Thomas Kunze, Martin Brückner, Martin Heß & Gerhard Haszprunar

Frontiers in Zoology: in preparation

What is a Skeneidae (Mollusca, Vetigastropoda)? 3D-interactive anatomy of the type species, *Skenea serpuloides* (Montagu, 1808), with comments on dwarfing

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Abstract

Background: Skeneidae were originally characterised by their minute size, a shell lacking nacre, and a rhipidoglossate radula. It has become obvious that these characters do not prove a phylogenetic relation; therefore Skeneidae became a well known example of a polyphyletic assemblage. Species descriptions are mostly based on shell and radula alone, features of the external body are poorly studied, and data on the internal anatomy are entirely lacking.

Results: Applying serial sectioning and 3D reconstruction methodology we studied the internal anatomy of the Skeneidae type species, *Skenea serpuloides* (Montagu, 1808) to provide a complete anatomical data set with histological information. In addition, comparative data are provided for four further species of Skeneidae, *Skenea profunda* Friele, 1879, *Dillwynella voightae* Kunze, 2011, *Leucorhynchia caledonica* Crosse, 1867, and *Lodderena minima* (Tenison-Woods, 1878).

Conclusions: Skeneidae *sensu stricto* (Skeneinae) are typical trochoidean vetigastropods with combined ESOs, eyes of the open-type and neck lobes. Besides the diagnostic propodial penis the genital system of the Skeneinae is characterised by simultaneous hermaphroditism with distinct testis and ovary, an urogenital opening, and the presence of a distinct seminal receptacle. These reproduction features and also other characteristics of Skeneidae such as shell structure, the radula type, or the gill type are explained by progenesis respectively paedomorphosis.

Keywords: Microgastropods, systematics, progenesis, paedomorphosis.

Introduction

"*Skeneidae are probably the most infamous case of a polyphyletic family in Vetigastropoda*" [1]. History of the family started, when *Helix serpuloides* Montagu, 1808 was transferred into the genus *Skenea* by Fleming [2], and Clark [3,4] designated it as the type species for the microgastropod family Skeneidae. Besides the minute, often colourless shell, McLean [in 5] summed up the characters as follows: "No other family combines the features of rhipidoglossate radula, lack of nacre, and multispiral operculum". However, in fact many small, unrelated snails share these characters, especially inhabiting deep sea habitats like sunken wood and hydrothermal vents [e.g. 6,7,8,9]. So some authors suggested numbers of skeneid species of up to hundreds of described and much more undescribed species [1,6]. It has become obvious that the diagnosis given above is not sufficient to prove any closer relationship. Accordingly, Hickman & McLean [10] regarded the family status as "highly provisional". Most recent authors agreed and assumed the family to be polyphyletic [6,7, Marshall in 10,11,12]. Indeed, for some decades Skeneidae acted as a provisional 'storage place' for small gastropods sharing the characters described above [7] (personal communication A. Warén]. Thus, several authors call these gastropods informally "skeneimorph" [11,13] or "skeneiform" [12]. Herein we follow this tradition, calling gastropods having the features described above skeneimorph, and restrict Skeneidae for those species forming a clade around the type species, *Skenea serpuloides* (Montagu, 1808). The higher taxon including these species has been assigned both, family status as Skeneidae [e.g. 3,4, McLean in 5,6,7,8,10,11,14,15,16,17,18] and subfamily status as Skeneinae [19,20,21]. Based on recent molecular studies the family status is accepted nowadays [18,22,23]. Skeneidae are incorporated with the families Calliostomatidae, Cyclostrematidae, Liotiidae, Margaritidae, Solariellidae, Tegulidae, Trochidae and Turbinidae as Trochoidea [21,23], whereas the "trochoid" Phasianelloidea and Angarioidea are accepted as separate clades.

Concerning the content of Skeneidae Warén [11,16] assumed the presence of a propodial penis as diagnostic and included the genera *Dikoleps*, *Lissospira*, *Skenea*, *Skeneoides, Pseudorbis* and *Lodderena,* later on also *Dillwynella* [6] and *Protolira* [7] from the hot-vent habitat were integrated, but many other "skeneimorph" genera still are doubtful. Herein we follow the taxonomy of the CLEMAM website [24], Appeltans et al. (World Register of Marine Molluscs) [25] and Gofas et al. [26].

Recent studies on skeneimorph microgastropods applying molecular and micromorphological methods excluded a good number of genera originally assigned to Skeneidae, some are not even Vetigastropoda: *Akritogyra*, *Anekes*, *Granigyra*, *Ventsia* and *Xyloskenea* were transferred to Seguenzioidea [1,13,27,28], *Bathyxylophila* to Scissurelloidea [13,27], *Leptogyra* and *Leptogyropsis* to Neomphalina [27,29], *Hyalogyra*, *Hyalogyrina* and *Xenoskenea* to Heterobranchia [7,27,30,31]. Whereas a high number of recent reports on skeneimorph microgastropods [11,16,17,32,33,34,35,36,37,38,39,40,41,42,43,44,45,46,47,48] provided SEM-data on shell, protoconch and radula, a severe lack of anatomical and molecular data is obvious (Tab. 3). Indeed, to now anatomy is known from only two species (Tab. 3). Since the diagnostic character of Skeneidae, the presence of a propodial penis [11,27], depends of soft bodies, most species described are in fact only tentatively assigned to Skeneidae.

Methodological progress in microanatomy including serial semi-thin sectioning, 3D reconstructions, and their interactive embedding in PDFs enables us to provide the first complete anatomical description with histological data for a species of the complete taxon within this article. With the data of the type species we want to define the family Skeneidae morphologically. Also we provide data on the internal anatomy of four other Skeneidae species. (1) A second species of the same genus, *S. profunda* Friele, 1879. (2) *Dillwynella voightae* Kunze, 2011 represents a genus supposed to be closely related to *Skenea* [13]. Furthermore *Dillwynella* was investigated with molecular methods and included in molecular phylogenies [13,18,21,22]. (3) *Leucorhynchia caledonica* Crosse, 1867 and (4) *Lodderena minima* (Tenison-Woods, 1887) are species lacking a propodial penis on the right side, but are still handled as Skeneidae. These data are particularly compared with those of *Wanganella fissura* Laseron, 1954 (Trochoidea: Liotiidae) which originally was also included in Skeneidae, but the genus is now placed in the Liotiidae [49].

Material and Methods

Skenea serpuloides (Montagu, 1808): Collected off Roscoff, Bretagne, France, on the surface of “amphioxus-sand” (48°43.532'N, 3°50.712'W; depth: 20–25 m). Collected and determined by Anders Warén (Naturhistoriska Riksmuseet, Stockholm: SMNH). Section series SMNH: 98643, 98644, 98645, 98646 were used for histological examination. 3D reconstructions were compiled based on the section series: SMNH-98643 and 98644 body and inner organs; SMNH-98643 and 98645 body and tentacles.

Methods applied: Specimens of *Skenea serpuloides* were fixed and stored in 70% ethanol. The shell was decalcified with Bouin`s fluid (picric acid, acetic acid and formaldehyde in a mix ratio of 15:1:5) and after a dehydration series of acetone the body was embedded in araldite resin. Semi-thin section series were performed with “Ralph”-glass knives with the glue-method according to Ruthensteiner [50], stained with a 1:1 mixture of Methylene blue and Azur II for approx. 5 seconds at 80 C° [51] and sealed with araldite resin.

The sections were photographed with a digital camera (Olympus Camedia 5060) mounted on a light microscope (Olympus CX 41, objective Plan C 10x). The digital images were pre-processed in Adobe Photoshop: RGB-images set to greyscale, contrast and brightness adjustment, unsharp masking, size reduction by resampling. Thereafter the images were imported in AMIRA Resolve RT 4.2 (TFG Template Graphics Software, Inc., USA). In AMIRA the 3D reconstructions were performed after manual alignment and segmentation (for details see [28]), snapshots of the surface-model were taken and morphometric measurements performed. Morphometric data are affected by the retraction grade of the specimen, anyway morphometric values are given here, to get an overview and an information basis about size dimensions in the examined species. The 3D-PDF was created with Adobe Acrobat 3D according to Ruthensteiner & Heß [52].

Results

All measurements are approximate values (aberrance max. 2 %), without mentioning approx. before every value in the text. Two section series and their 3D reconstruction of adult, hermaphroditic specimens of *Skenea serpuloides* were used for the descriptions of the inner organs. Measurements of the organ systems (size and volume) were done for both specimens

(Tab. 1). Both have almost the same size and arrangement of organs, but the retraction grade is different. Respiratory and circulatory system were better conserved in SMNH-98643, while in SMNH-98644 the nervous system and tentacles are in a better preserved condition. Because the epipodial tentacles were poorly preserved in the other series, this part was described and reconstructed based on SMNH-98645. So the results chapter is a synopsis of these series. In the figure captions the specimen number is quoted for every picture.

Shell

The shell, the protoconch, and the radula of *S. serpuloides* are described by multiple authors [e.g. 15,33,34,53,54,55,56,57]. Figures of this species are shown by following authors: drawings of the teleoconch [15,53,57]; SEM pictures of the teleoconch [16,33,34,56]; SEM pictures of the protoconch [15,16,33,34,56]; SEM pictures of the radula [11,33,34].

External morphology and structure of foot and tentacles

Caused by the retraction of the animals especially the foot and the tentacles of *S. serpuloides* were compressed. Due to the poor preservation sensory papillae could not be shown in the 3D reconstructions (but are verified histologically).

The (retracted) complete body has a maximum length of 870 µm. The visceropallium is located on the right side of the median plane and performs 1.5 whorls (height 350 µm; Fig. 1A). The operculum is round, multispiral and located on the dorso-posterior part of the epipodium. The anterior pedal gland is found in the dorsal part of the propodium. Its cells are rather big and voluminous (Fig. 2B, C, G). The anterior pedal gland opens via a channel at the dorso-anterior tip of the propodium.

The single pair of cephalic tentacles is long (350 µm) with a round profile and a diameter of only 30-40 µm (Fig. 1A-C), and is filled with longitudinal and diagonal muscles forming a complex grid. The anterior part of the cephalic tentacles is covered by sensory papillae (Fig. 3G).

The epipodium bears three pairs of “true” [see also 58] epipodial tentacles (Fig 1A-C: et1-3). The tentacles are strongly retracted, but with different grade of retraction, affecting length and shape (length 90-140 µm, diameter 25-50 µm). All of these tentacles are covered with sensory papillae distally (Fig. 3D). The most anterior pair of epipodial tentacles (et1) is short, situated on the level of the pedal ganglia, and slightly anterior to the operculum (Fig. 1). The second and third pair is located beyond the operculum. The epipodial sense organs (ESOs) are of the “combined” type as usually found in trochoids being small, smooth knobs, which are attached ventrally to the first pair of epipodial tentacles, with the sensory epithelium lying distally.

An eye stalk is located dorsal of each eye. While the left one is small (length 30 µm, diameter 5 µm) and inconspicuous, the right eye stalk is large (length 140 µm, diameter 40 µm; Fig. 1A), smooth and oriented parallel (latero-dorsal) to the right cephalic tentacle. Both sides bear a smooth neck lobe (Fig. 1A-C), originating on the level of the mouth cavity and leading backwards. The right one is 130 µm long, while the left one has a length of 90 µm (diameter of

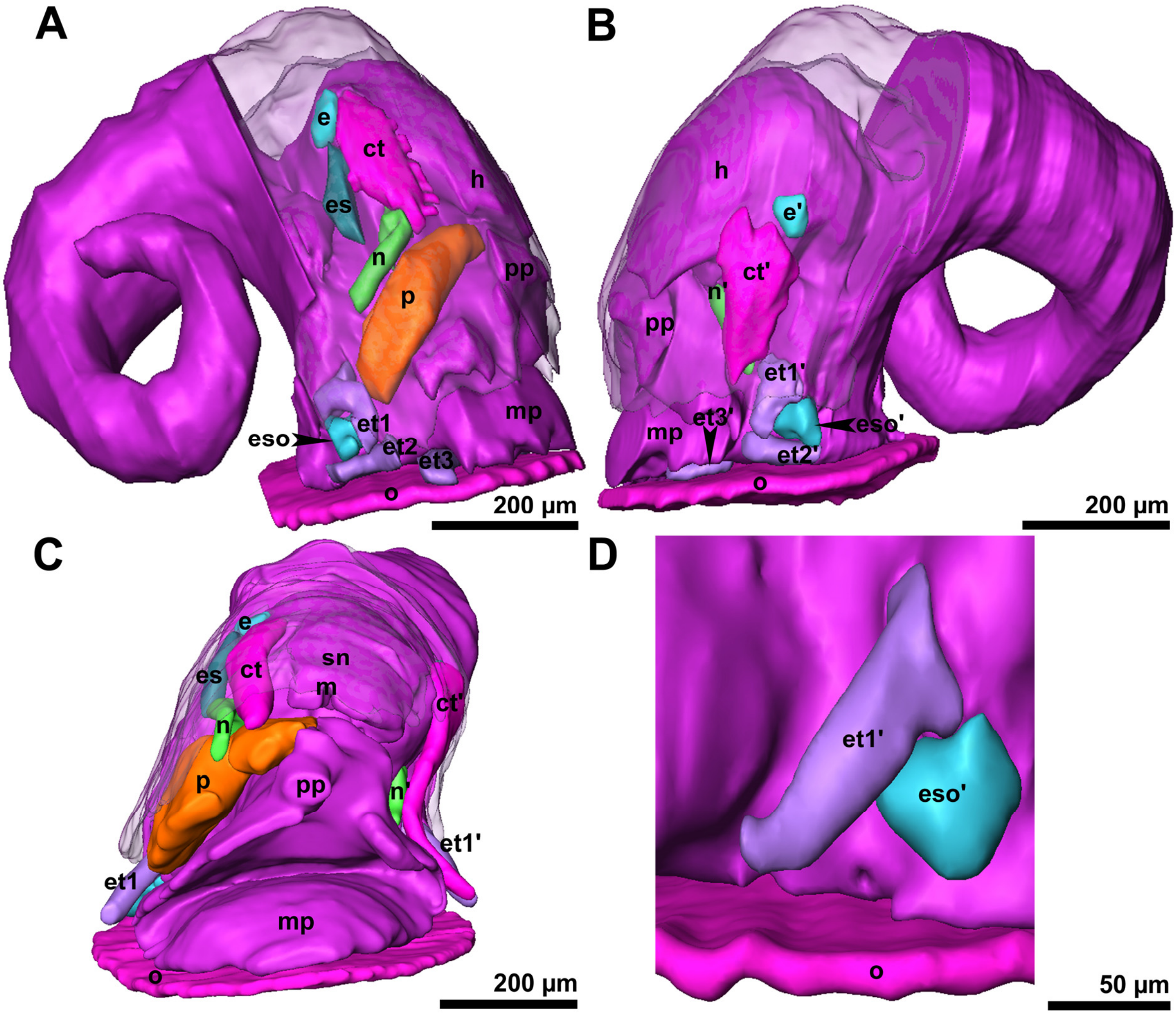


Figure 1. 3D reconstructions of the body and tentacles of *Skenea serpuloides*.

A: Latero-frontal view of the right side, mantle roof transparent. **B:** Latero-frontal view of the left side, mantle roof transparent. **C:** Frontal view, mantle roof transparent. **D:** Right side view onto epipodial tentacle and epipodial sense organ, mantle roof removed. (**A**/**B**: SMNH-98645; **C**/**D**: SMNH-98644).

Abbreviations: **ct/ct'**, right/left cephalic tentacle; **e/e'**, right/left eye; **es**, right eyestalk; **eso/eso'**, right/left epipodial sense organ; **et1-3/et'1-3**, right/left first, second, third epipodial (anterior to posterior) tentacle; **h**, head; **m**, mouth opening; **mp**, metapodium, **n/n'**, right/left neck lobe; **o**, operculum; **p**, penis; **pp**, propodium; **sn**, snout.

both neck lobes: 25 µm). They are innervated by the right/left pedal ganglion. The right frontal edge of the propodium forms a propodial penis. This penis is 160 µm long in the given state of retraction (height 250 µm, width 100 µm). The epithelium appears strongly folded suggesting a high potential for extension. A penis channel is formed by a fold running along the complete penis. It starts latero-proximally and proceeds dorsally. The apical channel of the penis is equipped by cilia. The foot is folded due to retraction, but the bad state of conservation does not allow describing further details. There are two shell muscles. The right shell muscle has its attachment zone at the level where the posterior oesophagus begins and the left one beneath the osphradial ganglion.

Mantle cavity

The mantle cavity of *S. serpuloides* is 650 µm deep and extends around a quarter whorl of the shell into the soft body. The anterior part of the mantle roof is thin and thickens as soon as the enclosed organs, e.g. rectum, emerge (Fig. 3G). The middle part of the mantle roof was largely occupied by the rectum, performing two semicircular loops here. Posterior right of the mantle cavity the hypobranchial gland, rectum and left kidney are found, at the left side the ctenidium is situated (Fig. 2C). The end of the mantle cavity hosts the seminal receptacle dorsally, while ventrally the right and the left kidney, the urogenital opening and the heart are found (interactive Fig. 2). At the posterior left end of the mantle cavity the seminal receptacle opens into the mantle cavity dorsally, while the urogenital opening emerges medio-ventrally into the mantle cavity. Cilia are present at the bottom of the mantle cavity opposite to the seminal receptacle opening, and a ciliary tract runs to the right side in the direction of the penis. Also the opening of the penis channel is ciliated (Fig. 3B).

The single (left) monopectinate ctenidium shows eight leaflets with skeletal rods and bursicles (Fig. 3H). It is located on the left part of the mantle roof (Fig. 2C), at the level of the transition zone of anterior and posterior oesophagus. The ctenidial axis is attached on its entire length to the mantle roof. The leaflets are positioned slightly obliquely to the axis with a length of 110 up to 170 µm, the fourth one is the longest. Their whole surface is densely ciliated. The ctenidial leaflets are supported by skeletal rods. Bursicles occupy the anterior, efferent part of the leaflets, showing a small channel. The epithelium of the mantle roof is thin.

The large hypobranchial gland occupies the lateral right side of the mantle cavity, between gill and left kidney (interactive Fig. 2). Three different parts can be distinguished by histology: the cells of the anterior part stain darkly, showing secretion. Posteriorly it is followed by the largest section, containing big, voluminous cells. The third part runs parallel at first, continuing posteriorly and consists of two secreting cell types, one apocrine and the other one mesocrine. The opening of the seminal receptacle is situated at the left dorsal end of the mantle cavity (Figs. 2E; 3I-K), while the urogenital opening is placed more ventrally.

Beyond the right part of the mantle lappet several specimens were infected by a parasite (Fig. 3E). The parasite stuck anterio-laterally of the hypobranchial gland and was attached to the epithelium of the mantle cavity. Its anatomy was highly simplified, but histology suggests a crustacean (probably copepod) relationship.

Vascular and excretory system

The heart consists of a single (left) auricle and a ventricle, both being surrounded by a pericardium (Fig. 3K). The heart is located just behind the mantle cavity on the right side of the visceral body (Fig. 2C). The irregular shape of the heart results from wedging between intestine, seminal receptacle and both kidneys. The wall of the pericardium is very thin. Both kidneys are connected with the pericardium via a ciliated renopericardial duct. Auricle and

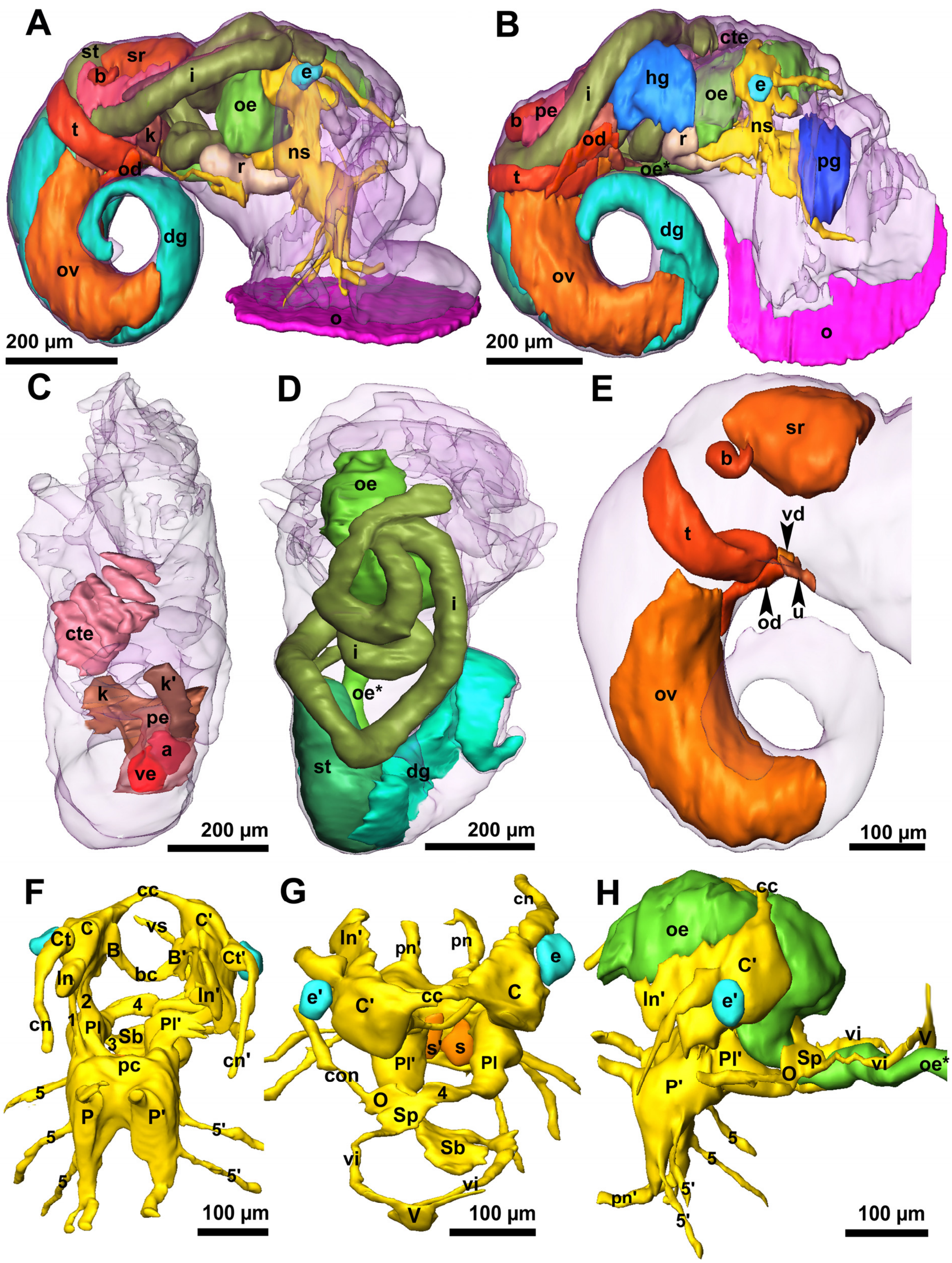
Figure 2. 3D reconstructions of inner organs of *Skenea serpuloides*.

A/B: Right side view of body with all inner organs (2 specimens), body surface transparent. **C:** Dorsal view of vascular and excretory system with ctenidium, body surface transparent. **D**: Dorsal view of the digestive system, body surface transparent. **E:** Right side view of the reproduction system, body surface transparent. **F:** Frontal view of the nervous system. **G:** Dorsal view of the nervous system. **H:** Left side view of the nervous system and oesophagus. (**A**, **D**-**H**: specimen SMNH-98644. **B**/**C**: specimen SMNH-98643).

Abbreviations: **a**, auricle; **B/B'**, right/left buccal ganglion; **b**, bursa copulatrix; **bc**, buccal commissure; **C/C'**, right/left cerebral ganglion; **cc**, cerebral commissure; **cn/cn'**, right/left cephalic tentacle nerve; **con**, ctenidial-osphradial nerve ; **Ct/Ct'**, right/left cephalic tentacle ganglion; **cte**, ctenidium; **dg**, digestive gland; **e/e'**, right/left eye; **hg**, hypobranchial gland; **i**, intestine; **k/k'**, right/left kidney; **ln/ln'**, right/left labial nerve; **ns**, nervous system; **O**, osphradial ganglion; **o**, operculum; **od**, oviduct; **oe/oe***, anterior/posterior oesophagus; **ov**, ovary; **P/P'**, right/left pedal ganglion; **pc**, pedal commissure; **pe**, pericardium; **pg**, anterior pedal gland; **Pl/Pl'**, right/left pleural ganglion; **pn/pn'**, right/left pedal nerves; **r**, radula and radular sack; **s/s'**, right/left statocyst; **Sb**, suboesophageal ganglion; **Sp**, supraoesophageal ganglion; **sr**, seminal receptacle; **st**, stomach; **t**, testis; **u**, urogenital duct; **V**, visceral ganglion; **vd**, vas deferens; **ve**, ventricle; **vi**, visceral loop; **vs**, visceral nerve; **1**, right cerebro-pedal connective; **2**, right cerebro-pleural connective; **3**, pleuro-suboesophageal connective; **4**, pleuro-supraoesophageal connective; **5/5'**, right/left pedal nerves.

The **interactive 3D model** of *Skenea serpuloides* can be accessed by clicking into Fig. 2 (Adobe Reader Version 7 or higher required). Click letter A for a 3D model of specimen SMNH-98644 or letter B of specimen SMNH-98643. Rotate model by dragging with left mouse button pressed, shift model: same action + ctrl, zoom: use mouse wheel (or change default action for left mouse button). Select or deselect (or change transparency of) components in the model tree, switch between prefab views or change surface visualization (e.g. lightning, render mode, crop etc.).

ventricle are of oval shape (only preserved in specimen SMNH-98643). The auricle is located anterio-dorsally and it is connected ventrally with the ventricle. The heart is attached to the intestine, but does not encircle it completely. Due to the poor initial fixation, the preservation of the small blood vessels was not sufficient for reconstruction. Small blood sinuses from the



gill leaflets merge into the efferent gill sinus. This sinus proceeds on the left part of the mantle roof and leads into the auricle. A second efferent sinus from the left kidney pipes ventrally into the auricle. The anterior aorta emerges posterio-ventrally from the ventricle and runs in the same direction.

Skenea serpuloides has two kidneys, both located at the right side of the animal (Fig. 2C). The left kidney is a papillary sac, lying in the right part of the body, but ventro-laterally left of the intestine (Figs. 2A; 3J: k´). It borders on the rear part of the mantle cavity, behind the ctenidium, to the right of the midline and runs in a slight curve latero-caudally. The left kidney is a longish tube with a diameter of about 50 µm (Fig. 3J: k'). Its anterio-dorsal part lies close to the pericardium. Here it is connected with the pericardium via a renopericardial duct. The nephroporus is located in the anterior part of the left kidney and is equipped with a sphincter muscle. The right kidney is placed ventrally at the same level as the heart. It forms irregular lobes between the viscera and has a large lumen (Fig. 3 I, J: k), epithelial cells are small and weakly stained. A renopericardial duct connects the right kidney with the ventral side of the pericardium. Anterio-ventrally both, the oviduct and the vas deferens open into the right kidney. From here the very short urogenital duct opens into the mantle cavity.

Genital system

Skenea serpuloides is a hermaphroditic species. The genital apparatus consists of separate ovary and testis, oviduct and vas deferens, also a seminal receptacle, a bursa copulatrix, and a propodial penis are present (Fig. 2E; see also external morphology: Fig. 1A-C). Ovary and testis were fully mature in the examined specimens; sperm and eggs were produced concurrently and are found in all stages of development.

The large ovary together with the digestive gland occupies the last whorl of the animal. The lumen contains eggs of various developmental stages (Fig. 3L), which are not sorted by size. Yolky, mature eggs have diameters of 150 µm, each is covered by an irregularly shaped vitelline layer (up to 30 µm thick). Yolk granules are small; the nucleus has a diameter of about 40 µm and contains a prominent nucleolus. The anterio-ventral end of the ovary is continued by the oviduct, which is a compressed tube (about 100 µm long) being situated between body wall and testis. The oviduct entirely lacks glandular cells or cilia and opens into the right kidney.

The testis is located anterio-ventrally of the ovary. It has a long cylindrical, curved shape, orientated horizontally in the animal (Figs. 2E; 3L). The anterior part of the testis is filled with fibrous spermatids. The posterior testis contains spermatogonia (diameter 4 µm)

Table 1. Size and volume of the inner organs of *Skenea serpuloides*.

Measurements were calculated with the AMIRA software and are given in µm/µm^3.

