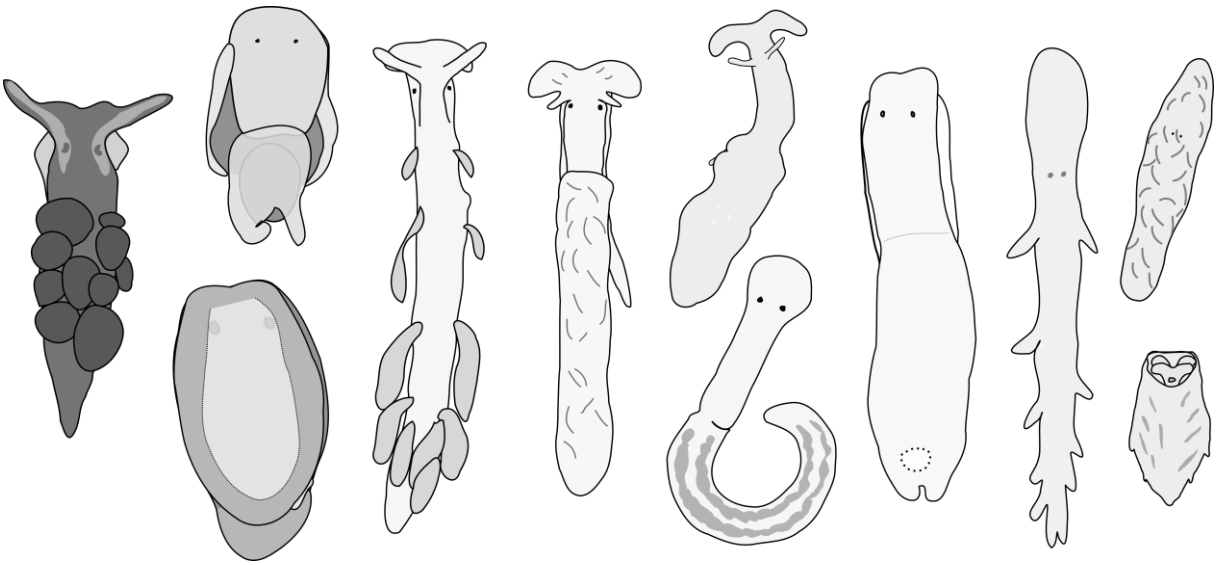
Identification guide to Northern European interstitial opisthobranchs (Gastropoda: Heterobranchia)

Bastian Brenzinger

Bavarian State Collection of Zoology, Munich (SNSB - Zoologische Staatssammlung München, ZSM)
Sektion Mollusca
Münchhausenstr. 21
81247, Munich, Germany

bastian.brenzinger@arcor.de

Version 2.1, August 2015



This guide prepared for NMBAQC Taxonomic Workshop, November 2014
at Dove Marine Laboratory, Cullercoats, Tynemouth, UK

Table of Contents

Introduction

Opisthobranchia include most seaslugs and their shelled relatives, and is one of the three most basic traditional taxa of the Gastropoda (besides Prosobranchia and Pulmonata). Recent research has shown that, from a phylogenetic point of view, none of these groups are monophyletic and that marine opisthobranchs are paraphyletic with respect to coastal, limnic and terrestrial Pulmonata and also some marine, formerly prosobranch, groups. These are all being included into one (also classical) major taxon, the Heterobranchia (e.g. Jörger et al., 2010a, Wägele et al., 2013). Current classification therefore contrasts with classical ideas found in most textbooks.

Interstitial opisthobranchs are a special group of minute heterobranch sea slugs that inhabit the interstices of worldwide marine sands and gravel habitats (Arnaud et al., 1986; Jörger et al., 2014a). They show many morphological adaptations in common with other minute interstitial, or meiofaunal, fauna. These adaptations are largely related to three sets of ecological factors: the spatial restriction of the habitat (reduction in size following miniaturization and/or progenesis, development of elongate body forms without appendages, reduction of bulky internal organs, development of sperm transfer via spermatophores), the lack of light (loss of pigmentation and, often, eyes), or to specialties of the sometimes highly turbulent interstitial habitat (development of secondary spicule 'skeletons', adhesive mechanisms) (Swedmark, 1964, 1968a; Rieger & Sterrer, 1975; Westheide, 1987). In total, only about 70 species of interstitial opisthobranchs have been described from around the world. This is a low number, but the study of interstitial opisthobranchs has led to novel perspectives on the much larger group of "opisthobranchs", on biological novelties, and for the use as ecological indicator organisms (Jörger et al., 2010a, 2014a, Poizat, 1985). Also, a much higher number of undiscovered and perhaps morphologically cryptic taxa can be expected (Jörger et al., 2014a). Interstitial opisthobranchs belong to several independently evolved lineages among lower heterobranch Rhodopemorpha, Nudipleura (among aeolidacean nudibranchs), Euopisthobranchia (among Cephalaspidea), and panpulmonate Acochlidia and Sacoglossa (Jörger et al., 2010a, 2014a). Most lineages also occur in European waters where 9 families with approximately 25 valid species of interstitial opisthobranchs are found.

The present guide will cover all recorded Northern European species (at least 10) of the interstitial families Philinoglossidae, Hedylopsidae, Asperspinidae, Microhedylidae, Platyhedylidae, and Pseudovermidae. Exemplarily, it also covers *genera* of the aforementioned families that have so far only been recorded from the Mediterranean (*Abavopsis*, *Parhedyle*, *Pontohedyle*, *Platyhedyle*) but could be expected to range into the Northern Atlantic, besides those European species of families Philinidae, Embletoniidae and Rhodopidae that are also interstitial (3 species). Some other sea slug taxa are not interstitial but reasonably often found in bulk sediment samples (some species of *Runcina*, or the sacoglossan *Calliopaea*); these are also covered here in brief. Not included in the present key are juvenile specimens of opisthobranch taxa, such as those of dorid or aeolid nudibranchs, which may also on occasion be found in sediment samples.

Acknowledgments

The present guide was prepared for the NMBAQC taxonomic workshop at Dove Marine Laboratory, Cullercoats, Tynemouth, UK, in November, 2014.

I am indebted to Tim Worsfold, Carol Milner, David Hall and Nicola Pennisi (of APEM Ltd., Letchworth) for inviting me to speak at this workshop, for their invaluable help in organising it and their practical help during my stay, and their patience afterwards. All workshop participants are gratefully thanked for their feedback, discussion, and company during the workshop.

This work relied heavily on the past and present enthusiasm, time and energy of three people: Timea Neusser, Katharina Jörger, and Michael Schrödl.

Layout of this guide was partially inspired by the workshop “Guide to identification of Lumbrineridae (Polychaeta) in north east Atlantic waters” by Eivind Oug. This work has received financial support from NMBAQC.

How to collect interstitial opisthobranchs

Interstitial opisthobranchs are found in marine inter- or subtidal sands, gravel, or shell grit in areas with hydrodynamism that is strong enough to prevent clogging with silt particles and at the same time weak enough to provide sufficient re-oxygenation without disturbing the sediment too much (the latter would be the case e.g. in the surf zone of many strongly exposed beaches).

For biological study, a simple sampling method suitable for interstitial opisthobranchs (but maybe not other groups of meiofaunal animals; Jörger et al., 2014a, Higgins & Thiel, 1988) is to collect sand (not too fine or silty/muddy, without traces of black sulphides) by snorkelling, scuba, or dredging. Place the sand in a reasonably large container and then let this sit for a period of time in an undisturbed, preferably cool and dark place. Ideally, the top layer of sand remains wet, in contact with the air but not covered by water. After a while, interstitial animals will accumulate in the still oxygenated top layer of the sand. This top layer can then be removed (e.g. to an Erlenmeyer flask) and washed with isotonic magnesium chloride solution to narcotize animals. Narcotized animals can be resuspended by swirling, then decanted through a 200 µm sieve and washed into a petri dish with the help of a wash bottle containing fresh sea water. Animals will then slowly revive again and can be examined under a stereo microscope.

How to identify interstitial opisthobranchs

When collected in bulk sediment samples, two things may hinder identification of interstitial opisthobranchs: the use of sieves with a mesh size larger than 200 µm may lead to the loss of most interstitial opisthobranch specimens from the sample. In samples that have been fixed together with the sediment, specimens may be distorted or badly damaged (e.g. cerata may be torn off) through compaction of the sediment.

Interstitial opisthobranchs may sometimes be, at first glance, mistaken for “worms” such as platyhelminths or nemerteans. Several characters (or a combination of those) can be used to distinguish reliably between the groups: among others, “worms” are usually bilaterally symmetric, and never possess a shell, a laterally demarcated ventral foot, a retractable head, or cylindrical tentacles at the sides of the (terminal) mouth. Gastropods never possess a shiny cuticle, numerous epidermal eyespots, or body openings on the ventral, median side. Gastropods possess paired statocysts, and a translucent, fluid-filled body cavity just below the skin in preserved specimens; the aforementioned worms possess a body cavity that is opaque and filled with cells.