	SMNH-98644		**SMNH-98643**	
	Size [µm]	Volume [µm^3]	Size [µm]	Volume [µm^3]
Soft part	l: 860, w; 370, h: 700	79.9 10^6	l: 880, w: 350, h: 710	77.17 10^6
Operculum	d: 550	-	d: 550	-
Mantle cavity				
Hypobranchial gland	-	-	l: 210, w: 175, h: 100	1.53 10^6
Anterior pedal gland	-	-	l: 110, w: 105, h: 230	1.09 10^6
Ctenidium	-	-	l: 150, w: 290, h: 80	1.29 10^6
Vascular and excretory system				
Pericardium	l: 190, w: 105	0.49 10^6	l: 225, h: 145	0.77 10^6
Auricle	-	-	l: 75, h: 100	0.16 10^6
Ventricle	-	-	l: 70, h: 120	0.24 10^6
Right kidney	l: 260, w: 260, h: 55	0.69 10^6	l: 180, w: 240, h: 75	0.88 10^6
Left kidney	l: 230, w: 60, h: 30	0.22 10^6	l: 205, w: 65, h: 55	0.33 10^6
Urogenital duct	l: 50, w: 65	0.03 10^6	l: 30, w: 70	0.04 10^6
Genital system				
Ovary	l: 245, w: 125, h: 130	3.92 10^6	l: 260, w: 135, h: 150	4.46 10^6
Oviduct	l: 100, w: 60	0.07 10^6	l: 200, w: 60	0.08 10^6
Testis	l: 285, d: 70	0.72 10^6	l: 300, d: 80	0.75 10^6
Vas deferens	l: 20, w: 50	0.02 10^6	l: 35, w: 40	0.02 10^6
Seminal receptacle	l: 185, w: 175, h: 145	1.57 10^6	l: 195, w: 125, h: 90	1.10 10^6
Bursa copulatrix	l: 80, d: 45	0.07 10^6	l: 115, d: 60	0.26 10^6
Alimentary tract				
Radula incl. caecum	l: 450	0.99 10^6	l: 450	0.80 10^6
Radular cartilage	l: 75, w: 60, h: 160	0.57 10^6	l: 60, w: 90, h: 95	0.29 10^6
Anterior oesophagus	l: 430, w: 170, h: 135	3.82 10^6	l: 420, w: 200, h: 130	4.09 10^6
Posterior oesophagus	l: 325, d: 50		l: 300, d: 45	
Stomach	l: 380, w: 145, h: 180	5.54 10^6	l: 420, w: 160, h: 185	6.96 10^6
Intestine	l: 2150, w: 55-70	5.45 10^6	l: 2350, w: 60-70	8.34 10^6
Midgut gland	l: 890, w: 150	5.31 10^6	l: 700, w: 110	6.12 10^6
Nervous system		3.59 10^6		1.72 10^6
Cerebral ganglia	l: 100, w: 80, h: 110	-	-	-
Pedal ganglia	l: 120, w: 90, h: 210	-	-	-
Pleural ganglia	l: 100, w: 60, h: 70	-	-	-
Sense organs				
Statocysts	l: 55, w: 40, h: 20	0.05 10^6	-	-
Eyes	d: 50	0.10 10^6	d: 55	0.09 10^6

Abbreviations: **d**, diameter; **h**, height; **l**, length; **w**, width.

stuffed with small granulae. Anteriorly the testis merges into the vas deferens. This channel is very short and opens into the right kidney close to the opening of the oviduct.

The oval, large seminal receptacle is located posterio-ventral to the mantle cavity on the left side (Fig. 2E). The opening into the mantle cavity is at the anterio-ventral end of the seminal receptacle, containing sperms in its front part. Sperm cells form a thick, unordered cluster in the posterior part close to a distinct bursa copulatrix (Fig. 3K). The latter is located anterio-proximally of the seminal receptacle and is filled with a sperm mass, which is in progress of disintegration. It is connected with the seminal receptacle via a narrow channel.

Alimentary tract

The blunt snout is retracted far inside the mantle cavity (Fig. 1A-C) in the examined specimens of *S. serpuloides*. The mouth opening lies fronto-dorsally and has a small lappet on each side. The mouth opening is approx. 50 µm long and then merges into a straight channel, which enlarges to the buccal cavity with the radula (Fig. 3E-G). The pharynx is short and has small pouches laterally and dorsally. Salivary glands could not be found, so they are lacking or at least very small and inconspicuous.

The delicate, paired jaws are fused dorsally and consist of small rod like elements. The radula is rhipidoglossate and lacks a radular caecum. It is located latero-dorsally of the jaws. Due to contraction of the body the radula is s-shaped and has an overall length of 400 µm. The radular diverticulum occupies around 210 µm of this length, is not bifid and thickened at its posterior end. Contrary to the smooth shell muscles and head retractors all buccal muscles are cross striated. The radula is associated with two pairs of radular cartilages. The anterior pair of

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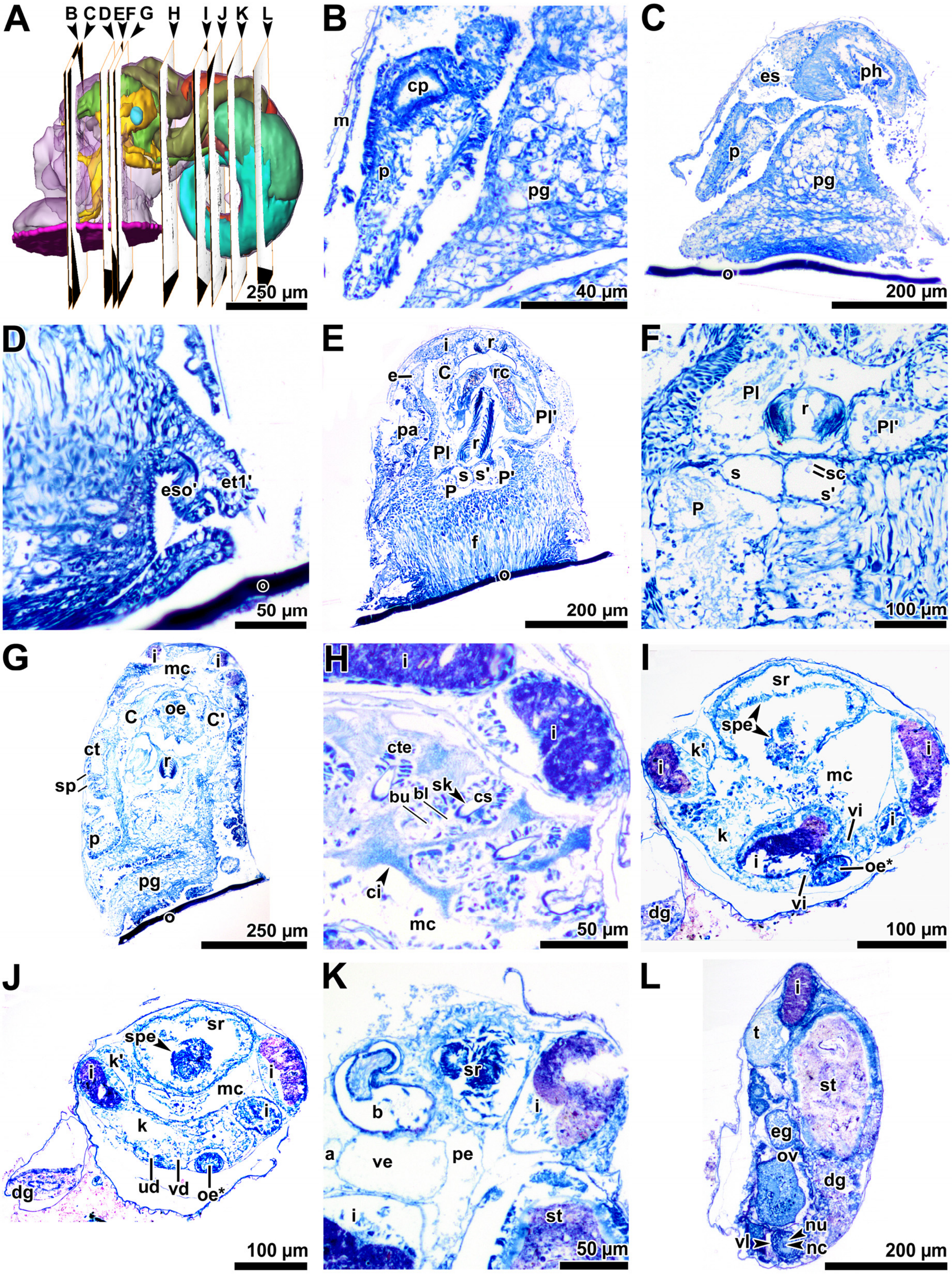
Figure 3. Histological details of *Skenea serpuloides*.

A: Overview: 3D reconstruction with the relative location of the section planes. **B:** Propodial penis with penis channel. **C:** Transversal section of the anterior soft body with propodial penis. **D:** Epipodial tentacle and epipodial sense organ (ESO). **E:** Transversal section of the soft body with ganglia. **F:** Statocysts with statoconia. **G:** Section of the soft body with cephalic tentacle and sensory papillae. **H:** Ctenidium with skeletal rods and bursicles. **I:** Transversal section of the soft body with seminal receptacle opening to the mantle cavity and kidneys. **J:** Transversal section of the soft body with seminal receptacle and gonoducts. **K:** Heart and bursa copulatrix. **L:** Transversal section of the posterior soft body with testis, ovary and egg details. (**A**-**C**, **E**, **I**, **J**, **L** specimen SMNH-98644; **D**, **F**, **G** specimen SMNH-98645; **H**, **K** specimen SMNH-98643).

Abbreviations: **a**, auricle; **b**, bursa copulatrix; **bl**, bursicle lumen; **bu**, bursicle; **C/C'**, right/left cerebral ganglion; **ci**, cilia; **cp**, penis channel; **cs**, ctenidium sinus; **ct**, right cephalic tentacle; **cte**, ctenidium; **dg**, digestive gland; **e**, right eye; **eg**, egg; **es**, right eyestalk; **eso'**, left epipodial sense organ; **et1'**, left (most anterior) epipodial tentacle; **f**, foot; **i**, intestine (including pallial rectal loops); **k/k'**, right/left kidney; **m**, mantle; **mc**, mantle cavity; **nc**, nucleolus; **nu**, nucleus; **o**, operculum; **oe/oe***, anterior/posterior oesophagus; **ov**, ovary; **P/P'**, right/left pedal ganglion; **p**, penis; **pa**, parasite; **pe**, pericardium; **pg**, anterior pedal gland; **ph**, pharynx; **Pl/Pl'**, right/left pleural ganglion; **r**, radula and radular sack; **rc**, radular cartilage; **s/s'**, right/left statocyst; **sc**, statoconia; **sk**, skeletal rods; **sp**, sensory papillae; **spe**, sperm; **sr**, seminal receptacle; **st**, stomach; **t**, testis; **ud**, urogenîtal duct; **vd**, vas deferens; **ve**, ventricle; **vi**, visceral loop; **vl**, vitelline layer.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cartilages is drop-shaped located anterio-ventral of the radula, the left and right cartilages contact each other closely proximal (interactive Fig. 2). The cartilage cells are largest at the ventral side (max. diameter 14 µm), getting smaller dorsally (Fig. 3E). The second pair of radular cartilages is located posterio-dorsal of the other pair. It is rather small and the separation is so inconspicuous, that they could not be shown in the reconstructions. A subradular organ is missing.

After 80 µm the dorsal pharynx passes into the large anterior oesophagus (see interactive Fig. 2). The epithelium of the anterior oesophagus bears long cilia. The dorsal food channel shows a slight, but not complete, torsion of approximate 45°. The posterior part of the anterior oesophagus forms two blind, glandular pouches (about 40 µm long) and it is continued by the posterior oesophagus, which is a 200 µm long, quite thin (diameter 50 µm) tube with star-shaped lumen leading straight backwards (Fig. 3I, J). The oesophagus opens dorso-medially into the stomach, between the openings of the digestive glands.

The stomach is of oval shape and slightly curved (Figs. 2D; 3L). The epithelium is quite thin in the anterior part (10 µm). The cells have long cilia (8 µm) and additionally they are covered completely with microvilli. In the posterior part, around the opening of the digestive glands, the epithelium changes to high prismatic, ciliated cells (height 30 µm, width 2 µm). A gastric shield covers the posterior part of the gut. There are two digestive glands, each with a separate opening to the stomach. Together with the ovary the digestive glands occupy the last whorl of the soft body, but they reach distally further out then the ovary (Fig. 2A, B, D). The digestive glands form lobes with a curved lumen. The darkly stained cells (Fig. 3J, L) suggest intense secretion.

The intestine emerges in the most anterior part of the gut. The epithelium is ciliated, but a typhlosolis is absent. First the intestine leads 130 µm straight forward and then to the right side (Fig. 2D). Afterwards it loops 180° backwards to the left and passes the heart. Then the rectum loops 180° forward to the right and leads 450 µm in the same direction. This is followed by a narrow 180° turn to the left side. After 160 µm the intestine performs a last 180° loop to the left and finally it leads straight forward (260 µm). The anus opens into the right part of the mantle cavity at the level of the anterior edge of the ctenidium.

Nervous system

The central nervous system consists of four paired ganglia (cerebral, buccal, pleural and pedal ganglia) and four unpaired ganglia (osphradial, suboesophageal, supraoesophageal and visceral ganglion). Due to contraction and the poor conservation not all nerves could be detected (e.g. those of the epipodial sense organs or the neck lobe).

Each cerebral ganglion is situated below the basis of a cephalic tentacle flanking the transition zone of pharynx and oesophagus latero-distally. Both ganglia are interconnected by the cerebral commissure (Figs. 2F-H; 4A, B). Each cephalic tentacle nerve forms a small cephalic tentacle ganglion at its basis. These ganglia are located dorso-frontal of the cerebral ganglia and in front of the eyes. The buccal ganglia are located proximally to the cerebral ganglia and ventral of the pharynx (Figs. 2F; 4A, B). Dorso-frontally the short and thin buccal-cerebral connectives emerge. The buccal ganglia are interconnected via the buccal commissure, which forms a ventral loop in front of the anterior oesophagus.

The pedal ganglia (Figs. 2F; 3E; 4A) are the largest ganglia and quite elongated. They are close to each other, so that the pedal commissure is formed by the proximal attachment zone of both ganglia. Further pedal commissures were not found. The flat statocysts (see also sense organs) were attached posterior to the pedal ganglia (Figs. 2G; 3E). Nerves emerging from the pedal ganglia innervate the foot and the epipodial tentacles. A nerve emerges from the right pedal ganglion leading into the right parts of body and mantle roof. The left counterpart of this nerve is not visible or missing. Anterio-dorsally the cerebro-pedal connectives run to the

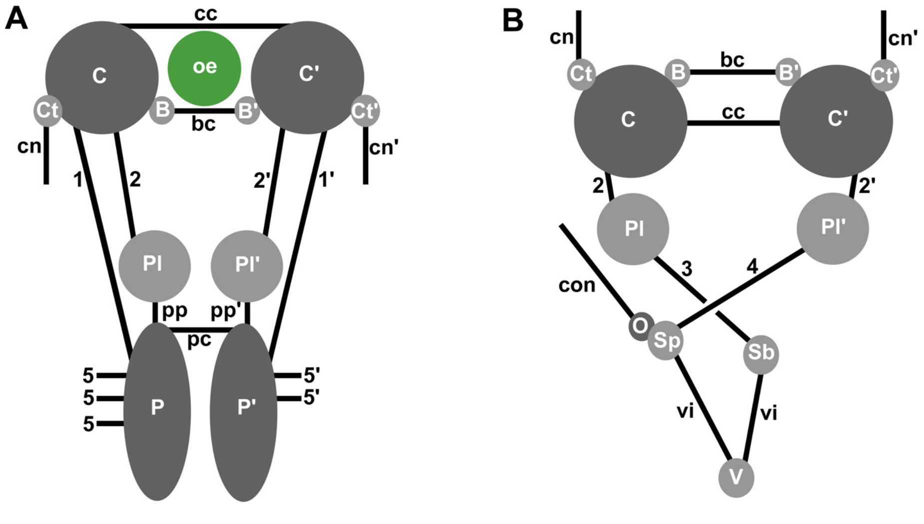

Figure 4. Schematic view of the central parts of the nervous system in *Skenea serpuloides*.

A: Frontal view (visceral loop removed). **B:** Dorsal view (pedal ganglia removed).

Abbreviations: **B/B'**, right/left buccal ganglion; **bc**, buccal commissure; **C/C'**, right/left cerebral ganglion; **cc**, cerebral commissure; **cn/cn'**, right/left cephalic tentacle nerve; **con**, ctenidial-osphradial nerve ; **Ct/Ct'**, right/left cephalic tentacle ganglion; **O**, osphradial ganglion; **oe**, anterior oesophagus; **P/P'**, right/left pedal ganglion; **pc**, pedal commissure; **Pl/Pl'**, right/left pleural ganglion; **pp/pp'**, pleuro-pedal connective; **Sb**, suboesophageal ganglion; **Sp**, supraoesophageal ganglion; **V**, visceral ganglion; **vi**, visceral loop; **1/1'**, right/left cerebro-pedal connective; **2/2'**, right/left cerebro-pleural connective; **3**, pleuro-suboesophageal connective; **4**, pleuro-supraoesophageal connective; **5/5'**, right/left pedal nerves.

pedal ganglia. They are located in front of the cerebro-pleural connectives. The long, conic pleural ganglia are located close to the pedal ganglia (hypoathroid situation; Figs. 2H; 4A). While the left pleuro-pedal connective is thin and short, but distinct, the right pleural ganglion is closely attached to the right pedal ganglion.

The visceral loop is streptoneurous. The pleuro-supraoesophageal commissure emerges posteriorly from the right pleural ganglion, crosses the anterior oesophagus dorsally and leads to the supraoesophageal ganglion (interactive Figs. 2; 4B). This ganglion is located dorso-laterally above the posterior oesophagus. From there the left visceral connective emerges backwards and reaches the visceral ganglion. The osphradial ganglion is found above the supraoesophageal ganglion. Both are interconnected by a short but broad connective. The oesophageal ganglion supplies the left mantle roof and the ctenidium. The left pleural ganglion is continued by the short pleuro-suboesophageal connective, which reaches the suboesophageal ganglion (Figs. 2G; 4B) by crossing the posterior oesophagus at its ventral side. The suboesophageal ganglion is quite large, round and depressed dorso-ventrally. A thin nerve emerges latero-frontally and leads in a loop backwards to the visceral ganglion, thus forming the right part of the visceral loop. The small visceral ganglion lies quite medially, at the level of the posterior end of the mantle cavity.

Sense organs

Cephalic and epipodial tentacles are covered with sensory papillae (Fig. 3D, G). The epipodial sense organs (ESOs) are placed at the base of the epipodial tentacles. The eyes are of the open-type and lie slightly below the body surface (Figs. 2F-H; 3E). In the section series the eyes were colourless (see discussion). The depressed statocysts are located adjacent to the pedal ganglia (Figs. 2G; 3E). Each statocyst contains several statoconia (Fig. 3F). Bursicles (of the ctenidial leaflets) have been described above. The single osphradium (diameter 30 µm) is located on the left side of the mantle roof and is directly underlain by the osphradial ganglion.

Discussion

Character analysis

Morphological data not only are suitable to infer the phylogenetic affiliations of skeneimorph/skeneid gastropods, but also shed light on ecology and function.

In the following discussion genera with a propodial penis, i.e. *Skenea* (type genus), *Dikoleps, Dillwynella, Lissospira, Protolira, Pseudorbis,* and *Skeneoides* are classified as Skeneinae. Descriptions of the external body of Skeneidae are quite rare (Tab. 3), morphological data were so far restricted to an unpublished diploma-thesis on *Skenea serpuloides* [cf. 59, data included herein] and *Protolira valvatoides* Warén & Bouchet, 1993 [7]. With this study anatomical and morphological data for three plus two Skeneidae become available (Tab. 2): the type species, *Skenea serpuloides, S. profunda,* and *Dillwynella voightae* are Skeneinae with propodial penis; *Leucorhynchia caledonica* and *Lodderena minima* do not have a right propodial penis but are still assorted to Skeneidae; finally we add data on *Wanganella fissura*, which was previously listed in this family, but is now grouped in Liotiidae.

Epipodial conditions: In living animals the epipodial tentacles are quite long [4,34]. However, all examined specimens were heavily retracted in the shell, thus these tentacles appear short and stumpy in the reconstructions (Fig. 1 A, B). Although Fretter & Graham [15] provided a comprehensive description of the body of *Skenea serpuloides*, ESOs were not mentioned. For *Dikoleps nitens* (Philippi, 1844) three pairs of epipodial tentacles were reported, whereas Rubio-Salazar [34:fig. 2] reported three ESOs: one at the 1st epipodial tentacle on the left side and one each at the 2nd one on both sides. In *Skenea serpuloides* Rubio-Salazar [34:fig. 1] described also three ESOs: one (larger?) ventral to the rightmost anterior epipodial tentacle and two ESOs associated with the 1st one left. In contrast we found only a single, equally sized pair of ESOs attached to the most anterior pair of epipodial tentacles (Figs. 1A, B, D; 3D). As outlined elsewhere [58,60] epipodial tentacles and ESOs are module-like in vetigastropods, and multiplications and malformations have been frequently reported. All in Skeneidae species examined ESOs are located at the ventral base of an epipodial tentacle, a condition generally found in Haliotidae, Trochoidea and Phasianelloidea [60] (Tab. 2; Tab. 3).

The two necklobes (Fig. 1A) of *S. serpuloides* were also reported by Fretter & Graham [15] and Rubio-Salazar [34]. As the right eyestalk is much larger than the small and inconspicuous left one (Fig. 1A, B), it was interpreted originally as a penis [15], but Warén & Bouchet [7] and our data identify it as an enlarged eyestalk. *S. serpuloides* has pigmented eyes, which are black in living animals [15,34,54], but the eyes in our sectioned animals lack pigments, a known bleaching artefact of the alcohol storage (personal communication A. Warén). The eyes are of an open-type with a vitreous body [sensu 61] like found in several haliotid (e.g. *Haliotis tuberculata* Linné, 1758 [62]) and trochoidean species (e.g. *Cantharidus clelandi* (Wood, 1828), *Turbo stenogyrum* Fischer, 1873 or *Stomatia phymotis* Hebling, 1779 [61,63]), and not closed like in the scissurellids (e.g. *Scissurella jucunda* Smith, 1890 [64]) or phasianelloid-tricoliid species *Tricolia pullus* (Linné, 1758) (personal observation G.H.) or *Eulithidium affine* (Adams, 1850) [65].

Simultaneous hermaphroditism with separated ovary and testis seems to be present in all Skeneinae (Tab. 2), whereas several skeneimorph genera (e.g. *Wanganella*, *Ventsia* and *Bathyxylophila*), now placed in other (super-)families, have separated sexes. *Leucorhynchia caledonica* is a true hermaphrodite (Tab. 2), but ovary and testis are not separated locally like in *Skenea* and *Dillwynella*, and it seems to be a true hermaphroditic gland opening via a

Table 2. Comparison of the anatomy of six skeneimorph microgastropods.

	Skenea serpuloides (Montagu, 1808)	***Skenea profunda*** Friele, 1879	***Dillwynella voightae*** Kunze, 2011
Data resource	pers. obs. TK	pers. obs. TK	pers. obs. TK
Family	Skeneidae/Skeneinae	Skeneidae/Skeneinae	Skeneidae/Skeneinae
Teleoconch	1.5 mm	3.2 mm	5.8 mm
Cephalic tentacles	with sensory papillae	with sensory papillae	with sensory papillae
Epipodial tentacles (ET)	3 pairs	3 pairs	3 pairs
Papillae at ET	with sensory papillae	with sensory papillae	with sensory papillae
ESO-type	combined	combined	combined
ESO	1 at 1st ET per side	1 at 2nd ET per side	1 at 1st ET per side
Mantle edge	no sensory papillae	no sensory papillae	with sensory papillae
Shell muscles	2	?	2
Ctenidium	monopectinate	monopectinate	monopectinate
Skeletal rods	+	+	+
Bursicles	+	+	+
Right kidney	voluminous	voluminous	voluminous
Left kidney	papillary sack	papillary sack	papillary sack
Genital system	hermaphrodite	hermaphrodite	hermaphrodite
Specimens observed	hermaphrodite	hermaphrodite	hermaphrodite
Propodial penis	right side	right side	right side
Seminal receptacle	left mantle cavity	left mantle cavity	left mantle cavity
Bursa copulatrix	+	-	-
Eggs	yolky	yolky	yolky
Vitelline layer	thick	thick	thick
Alimentary system			
Jaws	thin	thin	thin
Radula	rhipidoglossate	rhipidoglossate	rhipidoglossate
Radular cartilage	2 pairs	2 pairs	2 pairs
Oesophagus	papillate	papillate	papillate
Heart encircling rectum	partly	completely	partly

common duct. The examined specimen of *Lodderena minima* (female specimen; Tab. 2; personal observation T.K.) has separated sexes, no seminal receptacle and thus should be excluded from the Skeneinae. For *Bruceiella globulus* Warén & Bouchet, 1993, only provisionally assigned to Skeneidae, we (personal observation T.K.) confirm the lack of a propodial penis [7], but the specimen investigated is a true hermaphrodite and not a gonochoristic as stated in the original description (personal observation T.K.). The most striking feature of *S. serpuloides, S. profunda,* and *Dillwynella voightae* (see also Tab. 2) is the

Table 2. Continued.

	Leucorhynchia caledonica Crosse, 1867	***Lodderena minima*** (Tenison-Woods, 1878)	***Wanganella fissura*** Laseron, 1954
Data resource	pers. obs. TK	pers. obs. TK	pers. obs. TK
Family	Skeneidae/ '?'	Skeneidae/ '?'	Liotiidae
Teleoconch	2 mm	0.8 mm	1.7 mm
Cephalic tentacles	with sensory papillae	with sensory papillae	with sensory papillae
Epipodial tentacles (ET)	4 pairs	? 3 pairs	3 pairs
Papillae at ET	with sensory papillae	with sensory papillae	with sensory papillae
ESO-type	combined	combined	combined
ESO	1 at 2nd ET per side	1 at the 2nd (?) per side	1 at 1st ET per side
Mantle edge	no sensory papillae	no sensory papillae	no sensory papillae
Shell muscles	?	?	1
Ctenidium	mono-/bipectinate	monopectinate	monopecinate
Skeletal rods	+	+	+
Bursicles	+	+	+
Right kidney	voluminous	voluminous	voluminous
Left kidney	papillary sack	papillary sack	papillary sack
Genital system	hermaphrodite ?	separated sex	separated sex
Specimens observed	hermaphrodite	female	female/male
Propodial penis	left side	not applicable	-
Seminal receptacle	?	-	-
Bursa copulatrix	-	-	-
Eggs	yolky	yolky	yolky
Vitelline layer	thick	mediate	+
Alimentary system			
Jaws	thin	thin	thin
Radula	rhipidoglossate	rhipidoglossate	rhipidoglossate
Radular cartilage	2 pairs	2 pairs	2 pairs
Oesophagus	papillate	papillate	papillate
Heart encircling rectum	completely	completely	completely

propodial penis (Figs. 1A; 3C, G), up to now the only synapomorphy for the Skeneidae family [7,11,16], but missing in *Bruceiella* and *Lodderena*. *Leucorhynchia* has a propodial penis but on the left side (personal observation T.K.). Special copulatory appendages are rare in Vetigastropoda [66], but are also found in certain species of Seguenzioidea [1].

The eggs of *S. serpuloides* have a vitelline layer as diagnostic for Vetigastropoda [67]. Also all three Skeneidae species (Tab. 2) investigated have a seminal receptacle in the left mantle cavity; only in *S. serpuloides* also a bursa copulatrix is present (Fig. 3K). Oviduct and vas deferens both open close to the opening of the renopericardial duct into the right kidney and a common urogenital opening is present, conditions typical for most vetigastropod clades like Haliotidae, Scissurellidae or Trochoidea [68].

The ctenidium is monopectinate in all Skeneidae, but *Leucorhynchia caledonica* has a bipectinate one (personal observation T.K.; Tab. 2). As typical for most Vetigastropoda and several Neomphalina the ctenidial leaflets are equipped with bursicles and skeletal rods [27,28,68,69]. Retention of two kidneys with different functions is diagnostic for the Vetigastropoda and Patellogastropoda [61,67,68,70,71].

Many skeneimorph species show a quite similar radula type. However, Warén [72] showed that many turbinid or trochid species have as juveniles a very similar rhipidoglossate radula, even if the radula type substantially differs in adults. This similarity might be due to similar nourishment in juveniles, namely grazing on different substrates [72], or but might recapitulate the radula type of the vetigastropod (plus neomphalinan) stem species. In both cases the similar rhipidoglossate radula type of skeneimorph gastropods probably is the result of parallel evolution.

It is rather difficult to determine whether the rectum is encircling the heart completely, because this region is often damaged by blood, hardened during fixation. In *S. serpuloides* the heart is encircling the rectum partly (interactive Fig. 2B), while in *S. profunda* and many other vetigastropods the rectum is encircled completely. Jaws with teeth-like elements are typical for Neomphalina and Vetigastropoda, but also for hyalogyrinid Heterobranchia [31]. Two pairs of radular cartilages and a papillate oesophagus were found in many vetigastropod clades [e.g. 61,73] (Tab. 2). A complexly coiled rectum has been also reported in *Turbo stenogyrum* [61], certain Seguenzioidea and again in ectobranch (valvatoidean) Heterobranchia. Conditions of the statocysts with several statoconia reflect again vetigastropod relationships.