In principle, every beach with suitable sand can yield forms unknown to science – among interstitial opisthobranchs, or other meiofaunal animals.

Overview of morphology and terms

Interstitial opisthobranchs are usually morphologically highly derived from their closest ancestors, but they still retain basics of the bauplan of these related groups. To explain terms used in the following key and the taxon accounts, the morphology of a "typical" philinid, acochlidian, and a cerata-bearing nudibranch are explained in the following figure (schematized dorsal views).

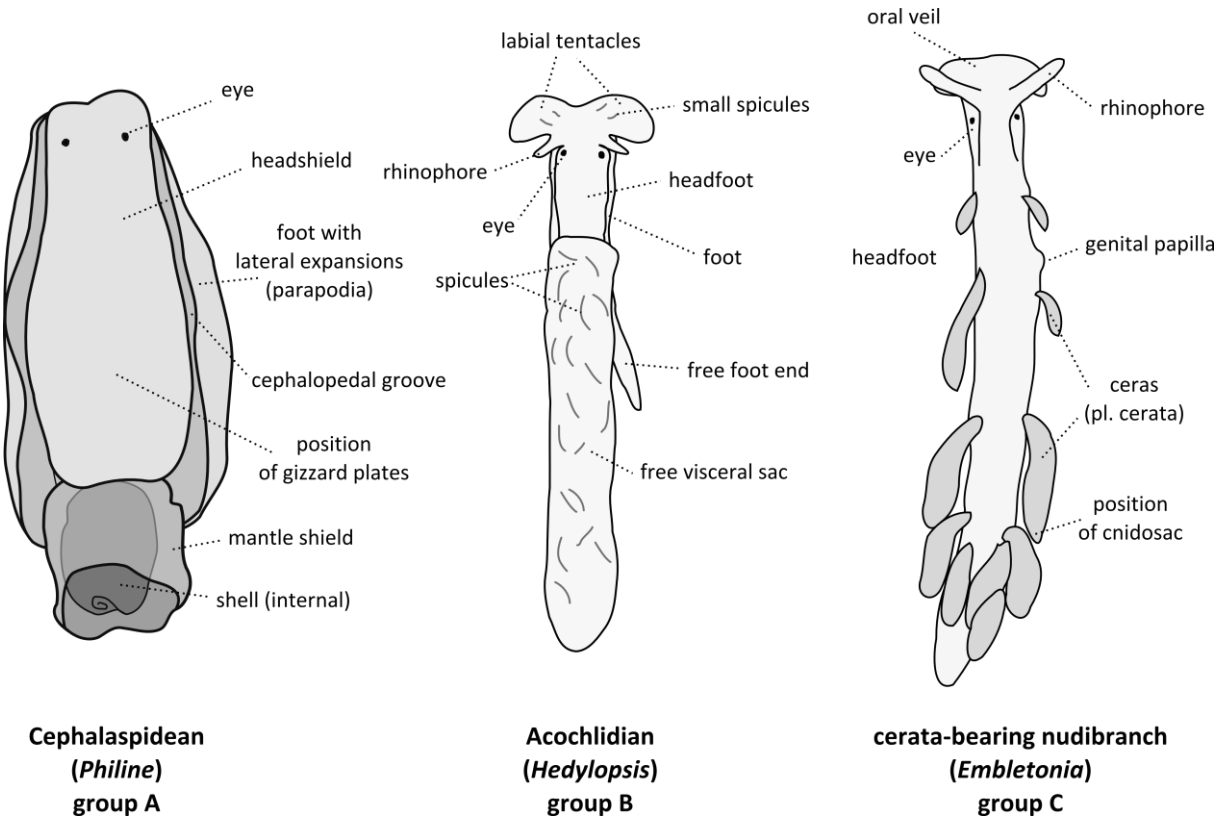


Figure 2. General bauplan of three major taxa of interstitial opisthobranchs.

Even the most derived interstitial opisthobranchs such as rhodopemorphs (group D) or philinoglossid cephalaspideans show at least some ancestral characters of gastropods, i.e. distinction of a headfoot and visceral sac, asymmetry of internal organs as relict of torsion (with some body openings located on the right side), and in most cases a radula (Brenzinger et al., 2010, 2013).

Key to genera in North East Atlantic and adjacent waters

This key is based on external morphology and externally detectable hard structures, and is thus only semi-phylogenetic. **?**: potentially found in N Atlantic, but so far recorded only from Mediterranean. *: includes benthic species.
Four principal groups used in this key:

Group A – With headshield (squarish front end, no tentacles)

A1 – Dorsum continuous, tail end fin-like, notched, without shell; no gizzard plates

A1a – without parapodia, foot narrow posteriorly …….. *Philinoglossa* Hertling, 1932

A1b – with parapodia, foot wide posteriorly ……..….. *Abavopsis* Salvini-Plawen, 1973[?]

A2 – With shell or externally visible gill; with gizzard plates in middle of body

A2a – with internal shell, three gizzard plates ……..…….. *Philine* Ascanius, 1772*

A2b – with gill, four gizzard plates …… *Runcina* Forbes [in Forbes & Hanley], 1851*

Group B – With free visceral sac, foot short

B1 – With two pairs of head tentacles

B1a – with dense spicules in visceral sac (spicule shell), midgut gland straight posteriorly

B1a1 – Labial tentacles flat, foot large, eyes present ….…..… *Hedylopsis* Thiele, 1931

B1a2 – Labial tentacles round, foot small, no eyes ……...… *Asperspina* Rankin, 1979

B1b – without distinct spicule shell, midgut gland hooked posteriorly

B1b1 – Rhinophores shorter than labial tentacles …….. *Microhedyle* Hertling, 1930

B1b2 – Rhinophores as long as labial tentacles ……..……. *Parhedyle* Thiele, 1931[?]

B2 – With one pair of head tentacles or none

B2a – With labial tentacles only…..……... *Pontohedyle* Golikov & Starobogatov, 1972[?]

B2b – Without head tentacles……..…….…….. *Platyhedyle* Salvini-Plawen, 1973[?]

Group C – With dorsal appendages (cerata)

C1 – cerata large, club- or balloon shaped

C1a – cerata balloon-shaped, animal dark …….….. *Calliopaea* d'Orbigny, 1837*

C1b – cerata club-shaped, animal white ....…...…..… *Embletonia* Alder & Hancock, 1851*

C2 – cerata short to knob-shaped, no tentacles …….. *Pseudovermis* Perejaslavtzeva, 1891

Group D – Worms, with curved spicules

D1 – stout, with retractable front end ……..……..… *Rhodope* Koelliker, 1847*

D2 – very thin, curls up when disturbed …...……..…… *Helminthope* Salvini-Plawen, 1991[?]

Illustrations to all taxa are found in appendices 1-3. More detailed information is found on the following pages.

Taxon Accounts

Graphical keys to all taxa covered in this key and the following accounts are provided in the appendix. Numbers herein refer to illustrations in the key.

Cephalaspidea (group A)

Euopisthobranch snails (bubble-shells), semi-slugs or slugs. Head characteristically without tentacles, but with squarish front end and flattened surface used as a plough (headshield). Sides of foot often expanded to form-wing-like parapodia that extend dorsally. Shell, if present, often covered by extension of the mantle (mantle shield). Often with 3-4 calcified gizzard plates behind pharynx (visible in transmitted light). Marine, benthic or interstitial, with worldwide distribution; diverse group (Malaquias et al. 2009, Oskars et al. 2015). Interstitial members found in two families, plus occasional records from a third:

Philinoglossidae Hertling, 1932

Interstitial cephalaspideans, with wormlike body and reduced separation of headshield and mantle, without a shell. Distinct longitudinal grooves between dorsum and foot. Tail end with fin-like horizontal overhang, with spherical yellow gland sometimes visible. Radula 3.0.3; no gizzard plates. Worldwide distribution, with two genera and four species described from European waters.

Philinoglossa Hertling, 1932 [1-8]

Diagnosis. Elongate philinoglossids, without parapodia, with posteriorly tapering foot. Separation of headshield and mantle only visible in contracted specimens, at approximately one third of body. Large epidermal glands along margin of dorsum. Female genital opening at anterior right. Caudal overhang wide, posteriorly notched. Live specimens orange-brown, sometimes with black speckles. Preserved specimens curl up [6].

Taxonomy. Three species described from Europe, two with records from N Europe* (Marcus & Marcus, 1954):

P. helgolandica Hertling, 1932

Species described from Heligoland Island (N Germany); further records from Britain to N Spain. Up to 3 mm in size, comparatively stout (length-to-width ratio 4.5 [1]). Radula with denticulate first lateral teeth [2], digestive gland s-shaped. Common species with records from Scandinavia to N Spain.

P. praelongata Salvini-Plawen, 1973

Species described from Mediterranean (Livorno, NW Italy), further records from Adriatic and S France. Up to 4 mm in size, elongate (length-to-width ratio 6; [3,6]). First laterals of radula smooth [4], digestive gland screw-shaped. Only single record from N Atlantic (Plymouth, SW Britain: Salvini-Plawen, 1984); common in Mediterranean.