Ecology of Skeneidae

Skeneidae species are found in various marine habitats from the shallow coastal waters down to the bathyal plan, but for many locations detailed data about the habitat or bottom structure are not available [e.g. 55,74]. *Skenea serpuloides* is known from infra- and circalitoral, amphioxus sand and maerl in depths between 25 to 145 m [34, herein]. Other *Skenea* species live in depths between 50 and 3,500 m on algae, rock, sunken wood, sand and silty bottoms [16,17,34] (personal communication C. Schander; personal observation T.K.). The *Dikoleps* and *Skeneoides* species shown in Table 3 live in shallow water from 0 to up to 160 m on different bottoms like sand, maerl, intertidal gravel and also on stones, algae and corals [11,34]. Both known species of *Protolira*, *P. thorvaldssoni* Warén, 1996 and *P. valvatoides* live in depths between 850 to 3,700 m in hydrothermal vent habitats, among mussels in sediments, and also on whale bone [7,8]. All species of the genus *Dillwynella* inhabit sunken wood and algal holdfasts [6,9,75].

Most *Skenea*, *Dikoleps* and *Skeneoides* species are mainly known from the European Atlantic coast, from Spain to Spitsbergen and around Iceland, while many *Dillwynella* species were exclusively found in the Pacific Ocean.

Constraints of small size

Skeneimorph gastropods show some special adaptations to their small size. Based on various similarities with trochid or turbinid juveniles (ESO-conditions, radula type, see also below), we assume, that dwarfing has probably been reached by progenesis, i.e. acceleration of sexual matureness into a juvenile stage of forerunners.

Nacre, otherwise typical for trochoid Vetigastropoda, is often missing in very small species [76]. Trochoidean microgastropods have 3-4 pairs of epipodial tentacles, but the number of ESOs is reduced. So larger species, like *Gibbula* or *Osilinus* have mostly one ESO per epipodial tentacle [60], while the small ones have often only a single pair of ESO. This is adjacent to the first or second epipodial tentacle pair, but also a scattered distribution on the epipodial tentacles is known (Tab. 3).

In small species ripe eggs are extremely large compared to the body size, because the eggs have a kind of minimum size to include enough yolk for the developing embryo and obligatory lecithotrophic larva. With a decreasing body size the number of ripe eggs decrease dramatically (50% body size equals only 12,5% of volume, 20% body size equals 0.8% of volume and thus egg numbers!), thus fertilization success by internal or entaquatic (pallial) contact of sperm and eggs becomes a must. Hence, most microgastropods have copulatory structures or seminal receptacles. However, there are exceptions: so for example the small (1.7 mm) Liotiidae species *Wanganella fissura* has neither any copulatory organ nor receptacula (personal observation T.K.; Tab. 2). The same is true for certain small Scissurellidae such as *Incisura lytteltonensis* (Smith, 1894) (size about 1 mm) [cf. 77] or *Scissurella jucunda* (size about 2 mm) [cf. 64,78], where fertilization success might be enhanced by special reproductive behaviour.

A monopectinate gill is also found in other minute vetigastropod species [13,66] (Tab. 2), and this condition might reflect the probably progenetic process of miniaturization, since a monopectinate condition occurs during early ontogeny of bipectinate species [e.g. 78,79]. However, there are small species with bipectinate ctenidia like *Leucorhynchia caledonica* (2 mm), and large species like *Dillwynella voightae* (5.8 mm) with a monopectinate ctenidium, so this is not a strict rule.

Systematic notes

At current stage of knowledge the arrangement of the genital apparatus seems to provide the best characters to define Skeneidae (Tab. 2). All Skeneinae species investigated morphologically are true hermaphrodites with separated ovary and testis. The setting of the genital organs in the other species investigated is very diverse: *Burceiella globulus* is a hermaphrodite without penis, but with separated ovary and testis. *Leucorhynchia caledonica* is a true hermaphrodite with most likely a true hermaphroditic gland (testis and ovary not separated) and a copulatory organ on the left (not right) propodium. *Cirsionella* also lacks a propodial penis [11], but the specimen examined was too young to allow any final statement about the reproductive system. *Lodderena minima* has separate sexes, lacking a seminal receptacle, while the liotiid *Wanganella fissura* has separate sexes, no penis and no seminal receptacle. In the other features like heart encircling the rectum, the setting of epipodial appendages, papillae in the oesophagus or the number of radular cartilages all species are equal (Tab. 2).

Currently a right propodial penis has been confirmed for the genera *Skenea* (type genus), *Dikoleps*, *Skeneoides*, *Protolira, Dillwynella* and *Lissospira* [7,11] (personal observation T.K.). Warén [11] also described a propodial penis for *Pseudorbis* but neither the species nor the source is stated there. The record of a propodial penis in *Lodderena* [11] is obsolete, because *L. catenoides* is nowadays accepted as *Skenea catenoides* (Monterosato, 1877) [80].

For the numerous other genera, which have been assigned to Skeneidae, molecular or

Table 3. Overview of the available data on the soft bodies of Skeneinae.

Species	Method	Cross anatomy	Morphology	References
Dikoleps cutleriana (Clark, 1849)	SM SEM	as *S. serpuloides**, papillate CT & ET, 4 pairs ET, 1 left/2 right ESOs, right postoptic tentacle, neck lobes, propodial penis	n.r.	Fretter & Graham [15]; Jeffreys [54]; Rubio et al. [42]
Dikoleps marianae (Rubio, Dantart & Luque, 1998)	SEM	papillate CT & ET, 4 pairs ET, 1 left/2 right ESOs, right postoptic tentacle, neck lobes, propodial penis	n.r.	Rubio et al. [42]
Dikoleps nitens (Philippi, 1844)	SM, SEM	papillate CT & ET, 4 pairs ET or 4 left/3 right, 2 left/ 1 right ESOs, right eyestalk, right and left neck lobe, propodial penis	n.r.	Fretter & Graham [15]; Jeffreys [54]; Rubio et al. [46]; Rubio-Salazar [34]; Warén & Bouchet [7]
Dikoleps pruinosa (Chaster, 1896)	SEM	papillate CT & ET, 3 pairs ET, 1 pair ESOs, right postoptic tentacle, neck lobes, propodial penis	n.r.	Rubio et al. [46]
Dikoleps rolani (Rubio, Dantart & Luque, 1998)	SEM	papillate CT & ET, 3 left/4 right ET, 1 pair ESOs, big sense organ left, right postoptic tentacle, neck lobes, propodial penis	n.r.	Rubio et al. [42]
Dikoleps templadoi Rubio, Dantart & Luque, 2004	SEM	papillate CT & ET, 3 pairs ET, 1 left/1 right ESOs, right postoptic tentacle, neck lobes, propodial penis	n.r.	Rubio et al. [46]
Dikoleps umbilicostriata (Gaglini, 1987)	SEM	papillate CT & ET, 4 pairs ET, 1 pair ESOs, right postoptic tentacle, neck lobes, propodial penis	n.r.	Rubio et al. [46]
Protolira valvatoides Warén & Bouchet, 1993	SEM	papillate CT & ET, left & right eyestalk, left & right (different) neck lobes, propodial penis	ctenidium, pallial skirt, kidney, rectum	Warén & Bouchet [7]
Skenea basistriata (Jeffreys, 1877)	SM, SEM	as in *S. serpuloides**, papillate CT & ET, right neck lobe, propodial penis, seminal grove	n.r.	Fretter & Graham [15]; Warén [17]
Skenea catenoides (Monterosato, 1877)	?	propodial penis	n.r.	Warén [11]
Skenea peterseni (Friele, 1877)	SM	as in *S. serpuloides**	n.r.	Fretter & Graham [15]
Skenea profunda Friele, 1879	SM	no eyes present	n.r.	Bouchet & Warén [74]
Skenea serpuloides (Montagu, 1808)	SM	papillate CT & ET, 3 pairs ET, 1 pair or 1 left/2 right ESOs, right eyestalk, left and right neck lobe, propodial penis	ctenidium reduced	Clark [4]; Fretter & Graham [15]; Jeffreys [54]; Rubio-Salazar [34]
Skenea trochoides (Friele, 1876)	SEM	papillate CT & ET, right eyestalk, propodial penis	n.r.	Warén [17]
Skenea turgida (Odhner, 1912)	SM	no eyes present	n.r.	Bouchet & Warén [74]
Skeneoides exilissima (Philippi, 1844)	?	propodial penis	n.r.	Warén [11]

Abbreviations: **CT**, cephalic tentacles; **ET**, epipodial tentacles; **n.r.**, not reported in literature – not known; **SEM**, scanning electron microscope; **SM**, stereo microscope; *, Fretter & Graham [15] described the anatomy as in *Skenea serpuloides*.

soft part studies (ideally both) are required for inclusion, hard part characters alone clearly are not sufficient. Only two Skeneinae with propodial penis, *Dillwynella* [11:152] and *Protolira* were included in molecular analyses [1,18,21,22]. Williams & Ozawa [18] used sequences of *Dillwynella vitrea* Hasegawa, 1997 and *Munditiella ammonoceras* Adams, 1863 (no data on penis) but both species only group in 28S rRNA tree together. Besides *Dillwynella* (*D. planorbis* Hasegawa, 1997; *D.* spec. cf. *lignicola* Marshall, 1998; *D.* spec.) and *M. ammonoceras* Kano [13] included three (undetermined) *Cirsionella* species (genus lacks penis; [11:152]), *Bruceiella globulus* Warén & Bouchet, 1993 (species lacks penis [7]), and *Lodderena* spec. in his study. In all trees *Dillwynella* and *Cirsionella* grouped together with a support between 98 % and 100 %. *Bruceiella* has high support of 100 % with *Cirsionella*/*Dillwynella* with COI and 98 % in the combined tree of COI and H3, but do not form a group in the analysis of H3 only. Aktipis & Giribet [22] used *Dillwynella vitrea* and *Protolira* spec. sequences in their analysis. Both grouped together in the five gene analysis, with a support of 78% in the cladogramm and 98% in the maximum-likelihood tree.

Accordingly, it is likely that “Skeneinae” is only a subclade within a broader clade which may also include taxa without a propodial penis. On the other hand there is little doubt that there are still many species listened as Skeneidae, which need to be excluded from this taxon and will be put in different vetigastropod families or even higher taxa.

Conclusions

As stated previously the propodial penis on the right side as an apomorphic character for Skeneinae can be verified. This is always combined with a special arrangement of the genital system including an ovary, testis and seminal receptacle. So for the characterisation data about the cross anatomy and better internal morphology are needed. From the 61 species described in the genera *Skenea*, *Dikoleps*, *Skeneoides*, *Lissospira*, *Dillwynella* and *Protolira* [81], the soft body is only known (partly very poor) from 17 species (Tab. 3). Even less data are available when it comes to the other species suspected to be Skeneidae. From the five genera assigned to Skeneidae examined morphologically, three (*Lodderena*, *Bruceiella*, *Leucorhynchia*) have not the special reproductive system. As maybe around 80 genera with 200 species are grouped in this family previously, a lot more have to be excluded presumably. As all trochoidean (and phasianelloid) skeneimorphs have a combined ESO (Tab. 2; Figs. 1, 3D; [58,75]) all species with a simple ESO can be excluded easily.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

TK carried out the morphological analyses, 3D reconstructions and drafted a manuscript version that was discussed and improved in concert by TK, MH and GH. MB performed the preparation and preliminary examination of *S. serpuloides* in his Diploma Thesis. TK and MH prepared the interactive 3D model. GH supervised the study and particularly provided literature advice. All authors read and approved the final manuscript.

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Paper 5

Epipodial appendages in basal gastropods (Mollusca): new insights, homology assumptions, and evolutionary scenarios

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Epipodial Appendages in Basal Gastropods (Mollusca): New Insights, Homology Assumptions, and Evolutionary Scenarios

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Abstract

Basal gastropods are known to have three different types of appendages. Besides of cephalic tentacles and (occasional) copulatory structures, epipodial tentacles and epipodial sense organs (ESOs) have been severely confused in the past. We provide clear definitions of these structures, check various representatives, and reconsider literature data on their occurrence throughout basal gastropod clades (Patellogastropoda, Cocculiniformia, Neritimorpha, Neomphalina, and in particular Vetigastropoda). "Epipodial tentacles" of Patellogastropoda, Cocculiniformia, Neomphalina, and of several vetigastropod subgroups are considered as ESOs, true epipodial tentacles appear restricted to certain vetigastropod clades (Scissurelloidea, Haliotoidea, Seguenzioidea, and the trochoid/turbinoid radiation). An evolutionary scenario of epipodial structures in basic gastropods is presented in the light of the new data and interpretations: a single pair of ESOs in posterior position is considered as part of the gastropod ground plan, being retained in early juvenile Patellogastropoda and many Cocculiniformia. Neomphalina and Vetigastropoda often multiply this ESO-modul, and within the latter taxon they may be combined with true epipodial tentacles, which are an iterative homologue of the cephalic tentacles.

Introduction

A single pair of cephalic tentacles is typical for the overwhelming majority of gastropods. Additionally the head, neck, mantle and especially the epipodium may be equipped with various kinds of appendages. Especially Vetigastropoda are known to have a large variety of appendages: accessory cephalic tentacles, penis, eyestalks, oral lappets, and neck lobes vary significantly in shape and show various combinations.

Vetigastropoda are unique in showing sensory papillae at the cephalic and epipodial tentacles. This character is variously described in the literature: setose tentacles, ‘seta’-like projections, tentacles with (sensory) papillae, papillate tentacles or papillated (e.g. Flemming 1884; Fretter & Graham 1977; Warén & Bouchet 1993; Fretter et al. 1998; Okutani et al. 2000; Geiger 2003). Tentacles lacking sensory papillae are described on the other hand as smooth or non-papillate (e.g. Haszprunar 1992; Geiger 2003).

Another sensory structure related to the epipodial tentacles in trochids is well known for more than a century: Boutan (1885: pls. 41, 42) marked them as “x” in early juveniles of *Scissurella* and *Fissurella*, Robert (1903) called these “organs sensoriels lateraux” in *Calliostoma zizyphinum* Linné, 1758. 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, since for other species in the same paper they called it only “sense organ”. Crisp (1981) added the acronym ESO and described and depicted its fine-structure (SEM and TEM) for various trochid species in detail. According to Crisp, the ESO is a knobbed structure at the base of an epipodial tentacle with a ciliary groove at the tip (Crisp 1981: fig. 5A). TEM revealed that the ESO is a mechanoreceptor with a distinct ultrastructure consisting of cells with so-called “collar receptors”, a unique structure (Crisp 1981: fig. 6A) characterised by a central cilium surrounded by 8 or 9 specialised microvilli. Later on ESOs were reported in (almost) all vetigastropod superfamilies, however, many authors did not describe them as ESOs or overlooked them (see below).

In order to clear up this mess of data we provide a survey on epipodial structures in basic gastropod taxa. We distinguish two types of ESOs: (a) “simple ESO” (not combined type), an ESO formed as an own tentacle; (b) “combined ESO”, a knobbed ESO located on the base of (mostly papillate) epipodial tentacles (Fig. 9D, F). We examined representatives of six vetigastropod superfamilies, of various Neomphalina and of Cocculiniformia by applying SEM, histological sectioning, and computer aided 3D reconstruction (Tab. 1). These new data were compared with the descriptions of tentacle conditions given in the literature (Tabs. 2-7). We discuss further the evolution of cephalic and epipodial tentacles, sensory papillae, and ESOs in lower gastropods and their systematic significance.

Methods

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; examined with a Hitachi SEM (SMNH).

The histological sections were performed as follows: dissolving of the shell with acid (hydrochloric acid or Bouin's fluid); dehydration in a graded acetone series; plastic embedding in epoxy resin, Spurr´s resin or historesin (Spurr 1969); serial sectioning with glass or diamond knives (thickness between 1.5 or 5 µm; Kunze et al. 2008; Ruthensteiner 2008); staining with a mix of methylene-azurblue after Richardson et al. (1960), 'Kernechtrot' (Mulisch & Welsch 2010) or a mixture of both; sealing with DPX (Agar Scientific, Essex) or cedar oil. Finally the slices were photographed with a digital camera set up (Olympus XC 10) on an Olympus CX41 light microscope (objectives Olympus Plan N 4x, Plan CN 10x, Plan CN 20x, Plan SA 40x). Using these digital images 3D reconstructions were compiled and selected perspective views displayed with the AMIRA software Resolve RT 4.2 (TFG Template Graphics Software, Inc., USA) according to Ruthensteiner (2008). Table 1 lists the species investigated in this study and the institutional references where the examined material is deposited.

Institutional abbreviations.
MNHN, Muséum national d'Histoire naturelle Paris, France;
SMNH, Swedish Museum of Natural History Stockholm, Sweden;
ZSM, Bavarian Zoological State Collection Munich, Germany.

Results

All measurements are approximate values with a tolerance of 2% and the µm values were rounded to decades. The possible shrinking caused by storage and sectioning were disregarded. An overview of the tentacle situation of the taxa investigated is given in Figure 1 and Table 1.

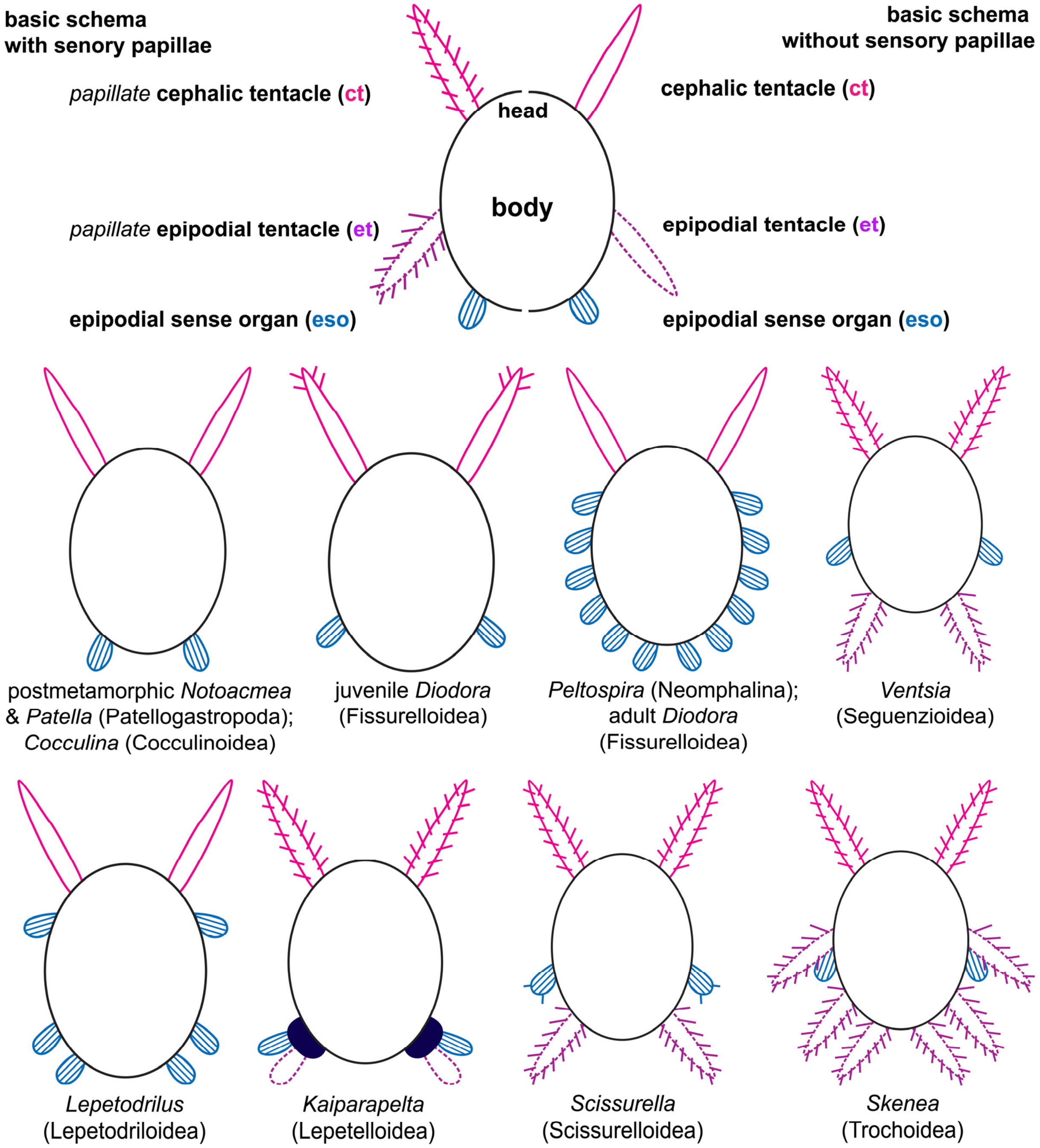


Fig. 1 Overview of the schemata of the taxa included in this study, showing the tentacle situations. Explanation: Dark blue (filled) body of epipodial tentacle (eb).

Table 1 Overview of the tentacles found in the taxa investigated and the methods used.

Species	**Family**	**Tentacles**			**Methods**			**Material stored**	**Figure**
		CT	**ET**	**ESO**	**HS**	**3D**	**SEM**		
Cocculiniformia									
Cocculina craigsmithi McLean, 1992	Cocculinidae	1 pair	no	1 pair	x	-	-	ZSM	Fig. 2E-F
Cocculina spec.	Cocculinidae	1 pair	no	1 pair	-	-	x	SMNH	Fig. 2B-D
Neomphalina									
Cyathermia naticoides Warén & Bouchet, 1989	Neomphalidae	1 pair, no papillae	no	several	-	-	x	SMNH	Fig. 3G-I
Peltospira operculata McLean, 1989	Peltospiridae	1 pair, no papillae	no	several	-	-	x	SMNH	Fig. 3B-C
Peltospira smaragdina Warén & Bouchet, 2001	Peltospiridae	1 pair, no papillae	no	several	-	-	x	SMNH	Fig. 3D-F
Vetigastropoda									
Diodora spec.	Fissurellidae	1 pair, papillae only in juveniles	no	several	x	x	x	ZSM	Fig. 4B-H
Kaiparapelta spec.-1	Pseudococculinidae	1 pair, papillae	1 pair	1 pair, ESO & ET fused on eb	x	x	-	MNHN	Fig. 5B-H
Kaiparapelta spec.-2	Pseudococculinidae	1 pair, papillae	1 pair	1 pair, ESO & ET fused on eb	-	-	x	SMNH	Fig. 5I-K
Clypeosectus curvus McLean, 1989	Lepetodrilidae	1 pair	no	1 pair (juvenile)	x	-	-	ZSM	Fig. 6G-H
Lepetodrilus fucensis McLean, 1988	Lepetodrilidae	1 pair	no	3 pairs	x	-	-	ZSM	Fig. 6I
Lepetodrilus spec. aff. *pustulosus* McLean, 1988	Lepetodrilidae	1 pair	no	3 pairs	-	-	x	SMNH	Fig. 6B-F
Larochea miranda Finlay, 1927	Scissurellidae	1 pair, papillae	2 pairs, papillae	? (1 pair ESO)	x	-	-	ZSM	Fig. 7J-L
Scissurella jucunda Smith, 1890	Scissurellidae	1 pair, papillae	1 pair, papillae	1 pair with few papillae	x	x	-	ZSM	Fig. 7B-F
Scissurella spec.	Scissurellidae	1 pair, papillae	1 pair, papillae	1 pair with few papillae	-	-	x	SMNH	Fig. 7G-I
Ventsia tricarinata Warén & Bouchet, 1993	Seguenzioidea i.s.	1 pair, papillae	1 pair, papillae	1 pair	x	x	x	MNHN	Fig. 8B-I
Lissospira spec.	Skeneidae	1 pair, papillae	4 pairs, papillae	1 pair, combined	-	-	x	SMNH	Fig. 9F
Skenea serpuloides (Montagu, 1808)	Skeneidae	1 pair, papillae	3 pairs, papillae	1 pair, combined	x	x	-	SMNH	Fig. 9B-E
Wanganella fissura Laseron, 1954	Liotiidae	1 pair, papillae	4 pairs, papillae	1 pair	x	x	x	SMNH	
Homalopoma spec.	Colloniidae	1 pair, papillae	? pairs, papillae	1 pair, combined	x	-	-	SMNH	

Abbreviations: CT, cephalic tentacles; eb, body of epipodial tentacle; ESO, epipodial sense organ; ET, epipodial tentacles; HS, histological sections; SEM, scanning electron microscopy; 3D, 3D-reconstructions.

Cocculiniformia Haszprunar, 1987 (emend.)

Cocculinidae Dall, 1882

Cocculina spec. (Fig. 2B-D)

Material examined. SMNH, Gorda ridge, off Northern California (41°00'N, 127°29'W), depth 3,271 m.

Tentacle features. Total body length 880 µm. Cephalic tentacles very short. No sensory papillae at the tentacles. No epipodial tentacles. A single pair of ESOs in posterior position (length 100 µm, width 40 µm) with ciliated groove at the tip. Macro papillae, a special kind of large sensory papillae (diameter 20 µm), around the mantle skirt.

Cocculina craigsmithi McLean, 1992 (Fig. 2E-F)

Material examined. ZSM Mol 20120005, Catalina Basin, California (33°12.0'N, 118°30.0'W), depth 1,240 m, on whale-fall.

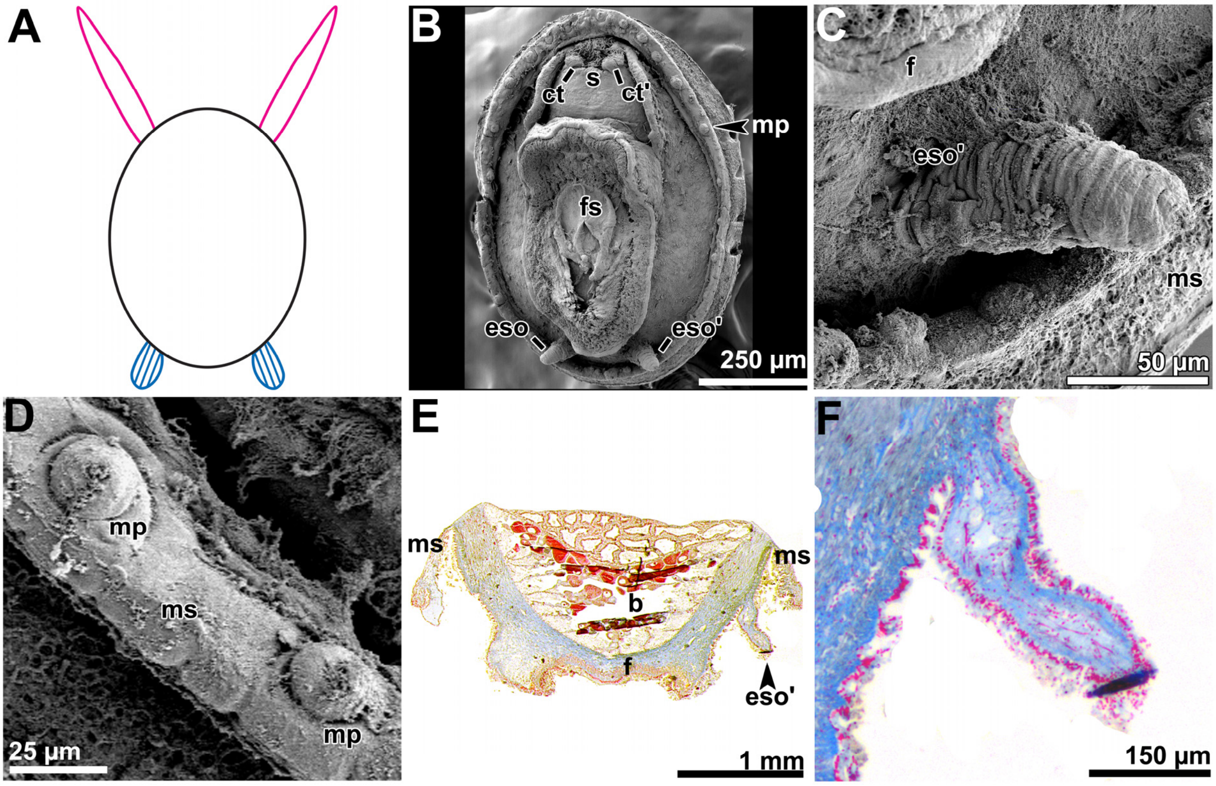


Fig. 2 Tentacles in *Cocculina* (Cocculiniformia: Cocculinidae).

A. Schema. **B-D.** SEM pictures of *C.* spec. **B.** Ventral view of the body. **C.** Left ESO. **D.** Mantle edge with papillae. **E,F.** Histological sections of *C. craigsmithi*. **E.** Cross section of the body. **F.** Longitudinal section of ESO. Abbreviations: b, body; 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.

Tentacle features. Body larger than in *C.* spec. No sensory papillae. No epipodial tentacles. Single pair of quite long ESOs in posterior position (length 350 µm, width 90 µm).

Neomphalina Warén & Bouchet, 1993

Neomphalidae McLean, 1981

Cyathermia naticoides Warén & Bouchet, 1989 (Fig. 3G-I)

Material examined. SMNH 43065, Western of Mexico (09°54’N, 104°12’W), depth 2,532 m, on hydrothermal vents, from vestimentiferan tubes.

Tentacle features. Total body length 2.5 mm. Cephalic tentacles long (length 930 µm, width 230 µm) lacking sensory papillae. No epipodial tentacles. Two pairs of ESOs lying posteriorly below the operculum, elongated (length/width of two ESOs: 200/110 µm, 160/110 µm), groove at the tip elongate, oval shaped and strongly ciliated.