---

*Genetics remain to confirm if *P. praelongata* is restricted to the Mediterranean.Thompson (1976) listed *Philinoglossa remanei* Marcus & Marcus, 1958 among British species. This species is, however, known only from a single locality in Italy.

Abavopsis Salvini-Plawen, 1973 [9-12]

Diagnosis. Philinoglossid with lateral parapodia and posteriorly rounded, wide foot [5]. Separation of headshield already visible in crawling specimens. Female genital opening at posterior right (Langegger-Weinbauer & Salvini-Plawen, 2013). Caudal overhang with lateroventral extensions. Live specimens whitish. Preserved specimens contract rather than curling up [82].

Taxonomy. Genus described only from Mediterranean (*A. latosoleata* Salvini-Plawen, 1973), but currently no records from N Europe.

Philinidae Gray, 1850

Benthic to interstitial cephalaspideans, with stout body. Headshield not fused with mantle. Thin shell with pattern of pitted lines, or smooth; partially or completely covered by mantle [10,12]. Foot with rounded posterior end, short, with ventral love of mantle [14]. Radula 3.0.3 or different; with three gizzard plates (sometimes one smaller plate). With pigment patterns, or colorless. Characteristic black spot (“larval kidney”) at posterior right in juvenile specimens [13]. Worldwide distribution, with several genera and up to 20 species in N European waters (Ohnheiser & Malaquias, 2013). Oskars et al. (2015) showed that there are at least four independent lineages; currently, European species remain allocated within one speciose genus:

Philine Ascanius, 1772 [9-15]

Diagnosis. Benthic to interstitial cephalaspideans, with characters of the family. With thin shell partially or completely covered by mantle shield.

Taxonomy. *Philine* represents a polyphyletic genus (Oskars et al., 2015). Numerous records from gravel and sand samples are currently recorded mostly as unidentified (?juvenile) *Philine* sp.. One commonly recorded and identifiable semi-interstitial species in Europe (Poizat, 1981, 1985):

P. catena (Montagu, 1803)

Species up to 4 mm in size, elongate, white or brownish. Headshield approx. two thirds of body length, mantle shield covers shell completely [9]. Shell thin, transparent, with wide aperture and characteristic pattern of distinct chain-like pits [10].

P. scabra (Müller, 1784)

Species up to 10 mm in size, white. Headshield approx. half of body length [11]. Shell elongate, with pattern of unconnected, rounded pits [12]. Common, not interstitial, species.

Note: Ohnheiser & Malaquias (2013) present a key to the identification of North Atlantic species of "*Philine*", including benthic species.

Runcinidae H. & A. Adams, 1854

Benthic cephalaspideans (or separate order?), with stout body. Headshield fused with mantle, covering entire dorsum. Thin and minute shell inconspicuous, partially or completely covered by mantle, or lost. Gill present at posterior right, or lost. Foot with rounded posterior end, longer than dorsal shield. Radula 1.1.1; with four equal gizzard plates. With variable pigment patterns, or with one color only. Worldwide distribution, with several genera and many species in European waters. Usually found among intertidal algae, but with occasional records from gravel:

Runcina Forbes [in Forbes & Hanley], 1851 [16-19]

Diagnosis. Intertidal slugs, with characters of the family [16-19].

Taxonomy. Approximately fifteen species described from Europe, especially from coralline algae, with two species occasionally recorded in gravel in N Europe (Salvini-Plawen, 1984, Arnaud et al., 1986):

R. coronata (Quatrefages, 1844)

Species found in the Mediterranean and N Atlantic, common in intertidal algae. Up to 4 mm in size, comparatively stout, sides of dorsum rounded, not parallel. Dorsum dark brown and speckled with yellow, with broad white transversal bands at level of eyes and at posterior end of dorsum [16]. Foot pale, with posterior black stripe bordered with white. Several similar species.

R. ferruginea Kress, 1977

Species described from Plymouth (SW Britain), further records from Iberian peninsula. Up to 5 mm in size, elongate [17]. Body elongate, with sides of dorsum parallel; colored brilliantly orange to red.

Acochlidia (group B)

Panpulmonate slugs, with characteristic separation of headfoot (with two, one, or no pairs of head tentacles) and free posterior visceral sac; foot usually short. Headfoot can be retracted into visceral sac. Usually colorless, sometimes with large subepidermal glands. Spicules often present. Most diverse group of interstitial opisthobranchs, with worldwide distribution (Schrödl & Neusser, 2010; Jörger et al., 2010a). Indo-Pacific also with benthic deepwater, freshwater, amphibious, or even terrestrial species (Kano et al., 2015).

Hedylopsidae Odhner, 1952

Interstitial acochlidians with irregular spicule shell and a large copulatory organ with injection devices (hypodermic cuticular needles).

Hedylopsis Thiele, 1931 [20-23, 30-31]

Diagnosis. Labial tentacles large, flattened; rhinophores shorter, finger-like [20,22]. Eyes behind base of rhinophores [20]. With large copulatory organ in headfoot, behind pharynx. Foot wide and separated from headfoot by distinct longitudinal grooves [22]. Tail end of foot rather long and flat. Visceral sac large, flattenable, with dense yet irregular covering of spicules [21,22,30-31]. Spicules fusiform, with rounded ends, surface rather smooth [23]. Colorless.

Taxonomy. Sole genus in family. Single species in Mediterranean but also recorded from N Atlantic (Sweden, Britain), with characters of the genus:

Hedylopsis spiculifera Kowalevsly, 1901

Syn. *H. suecica* Odhner, 1937

Largest acochlidian in the area, locally common. Characterised by its moustache-like labial tentacles, distinct eyes and spicules, and large visceral sac and foot. Size up to 6 mm but frequently smaller (Poizat, 1981a,b; Wawra, 1989).

Asperspinidae Rankin, 1979

Interstitial acochlidians with regular spicule shell, rather uniform and finger-shaped head tentacles, and no eyes.

Asperspina Rankin, 1979 [24-29, 32]

Diagnosis. Labial tentacles and rhinophores similar, round in cross-section, rather stiff [26-28]. No eyes. Foot as wide or narrower than headfoot [26-28]; free end does not reach beyond half of visceral sac [24,29]. Visceral sac cylindrical to triangular in cross-section, rather stiff, with dense and usually regular covering of spicules [24,29,32]. Anterior margin of headfoot distinct [29]; posterior end slightly pointed [24]. Spicules fusiform, with thinner ends, surface smooth or knobby [25]. Colorless, or rosy-brown.

Taxonomy. Sole genus in the family. Four species described from Europe (Swedmark, 1968b; Poizat, 1981a, 1991; Neusser et al., 2009), three of which occur in N Europe:

A. brambelli (Swedmark, 1968) [24-26]

Species described from N Wales (Menai Bridge, Anglesey); further records from Scandinavia. Up to 3 mm in size. Rhinophores with thicker part in middle, shorter than labial tentacles [26]. Radula 2.1.2. Foot as wide as headfoot, not separated by cephalopedal groove. Spicule shell rather irregular, spicules knobby, up to 225 µm long.

A. loricata (Swedmark, 1968) [28,32]

Species described from N France (Roscoff, Brittany). Up to 1 mm in size. Labial tentacles and rhinophores stout, with rounded ends, of equal length [27]. Radula 1.1.1. Foot narrow and very short. Spicule shell very regular, visceral sac rigid, triangular in cross-section. Spicules smooth, up to 180 µm long.

A. murmanica Kudinskaya & Minichev (1978) [27,29]

Only known polar acochlidian, species described from NW Russia (Barents Sea). Up to 3 mm in size. Labial tentacles and rhinophores stout, with rounded ends, rhinophores longer than labial tentacles [28]. Radula 1.1.2. Foot narrow. Spicule shell dense, spicules up to 120 µm long (Neusser et al., 2009).

Microhedylidae Hertling, 1930

Interstitial acochlidians with reduced copulatory organ and foot. Eyes small and shifted posteriorly, or lacking. Visceral sac elongate, round in cross-section, often with glandular skin. Spicules present yet inconspicuous, different types in same individual. Digestive gland looped posteriorly [35,38]. Some species very small. Several genera worldwide, 3 found in Europe:

Microhedyle Hertling, 1930 [33-36, 45, 46]

Diagnosis. Labial tentacles slightly flattened, curved, usually rather distinctly bent, tapering [33]. Rhinophores round in cross-section, tapering, shorter than labial tentacles [33]. Eyes generally present. Radula 1.1.1. Foot narrower than headfoot; free end short. Visceral sac cylindrical, long, with dense subepidermal layer of large, spherical glands [34,35]. Spicules fusiform, bean-shaped, triaxonic, or shaped like a ring of beads [36]. Colorless, sometimes with brownish digestive gland.