Peltospiridae McLean, 1989

Peltospira operculata McLean, 1989 (Fig. 3B, C)

Material examined. SMNH 81963, East Pacific Ridge (12°48’N, 103°56’W), depth 2,621 m, on hydrothermal vents.

Tentacle features. Total body length 3.4 mm. Cephalic tentacles quite broad (length 580 µm, width 400 µm). No sensory papillae at the tentacles. No epipodial tentacles. Knobbed ESOs all around the epipodial ridge except the frontal part, more than 30 per side, smaller and larger ones mixed, but smaller ventrally and dorsal ones larger (length/width of three ESOs: 50/90 µm, 70/100 µm, 75/120 µm), ciliated groove at the tip of the ESOs irregularly stellate.

Peltospira smaragdina Warén & Bouchet, 2001 (Fig. 3D-F)

Material examined. SMNH 50408, Sintra site, Lucky strike, Mid-Atlantic ridge (37°17.5’N, 32°16.47’W), depth 1,622 m, on hydrothermal vents.

Tentacle features. Total body length 3.5 mm. Cephalic tentacles rather broad (length 730 µm, width 370 µm). No sensory papillae at the tentacles. No epipodial tentacles. About 10 knobbed ESOs per side are situated at the posterior part of the epipodium. ESOs are almost as broad as long (length/width of four ESOs: 70/110 µm, 170/130 µm, 180/170 µm, 125/200 µm), the largest ones posterior, getting smaller anteriorly, ciliated groove at the tip with oval shape.

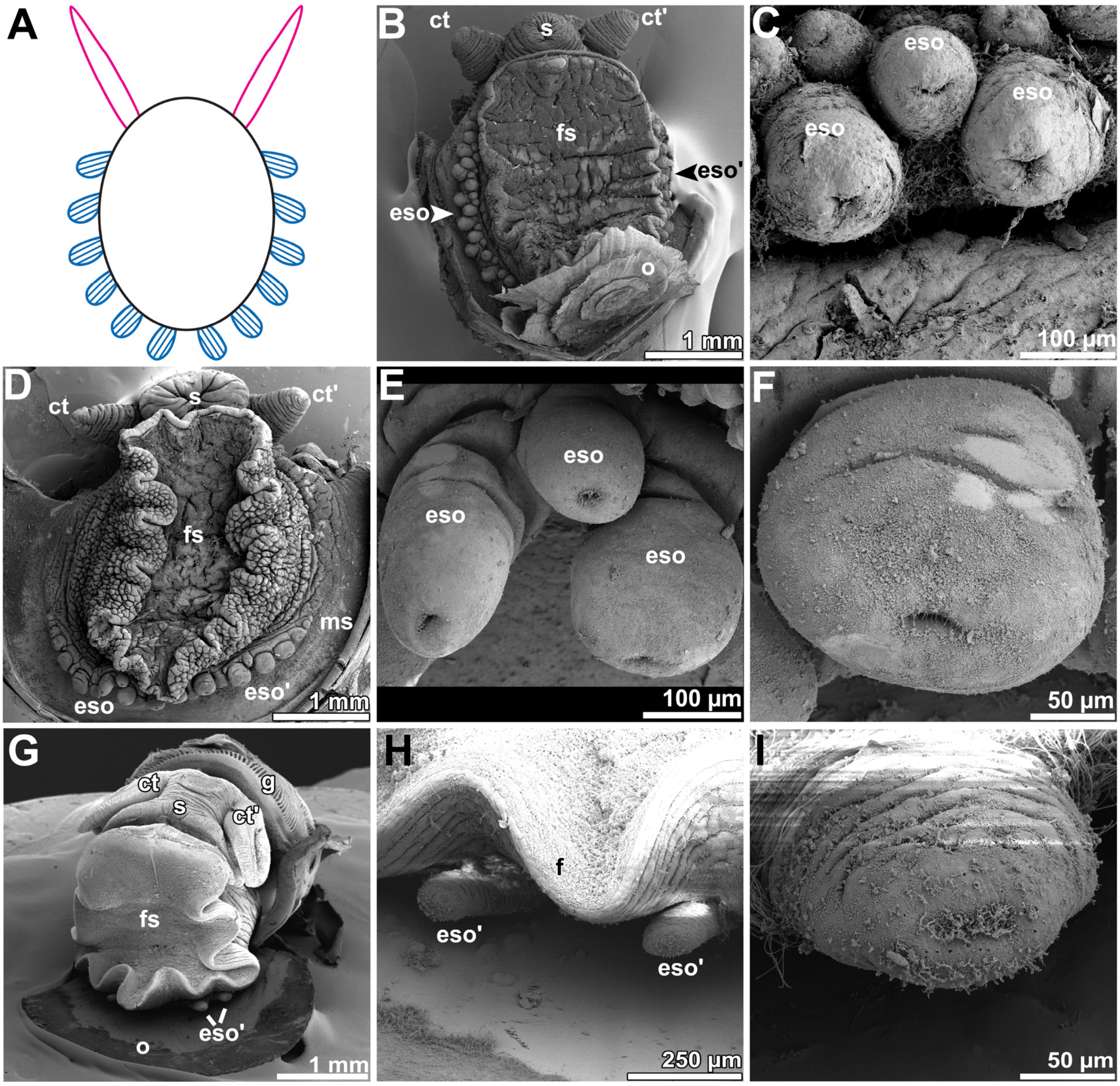


Fig. 3 Tentacles in Neomphalidae and Peltospiridae (Neomphalina).

A. Schema. **B,C.** SEM pictures of *Peltospira operculata*. **B.** Ventral view of the body. **C.** Epipodial sense organs (ESOs). **D-F.** SEM pictures of *P. smaragdina*. **D.** Ventral view of the body. **E.** ESOs **F.** ESO. **G-I**. SEM pictures of *Cyathermia naticoides*. **G.** Fronto-ventral view of the body. **H.** Foot with ESOs. **I.** 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.

Vetigastropoda Salvini-Plawen, 1980

Fissurelloidea Fleming, 1822

Diodora spec. (Fig. 4B-H)

Material examined. ZSM Mol 20120006, tropical aquarium probably from the Indian Ocean, breeding *Diodora* species.

Tentacle features. Total body length of a juvenile 500 µm. Cephalic tentacles (length: 140 µm; diameter: 40 µm) with few sensory papillae at the distal part (Fig. 4D, G) only in juveniles, adult specimens lack sensory papillae (G.H. and T.K. personal observation). No epipodial tentacles. Juveniles with single pair of ESOs (length 45 µm, width 30 µm), whereas adults show several ESOs along the epipodial ridge in adult animals, but less and more distantly spaced than in Peltospiridae.

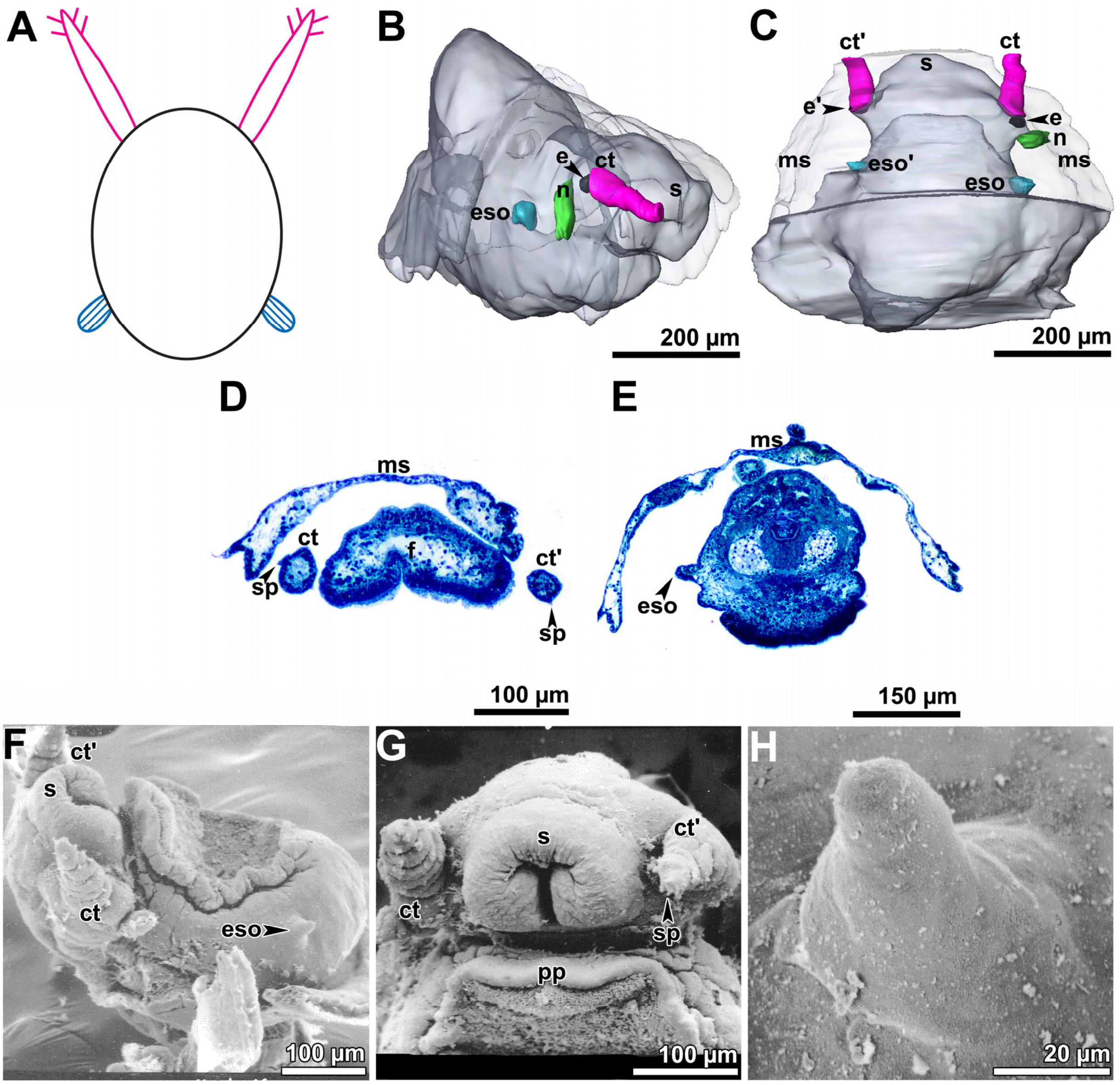


Fig. 4 Tentacles in juvenile *Diodora* spec. (Vetigastropoda: Fissurelloidea).

A. Schema. **B-C.** 3D reconstructions. **B.** Lateral-right side view, only appendages of the right side are shown, body transparent. **C.** Ventral view, body transparent. **D,E.** Histological sections. **D.** Cross section anterior body. **E.** Cross section posterior body. **F-H.** SEM pictures. **F.** Ventro-lateral view of the right side. **G.** Ventral view of the head. **H.** ESO.

Abbreviations: ct/ct', right/left cephalic tentacle; e/e', right/left eye; eso/eso', right/left epipodial sense organ; f, foot; fs, foot sole; ms, mantle skirt; n, neck lobe; pp, propodium; s, snout; sp, sensory papillae.

Lepetelloidea Dall, 1882

Pseudococculinidae Hickman, 1983

Kaiparapelta spec.-1 (Fig. 5B-H)

Material examined. MNHN Molluscan collection, Ua Huka, Marquesa Islands, French Polynesia (8°53'S, 139°38'W), depth 341-344 m, on rocks.

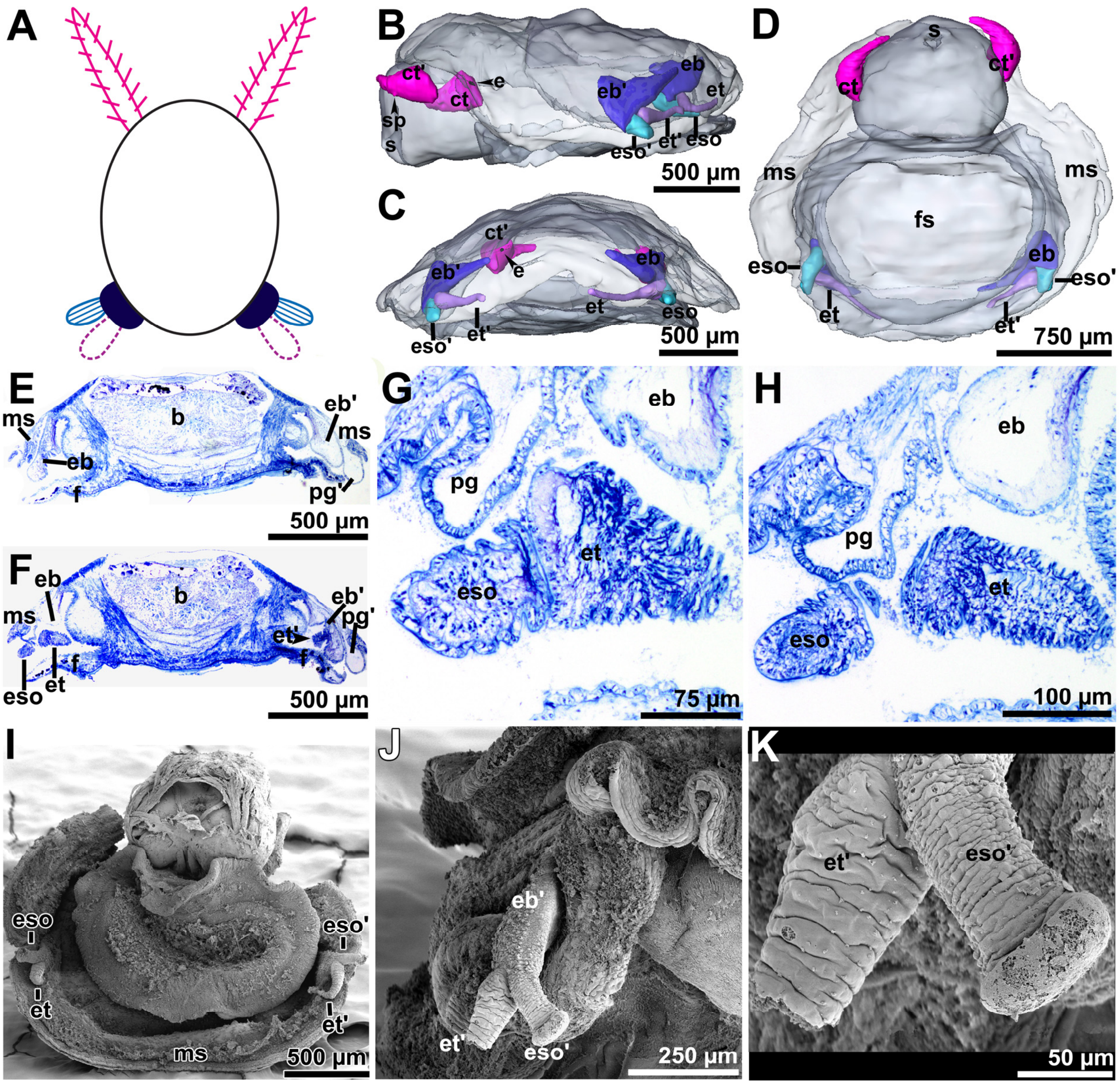


Fig. 5 Tentacles in *Kaiparapelta* (Vetigastropoda: Lepetelloidea).

A. Schema. **B-D.** 3D reconstructions of *K.* spec.-1. **B.** Lateral-left side view, body transparent. **C.** Posterior view, body transparent. **D.** Ventral view, body transparent. **E-H.** Histological sections of *K.* spec.-1. **E,F.** Cross section of the body with tentacles. **G,H.** Cross section of the right ESO and tentacle. **I-K.** SEM pictures of *K.* spec.-2. **I.** Ventral view. **J.** Epipodium with tentacles. **K.** Epipodial tentacle and ESO.

Abbreviations: b, body; ct/ct', right/left cephalic tentacle; e/e', right/left eye; eb/eb', right/left body of epipodial tentacles; eso/eso', right/left epipodial sense organ; et/et', right/left epipodial tentacle; f, foot; fs, foot sole; ms, mantle skirt; pg/pg', right/left pedal gland; s, snout; sp, sensory papillae.

Tentacle features. Total body length 2 mm. Cephalic tentacles short and sturdy (length 370 µm, width 160 µm). Sensory papillae at the cephalic tentacles, none at the epipodial appendages. Special tentacle structure at the posterior third of the epipodium, “bifid tentacle” consisting of a epipodial body (length 280 µm, width 320 µm) and two appendages: one is an ESO (length

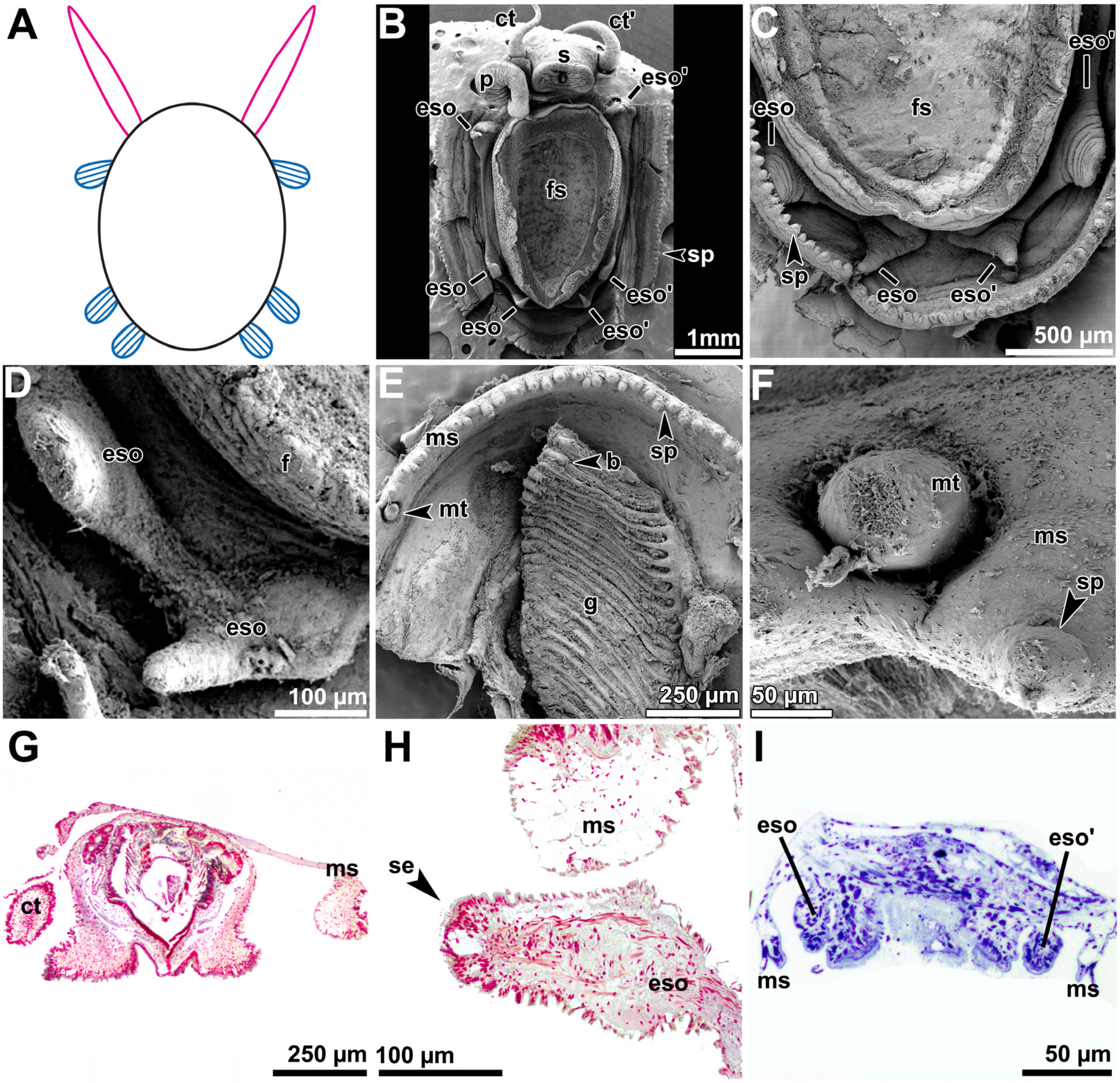


Fig. 6 Tentacles in Lepetodrilidae (Vetigastropoda: Lepetodriloidea).

A. Schema. **B-F.** SEM pictures of *Lepetodrilus* aff. *pustulosus*. **B.** Ventral view of the body. **C.** Ventral view of the posterior body with mantle skirt and ESOs. **D.** Right posterior ESOs. **E.** Ventral view of the mantle skirt with gill, body removed. **F.** Mantle skirt with tentacle and sensory papillae. **G,H.** Histological sections of *Clypeosectus curvus*. **G.** Cross section of the body. **H.** Longitudinal section of the right ESO. **I.** Histological cross section of the body of *L. fucensis*.

Abbreviations: b, bursicle; ct/ct`, right/left cephalic tentacle; eso/eso’, right/left epipodial sense organ; f, foot; fs, foot sole; g, gill; ms, mantle skirt; mt, mantle tentacle; p, penis; s, snout; se, sensory epithelium; sp, sensory papillae.

140 µm, width 95 µm) with a swollen tip, the other is an epipodial tentacle without sensory papillae or a derived part of the ESO (length 250 µm, width 60 µm).

Kaiparapelta spec.-2 (Fig. 5I-K)

Material examined. SMNH 29009, Tonga (21°05'S, 175°22'W), depth 487 m.

Tentacle features. As in *K.* spec.-1, but body smaller (total body length 1.5 mm). Epipodial body longer and more slender (length 230 µm, width 120 µm). ESO (length 160 µm, width 70 µm), epipodial tentacle or derived part of the ESO (length 160 µm, width 80 µm).

Lepetodriloidea McLean, 1988

Lepetodrilidae McLean, 1988

Lepetodrilus spec. aff. *pustulosus* McLean, 1988 (Fig. 6B-F)

Material examined. SMNH, East pacific rise.

Tentacle features. Total body length 4.6 mm. Cephalic tentacles very slender (length 1.1 mm, width 220 µm). No sensory papillae. No epipodial tentacles. Three pairs of slightly differently shaped ESOs, anterior edge of epipodium on both sides drawn out to ESO (length 200 µm, width 60 µm), pointed, ciliary groove not very distinct, two pairs in the most posterior quarter of epipodium, middle one broader with large, oval shaped ciliary groove (length 80 µm, width 125 µm), posterior one slender and small ciliary groove at the tip (length 140 µm, width 60 µm). Mantle skirt equipped with a line of large papillae. A mantle tentacle (diameter 60 µm) embedded in the anterior right end of the mantle skirt, tip of mantle tentacle with cilia.

Lepetodrilus fucensis McLean, 1988 (Fig. 6I)

Material examined. ZSM Mol 20120004, Juan de Fuco ridge of Washington (47°57.0'N, 129°04.0'W), depth 2,208 m, on hydrothermal vents.

Fig. 7 Tentacles in *Scissurella* and *Larochea* (Vetigastropoda: Scissurelloidea).

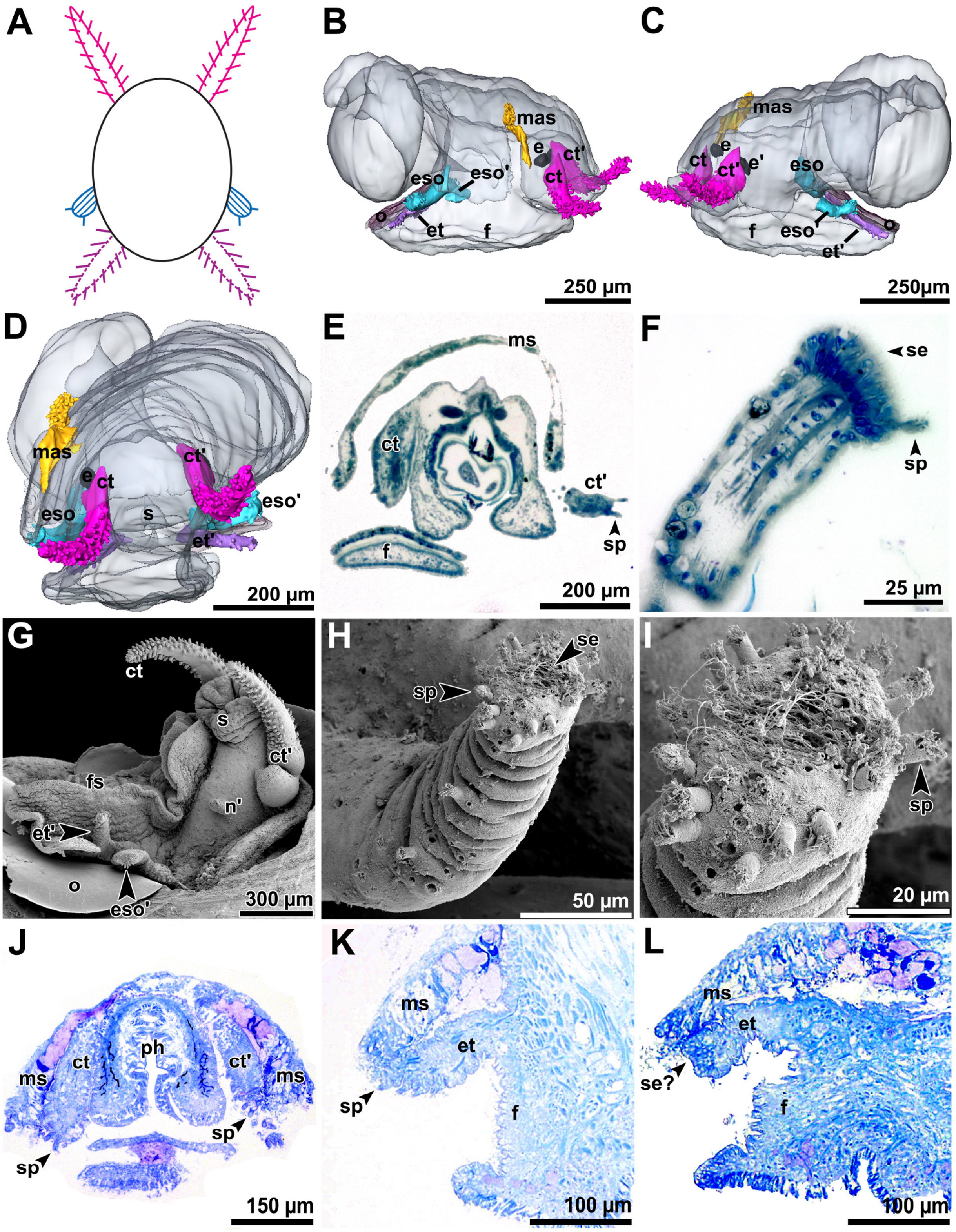
A. Schema. **B-D.** 3D reconstructions of *S. jucunda*. **B.** Lateral-right side view, body transparent. **C.** Lateral-left side view, body transparent. **D.** Frontal view, body transparent. **E,F.** Histological sections of *S. jucunda*. **E.** Cross section of the body. **F.** Longitudinal section of the ESO. **G-I.** SEM pictures of *S.* spec. **G.** Lateral-left side view of the body. **H.** ESO. **I.** Tip of ESO. **J-L.** Histological sections of *L. miranda*. **J.** Cross section with cephalic tentacles. **K.** Cross section with epipodial tentacle. **L.** Cross section with epipodial tentacle or 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; o, operculum; ph, pharynx; s, snout; se, sensory epithelium; sp, sensory papillae.

Tentacle features. No sensory papillae. No epipodial tentacles. ESO well beyond mantle skirt (length 30 µm, width 20 µm).

Clypeosectus curvus McLean, 1989 (Fig. 6G, H)

Material examined. ZSM Mol 20120003, Juan de Fuco ridge of Washington (45°59.5'N,



130°03.5'W), depth 1,575 m, on hydrothermal vents.

Tentacle features. Juvenile specimen. Cephalic tentacles without papillae. No epipodial tentacles. Single pair of ESOs (length 230 µm, width 90 µm), with sensory epithelium at the tip.

Scissurelloidea Gray, 1847

Scissurellidae Gray, 1847

Scissurella jucunda Smith, 1890 (Fig. 7B-F)

Material examined. ZSM Mol 20120002, tropical seawater aquarium.

Tentacle features. Total body length 800 µm. Cephalic tentacles short and slender (length 240 µm, width 50 µm). Cephalic and epipodial tentacles covered densely with sensory papillae. Epipodial tentacles posterior below the operculum (length 120 µm, width 25 µm). Single pair of ESOs slightly more anterior, also under the operculum, long and thickened distally (length 160 µm, width 30 µm), around the edge of the tip several sensory papillae (Fig. 7F, H, I), very few on the rest of the ESO, groove at the tip flat and large with long cilia. Mantle slit equipped with a small papillate tentacle.

Scissurella spec. (Fig. 7G-I)

Material examined. SMNH, Vanuatu, Santos 2006, shallow water.

Tentacle features. Setting like in *S. jucunda*, but animal larger, total body length 1.2 mm. Cephalic tentacles (length 550 µm, width 120 µm). Single pair of epipodial tentacles (length 150 µm, width 40 µm). Single pair of simple ESO (length 120 µm, width 40 µm).