Taxonomy. Genus with worldwide distribution. Apparently one single widespread species in Europe (Eder et al., 2011), with several synonyms:

Microhedyle glandulifera (Kowalevsky, 1901)

Syn. in Northern Europe: *M. lactea* Odhner, 1937

Species originally described from Bosphorus, but numerous records from N Europe. Locally abundant. Size 1-2.5 mm (records up to 5 mm). With distinct glands in visceral sac, triaxonic spicules present. Radula 1.1.1

Parhedyle Thiele, 1931 sp. [37-40, 45]

Diagnosis. Labial tentacles slightly flattened, curved, usually rather distinctly bent, tapering [37]. Rhinophores round in cross-section, tapering, as long as labial tentacles [37]. Eyes present but small, or lost. Radula 1.1.2. Foot narrower than headfoot; free end short [38-39]. Visceral sac cylindrical, long, with dense subepidermal layer of large, spherical glands. Spicules fusiform or bean-shaped [40]. Colorless, sometimes with brownish digestive gland.

Taxonomy. Genus endemic to N Atlantic and Mediterranean (2-3 species in Med.), but currently no species recorded from N Europe. Similar to *Microhedyle*, but distinguished by relatively longer and thinner rhinophores, generally smaller, radula 1.1.2 (Jörger et al., 2010b). Widespread Mediterranean species: *P. cryptophthalma* (Westheide & Wawra, 1974).

Pontohedyle Golikov & Starobogatov, 1972 sp. [41-44, 47-48]

Diagnosis. Labial tentacles flattened, tapering, rather short. Rhinophores lost [41-42-43]. Eyes set far behind, or lost [42]. Radula 1.1.1. Foot narrower than headfoot; free end short. Visceral sac cylindrical, long, often with dense subepidermal layer of spherical glands [42,43]. Spicules fusiform [44]. Sometimes with brownish or green digestive gland. Tun-like shape when retracted [47-48]

Taxonomy. Genus with worldwide distribution (single abundant species in Mediterranean: *P. milaschewitchii* Golikov & Starobogatov, 1972; Jörger et al., 2008), but currently no species recorded from N Europe.

Sacoglossa (groups B+C)

Panpulmonate snails or slugs, marine intertidal, interstitial, or even amphibious. Specialised herbivores (or rarely egg-feeders), radula with single row of puncturing teeth (0.1.0), discarded teeth stored in special pharyngeal sac. Digestive gland often forming two parallel tubes, sometimes branching into dorsal appendages (cerata). One truly interstitial family:

Platyhedylidae Salvini-Plawen 1973

Family of interstitial sacoglossans, externally similar to an acochlidian. No cephalic appendages or cerata, with free posterior visceral sac. Headfoot cannot be retracted into visceral sac, curls or coils up when disturbed. Digestive gland with two parallel tubes, green.

Platyhedyle Salvini-Plawen, 1973 [49-53]

Diagnosis. Head with wide and rounded anterior margin, no labial tentacles or rhinophores [48]. Eyes set slightly behind. Body flat, foot narrow, tail end of foot very short [51,52]. Visceral sac long, slightly flattened [50-53]. Small spicules present. Living animal brownish, with green digestive gland. Preserved animals do no retract headfoot but curl or coil up (Poizat, 1978) [51-53].

Taxonomy. Sole genus in family, with worldwide distribution. Only described species from Mediterranean, rare: *P. denudata* Salvini-Plawen 1973, with characteristics of the genus. 2-4 mm. So far no records from N Atlantic:

Limapontiidae Gray, 1847

Family of intertidal to amphibious Sacoglossa, with or without head appendages and lateral rows of appendages (cerata). If present, branches of digestive gland and albumen gland reach into cerata. Intertidal species often darkly pigmented, with large clear areas above eyes; anus dorsal. Members of one genus occasionally found in gravel or sand samples, yet not strictly interstitial:

Calliopaea d'Orbigny, 1837 [53, 54, 57]

Diagnosis. Genus with two rows of balloon-shaped, darkly pigmented cerata (can be autotomized) [53]. Labial tentacles incorporated into oral veil, rhinophores long, smooth. Bean-shaped eyes in clear window behind rhinophores. Long penial stylet. Skin pigment blackish-brown to ochre.

Taxonomy. Two species in N Europe, one of which was recorded from algae, gravel, or sand samples (Todd, 1982; Arnaud et al., 1986):

Calliopaea bellula d'Orbigny, 1937, with external characters of the genus. Feeds on eggs. 3-5 mm.

Nudibranchia (group C)

Marine slugs with dorsal gills and mantle covering the entire dorsum (Doridacea = Anthobranchia), or lateral appendages (cerata) with or without gills and reduced mantle (Aeolidacea = Cladobranchia). Carnivores. Aeolidacea with one fully and one partially interstitial family:

Embletoniidae Pruvot-Fol, 1954

Family with two rows of club-shaped cerata without cnidosacs. Upper lip forming rounded velum (no distinct labial tentacles), rhinophores fusiform, smooth. Anus lateral, with genital papilla. Sole genus with benthic or interstitial species.