Larocheidae Finlay, 1927

Larochea miranda Finlay, 1927 (Fig. 7J-L)

Material examined. ZSM Mol 20120001, eastern side of North Cape New Zealand, on red algae.

Tentacle features. Total body length 900 µm. Cephalic tentacles short (length 230 µm, width 80 µm). Cephalic and epipodial tentacles papillate. Three epipodial appendages: 1st and 3rd epipodial tentacles (length 230 µm, width 50 µm), 2nd one without papillae. 2nd appendage most likely a single pair of ESOs, but sensory epithelium not clearly visible (Fig. 7L: se?).

Seguenzioidea Verril, 1884

[Unassigned] Seguenzioidea

Ventsia tricarinata Warén & Bouchet, 1993 (Fig. 8B-I)

Material examined. Histology and 3D reconstruction: MNHN Moll 20948, Hine-Hina, Lau Basin, Fiji (22°32'S, 176°43'W), depth 1,900 m, on hydrothermal vents.

SEM: SMNH 78573, Hine-Hina, Lau Basin, Fiji, (ROV Jason 2, Dive 145), depth 1,847 m, on hydrothermal vents.

Tentacle features. Body almost completely retracted (diameter 1.15 mm). Cephalic tentacles

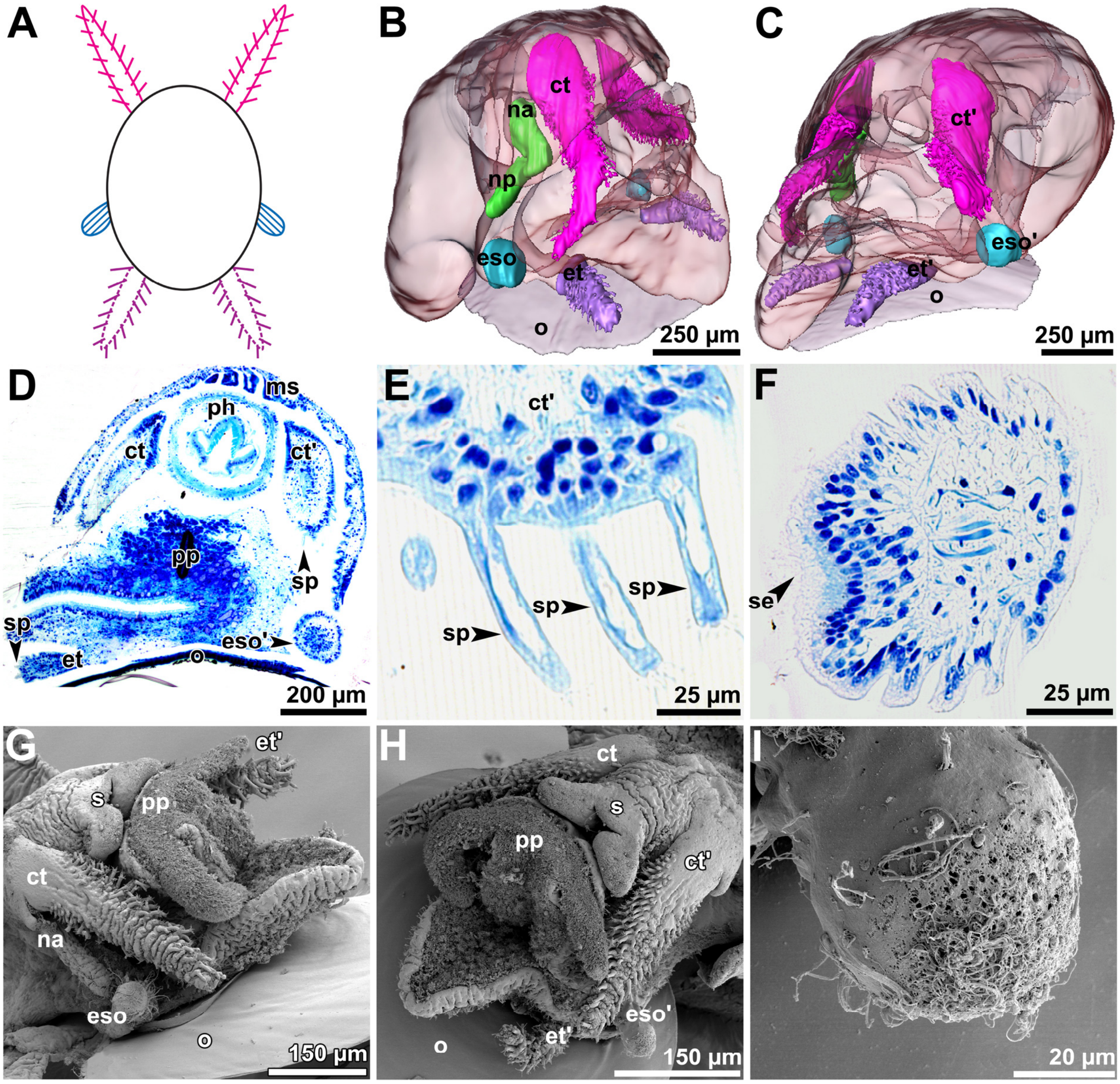


Fig. 8 Tentacles in *Ventsia tricarinata* (Vetigastropoda: Seguenzioidea).

A. Schema. **B,C.** 3D reconstructions. **B.** Lateral-right side view, body transparent. **C.** Lateral-left side view, body transparent. **D-F.** Histological sections. **D.** Cross section of the body. **E.** Longitudinal section of the anterior part of the left cephalic tentacle. **F.** Cross section of the left ESO. **G-I.** SEM pictures. **G.** Latero-frontal view of the right side. **H.** Frontal view. **I.** Left ESO.

Abbreviations: ct/ct', right/left cephalic tentacle; eso/eso', right/left epipodial sense organ; et/et', right/left epipodial tentacle; ms, mantle skirt; na/np, anterior/posterior neck lobe; o, operculum; ph, pharynx; pp, propodium; s, snout; se, sensory epithelium; sp, sensory papillae.

long (length 600 µm, width 100 µm). Cephalic and epipodial tentacles with sensory papillae, papillae quite large and very densely arranged. Single pair of epipodial tentacles long (length 300 µm, width 90 µm). Single pair of simple ESOs (length 80 µm, width 100 µm) anterior to the epipodial tentacle, sensory epithelium well developed, many cilia at the tip.

Trochoidea Rafinesque, 1815

Skeneidae Clark, 1851

Skenea serpuloides (Montagu, 1808) (Fig. 9B-E)

Material examined. SMNH 98645, off Roscoff, Bretagne, France (48°43.532'N, 3°50.712'W), depth 20–25 m, on the surface of "amphioxus-sand".

Tentacle features. Body completely retracted (diameter 670 µm). Cephalic tentacles (length 200 µm, width 70 µm) and epipodial tentacles with sensory papillae. Three pairs of epipodial tentacles (length 90-140 µm, width 25-50 µm), the most anterior one in front of the operculum,

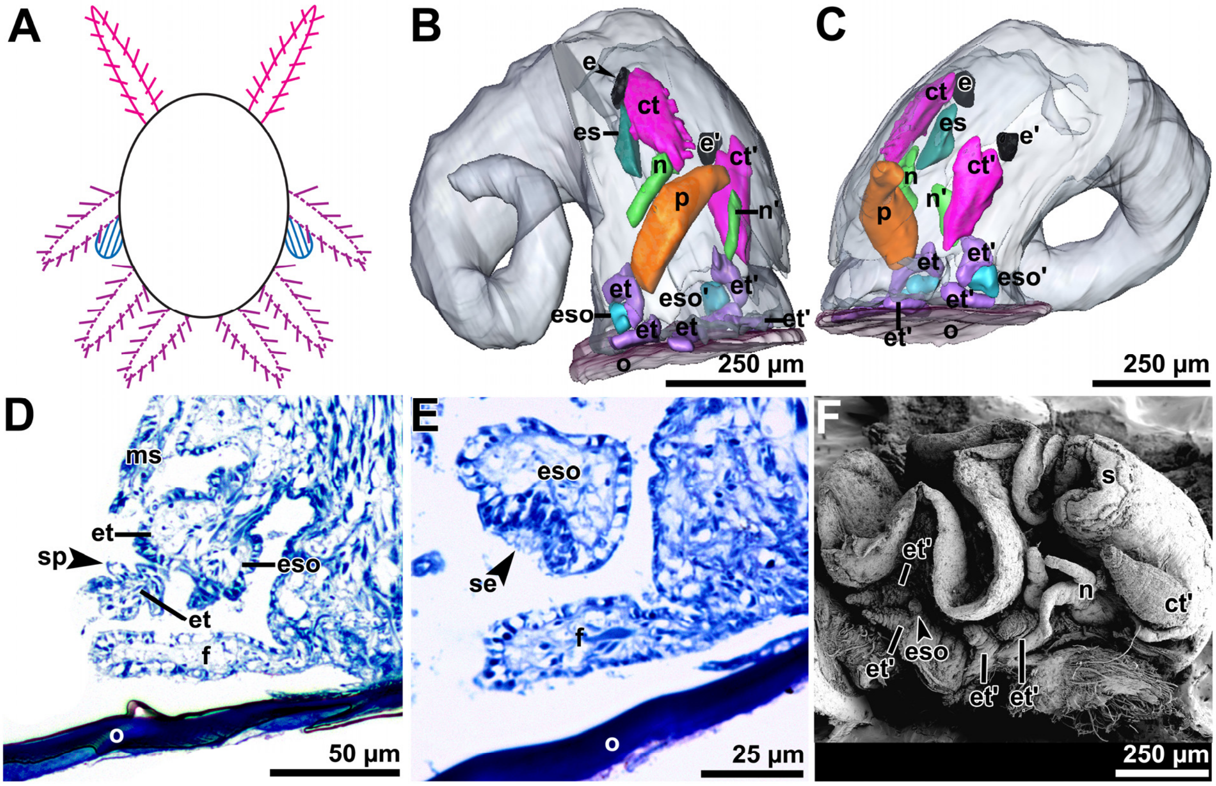


Fig. 9 Tentacles in Skeneidae (Vetigastropoda: Trochoidea).

A. Schema. **B,C.** 3D reconstructions of *Skenea serpuloides*. **B.** Lateral-right side view, body transparent. **C.** Lateral-left side view, body transparent. **D-E.** Histological sections of *S. serpuloides*. **D.** Cross section of epipodial tentacle. **E.** Cross section of the ESO. **F.** SEM picture of *Lissospira* spec., ventro-lateral left side view.

Abbreviations: ct/ct', right/left cephalic tentacle; e/e', right/left eye; es, right eyestalk; eso/eso', right/left epipodial sense organ; et/et', right/left epipodial tentacle; f, foot; ms, mantle skirt; n/n', right/left neck lobe; o, operculum; p, penis; s, snout; se, sensory epithelium; sp, sensory papillae.

the others beyond it. An ESO of the “combined type” attached to the base of the most anterior epipodial tentacle (length 45 µm, width 45 µm), sensory epithelium at the tip.

Lissospira spec. (Fig. 9F)
Material examined. SMNH, from off Cadiz, Spain, shallow water.
Tentacle features. Total body length 1.1 mm. Cephalic tentacles long and broad (length 300 µm, width 120 µm). Cephalic and epipodial tentacles with sensory papillae. Four pairs of epipodial tentacles (length 130 µm, width 40 µm), the posterior two below the operculum. A combined ESO (length 50 µm, width 35 µm) attached to the 3rd pair of epipodial tentacles.

Literature review

In the following we correlate our findings with the data found in the literature (Tab. 2). As outlined several quite different epipodial conditions do occur in basic gastropods (Fig. 1).

Patellogastropoda

All adult Patellogastropoda show smooth cephalic tentacles (Künz & Haszprunar 2001) and entirely lack epipodial appendages. However, Anderson (1965: fig. 8) figured a 10 day old, settled larvae of the lottiid *Notoacmea petterdi* (Tenison-Woods, 1876) with a pair of small appendages slightly ahead the operculum. This structure is obviously difficult to see at the transparent body and thus probably has been overlooked by Smith (1935), Dodd (1957), Kay & Emlet (2002) and others, but has been confirmed by Wanninger et al. (1999: fig. 3D “et”) in postmetamorphic early juveniles of the patellid *Patella caerulea* Linné, 1758. These paired appendages show striking similarities in position and structure with those of *Scissurella* and *Fissurella* described by Boutan (1885: pl. 41, 42: “x”) – and thus we regard them as ESOs too.

Cocculiniformia

Originally Cocculiniformia included also the Lepetelloidea, nowadays a vetigastropod clade, currently it comprises only Cocculinidae and Bathysciadiidae. No sensory papillae are reported for all tentacles of Cocculiniformia. Similar epipodial conditions as described for *Cocculina craigsmithi* McLean, 1992 (Fig. 2) have been described by SEM e.g. for *C. rathbuni* Dall, 1882 by McLean & Harasewych (1995). Strong et al. (2003) already homologized the cocculiniform epipodial appendages (see below) with ESOs rather than with epipodial tentacles of vetigastropods.

A pair of ESOs at the posterior end of the epipodium are positively reported for a series of species and genera: *Cocculina craigsmithi*; *C. emsoni* McLean & Harasewych, 1995; *C. fenestrata* Ardila & Harasewych, 2005; *C. messingi* McLean & Harasewych, 1995; *C. nipponica* Kuroda & Habe, 1949; *C. rathbuni*; *Coccocrater portoricensis* (Dall & Simpson, 1901); *Fedikovella beanii* (Dall, 1882); *F. caymanensis* Moskalev, 1976; *Macleaniella moskalevi* Leal & Harasewych, 1999, and *Teuthirostria cancellata* Moskalev, 1976 (Marshall 1986; Haszprunar 1987; McLean 1992b; McLean & Harasewych 1995; Sasaki 1998; Leal & Harasewych 1999; Strong & Harasewych 1999; Ardila & Harasewych 2005).

Several authors mentioned the absence of epipodial tentacles in the cocculinid genus *Coccopigya* (Marshall 1986; Haszprunar 1987; Dantart & Luque 1994; McLean & Harasewych 1995; Strong et al. 2003). Thiele (1908) did not mention any epipodial tentacles for *Bathypelta pacifica* (Dall, 1908). The recent study by Hartmann et al. (2011: 263) positively confirmed this lack for 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

Table 2 Comparison of the tentacle situation described in the literature and proposed in this paper.

	Previous literature			Proposed in this study		
	ET	**ESO**	**papillae***	**ET**	**ESO**	**papillae***
Patellogastropoda	-[d,e]	-[d,e]	-[d,e]	-	(+)[1]	-
Cocculiniformia	+[a,(d),e]	-[d,e]	-[d,e]	-	+	-
Neomphalina	+[d,e]	-[d,e]	-[d,e]	-	+	-
Vetigastropoda						
Fissurelloidea	+[e]; -[d]	+[b,d,e]	+[d]; -[e]	-	+	+[2]
Haliotoidea	+[d,e]	+[b,d,e]	+[d,e]	n.e.	n.e.	n.e.
Lepetelloidea[3]	+[d]	-[d]	+[d]	(+)	+	+
Lepetodriloidea	+[d,e]	+[b,d,e]	+[d;] -[e]	-	+	-
Pleurotomarioidea	+[e]; -[c,d]	+[b]; -[c,d]	-[c,d,e]	-	+	-
Scissurelloidea	+[d,e]	+[b,d]; ?[e]	+[(d),e]	+	+	+
Seguenzioidea	+[d,e]	+[a,b,d,e]	+[d,e]	+	+	+
Trochoidea	+[d,e]	+[b,d,e]	+[d,e]	+	+	+

References: a, Haszprunar 1988b; b, Haszprunar 1993; c, Hickman 1996; d, Ponder & Lindberg 1997; e, Sasaki 1998.

Abbreviations: n.e., not examined; 1, probably in juveniles; 2, in juveniles; 3, reduced in some families, here given for Pseudococculinidae.

prominent epipodial lappets [ESOs] near the posterior end of the animal".

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

In conclusion we rediagnose the Cocculiniformia in its present understanding: Cephalic tentacles without sensory papillae. No epipodial tentacles. If present, a single pair of ESOs, simple type.

Neritimorpha

Neritimorph gastropods have smooth cephalic tentacles. However, TEM revealed that the ciliary 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 hydrothermal vent inhabiting genera *Shinkailepas* (Okutani et al. 1989) and *Olgasolaris* (Beck 1992b) where several (14 to 30) "epipodial papillae" occur in posterior position (Beck 1992b; Sasaki et al. 2006). SEM photos of these papillae were provided by Sasaki et al. (2006) and suggest an interpretation as ESOs, although this needs confirmation by histological or (better) TEM-studies.

Neomphalina

Neomphalina are currently considered as a major clade of rhipidoglossate gastropods distinct from the Vetigastropoda (e.g. Sasaki 1998; Heß et al. 2008; Bouchet 2011).

The absence of sensory papillae at the tentacles is 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 described "epipodial tentacles", but their structure (Fig. 3: concave ciliary groove at the tip, but no TEM-data up to now to confirm collar receptors) reveals them to be ESOs.

Their number ranges from a single pair in *Retiskenea* cf. *diploura* Warén & Bouchet, 2001 to up to over a hundred in *Echinopelta fistulosa* McLean, 1989 (Fretter 1989; Warén & Bouchet 2001). The tentacles may differ in size as in *Lirapex humata* Warén & Bouchet, 1989, in the numbers on both sides as in *Neomphalus fretterae* McLean, 1981, in shape like in

Peltospira smaragdina Warén & Bouchet, 2001 (irregularly shaped) and may have a decreasing size from posterior to anterior e.g. *P. smaragdina* (Fretter 1989; Warén & Bouchet 1989; Warén & Bouchet 2001; Fig. 3).

The melanodrymiid genera *Leptogyra* and *Leptogyropsis* have two pairs of ESOs (Marshall 1988b; Heß et al. 2008), while the type species *Melanodrymia aurantiaca* Hickman, 1984 is equipped with four to five quite short pairs (Haszprunar 1989; Warén & Bouchet 2001).

The number of ESOs in Neomphalidae varies: 4 pairs in *Cyathermia naticoides* Warén & Bouchet, 1989; 6 pairs in *Lacunoides exquisitus* Warén & Bouchet, 1989; 5 to 6 pairs in *L. vitreus* Warén & Bouchet, 2001; 6 to 11 pairs on the right and less on the left side in *Neomphalus fretterae* McLean, 1981; 4 pairs in *Solutigyra reticulata* Warén & Bouchet, 1989; "more tentacles than in *Neomphalus*" in *Symmetromphalus regularis* McLean, 1990, and approx. 10 pairs in *S. hageni* Beck, 1992 (McLean 1981; Warén & Bouchet 1989; McLean

Table 3 Epipodial sense organs in Peltospiridae.

Species	Shell size	Methods	ESOs	References
Ctenopelta porifera Warén & Bouchet, 1993	l: 10.3 mm	SM/SEM	6	Warén & Bouchet 1993
Depressigyra globulus Warén & Bouchet, 1989	d: 5.4 mm	SM	8-10	Warén & Bouchet 1989
Depressigyra planispira Warén & Bouchet, 1989	d: 5.1 mm	SM	12	Warén & Bouchet 1989
Echinopelta fistulosa McLean, 1989	l: 8.8 mm	SEM	over 100	Fretter 1989; McLean 1989; Warén & Bouchet 2001
Hirtopelta hirta McLean, 1989	l: 12 mm	SM	numerous	Fretter 1989; McLean 1989
Lirapex costellata Warén & Bouchet, 2001	d: 3.6 mm	SEM	10	Warén & Bouchet 2001
Lirapex humata Warén & Bouchet, 1989	h: 3.4 mm	SM	18	Warén & Bouchet 1993
Nodopelta heminoda McLean, 1989	l: 19 mm	SEM	38-40	Fretter 1989; McLean 1989; Warén & Bouchet 2001
Nodopelta rigneae Warén & Bouchet, 2001	d: 8.7 mm	SEM	approx. 30	Warén & Bouchet 2001
Nodopelta subnoda McLean, 1989	l: 9.6 mm	SEM	26-28	McLean 1989; Warén & Bouchet 2001
Pachydermia laevis Warén & Bouchet, 1989	h: 4.6 mm	SM/SEM	10	Israelsson 1998; Warén & Bouchet 1989
Pachydermia sculpta Warén & Bouchet, 1993	h: 2.8 mm	SEM	approx. 10	Warén & Bouchet 1993
Peltospira operculata McLean, 1989	l: 10.1 mm	SM	numerous	Fretter 1989; McLean 1989; pers. obs. TK; Fig. 3
Peltospira delicata McLean, 1989	l: 6.5 mm	SM	numerous	Fretter 1989; McLean 1989
Peltospira smaragdina Warén & Bouchet, 2001	d: 12 mm	SEM	approx. 20	Warén & Bouchet 2001; pers. obs. TK; Fig. 3
Rhynchopelta concentrica McLean, 1989	l: 12.6 mm	SM	14 or 16	Fretter 1989; McLean 1989

Abbreviations: d, diameter; l, length; SEM, scanning electron microscope; SM, stereo microscope.

1990; Beck 1992a; Warén & Bouchet 2001; Fig. 3G-I).

Peltospiridae have up to hundred ESOs around the epipodium, often densely packed and mostly stubby (Tab. 3; Fig. 3B-F).

Retiskenea diploura (about 2 mm size) is not assigned to a family yet and only has a single pair of simple ESOs (Warén & Bouchet 2001).

In conclusion we redefine the conditions of Neomphalina as follows: Cephalic tentacles without sensory papillae. No true epipodial tentacles. From 2 pairs up to over hundred ESOs, simple type.

Vetigastropoda

Fissurelloidea

We follow here the recent phylogeny of Aktipis et al. (2011, Aktipis & Giribet 2012) and exclude Clypeosectidae (see Lepetodriloidea below).

Sensory papillae are lacking in all adults of the Fissurelloidea. However, the cephalic tentacles of juvenile *Diodora* have few sensory papillae at the tip (Fig. 4), as also shown by Boutan (1885: pl. 42, figs. 1, 3).

According to the definitions presented above all “epipodial tentacles” described for Fissurelloidea are ESOs. Thus, the ESOs in Fissurelloidea show a similar condition as in Neomphalina, being arranged in a more or less horseshoe-shaped formation around the foot. The number of ESOs ranges from a single pair up to 40 pairs in large representatives (Tab. 4). ESOs are either of equal size, or but small and larger ones are alternating.

Both, the juvenile *Diodora* of the present study and that of Boutan’s (1885), have a single pair of ESOs, and development starts with the most anterior one. The same condition is retained (probably by progenesis) in the very small (max. 2.6 mm) *Manganesepta hessleri* McLean & Geiger, 2011 and in part also in the small (max. 5 mm) *Profundisepta profundi* (Jeffreys, 1877), where three pairs of ESOs are present, the most anterior one is by far the largest (McLean & Geiger 1998).

Certain genera (*Manganesepta, Clathrosepta, Fissurisepta*) additionally show a single posterior “foot-tentacle” of unknown histology and homology. We agree with McLean & Geiger (1998) that this probably is an apomorphic character within Fissurellidae.

Table 4 Epipodial sense organs in Fissurelloidea.

Genus	Shell length	ESOs	References
Diodorinae			
Diodora	27 mm	30-35, numerous, 21	Fretter & Graham 1976; McLean & Geiger 1998; Ziegenhorn & Thiem 1926
Emarginulinae			
Clathrosepta	13 mm	3 pairs	McLean & Geiger 1998
Cornisepta	7.1 mm	2 pairs	McLean & Geiger 1998
Cranopsis	4.5 mm	numerous	McLean & Geiger 1998
Emarginula	6-21 mm	10-15 pairs, numerous	Fretter & Graham 1976; McLean & Geiger 1998
Fissurisepta	4.3 mm	6-8 pairs, 6 pairs	McLean & Geiger 1998; Warén 1972
Manganesepta	2.6 mm	1	McLean & Geiger 1998
Profundisepta	4.2 mm	3	McLean & Geiger 1998
Puncturella	7 mm	20-23, numerous, 7-8 pairs	Fretter & Graham 1976; McLean & Geiger 1998
Scutus	35 mm	several	Marshall 1987
Fissurellinae			
Fissurella	110 mm	75	McLean 1992c

Haliotoidea

The superfamily Haliotoidea comprehends only one family, with the single genus *Haliotis* including 13-17 subgenera.

In *Haliotis* cephalic, mantle tentacles, and the long epipodial tentacles are equipped with sensory papillae, and their fine structure has been studied by TEM (Künz & Haszprunar 2001; Li et al. 2006a). According to 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 type of epipodial tentacles is found, which is short and dendritic as figured in *H. diversicolor* Reeve, 1846 by Li et al. (2006b: pl. 1, figs. 3, 7).

ESOs were already described and figured by Crofts (1929: 128) in *Haliotis tuberculata* Linné, 1758 as “subtentacular sense organ” lying at the ventral base of the papillate epipodial tentacle. This agrees with the description provided by Sasaki (1998: 51) in *Haliotis diversicolor* as follows: “Epipodial sense organs present only at bases of long tentacles, taking form of simple ciliary tufts”. Although Wanichanon et al. (2004) did not mention any ESO in their work about the tentacles of *Haliotis asinina* Linné, 1758, it is likely that combined ESOs occur in all *Haliotis* species.

According to Crofts (1937) and Ino (1952) the epipodial tentacles develop from posterior to anterior. Bevelander (1988: figs. 2.7, 2.8, not labelled) figured a postmetamorphic early juvenile of *Haliotis rubescens* Swainsson, 1822 with a single pair of epipodial appendages similar to those of Boutan (1885) and Anderson (1965).

Lepetelloidea

Formerly classified as Cocculiniformia, all recent authors agree upon the vetigastropod nature of Lepetelloidea. The superfamily consists of 7 to 10 families, the majority of them only comprehend one to four genera each (Bouchet et al. 2005), only the Pseudococculinidae (including Caymanabyssiinae: cf. Aktipis & Giribet 2012; excluding *Kaiparapelta*: cf. Graf 2011; Graf et al. in review) include 10 genera.

Sensory papillae at cephalic tentacles and mantle margin are restricted to the Pseudococculinidae and *Kaiparapelta* and absent in adults (no data on juveniles) of all other families. All epipodial appendages (if present) lack papillae and according to our definition are in fact ESOs. Bathyphytophilidae and Cocculinellidae lack epipodial appendages completely, while within other families the presence and number of epipodial appendages is heterogeneous (Tab. 5). Dantart & Luque (1994) recognized and figured an unpaired epipodial appendage median at the posterior end of the epipodium of three Mediterranean *Lepetella* species. They described this structure as possible “posterior central (epipodial?) papilla” respectively “posterior (epipodial?) tentacle” (Dantart & Luque 1994: pp. 287, 290). Comparing the structure figured with the ESOs examined within this study we consider this structure to be most likely an unpaired ESO, but TEM-studies are needed to confirm this view.

A single pair of epipodial appendages (in fact ESOs) is described for several pseudococculinid species: *Amphiplica*, *Caymanabyssia*, *Colotrachelus*, *Copulabyssia*, *Kurilabyssia*, *Mesopelex*, *Notocrater*, *Pseudococculina*, *Punctabyssia*, *Tentaoculus*, *Yaquinabyssia* (Marshall 1986; Haszprunar 1988a; McLean 1988b, 1991; Leal & Harasewych 1999; Ardila & Harasewych 2005). Certain pseudococculinids (*Notocrater houbricki* McLean & Harasewych, 1995; *N. youngi* McLean & Harasewych, 1995; *Caymanabyssia spina* Moskalev, 1976; *Copulabyssia riosi* Leal & Simone, 2000) show bifid epipodial appendages (cf. McLean & Harasewych 1995: figs. 61, 70; Leal & Harasewych 1999: fig. 7A, C; Leal & Simone 2000: fig. 9). However, there are no histological data available, thus we hesitate to conclude about this condition.

Another case of bifid epipodial appendage is present in *Kaiparapelta askewi* McLean & Harasewych, 1995 and *K.* spec. (Warén & Gofas 1996: figs. 3B, 5B), and histological data are available in this case (Graf 2011; Fig. 5). Of the two branches, the outer one is doubtlessly an ESO, but the nature of the second (inner) one remains unclear (Fig. 5). It may be a true epipodial tentacle or but is a specialized part of the ESO. Because of the structure and general appearance we consider it within this analysis as an epipodial tentacle without sensory papillae. Both branches are set on a common base, more or less elongate.

Table 5 Epipodial sense organs in the Lepetelloidea families (excluding Pseudococculinidae).

Familiy	Shell size	ESOs		References
		present	lacking	
Addisoniidae				
Addisonia	l: 20 mm	-	+	Thiele 1908; McLean 1985b; Dantart & Luque 1994
Helicopelta	d: 1.9 mm	1 pair	-	Marshall 1996
Bathyphytophilidae				
Bathyphytophilus	l: 2.8 mm	-	+	Moskalev 1978
Cocculinellidae				
Cocculinella	l: 3.5 mm	-	+	Moskalev 1971; Thiele 1909
Pyropeltidae				
Pyropelta	l: 5.5 mm	1 pair	-	McLean & Haszprunar 1987; Sasaki et al. 2008; Warén & Bouchet 2009
Osteopeltidae				
Osteopelta	l: 8.1 mm	1 pair	-	Marshall 1987
Lepetellidae				
Lepetella	l: 3 mm	1 single / 1 pair	+	Thiele 1908; Warén 1972; Dantart & Luque 1994; pers. obs. GH
Tectisumen	l: 2 mm	1 pair	-	pers. obs. GH

Abbreviations: d, diameter; l, length.

Lepetodriloidea

We follow here the most recent molecular studies (Kano 2008; Aktipis & Giribet 2010, 2012) and include here the Lepetodrilidae with the genera *Lepetodrilus*, *Gorgoleptis*, *Clypeosectus,* and *Pseudorimula* (the latter two formerly Clypeosectidae/Fissurelloidea), and the Sutilizonidae with the genera *Temnocinclis*, *Temnozaga,* and *Sutilizona* (formerly Scissurelloidea).

The lack of any sensory papillae at all tentacles for Lepetodriloidea is described for the following species: *Lepetodrilus nux* (Okutani, Fujikura & Sasaki, 1993); *Clypeosectus delectus* McLean, 1989; *C. curvus* McLean, 1989; *Pseudorimula marianae* McLean, 1989, and *Sutilizona theca* McLean, 1989 (Haszprunar 1989; McLean 1989; Sasaki 1998). For all other species investigated the state of papillae is not mentioned. In contrast, Ponder & Lindberg (1997) coded papillae as present in this superfamily, because Fretter (1988: fig. 26) described and figured a special kind of retractable ciliary tufts, which might represent somewhat reduced (or heavily contracted or both) papillae. The latter view is supported by the fact that the mantle margin of *L.* spec. aff. *pustulosus* McLean, 1988 shows sensory papillae (Fig. 6F).

In both *Sutilizona* species studied, *S. theca* and *S. pterodon* Warén & Bouchet, 2001, a single pair of ESOs is present (Haszprunar 1989; McLean 1989, Warén & Bouchet 2001).

Temnocinclis euripes McLean, 1989 has three differently shaped tentacles, but only the middle one is an ESO, while by *Temnozaga parilis* McLean, 1989 each of the three uniform appendages is an ESO (Haszprunar 1989; McLean 1989; Marshall 1993). *Clypeosectus curvus* and *C. delectus* have one anterior and two posterior ESOs with the sensory epithelium located ventrally in the anterior ones, but at the tips in the posterior ones (Haszprunar 1989; McLean 1989). *Pseudorimula* shows the same condition, but the number of ESOs varies between species: 2 to 4 pairs in *Pseudorimula marianae* (Haszprunar 1989; McLean 1989) and 1 to 2 pairs in *P. midatlantica* McLean, 1992 (McLean 1992a).

According to McLean (1985a, 1988a) *Lepetodrilus* is characterised by three, blunt epipodial appendages (ESOs), one anterior (at the anterior end of the epipodium) and two posterior ones, and we confirm this for *Lepetodrilus* spec. aff. *pustulosus* (Fig. 6B-F). Also Sasaki (1998) found three pairs of ESOs in *L. nux*. In contrast, *L. shannonae* Warén & Bouchet, 2009 differs by having only a single, posterior one with lateral additional tentacles (Warén & Bouchet 2009: figs. 6B, 7G).

There are 5 pairs of epipodial appendages in *Gorgoleptis* (McLean 1985b, 1988a; Fretter 1988: fig. 18 - drawing): four of them are very long and slender, the third one is thick and truncated, however. In *G. emarginatus* McLean, 1989 Fretter (1989: 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 all three types, a simple ESO (appendage 3), true epipodial tentacles (appendages 4 and 5), and combined types (appendage 1 and 2) be present in a single species. Here a specimen of the same species was examined too (A.W. personal observation), and the ESO at appendage 1 can be confirmed. However, it is not possible to infer whether or not the other tentacles contain also ESOs. Needless to say that confirmation of this presumably unique condition at least by histology better by TEM is badly needed.

Lepetodrilus and *Pseudorimula* develop a single pair of ESOs first, followed by the other posterior epipodial appendages (A.W. personal observation).

Pleurotomarioidea

All recent molecular phylogenies place Pleurotomariidae as the earliest vetigastropod offshoot (Harasewych 2002; Williams et al. 2008; Aktipis & Giribet 2010, 2012).

Extant Pleurotomariidae are exceptional among the Vetigastropoda, because all authors reported the entire absence of epipodial appendages and of sensory papillae on the cephalic tentacles: *Bayerotrochus midas* (Bayer, 1965); *Entemnotrochus adansonianus* (Crosse &

Fischer, 1861); *Mikadotrochus beyrichii* (Hilgendorf, 1877); *Perotrochus amabilis* (Bayer, 1963); *P. lucaya* Bayer, 1965, and *P. quoyanus* (Fischer & Bernardi, 1856) (Dall 1889; Woodward 1901; Fretter 1964, 1966). Harasewych (2002) proclaimed to assume the secondary loss of these assumed vetigastropod synapomorphies like the absence of a faecal groove. However, there are papillae at the mantle fold (Fretter 1964, 1966; Harasewych & Askew 1993). Due to the lack of data concerning juvenile pleurotomariids it is not possible to exclude the possibility that there are papillae at the cephalic tentacles during development like in Fissurelloidea (see below).

Sasaki (1998: fig. 27c) observed a bunch of tentacular structures located at the margin of the epipodial flaps of *Mikadotrochus beyrichii* and assumed they are "presumably" ESOs. So in his phylogenetic analysis he coded both epipodial tentacles and ESOs as present in Pleurotomariidae. The tentacle structure identifies them as ESOs, so Pleurotomariidae might have several simple ESOs, but no true epipodial tentacles.

Scissurelloidea

According to Gofas (2012a) the Scissurelloidea contain four families, the Scissurellidae, Anatomidae and Larocheidae, and the monotypic Depressizonidae. Temnocinclinae and Sutilizoninae, formerly included in the Scissurelloidea (Haszprunar 1989; McLean 1989), are currently considered as the lepetodriloidean family Sutilizonidae (Warén & Bouchet 2001; Bouchet et al. 2005) and are thus dealt above

Only two species of *Depressizona* are known, and unfortunately no soft body have been found yet. Data on the soft body are quite restricted in this superfamily, since up to now species are designated mostly by shell and sometimes also by radula characters alone (Geiger 2006; Geiger 2008; Geiger & Sasaki 2008; Geiger 2009). The tentacle situation in the superfamily Scissurelloidea is quite heterogeneous. For Anatomidae and Scissurellidae sensory papillae are reported for cephalic and epipodial tentacles (e.g. Pelseneer 1899; Batten 1975; Strasoldo 1991; Marshall 1993; Ponder & Lindberg 1997; Sasaki 1998; Geiger 2003).

Only few histological descriptions of the epipodial conditions of Scissurellidae species are available. All detailed reports agree that cephalic tentacles, the epipodial tentacles, and the distal parts of the ESOs are covered with sensory papillae. The ESO in Scissurellidae is therefore unique in showing direct combination with sensory papillae (we regard the trochoidean "combined ESO" at the base of a papillate epipodial tentacle as a different form). Indeed, this character appears to be diagnostic for Scissurellidae.

The best and most comprehensive data are available for *Scissurella jucunda* Smith, 1890 by the (still unpublished) work of Strasoldo (1991) and Baborka (2007; herein Fig. 7). Both authors agree that there is only a single pair of true epipodial tentacles plus one pair of ESOs, the smallest number of epipodial appendages among Scissurellidae: *Scissurella costata* d'Orbigny, 1824 has a subocular tentacle, 2 true epipodial tentacles and 2 ESOs per side (Vayssière 1894); *Incisura lyttleltonensis* Smith, 1894 has 2 true epipodial tentacles and 1 ESO per side (Pelseneer 1899; Bourne 1910). For *Sinezona costulata* Geiger & Sasaki, 2009 papillae at the epipodial tentacles are reported (Geiger & Sasaki 2009), but nothing about the cephalic tentacles or any ESO is mentioned there.

Anatomidae have sensory papillae at the cephalic and epipodial tentacles, at least four epipodial tentacles on each side and a regular ESO without papillae (Fretter & Graham 1976; Strasoldo 1991; Marshall 1993; Geiger 2003; Geiger & McLean 2010). Typically the ESO forms a cluster together with one or two papillate epipodial tentacles, but is not fused on the base as known from Trochoidea. The presence of non-papillate cephalic tentacles in *Thieleella peruviana* Geiger & McLean, 2010 cannot be substantiated, because the specimen examined shows pealing of the upper epithelium in the SEM pictures (Geiger & McLean 2010: fig. 21A, B). Contrary to *S. jucunda* a tendency of accumulation of the epipodial appendages can be observed. Unlike as in *S. jucunda* represented for the Scissurellidae, the ESO in Anatomidae is not the most anterior epipodial appendage. Fretter & Graham (1976) described 7 pairs of "epipodial tentacles" in *Anatoma crispata* (Fleming, 1828), however, the two most anterior ones are rather smooth and most likely represent an accessory cephalic tentacle or a suboptic tentacle, compared with the data on *Thieleella peruviana* (Geiger & McLean 2010). The other five tentacles split in two groups, three near the midline of the epipodium and two more posteriorly. Most of these tentacles are equipped with sensory papillae. Only the third one in the first group is smooth and we suggest it to be an ESO, corresponding with the data for *Thieleella kelseyi* (Dall, 1905) (Geiger & McLean 2010). *Anatoma janetae* Geiger, 2006 has four papillate epipodial tentacles on each side and also the cephalic tentacles are equipped with papillae, but no ESO is described (Geiger 2006). The *Anatoma* spec. Strasoldo (1991) included in her study has 4 epipodial tentacles and two ESOs on each side. She described "Pinselzellen" according to (Flemming 1884) for all epipodial tentacles, but we consider according to the figures (Strasoldo 1991: fig. XXb) that the ESOs lack sensory papillae. This *Anatoma* spec. has two clusters of three tentacles each: each cluster consists of two epipodial tentacles and one ESO. In another *Anatoma* spec. investigated by Sasaki (Sasaki 1998: figs. 42B, 43A) the 4-5 epipodial tentacles cluster as well, but Sasaki did not find any ESO in that species. Geiger & McLean (2010) examined two species of *Thieleella* by SEM. *Thieleella kelseyi* has four epipodial tentacles. The

Table 6 Epipodial appendages in Seguenzioidea.

Species	Shell size	ESOs	ET	Papillae	References
Calliotropidae					
Bathybembix bairdii (Dall, 1889)	h: 50 mm	-	4 pairs	CT/ET	Hickman & McLean 1990
Calliotropis carlotta (Dall, 1902)	h: 11 mm	-	4 pairs	CT/ET	Hickman & McLean 1990
Calliotropis regalis (Verrill & Smith, 1880)	h: 18 mm	-	3 pairs	CT/ET	Hickman & McLean 1990
Cataegidae					
Cataegis meroglypta McLean & Quinn, 1987	d: 19 mm	-	some	CT	Warén & Bouchet 1993
Chilodontidae					
Herpetopoma pauperculum (Liscke, 1872)	d: 4 mm	-	several	CT/ET	Hickman & McLean 1990
Euchelus atratus (Gmelin, 1791)	h: 18 mm	-	approx. 17 pairs	CT/ET	Hickman & McLean 1990
Granata lyrata (Pilsbry, 1890)	h: 8.5 mm	-	3 pairs	CT/ET	Hickman & McLean 1990; Kano 2008
Seguenziidae					
Seguenzia sp.	d: 1.5 mm	(?)	3 pairs	CT/ET	Sasaki 1998
Seguenzia sp. cf. *eritima* Verrill, 1884	n.r.	-	4 pairs	CT/ET	Quinn 1983
Seguenzia megaloconcha Rokop, 1972	n.r.	(?)	(?) 3-6 left / 6 right	CT/ET	McLean in Quinn 1983
Carenzia carinata (Jeffreys, 1877)	d: 4.5 mm	1 pair	some	CT/ET	Haszprunar 1988b; pers. obs. GH & TK
Bathymargarites symplector Warén & Bouchet, 1993	d: 9.8 mm	-	4 left / 7 right	CT/ET	Warén & Bouchet 1989
Guttula galatheae Knudsen, 1964	d: 3 mm	-	3-4	CT/ET	Knudsen 1964; Quinn 1991
Hadroconus altus (Watson, 1879)	d: 8.2 mm	-	4 or 5	CT	Quinn 1987
Asthelys antarctica Marshall, 1988	d: 5.8 mm	-	4 left/7 right	-	Marshall 1988a
Halystes chimaera Marshall, 1988	d: 8.7 mm	-	6-7 left/5-6 right*	-	Marshall 1988a
Seguenzia matara Marshall, 1988	d: 3.9 mm	-	5 left/2 right	-	Marshall 1988a
Sericogyra metallica Marshall, 1988	d: 5 mm	-	3	-	Marshall 1988a
Sericogyra periglenes Marshall, 1988	d: 6.6 mm	-	3	-	Marshall 1988a
'Skeneimorph Seguenzioidea'					
Adeuomphalus collinsi Kano et al., 2009	d: 2.3 mm	1 pair	1 pair	CT/ET	Kano et al. 2009
Ventsia tricarinata Warén & Bouchet, 1993	d: 2,5 mm	1 pair	1 pair	CT/ET	Warén & Bouchet 1993; Kunze et al. 2008; Fig. 8
Anekes paucistriata Warén, 1992	d: 1.0 mm	-	4 pairs	CT/ET	Warén 1992
Vetulonia jeffreysi Dall, 1913	d: 3.3 mm	-	7 pairs	CT/ET	Warén & Bouchet 1993
Akritogyra similis (Jeffreys, 1883)	d: 2.2 mm	-	several per side	-	Warén 1992
Granigyra arenosa Warén, 1993	d: 2.2 mm	-	3 pairs	-	Warén 1993
Xyloskenea costulifera Marshall, 1988	d: 2.6 mm	1 pair	1 or 2 pair(s)	CT/ET	Marshall 1988b; pers. obs. GH & TK
Xyloskenea consors Marshall, 1988	d: 2.1 mm	-	2 pairs	-	Marshall 1988b
Xyloskenea grahami Marshall, 1988	d: 1.9 mm	-	2 pairs	-	Marshall 1988b
Xyloskenea depressa Marshall, 1988	d: 2 mm	-	1 pair	-	Marshall 1988b

Abbreviations: CT, cephalic tentacles; d, diameter, ET, epipodial tentacles; h, height; n.r.; not reported in the original paper; *, female: 7 tentacles on the left/6 on the right side, male: 6 left/5 right.

two most anterior ones cluster together with an ESO, while the third and fourth one have a more separate location. For *T. peruviana* the authors stated 4 epipodial tentacles, but marked the ESO situation with a question mark. However, we think that the smooth tentacle (Geiger & McLean 2010: fig. 21E) represents very likely an ESO.

In the Larocheidae, the reports about the conditions of sensory papillae differ, while ESOs are not described yet: in *Larochea miranda* Finlay, 1927 Haszprunar (in Marshall 1993) could not find any papillae at the tentacles, but the animal used for histological sectioning was in a poor state of conservation (T.K. personal observation). In a second, more recent series of *L. miranda*, we found sensory papillae, both at the cephalic and the epipodial tentacles (Baborka 2007; T.K. personal observation; Fig. 7J, K). Unfortunately also the poor preservation of the latter series hinders statements about the unequivocal presence of an ESO in Larocheidae, but the most posterior epipodial appendage represents most likely an ESO. In contrast, *Trogloconcha ohashii* Kase & Kano, 2002 shows papillae at the cephalic tentacles alone and has smooth epipodial tentacles (Kase & Kano 2002).

Bathyxylophila excelsa Marshall 1988, originally described as a skeneimorph species, was put close to *Anatoma* resp. Scissurelloidea (but weakly supported in both cases) by molecular analysis (Kano 2008, Aktipis & Giribet 2012) and thus may represent another slit-less scissurelloid species. Marshall (1988b) did not provide any comment on papillae or ESOs for *B. excelsa*, *B. pusilla* Marshall, 1988 or *B. iota* Marshall, 1988. By means of semithin sectioning Kunze et al. (2008) showed that *B. excelsa* has papillate cephalic and epipodial tentacles (a single pair), but due to the poor conservation data about the ESO cannot be provided.

Seguenzioidea

We follow the recent molecular studies (Williams & Oszawa 2006; Kano 2008; Williams et al. 2008; Aktipis & Giribet 2010, 2012) in the largely extended content of this vetigastropod clade. Choristellidae, originally placed in the Lepetelloidea (Haszprunar 1992, McLean 1992), have to be included now in the Seguenzioidea as well (Y. Kano personal communication).

The tentacle conditions in Seguenzioidea are diverse and the descriptions available are somewhat confusing (Tab. 6), but the ESO is always a single pair of knobbed tentacles, not combined with any other tentacular structure and free of sensory papillae (Fig. 8B, F, I).

Trochoidea, Angarioidea and Phasianelloidea

The relation and affiliation of the former ‘Trochacea’ are still under discussion. Two superfamilies (Trochoidea, Turbinoidea) were considered by Bouchet et al. (2005), but nowadays three distinct clades Trochoidea, Angarioidea and Phasianelloidea are accepted (Williams et al. 2008, 2010; Aktipis & Giribet 2010, 2012; Gofas 2012b). Due to the similarities of all relevant characters we deal these three taxa together.

Cephalic and epipodial tentacles are always equipped with sensory papillae, ESOs are always of the combined type, however, losses or but duplication of ESOs occur in many species, also intraspecifically (Tab. 7). A correlation of epipodial tentacles and ESO is found in the larger species, while a reduction of the ESOs to a single pair is typically found in smaller species like Skeneidae. The phasianelloid species *Homalopoma* spec. aff. *ammusitatum* (Gould,

Table 7 Epipodial appendages in Trochoidea.

Species	Shell size	ESOs	ET	Papillae	References
Calliostomatidae					
Calliostoma granulatum (Born, 1778)	d: 31 mm	no	3 pairs	CT	Fretter & Graham 1977
Calliostoma occidentale (Mighels & Adams, 1842)	d: 10 mm	no	3-4 pairs	CT	Fretter & Graham 1977
Calliostoma zizyphinum (Linné, 1758)	d: 22 mm	no	4-5 pairs	CT	Fretter & Graham 1977
Liotiidae					
Wanganella fissura Laseron, 1954	d: 1.3 mm	1 on 1st pair of ET	3 pairs	CT/ET	pers. obs. TK
Margaritidae					
Margarites helicinus (Phipps, 1774)	d: 5 mm	1 per ET*	3*/5-6 pairs	CT/ET	Fretter & Graham 1977; Crisp 1981
Margarites groenlandicus (Gmelin, 1791)	d: 6.2 mm	1 per ET	7 pairs	?	Fretter & Graham 1977
Skeneidae					
Skenea serpuloides (Montagu, 1808)	d: 1.4 mm	1 pair or 2 left/1 right	3 pairs	CT/ET	Fretter & Graham 1977; Kunze 2011; Rubio-Salazar 1990; Fig. 9
Dikoleps cutleriana (Clark, 1849)	d: 2.4 mm	1 left/2 right	4 pairs	CT/ET	Rubio et al. 1998
Dikoleps marianae (Rubio, Dantart & Luque 1998)	d: 0.91 mm	1 left/2 right	4 pairs	CT/ET	Rubio et al. 1998
Dikoleps nitens (Philippi, 1844)	d: 0.9 mm	2 left/1 right	4 pairs	CT/ET	Rubio-Salazar 1990
Dikoleps pruinosa (Chaster, 1876)	d: 1 mm	1 pair	3 pairs	CT/ET	Rubio et al. 2004
Dikoleps rolani (Rubio, Dantart & Luque 1998)	d: 1.1 mm	1 pair	3 left/4 right	CT/ET	Rubio et al. 1998
Dikoleps templadoi (Rubio, Dantart & Luque 2004)	d: 0.95 mm	1 left/1 right	3 pairs	CT/ET	Rubio et al. 2004
Dikoleps umbilicostriata (Rubio, Dantart & Luque 2004)	d: 0.86 mm	1 left/ 1 right	4 pairs	CT/ET	Rubio et al. 2004
Dillwynella voightae Kunze, 2011	d: 5.8 mm	1 per 1st ET	3 pairs	CT/ET	Kunze 2011
Solariellidae					
Solariella amabilis (Jeffreys, 1865)	d: 6 mm	no	3 pairs	?	Fretter & Graham 1977

Table 7 Continued.

Species	Shell size	ESOs	ET	Papillae	References
Tegulidae					
Chlorostoma lischkei (Tapparone-Canefri, 1874)	d: 21 mm$^{\#}$	1 per ET	4 pairs	CT/ET	Sasaki 1998
Trochidae					
Gibbula cineraria (Linné, 1758)	d: 12.5 mm	1 per ET	3 pairs	CT/ET	Fretter & Graham 1977; Crisp 1981
Broderipia iridescens (Broderip, 1834)	l: 8 mm$^{\#}$	1 per ET	3 pairs	CT/ET	Sasaki 1998; Geiger et al. 2008
Diloma nigerrima (Gmelin, 1791)	n.r.	1 per ET*	3 pairs*	CT/ET	Crisp 1981
Diloma zelandica (Quoy & Gaimard, 1834)	n.r.	1 per ET*	3 pairs*	CT/ET	Crisp 1981
Gibbula magus (Linné, 1758)	d: 28 mm	1 per ET	3 pairs	CT/ET	Fretter & Graham 1977
Gibbula umbilicalis (da Costa, 1778)	d: 16 mm	1 per ET*	3 pairs*	CT/ET	Fretter & Graham 1977; Crisp 1981
Jujubinus clelandi (Wood, 1828)	d: 14 mm	1 per ET	3 pairs	CT/ET	Fretter & Graham 1977
Jujubinus exasperatus (Pennant, 1777)	d: 4.5 mm	1 per ET	3 pairs	CT/ET	Fretter & Graham 1977
Jujubinus montagui (Wood, 1828)	d: 6.5 mm	1 per ET	3 pairs	CT/ET	Fretter & Graham 1977
Osilinus lineatus (da Costa, 1778)	d: 25 mm	2 per ET*	3 pairs*	CT/ET	Fretter & Graham 1977; Crisp 1981
Stomatia phymotis Hebling, 1779	l: 38 mm$^{\#}$	? 1 per ET	prob. 4 pairs	CT/ET	Sasaki 1998
Turbinidae					
Turbo stenogyrum (Fischer, 1873)	d: 13 mm$^{\#}$	1 per ET	4 pairs	CT/ET	Sasaki 1998

Abbreviations: d, diameter; ET, epipodial tentacles; l, length; n.r.; not reported in the original paper; *, described by Crisp (1981) 'as in *Gibbula cineraria*'; $^{\#}$, body size.

1861) investigated had papillae at cephalic tentacles and several epipodial tentacles, but only a single pair of ESOs (T.K. personal observation, Tab. 1). There are only very few data available for Angarioidea, so *Angaria delphinus* (Linné, 1758) has sensory papillae (Hickman 1998: fig. 15.56B), but no ESO is figured nor is its absence mentioned.

The development of the epipodial appendages in *Calliostoma zizyphinum* proceeds from anterior to posterior with tentacles and associated ESOs (Robert 1903, referred as "organs sensoriels lateraux").

Discussion

Limits of analysis

All sensory structures mentioned in this study may easily be overlooked even in the SEM or cannot be clearly histologically diagnosed in cases of poor fixation, suboptimal storage or other collecting or preserving artifacts such as deep freezing which caused pealing of external epithelia. In addition, also strong retraction of the animal into the shell might pack small ESOs making clear diagnosis difficult at least. Unequivocal identification should combine light microscopy ideally by means of semithin sectioning with associated 3D reconstruction and application of SEM plus ideally also TEM to distinguish the type of the ciliary sensory cells.

Concerning literature data, the situation is always problematic, if the absence of characters is inferred from “not mentioned”. Only if the lack is explicitly stated, it is obvious that attention was put on such details, otherwise doubts remain. Indeed, papillae, epipodial tentacles or ESOs are often not mentioned, yet present.

Homologies of epipodial structures

The main point of this review is the clear distinction between epipodial tentacles and the epipodial sense organs (ESOs), both structures have been severely confused by many authors in the past. Based on identical structure, in particular the papillate appearance in the Vetigastropoda, we conclude that true epipodial tentacles are serial (iterative) homologues of the cephalic tentacles and are likewise a combined chemo-mechanoreceptive sensory organ. In contrast, the epipodial sense organ (ESO) is an entirely distinct structure being equipped with collar receptors suggesting pure mechanoreceptive function.

Accordingly, there are two couples of homologous module structures: (1A) The cephalic/epipodial tentacle as an organ with a muscular hydraulic system and thus narrow blood sinuses; (1B) the papilla as part of the cephalic/epipodial tentacle with a tip consisting of encircling, ciliary receptor cells (see Künz & Haszprunar 2001). (2A) The ESO is an organ with a hollow appearance and thus a large blood sinus and simple ciliary receptor cells. (2B) The latter receptor cells bear mechanoreceptive “collar-receptors” of a distinct fine structure, which are present throughout the lophotrochozoans and also in various, non-homologous molluscan sense organs (see review by Haszprunar 1985).

Each of these modules is repeatedly and variously multiplied, lost or combined in basic gastropod taxa (Fig. 1).

Ground pattern of epipodium

There is a striking similarity in position and appearance of the lateral epipodial appendages in early juveniles of various taxa: Anderson (1965: fig. 8) described it for *Notoacmea petterdi* and Wanninger et al. (1999: fig. 3D "et") for *Patella caerulea* (Patellogastropoda); in *Scissurella* and *Fissurella* (Vetigastropoda) it was described and figured by Boutan (1885: pl. 41, 42: "x") and herein - the latter are ESOs without doubt - we accept also the former as ESOs. This structure looks very much like the epipodial appendage described and figured by Ino (1952: fig. 4.3-4) for a nine respectively ten day old larvae of *Haliotis discus* (again Vetigastropoda). The first epipodial appendage of the *Haliotis* juvenile is also located in front of the operculum. Both larvae figured have approximately the same state of development. The same condition is figured by Bevelander (1988: fig. 2.7, 2.8, not labelled) in *Haliotis rubescens*. Accordingly we conclude (as already pictured by Haszprunar 1988b) that a single pair of ESOs belongs to the ground pattern of Gastropoda, however, this may be originally a juvenile rather than an adult character.

Evolutionary scenarios

This original epipodial condition - just a single pair of ESOs - is still present and unchanged in most Cocculinidae and Lepetelloidea (Pseudococculinidae, Pyropeltidae), but now also in the adults. Like other characters (e.g. the pronounced asymmetry of the gills) of these taxa this condition might be due to a heterochronic shift (paedomorphosis). Within other taxa the single-pair-ESO-condition is often repeated during ontogeny.

Within Neomphalina and in parallel in Fissurellidae and Lepetodrilidae the ESO-modul is more or less multiplied forming a ring of ESOs surrounding the foot. In other vetigastropods ESOs also occur at the neck lobe or at the eyestalk showing its modul status as do asymmetrical appearances.

Künz & Haszprunar (2001) described by TEM encircling ciliary receptor cells in the cephalic tentacles of Vetigastropoda and Neritimorpha (no data on Neomphalina), whereas the ciliary sensory cells in Patellogastropoda show a different fine structure. If Patellogastropoda are still accepted as the earliest gastropod offshoot, this characteristic might be regarded as a synapomorphy of Orthogastropoda (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 and in the light of lacking data on juveniles - might be primary or secondary. Secondary loss of papillae is likely in Lepetodrilidae and Fissurellidae, the latter still show papillae in juveniles.

It is not unlikely that the multiplication of the cephalic tentacles as true epipodial tentacles occurred within the Vetigastropoda rather than in the stem species of this clade. If so, Pleurotomarioidea, Lepetelloidea, Lepetodriloidea, and Fissurelloidea never had this condition and form a lower level, whereas Scissurelloidea, Haliotoidea, Seguenzioidea, and the trochoid/turbinoid radiation are synapomorphically united by true epipodial tentacles. The latter condition has been independently evolved in certain taxa of the caenogastropod Cerithioidea such as Cerithiidae - Bittiinae, Litiopidae, or Plesiotrochidae (Healy & Wells 1995).

As a last step in the evolution of epipodial structures we consider the combined arrangement of true epipodial tentacles and ESOs as found in Haliotoidea and the trochoid/turbinoid radiation. A robust phylogenetic tree of Vetigastropoda is a prerequisite to decide whether this step occurred only once or several times in evolution.

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4 General discussion

Skeneimorph gastropods

Already first anatomical data on skeneimorph gastropods provide evidence for the extent of polyphyly (Paper 1). Several as Skeneidae described species are not members of this family, some do not even belong to the Vetigastropoda but have to be placed in other gastropod clades (Fig. 4.1). These species lack typical vetigastropod characters like sensory papillae at cephalic and epipodial tentacles, a retained right kidney or statocysts with several statoconia and thus could be excluded easily. *Leptogyra* and *Leptogyropsis* are placed nowadays in the Neomphalina (Heß et al. 2008; Kunze et al. 2008), while *Hyalogyra*, *Hyalogyrina* and *Xenoskenea* are assorted to the heterobranch superfamily Valvatoidea (Kunze et al. 2008; Haszprunar et al. 2011; Fig. 4.1).

Further 13 skeneimorph species originally described as Skeneidae were investigated morphologically (Tab. 4.1). The vetigastropod affiliation of all species is proved rather easily by the presence of two kidneys, statoconia in the statocysts, sensory papillae at cephalic and epipodial tentacles and epipodial sense organs (ESOs). ESO is an important character to designate the superfamilies affiliation. While the species of Trochoidea (incl. Skeneidae), Angarioidea and Phasianelloidea have an ESO combined on the base of an epipodial tentacle, all other superfamilies have a simple ESO (see below section 'Tentacles in lower gastropods'; Fig. 4.2). Haliotoidea have a kind of combined ESO too, but all members of this superfamily can be defined without any doubt by the shell. To assign those species with a simple ESO to a certain family or even superfamily is more difficult because the existing morphological data for these taxa are in most parts poor and incomplete as demonstrated for Seguenzioidea (Paper 3).

The examined specimens of *Bathyxylophila excelsa* Marshall, 1988 were deep-frozen before stored in alcohol. This causes an extremely poor state of preservation of the external epithelia and details like the ESOs were not conserved. However, Kano (2008) put this species in relation to the Larocheidae (Scissurelloidea) based on molecular data. The morphological data do not contradict this and so *Bathyxylophila* represents another genus of slit-less Scissurelloidea (common name: little slit snails).

The affiliation of *Ventsia tricarinata* Warén & Bouchet, 1993 to the Seguenzioidea was revealed by Kano (2008) using a molecular approach and can be confirmed by the unique seminal receptacle found also in the genera *Seguenzia*, *Carenzia* and *Xyloskenea* (personal

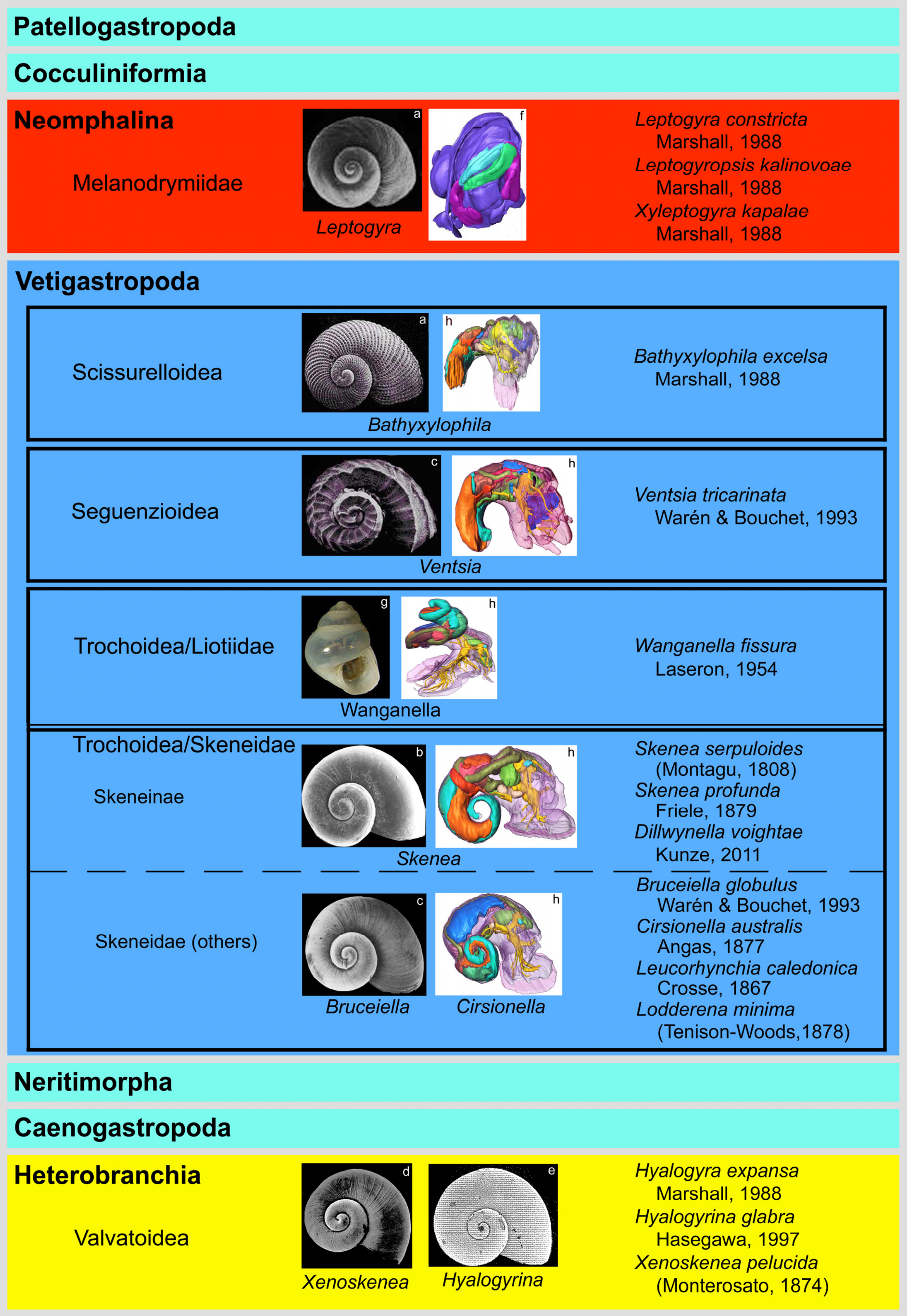


Figure 4.1 Overview of the recent affiliations of species originally described as Skeneidae.

Picture references: a, Marshall 1988; b, Warén 1991; c, Warén & Bouchet 1993; d, Warén et al. 1993; e, Hasegawa 1997; f, Kunze et al. 2008; g, Beechey 2009; h, Kunze (unpublished data).

observation G. Haszprunar & T. Kunze; personal communication T. Sasaki). *Ventsia tricarinata* has a very special mosaic of apomorphic (e.g. organs for inner fertilization) and plesiomorphic characters (e.g. subradular organ) and forms with other small skeneimorph genera (e.g. *Adeuomphalus*, *Akritogyra*, *Anekes*, *Granigyra*, *Xyloskenea*) most likely an early offshoot of the Seguenzioidea (Kano et al. 2009), currently named 'skeneimorph Seguenzioidea' as a working title (Fig. 2.2).

The angarioidean respectively phasianelloidean shells are very characteristically formed and species of these two superfamilies can be grouped into both taxa rather easily. All other species with a combined ESO belong to the Trochoidea.

Wanganella nowadays is placed in the trochoidean family Liotiidae (Rosenberg 2012). The examined species *Wanganella fissura* Laseron, 1954 has separate sexes lacking a copulatory organ.

Skeneidae sensu stricto (Skeneinae) can now be defined clearly. These are all species having a so-called propodial penis on the right edge of the propodium (Warén 1991, 1992). Copulatory organs are also found in other Vetigastropoda, but the location on the right propodium is unique for Skeneinae. A right propodial penis can be detected in the following genera: *Skenea*, *Dikoleps*, *Skeneoides*, *Lissospira*, *Dillwynella*, and *Protolira* (Warén 1992, 1993; Warén & Bouchet 1993; Rubio et al. 1998, 2004; personal observation T. Kunze). The record of a penis in *Lodderena* (Warén 1992) is invalid, because the examined species is nowadays accepted as *Skenea catenoides* (Monterosato, 1877) according to Oliverio (2006). Also the presence of a penis in *Pseudorbis* as given in Warén (1992) could not be reassessed because no source, respectively species, is specified there. The species examined in this study having a propodial penis (*Skenea serpuloides* (Montagu, 1808), *S. profunda* Friele, 1879 and *Dillwynella voightae* Kunze, 2011) are all true hermaphrodites with separate ovary and testis and a seminal receptacle. In most gastropods the gonad is situated in the very posterior part of the visceropallium next to the digestive gland. In Skeneinae this position is occupied by the ovary whereas the testis is located anteriorly in the body. All products are discharged via the right kidney and a common urogenital duct.

The other Skeneidae species treated do not have a right propodial penis combined with true hermaphrodism. These species are morphologically very diverse; the same is true for their reproductive biology. *Lodderena minima* (Tenison-Woods, 1878) has separate sexes. *Bruceiella globulus* Warén & Bouchet, 1993 is, contrary to the original description, a hermaphrodite (Warén & Bouchet 1993) but lacks a propodial penis. *Leucorhynchia*

Table 4.1 Species investigated in this study.

Species investigated	**Family**	**Methods**[1]	**Skeneidae**[2]	**Project**[3]	
				sken.	**tent.**
Cocculiniformia					
Cocculina craigsmithi McLean, 1992	Cocculinidae	LM	-	-	+
Cocculina spec.	Cocculinidae	SEM	-	-	+
Neomphalina					
Peltospira operculata McLean, 1989	Peltospiridae	SM, SEM	-	-	+
Peltospira smaragdina Warén & Bouchet, 2001	Peltospiridae	SM, SEM	-	-	+
Cyathermia naticoides Warén & Bouchet, 1989	Melanodrymiidae	SEM	-	-	+
Vetigastropoda					
Homalopoma spec.[4]	Colloniidae	LM	-	-	+
Diodora spec.	Fissurellidae	LM, 3D, SEM	-	-	+
*Clypeosectus curvu*s McLean, 1989	Lepetodrilidae	LM	-	-	+
Lepetodrilus fucensis McLean, 1988	Lepetodrilidae	LM	-	-	+
Lepetodrilus spec.[5]	Lepetodrilidae	SEM	-	-	+
Wanganella fissura Laseron, 1954	Liotiidae	LM, 3D, SEM	(+)	+	+
Kaiparapelta spec.	Pseudococculinidae	LM, 3D, SEM	-	-	+
Bathyxylophila excelsa Marshall, 1988	Scissurellidae	LM, 3D	(+)	+	-
Larochea miranda Finlay, 1927	Scissurellidae	LM			+
Scissurella jucunda Smith, 1890	Scissurellidae	LM, 3D, SEM	-	-	+
Carenzia carinata (Jeffreys, 1877)	Seguenziidae	LM	-	+	+
Ventsia tricarinata Warén & Bouchet, 1993	ua Seguenzioidea	LM, 3D, SEM	(+)	+	+
Bruceiella globulus Warén & Bouchet, 1993	Skeneidae	LM	+	+	-
Cirsionella australis Angas, 1877	Skeneidae	LM, 3D	+	+	-
Dillwynella modesta (Dall, 1889)	Skeneidae	SM	+	+	-
Dillwynella voightae Kunze, 2011	Skeneidae	SM, LM, SEM	+	+	+
Lissospira spec.	Skeneidae	SEM	+	-	+
Leucorhynchia caledonica Crosse, 1867	Skeneidae	LM, 3D	+	+	-
Lodderena minima (Tenison-Woods, 1878)	Skeneidae	LM, 3D	+	+	-
Munditiella ammonoceras (Adams, 1863)	Skeneidae	LM	+	+	-
Protolira valvatoides Warén & Bouchet, 1993	Skeneidae	LM, CT, S	+	+	-
Skenea profunda Friele, 1879	Skeneidae	LM	+	+	-
Skenea serpuloides (Montagu, 1808)	Skeneidae	LM, 3D	+	+	+

Explanations:

1, Methods: CT, computer tomography; LM, light microscopy (histological sections); S, synchrotron tomography; SEM, scanning electron microscopy of body; SM, stereo microscopy of body; 3D, 3D reconstructions based on histological sections.

2, Skeneidae: +, classified as Skeneidae nowadays; - never placed in Skeneidae; (+) classified as Skeneidae previously but not nowadays.

3, Project: sken., concerning skeneimorph gastropods; tent., concerning tentacles in lower gastropods.

4, *Homalopoma* spec. aff. *amussitatum* (Gould, 1861).

5, *Lepetodrilus* spec. aff. *pustulosus* McLean, 1998.

Abbreviation: ua, unassigned to a family yet.

caledonica Crosse, 1867 is a hermaphrodite. It has very likely a true hermaphroditic gland but at least ovary and testis are placed both closely together in the most posterior part of the body. Its propodial penis is located on the left side exceptionally and therefore is not the same as in Skeneinae. The examined specimen of *Cirsionella australis* Angas, 1877 turned out to be a juvenile, so the reproductive organs could not be described.

With the present data it is not possible to state whether the Skeneinae is a subgroup of a broader definition of Skeneidae together with the 'sensu lato' group or forming an own taxon. About 80 more unexamined genera of Skeneidae exist and most likely many more species have to be excluded.

Dwarfing in skeneimorph gastropods

All skeneimorph gastropods share a minute size from 0.8 mm in *Lodderena* up to 5.8 mm in *Dillwynella*, but most often sizes between 1 and 2 mm were found. A reduction of an animal's body size has an enormous influence on its volume. A size reduction of half the body size (diameter) results in volume of only 12.5 %, with a reduction of 80 % only 0.8 % of the original volume remains. One of the questions in this study was the examination of adaptation patterns of microgastropods to their small size and the influence of the miniaturization onto the inner organs. How do they dwarf? Are skeneimorph gastropods progenetic derived dwarfs or are they 'normal sized' with the related species being giants?

Nacre is common in Vetigastropoda and typical for Trochoidea. However, the shells of all skeneimorph gastropods lack nacre. Hickman (1983) described the correlation of shell size reduction and loss of shell layers in gastropods. One of the first reduced layers is nacre. This has happened independently in all skeneimorph gastropods.

In addition all of these snails have a more or less similar rhipidoglossate radula (Fig. 2.3). Warén (1990) found out that many juvenile trochoidean gastropods (members of the families Calliostomatidae, Solariellidae, Trochidae, and Turbinidae) have the same radula type. However, as adults the same species have very different radulae varying between species. The rhipidoglossate radula is suspected to be an adaptation to grazing, whereas from adults totally different diets are known. Grazing seems to be the most appropriate nutrition for small snails, while larger specimens are often specialised (like sucking or drilling). As skeneimorph gastropods never grow large they seem to stick to the 'original' feeding type. Unfortunately, the diet in most of the skeneimorph gastropods is unknown, but the rhipidoglossate radula speaks in favour of grazing like in juvenile trochoids. Paedomorphosis could well explain the rhipidoglossate radula and hence general dwarfing.

Larger trochoid species like *Gibbula* have 3-4 pairs of epipodial tentacles with a combined ESO attached to each of these tentacles (Crisp 1981; Paper 5 Tab. 7). In the course of dwarfing a reduction of the epipodial appendages could be expected. This situation is found in the Seguenzioidea where the number of epipodial tentacles is reduced in the micro-scaled genera *Adeuomphalus*, *Ventsia* and *Xyloskenea* to 1 or 2 pairs, while larger species have 3 or more pairs (Paper 5 Tab. 6). However, Skeneidae species like *Skenea*, *Dillwynella* or *Dikoleps* still have 3-4 pairs of epipodial tentacles like larger trochoidean species. One ESO per epipodial tentacle is found in most of the larger species, but ESOs are reduced in the Skeneidae with a single pair remaining in most of the cases. However, loss and duplication of ESO occur regularly both in dwarfed and large species. For example in *Dikoleps* species many different settings of ESOs were found (Paper 4 Tab. 3).

Most of the skeneimorph species have a monopectinate ctenidium. The only one with a partly bipectinate ctenidium is the medium sized *Leucorhynchia caledonica* (Skeneidae) with a shell diameter of 2 mm. In contrast, the largest skeneimorph species investigated, *Dillwynella voightae*, has a monopectinate ctenidium with a maximal shell diameter of 5.8 mm. Size reduction often causes a monopectinate ctenidium, but does not exclude a bipectinate one. This character is therefore quite variable and could not be used so far for classification of Skeneidae.

As described above with dwarfing the volume shrinks extraordinarily. However, eggs cannot shrink below a minimum size (150 µm diameter in *S. serpuloides*; 120 µm in *V. tricarinata*), so they appear rather large compared to the residual body of microgastropods. The eggs are always yolky and covered with a more or less thick vitelline layer. Only very few eggs are mature at the same time. In order to guarantee reproductive success internal fertilization including copulatory organs and sperm storage devices, like seminal receptacle, seem to be most appropriate.

The reproductive systems are very diverse in the investigated species. All Skeneinae are true hermaphrodites, having a right propodial penis, separated ovary and testis, and a seminal receptacle. *Skenea serpuloides* additionally has a bursa copulatrix. The species assorted as Skeneidae all have a different reproductive system, including separate sexes in *Lodderena minima* and hermaphrodites with a true hermaphroditic gland in *Leucorhynchia caledonica.* The liotiid *Wanganella fissura* has separate sexes lacking a penis and seminal receptacle, while the seguenzioid *Ventsia tricarinata* is gonochoristic as well, but with a seminal receptacle. Different strategies in the setting of the reproductive organs seem to be appropriate to manage dwarfing. Semi internal fertilization in the mantle cavity guaranteed by penes and sperm storage is found regularly. However, it is not the only possible solution and also small species like *Wanganella fissura* with separate sexes and aquatic fertilization are successful.

So far two of the characters originally described for Skeneidae, the rhipidoglossate radula and the loss of nacre, are modifications in favour of the miniaturization.

Small size is widely spread over Gastropoda and is especially found in the Heterobranchia (e.g. Neusser et al. 2006; Neusser et al. 2009; Martynov et al. 2011; Martynov & Schrödl 2011). Progenesis is one possible explanation for the origin of the dwarf size, but not all small species are progenetic ones. The progenetic species are smaller than the related species, the anatomy is simpler, juvenile organs are present and ontogenetic data are needed to prove progenesis. This was shown in detail e.g. for corambid nudibranchs (Martynov et al. 2011; Martynov & Schrödl 2011) driven by habitat change and a need for faster development. Several developmental stages could be observed in different *Loy* and *Corambe* species (Martynov et al. 2011: fig. 8).

Unfortunately, ontogenetic data are missing for most groups including skeneimorph species, e.g. Neomphalina and Seguenzioidea. The best examined character is the rhipidoglossate radula in Trochoidea, which is also known in many juvenile trochoidean species, while the adults grow to a size of 1 cm or even larger. Similarities of juvenile trochoidean and skeneimorph radulae suggest progenesis in a juvenile ancestor of Skeneidae.

Tentacles in lower gastropods

In Vetigastropoda two kinds of epipodial appendages exist: (a) epipodial tentacles and (b) epipodial sense organs (ESOs). Additionally cephalic and epipodial tentacles may be equipped with sensory papillae (Fig. 4.2). These characters of the tentacles turned out to be systematically important. The presence of ESOs is accepted by many authors to be an apomorphy for Vetigastropoda (Salvini-Plawen & Haszprunar 1987; Haszprunar 1993; Ponder & Lindberg 1997; Sasaki 1998). A combined ESO (ESO located at the base of an epipodial

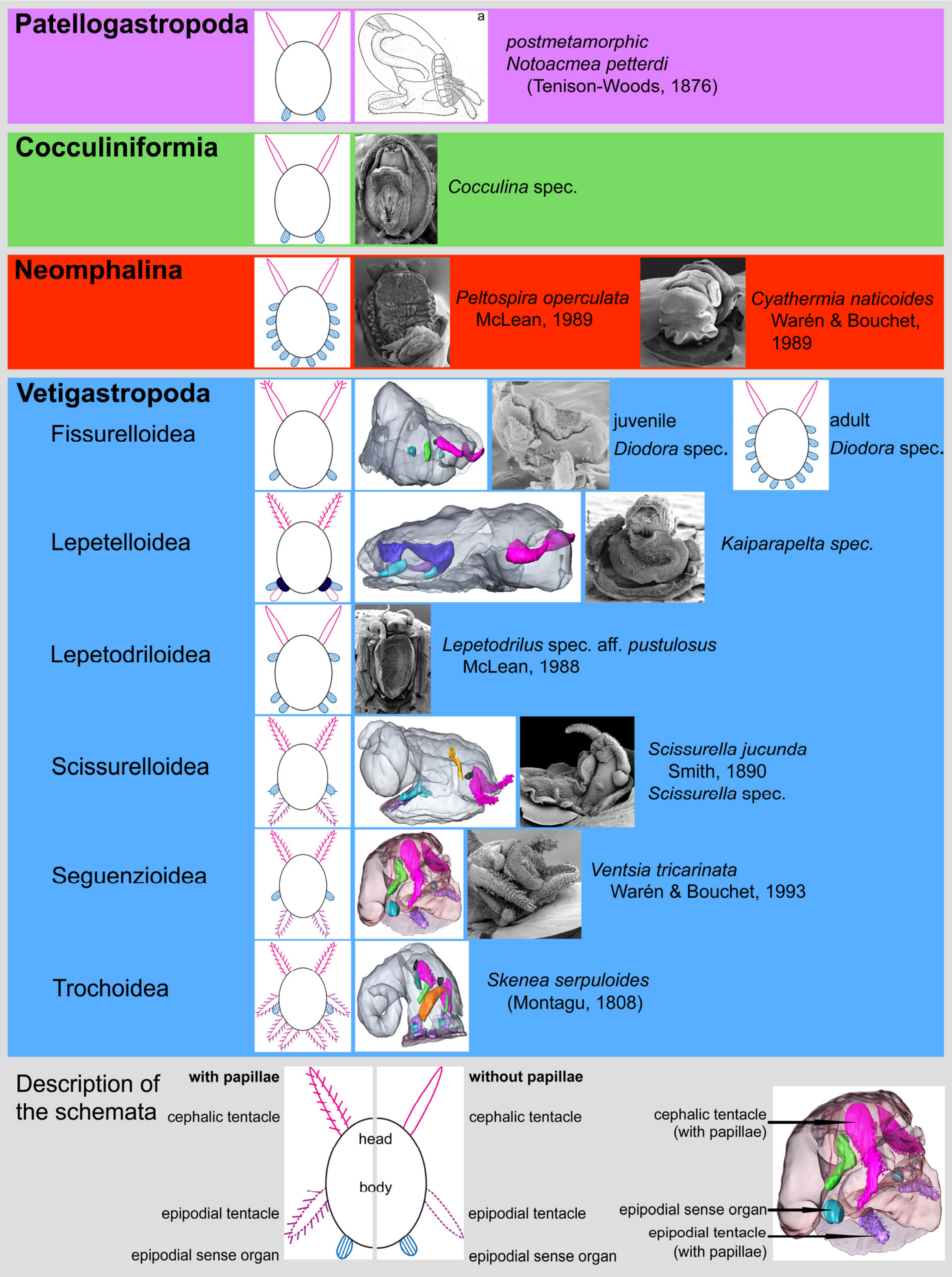


Figure 4.2 Overview of the tentacles found in lower gastropod taxa investigated.

Picture references: Schemata & 3D reconstructions, Kunze (unpublished data); SEM pictures, Kunze & Warén (unpublished data); a, Anderson 1965.

tentacle) is unique for Trochoidea, Angarioidea, and Phasianelloidea (Crisp 1981; Hickman 1998). Comparisons of the tentacle situations in the species investigated with the tentacles described in the literature showed that ESOs, as a rule, were poorly described and often overlooked, even in papers done after Crisp's (1981) description. In order to complete the data set specimens from the vetigastropod superfamilies Lepetelloidea and Lepetodriloidea, but also from the gastropod clades Cocculiniformia and Neomphalina were prepared (Tab. 4.1). Neritimorpha entirely lack epipodial appendages. ESOs were described in the literature variously as macropapillae, 'organs sensoriels' or sense organs (e.g. Robert 1903; Fretter & Graham 1977; Hickman 1998) only to name a few expressions used. A comprehensive literature review was a precondition to work with this character.

Formerly a single pair of epipodial tentacles was assumed to be the original state in Gastropoda (Haszprunar 1988) and all epipodial appendages in Patellogastropoda, Cocculiniformia and Neomphalina were regarded as epipodial tentacles. Vetigastropoda also had epipodial tentacles and were known to be additionally equipped with ESOs which were regarded as a vetigastropod apomorphy. However, the presence or absence of ESOs was reported diverging in the vetigastropod superfamilies (Paper 5 Tab. 2).

Taking into account the data of the present study this view has to be changed fundamentally. A comparison of SEM pictures and section series of the vetigastropod ESOs reveals several morphologic homologies of the epipodial appendages (formerly tentacles) in Cocculiniformia and Neomphalina. All these structures have cilia at the tip combined with a more or less distinctive groove. In the sections also a sensory epithelium was found in this area. Therefore all epipodial appendages in Cocculiniformia and Neomphalina are true ESOs. The figures of postmetamorphic Patellogastropoda (Anderson 1965; Wanninger et al. 1999) reveal the presence of a paired ESO being lost during juvenile development. This led to the diagnosis that ESOs are not restricted to the Vetigastropoda (Fig. 4.2).

Hence, the ESO is reported now for the first time in gastropod clades Patellogastropoda, Cocculiniformia and Neomphalina. Also for the vetigastropod superfamily Lepetelloidea an ESO is reported herein for the first time. In an unpublished study about Neritimorpha, a single pair of ESOs is figured by a juvenile *Nerita* species (personal communication L. Page).

In the new hypothesis a single pair of cephalic tentacles and a single pair of ESOs belongs to the ground pattern of Gastropoda and is found in postmetamorphic Patellogastropoda, juvenile Neritimorpha, adult Cocculiniformia and certain adult Vetigastropoda (e.g. certain Fissurelloidea and Lepetelloidea). In the next step the ESO is multiplied as happened, for example, in Neomphalina and Fissurelloidea. In Vetigastropoda a

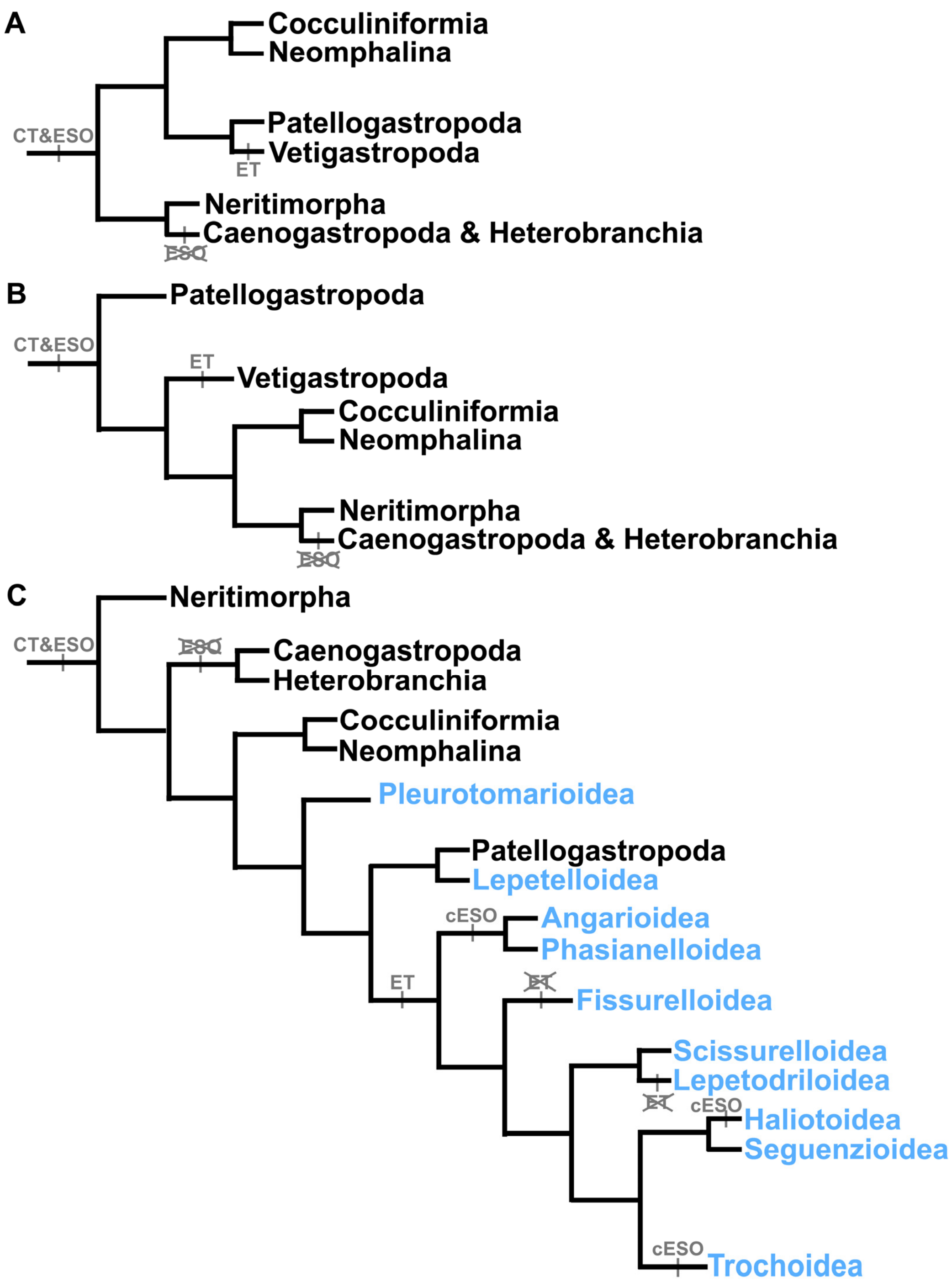


Figure 4.3 Evolutionary scenarios of gastropod tentacles plotted on different phylogenies.

A,B. Two topologies of relationships among gastropod clades, modified after Aktipis et al. (2008: fig. 9.6). **C.** Tree modified and simplified after a maximum-likelihood tree based on a five-gene combined analysis (Aktipis & Giribet 2012: fig. 3).

Abbreviations: cESO, combined epipodial sense organ; CT, cephalic tentacle; ESO, epipodial sense organ; ET, epipodial tentacle.

Vetigastropoda superfamilies shown in blue colour (e.g. Trochoidea). Light grey marks examplary evolutionary scenarios of the characters examined. Cancellation used for a reduction/loss of a character.

new kind of epipodial appendage occurs, the epipodial tentacle as an iterative homologue of the cephalic tentacle, but does not occur in all superfamilies (e.g. lacking in Pleurotomarioidea). Haliotoidea, Angarioidea, Phasianelloidea, and Trochoidea have the ESO situated at the base of an epipodial tentacle (ESO: combined type).

Also sensory papillae at cephalic and epipodial tentacles are restricted to Vetigastropoda. They are lacking due to secondary reduction in adult Fissurelloidea. In Pleurotomarioidea and Lepetodriloidea no papillae are described yet, but data about the juvenile development are lacking, as they do for Neomphalina. The combination of sensory papillae situated on an ESO was found the first time in *Scissurella jucunda* Smith, 1890 (Scissurelloidea) and is singular for Scissurellidae.

The position of Neomphalina as a vetigastropod superfamily or as an own clade was discussed throughout and the lack of epipodial tentacles in Neomphalina always supported the second view. Now this character can be eliminated as a vetigastropod apomorphy, but the findings of Aktipis & Giribet (2012) about the relations of lower gastropod groups reveal the data about tentacles in a new light. ESO might be a common character shared by the lower gastropod clades Patellogastropoda, Cocculiniformia, Neritimorpha, Neomphalina and Vetigastropoda.

The systematics of higher gastropod taxa is under permanent reconsiderations, therefore evolutionary scenarios are difficult to discuss. When the occurrence of appendages is plotted on the two tree topologies of the seven higher gastropod taxa (Fig. 4.3A, B), the evolution of these appendages can be infused: cephalic tentacles, ESO, and epipodial tentacles were each invented once, combined with a loss of ESO in a common ancestor of Caenogastropoda and Heterobranchia. Concerning cephalic tentacles and ESO the situation is the same, if the data are compared to an actual tree (Fig. 4.3C) calculated on five gene analyses (Aktipis & Giribet 2012). However, the distribution of epipodial tentacles cannot be explained with a single event. They might be invented or lost several times. Several most parsimoneous scenarios are possible with this tree: three independent inventions (Angarioidea & Phasianelloidea; Scissurelloidea; Haliotoidea & Seguenzioidea & Trochoidea) or one invention of epipodial tentacle (ET) and two independent losses (shown in Fig. 4.3C). A combined ESO evolved at least twice: [1] the *Haliotis*-type of ESO represent a unique development, [2] but the other type found in Angarioidea, Phasianelloidea, and Trochoidea seems to be very similar and might be invented most likely only once, as the position and relation of these three superfamilies are still doubtful. Otherwise this type has to be invented at least two times independently.

Methodological approaches

Serial semi-thin sectioning is a useful and well established method to investigate micro-scale gastropods with a size under 2 mm. The sections were made using glass or diamond knives mounted on a rotator microtome. During sectioning of *Protolira valvatoides* Warén & Bouchet, 1993, a snail from hydrothermal vents and suspected to be closely related to *Skenea* (Kano 2008), lots of small mineral particles in the gut (Fig. 4.4F) and mantle cavity did not allow

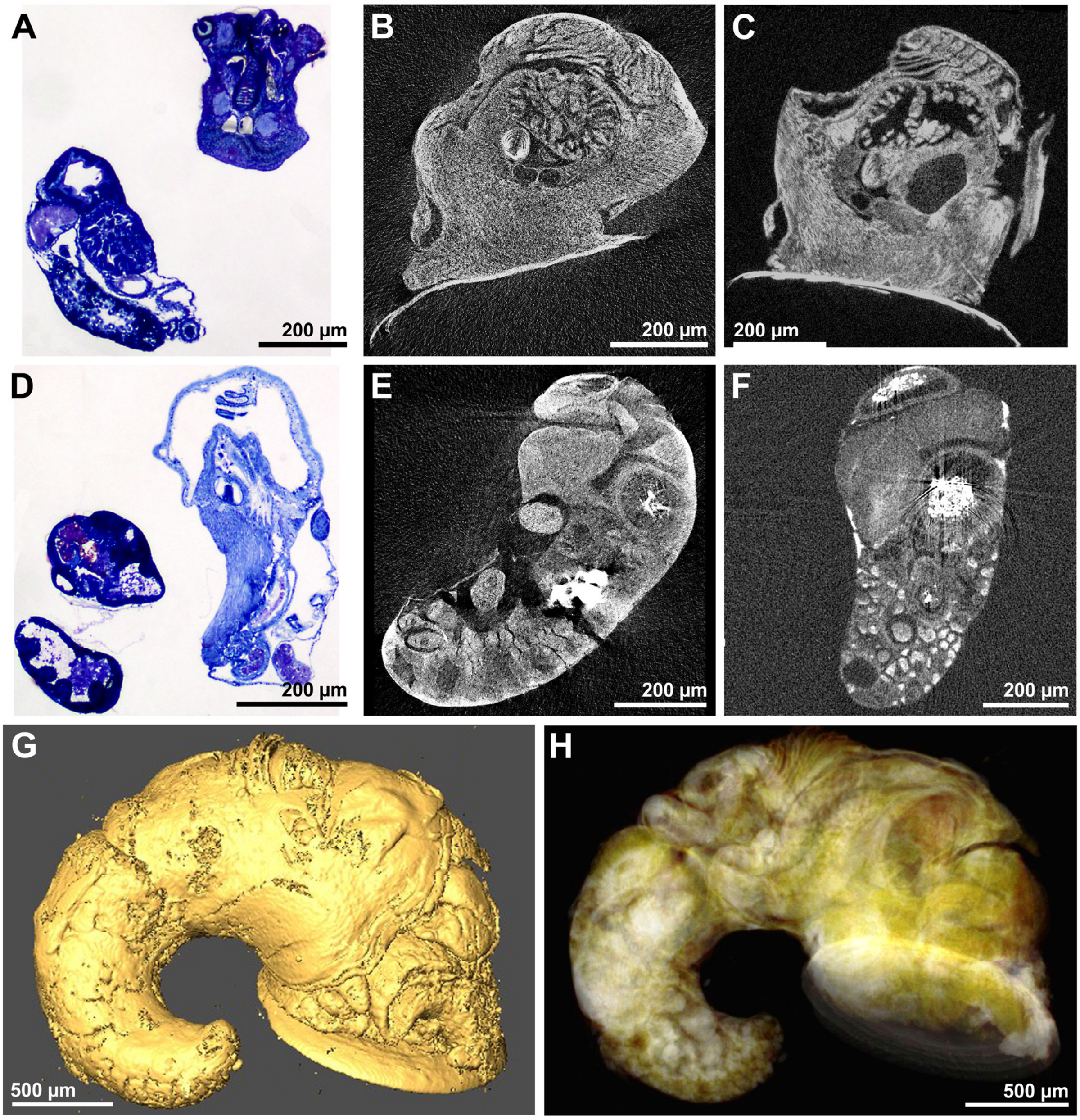


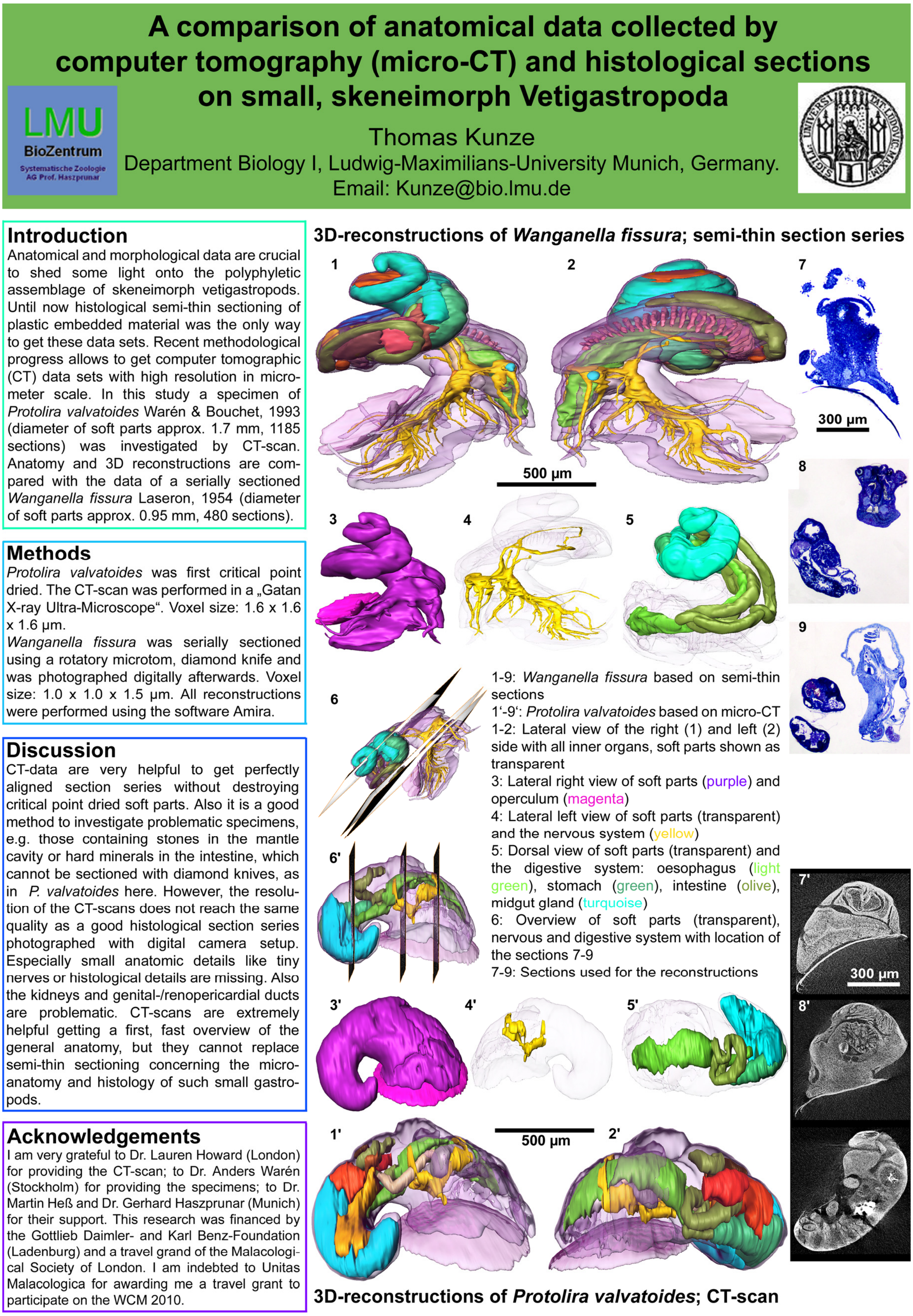
Figure 4.4 Serial sections prepared by histological sectioning, microCT and synchrotron tomography. **A,D.** Histological section of *Wanganella fissura*. **B,E.** MicroCT sections of *Protolira valvatoides*. **C,F.** Synchrotron tomographic sections of *P. valvatoides*. **G,H.** Automatic generated surfaces in AMIRA using the synchroton data of *P. valvatoides*. **G.** Surface rendering (autosurface). **H.** Direct volume rendering (voltex).

to perform useful sections. It became obvious that only non-invasive methods might help to get a data set suitable for 3D reconstructions.

Microcomputed X-ray computertomography (microCT) or synchrotron X-ray microtomography (SR-microCT) were used for various solid parts of invertebrates, e.g. shells, sea urchin pyramids, statoliths of medusae or parts of the arthropod exoskeleton (Stock et al. 2003; Prymak et al. 2005; Westneat et al. 2008; Heethoff et al. 2009; Heethoff & Norton 2009). However, also soft tissue can be examined using such microCT scans, e.g. woodlouse circulatory organs, honey bee brain, internal arthropod anatomy, sponges, marine worms or scorpion book lungs (Wirkner & Richter 2004; Nickel et al. 2006; Betz et al. 2007; Ribi et al. 2008; Westneat et al. 2008; Kamenz & Weidemann 2009; Dinley et al. 2010) especially when contrasting detergents like osmium tetraoxide are applied during preparation (Kamenz & Weidemann 2009; Metscher 2009a, b). Golding applied CT scans on whole snails (Golding & Jones 2007) and also for single organ systems, the radula supporting organs (Golding et al. 2009).

It seems to be promising to test this method for data acquisition combined with labelling and surface rendering in AMIRA on skeneimorph microgastropods (Figs. 4.4, 4.5). In cooperation with Lauren Howard from the Natural History Museum in London a CT scan was performed. The specimen was stained with osmium tetraoxide and critical point dried afterwards. As SR-microCT provides a better resolution such a scan was done at the Swiss Light Source in Zürich, made possible by cooperation with Stefan Bengston and Veneta Belivanova from the Swedish Museum of Natural History in Stockholm. This specimen was stained with osmium tetraoxide and plastic embedded afterwards.

The data of the microCT scan and the synchrotron microtomography of *P. valvatoides* were compared with those of *Wanganella fissura* based on sectioning (Figs. 4.4, 4.5). The thickness of the sections was around 1.5 µm by all three data sets, but the resolution and especially the contrast of the non-invasive methods did not reach the quality of histological sectioning. As shown in Fig. 4.5 larger organs like the complete digestive system, the kidneys, ovary and testis can be reconstructed rather well. When it comes to small organs or details like shown for the nervous system (Fig. 4.5: 4’) only the largest ganglia and commissures are detectable and all small details are lost. Especially those organs that can be only determined by the histology, like seminal receptacle, bursa copulatrix or hypobranchial gland, could not be detected at all. Small channels, e.g. urogential duct, renopericardial duct or oviduct, are not visible on the scans. It was also impossible to find epipodial sense organs there. The synchrotron data had a better resolution but even then the small nerves could not been seen.



A comparison of anatomical data collected by computer tomography (micro-CT) and histological sections on small, skeneimorph Vetigastropoda

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Introduction

Anatomical and morphological data are crucial to shed some light onto the polyphyletic assemblage of skeneimorph vetigastropods. Until now histological semi-thin sectioning of plastic embedded material was the only way to get these data sets. Recent methodological progress allows to get computer tomographic (CT) data sets with high resolution in micrometer scale. In this study a specimen of *Protolira valvatoides* Warén & Bouchet, 1993 (diameter of soft parts approx. 1.7 mm, 1185 sections) was investigated by CT-scan. Anatomy and 3D reconstructions are compared with the data of a serially sectioned *Wanganella fissura* Laseron, 1954 (diameter of soft parts approx. 0.95 mm, 480 sections).

Methods

Protolira valvatoides was first critical point dried. The CT-scan was performed in a „Gatan X-ray Ultra-Microscope“. Voxel size: 1.6 x 1.6 x 1.6 µm.
Wanganella fissura was serially sectioned using a rotatory microtom, diamond knife and was photographed digitally afterwards. Voxel size: 1.0 x 1.0 x 1.5 µm. All reconstructions were performed using the software Amira.

Discussion

CT-data are very helpful to get perfectly aligned section series without destroying critical point dried soft parts. Also it is a good method to investigate problematic specimens, e.g. those containing stones in the mantle cavity or hard minerals in the intestine, which cannot be sectioned with diamond knives, as in *P. valvatoides* here. However, the resolution of the CT-scans does not reach the same quality as a good histological section series photographed with digital camera setup. Especially small anatomic details like tiny nerves or histological details are missing. Also the kidneys and genital-/renopericardial ducts are problematic. CT-scans are extremely helpful getting a first, fast overview of the general anatomy, but they cannot replace semi-thin sectioning concerning the micro-anatomy and histology of such small gastropods.

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3D-reconstructions of *Wanganella fissura*; semi-thin section series

1-9: *Wanganella fissura* based on semi-thin sections
1'-9': *Protolira valvatoides* based on micro-CT
1-2: Lateral view of the right (1) and left (2) side with all inner organs, soft parts shown as transparent
3: Lateral right view of soft parts (purple) and operculum (magenta)
4: Lateral left view of soft parts (transparent) and the nervous system (yellow)
5: Dorsal view of soft parts (transparent) and the digestive system: oesophagus (light green), stomach (green), intestine (olive), midgut gland (turquoise)
6: Overview of soft parts (transparent), nervous and digestive system with location of the sections 7-9
7-9: Sections used for the reconstructions

3D-reconstructions of *Protolira valvatoides*; CT-scan

Figure 4.5 Comparison of methods using histological sections and computer tomography scans (Poster presented at the World Congress of Malacology in Phuket 2010).

After tomographic scanning, critical point dried specimens are still complete. Both gross anatomy and radula preparation can be examined afterwards in the SEM. Another big advantage of the non-invasive methods is the rather fast data acquisition. After preparation of the soft body including contrasting with osmium tetraoxide and combined with plastic embedding respectively critical point drying, the specimen has to be put into the analytic instrument and the scan will be performed in a few hours (maximum up to half a day). The pictures of the data set are perfectly aligned for the 3D reconstructions and no photographing, sorting and alignment is needed. The mineral particles influence the pictures rather little (Fig. 4.4E, F) and those artefacts can be eliminated easily using interpolation. Using automated surface reconstruction functions in AMIRA like autosurface and direct volume rendering (voltex) 3D models can be generated easily (Fig. 4.4G, H). Unfortunately, until the resolution can be raised substantially, the scans provide no more than a good, but sketchy, overview of the anatomy. For complete data sets substantial histological characters are missing. Thus, it turned out that the time consuming histological sectioning is still the best and only suitable method to investigate skeneimorph gastropods.

Conclusions and outlook

Histological sectioning combined with computer aided 3D reconstructions and SEM provide the best results to examine microgastropod morphology. Non-invasive approaches, like microCT and synchrotron based computertomography give promising results, but their resolution is still too poor to replace histological sectioning.

In this study 14 species from four families originally classified as Skeneidae were examined. Among Skeneidae a subclade Skeneinae can be diagnosed by a right propodial penis and true hermaphrodism. However, the relationship to the remaining species being defined as Skeneidae on molecular data is not solved yet. Before more data of other trochoidean snails are available, it is unclear if they group within the Skeneidae or belong elsewhere in the Trochoidea. Further studies are planned in close cooperation with the groups of Dr. Kano (Tokyo) and Dr. Williams (London) applying molecular approaches. The characters defining the taxon Skeneidae originally, namely the small shell, lack of nacre and the rhipidoglossate radula are convergences caused by dwarfing.

Additional 14 species from ten families were examined for the tentacle project. The data about microanatomy and histology of skeneimorph gastropods are not only the first for the taxon Skeneidae, but also substantially complement the matrix of structural data for Vetigastropoda. Unfortunately, these data are still far from being complete. Each comprehensive description of the anatomy and histology highlights new aspects. Especially the lack of comparative data made it often difficult to clear up systematic relations. It turned out that some morphologic characters differ largely among the examined species and are much more variable than expected. For example, mono- and bipectinate ctenidia are found in closely related species. This variability demands a change in the systematic interpretations. The occurrence of bursicles and sensory papillae correlates much better with modern phylogenetic data and underline their systematic relevance. However, in general the morphology of the vetigastropod soft bodies is very similar to each other, so (super)family characters are not very obvious and distinct characters like the special seminal receptacle in Seguenzioidea are rare. A further limit is that due to the few existing data the importance and emphasis of characters is often problematic to interpret. As shown for the epipodial sense organ even a seemingly well known and established character has to be re-interpreted, if new data are added. These data not only influence our knowledge of Vetigastropoda, but also concern four of the seven major gastropod clades and shed new light onto the evolution of tentacles in the complete lower gastropods.

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7 Authors' contributions

Paper 1

Skeneimorph gastropods in Neomphalina and Vetigastropoda – a preliminary report

Thomas Kunze, Martin Heß, Martin Brückner, Friederike Beck & Gerhard Haszprunar (2008). *Zoosymposia*, 1: 119-131.

TK had the idea for the paper, carried out the data acquisition, prepared the figures and drafted a manuscript version that was discussed and improved in concert by TK, MH and GH. MB performed the preparation and preliminary examination of *Skenea* in his diploma thesis, as FB did for *Leptogyra* and *Leptogyropsis* and TK did for *Ventsia* and *Bathyxylophila*. GH supervised the study and particularly provided literature advice.

Paper 2

***Dillwynella voightae* new species, a new skeneimorph gastropod (Turbinidae) from the western Atlantic and a new record of *Dillwynella modesta* (Dall, 1889)**

Thomas Kunze (2011). *The Nautilus*, 125: 36-40.

TK prepared the specimens and pictures, described the species and wrote the manuscript.

Paper 3

3D-interactive microanatomy of *Ventsia tricarinata* Warén & Bouchet, 1993 from Pacific hydrothermal vents (Vetigastropoda: Seguenzioidea)

Thomas Kunze, Martin Heß & Gerhard Haszprunar. *Journal of Molluscan Studies*: in review

TK carried out sample preparation, sectioning, 3D reconstructions, figures and drafted a manuscript version that was discussed and improved in concert by TK, MH and GH. TK and MH prepared the interactive 3D model. GH supervised the study and particularly provided literature advice. Basic parts (approx. 30%), namely sectioning, basic reconstructions and preleminary descriptions, were done within the diploma thesis of TK.

Paper 4

What is a Skeneidae (Mollusca, Vetigastropoda)? 3D-interactive anatomy of the type species, *Skenea serpuloides* (Montagu, 1808), with comments on dwarfing

Thomas Kunze, Martin Brückner, Martin Heß & Gerhard Haszprunar. *Frontiers in Zoology*: in preparation

TK prepared the morphological analyses, 3D reconstructions, figures and drafted a manuscript version that was discussed and improved in concert by TK, MH and GH. MB performed the preparation and preliminary examination of *S. serpuloides* in his diploma thesis. TK and MH prepared the interactive 3D model. GH supervised the study and particularly provided literature advice.

Paper 5

Epipodial appendages in basal gastropods (Mollusca): new insights, homology assumptions, and evolutionary scenarios

Thomas Kunze, Martin Heß, Anders Warén & Gerhard Haszprunar. *Zoologica Scripta*: in preparation

TK designed the concept and carried out the morphological analyses, 3D reconstructions, figures and drafted a manuscript version that was discussed and improved in concert by TK, MH, and GH. AW and TK performed the SEM preparation and pictures. GH supervised the study and particularly provided literature advice.

Die Richtigkeit der Angaben wird bestätigt.

Prof. Dr. Gerhard Haszprunar

Thomas Kunze

8 Publication list

Original papers

[2] Kunze T (2011). ***Dillwynella voightae* new species, a new skeneimorph gastropod (Turbinidae) from the western Atlantic and a new record of *Dillwynella modesta* (Dall, 1889).** *The Nautilus*, **125:** 36-40.

[1] Kunze T, Heß M, Brückner M, Beck F & Haszprunar G (2008). **Skeneimorph gastropods in Neomphalina and Vetigastropoda – a preliminary report.** *Zoosymposia*, **1:** 119-131.

Oral presentations on conferences

[6] Kunze T (2011). **What is really a Skeneidae? - Anatomy, histology and phylogeny of skeneimorph microgastropods (Mollusca: Vetigastropoda).** *5th EES Conference,* Abstracts: 31. Munich, October 2011.

[5] Kunze T & Haszprunar G (2010). **Tentacles in Vetigastropoda - What can we learn about all these sensory organs?** *World Congress of Malacology*, Abstracts: 122. Phuket, July 2010.

[4] Kunze T & Haszprunar G (2008). **What are Skeneimorph gastropods? – How 3D based anatomy can help to shed some light on the polyphyletic assemblage called Skeneidae.** *Molluscan Forum*, Abstracts: 11. London, November 2008.

[3] Kunze T, Heß M & Haszprunar G (2008). **What is a real skeneid? - The microanatomy of *Skenea serpuloides* (Montagu, 1808).** *5th Congress of the European Malacological Societies*, Abstracts: 32. Ponta Delgada (Azores), September 2008.

[2] Kunze T, Heß M & Haszprunar G (2008). **The microanatomy of the skeneimorph *Ventsia tricarinata* Warén & Bouchet, 1993, a small seguenzioid from Pacific hydrothermal vents (Vetigastropoda).** *American Malacological Society 74th annual meeting,* Abstracts: 33. Carbondale (Illinois), June 2008.

[1] Kunze T, Beck F, Brückner M, Heß M, Ruthensteiner B & Haszprunar G (2007). **Skeneimorph gastropods in Neomphalina and Vetigastropoda.** *World Congress of Malacology*, Abstracts: 122-123. Antwerp, July 2007.

Posters on conferences

[8] Gensler H & Kunze T (2011). **How to destroy a snail! - Problems and solutions working with histological samples of micro-scaled gastropods.** *4. Graduiertenforum der DZG*, Abstracts: 36. Munich, October 2011.

[7] Kunze T (2010). **A comparison of anatomical data collected by computer tomography (micro-CT) and histological sections on skeneimorph Vetigastropoda.** *World Congress of Malacology*, Abstracts: 346. Phuket, July 2010.

[6] Kunze T (2009). **A new species of *Dillwynella* in the Atlantic Ocean.** *Systematic Dagarna*, Abstracts: 32. Stockholm, November 2009.

[5] Kunze T (2009). **A new gastropod species of the skeneimorph genus *Dillwynella* from the western Atlantic Ocean.** *Molluscan Forum*, Abstracts: 8. London, November 2009.

[4] Kretzler F, Haszprunar G, Kunze T & Heß M (2008). **3D-reconstruction of bivalve compound eyes.** *5th Congress of the European Malacological Societies*, Abstracts: 70-71. Ponta Delgada (Azores), September 2008.

[3] Patzner I, Haszprunar G, Kunze T & Heß M (2008). **Comparative 3D-microanatomy of the visual system of cephalopod hatchlings.** *American Malacological Society 74th annual meeting*, Abstract: 46. Carbondale (Illinois), June 2008.

[2] Kunze T, Heß M & Haszprunar G (2007). **The microanatomy of *Bathyxylophila excelsa* Marshall, 1988, and *Ventsia tricarinata* Warén & Bouchet, 1993, two skeneimorph vetigastropods from Pacific deep sea habitats (Vetigastropoda).** *World Congress of Malacology*, Abstracts: 122. Antwerp, July 2007.

[1] Kunze T, Heß M & Haszprunar G (2007). **The microanatomy of *Ventsia tricarinata* Warén & Bouchet, 1993, a skeneimorph vetigastropod from Pacific hydrothermal vents (Mollusca).** *9th Annual meeting of the GfBS*, Abstracts: 141. Vienna, February 2007.

9 Curriculum vitae

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Education

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May 2007 – present	PhD-student at LMU Munich in the lab of Prof. Haszprunar: “Comparative 3D microanatomy and systematics of skeneimorph gastropods, with a survey on epipodial tentacles in lower gastropods”
April 2007	Diploma in Biology, LMU Munich
October 2001 – April 2007	Studies of Biology, LMU Munich. Diploma thesis: “Computergestützte 3D-Rekonstruktion und vergleichende Anatomie skeneimorpher Mikrogastropoden an *Bathyxylophila excelsa* Marshall, 1988 und *Ventsia tricarinata* Warén & Bouchet, 1993” supervised by Prof. Dr. Haszprunar, LMU Munich
June 2000	“Allgemeine Hochschulreife“ (baccalaureate), Obermenzinger Gymnasium Munich

September 1991 – June 2000	Grammar school at “Obermenzinger Gymnasium Munich”
September 1987 – July 1991	Primary school, “Grundschule an der Krenmoosstraße Karlsfeld”

Working experience (university)

August – December 2011	Technical assistant at the chair of systematic zoology (Prof. Dr. Haszprunar), LMU Munich
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Travel grant of Unitas Malacologica to the “World congress of Malacology” in Phuket, Thailand, in July 2010

ASSEMBLE research fellowship for three weeks at the Algarve Marine Sciences Centre Faro, Portugal

Travel grant of the Malacological Society of London to the course “Benthic fauna of Svalbard” at the University Centre in Svalbard (UNIS), Norway

PhD course “Benthic fauna of Svalbard” at the University Centre in Svalbard (UNIS), Norway, August and September 2009

Travel grant of the Malacological Society of London to the Molluscan Forum in London November 2008 and 2009

Two year fellowship at the Swedish Museum of Natural History, Stockholm, financed by the Daimler- and Benz Foundation, Ladenburg, March 2008 to March 2010

DAAD travel grant, for research cooperation and sampling at the marine biological station Espeland and the University of Bergen, Norway, November 2007

Other (selected) occupations

Since September 2005	Complimentary coxswain at “Segelzentrum der Technischen Universität München“ in Starnberg
January 2002 – June 2004	Employment at the “Friedrich-Meinzolt-Haus, an old people’s home in Dachau
October 2000 – September 2001	Civilian service at the “Friedrich-Meinzolt-Haus“, an old people’s home, in Dachau
September 1994 – June 1999	During High school additional education to “Staatlich geprüfter kaufmännischer Assistent“ at “Obermenzinger Gymnasium“ Munich

10 Declaration

Eidesstattliche Erklärung

Ich versichere hiermit an Eides statt, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt ist.

München, den 27. September 2012

Erklärung

Hiermit erkläre ich, dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

München, den 27. September 2012