Embletonia Alder & Hancock, 1851 [55-56, 58-59]

Diagnosis. Genus with characters of the family. No distinct labial tentacles, instead large rounded oral veil [56]. Rhinophores long, smooth. Two rows of fusiform to flask-shaped cerata (can be autotomized) [59], posterior ones largest. Spherical eyes behind rhinophores. Body white on back, head and cerata. Cerata orange-brown internally.

Taxonomy. One widespread and common species in Europe, frequently recorded from sand or gravel (Poizat, 1981b, 1991, Marcus & Marcus, 1955, 1958) but also (rarely) from rocks and algae:

Embletonia pulchra (Alder & Hancock, 1844)

Syn. *E. faurei* Labbé, 1923

Only embletoniid in the area, locally common.

Pseudovermidae Thiele, 1931

Family of strictly interstitial aeolidaceans. Body vermiform. Head without appendages, with large, acorn-shaped snout, mouth subterminal [60-63]. Eyes set slightly behind, or lost. With lateral rows of short, knob- to finger-shaped shaped cerata (with cnidosacs). First cerata paired, others alternating. Body colorless, digestive gland yellowish to brown. One genus:

Pseudovermis Perejaslavtzeva, 1891 [57-60]

Diagnosis. Genus with characters of the family. Cerata sometimes very small and reduced to cnidosacs only. Radula 1.1.1, with large jaws. Prey on interstitial hydrozoans, and possibly opisthobranchs (Jörger et al., 2014b).

Taxonomy. Nine described species in Europe, usually rare. Three species recorded in N Europe:

P. schulzi Marcus & Marcus, 1955

Species described from W France (Arcachon, Bay of Biscay). Only up to five, very small cerata [60]. Up to 2 mm in size.

P. boadeni Salvini-Plawen & Sterrer, 1968

Species described from N Wales (Menai Bridge, Anglesey). Up to 15, small and knob-shaped cerata () 7-8 per side) [61]. Up to 3 mm in size.

P. artabrensis Urgorri, Cobo & Besteiro, 1991

Species described from N Spain. Up to 15, rather large cerata [62]. Up to 3 mm in size.

Other small Aeolidacea sometimes found in dredged samples, with paired tentacles instead of flat oral veil: family Tergipedidae. Colour and pattern of cerata are important for species identification. Thompson (1988) provides a key for the British species.

Rhodopemorpha (group D)

"Lower heterobranch" slugs, marine interstitial or benthic. Body completely vermiform, resembling a turbellarian or nemertean. Body round in cross-section; no separation into headfoot and visceral sac, without any appendages. Internal organs reduced (no pharynx or radula, no heart). Eyes at anterior third of body, or lost. With curved or cross-shaped subepidermal spicules in entire body. With caudal adhesive gland. Distinguishable from "worms" by spicules, paired statocysts, and slow movement. Worldwide distribution (Brenzinger et al., 2010, 2013).

Rhodopidae Ihering, 1876

Family with characters of the order. Two genera:

Rhodope Kölliker, 1847 [64-66, 69-70]

Diagnosis. Body vermiform, ratio of body length to width 3-9. Slightly retracts front end when disturbed (Riedl, 1959) [69-70]. Snout slightly pointed, tail end slightly widened and flat. Eyes spherical, present or lost. Spicules bent, with verrucose surface, sometimes with notch at outer side of bend. Colorless, or with dorsal pigmented bands colored orange or yellow. Size 0.5 to 6 mm. In gravel, sand, or among intertidal algae. Rare.

Taxonomy. Five described species, many undescribed ones. Three records from N Europe:

Rhodope roskoi Haszprunar & Hess, 2005

Species described from subtidal shelly gravel in N France (Roscoff, Brittany). With transversal, orange-yellow band at first third and more posterior, longitudinal dorsal band [64]. Spicules thick, verrucose, 90-120 µm long [65]. Size up to 1.5 mm.

Rhodope "veranyi" in Swedmark, 1958; Karling, 1966

Species recorded from subtidal shelly gravel in N France (Roscoff) and Norway [66]. Without orange bands, white. Spicules thick, verrucose, or thin, or "branched". Size up to 1.5 mm.

Helminthope Salvini-Plawen, 1991 sp. [73-74, 77]

Diagnosis. Body extremely vermiform, ratio of body length to width 8-25 [67]. Curls up and slightly contracts when disturbed [71]. Snout long and rounded, tail end slightly widened and flat. Eyes spherical, present or lost. Spicules bent, with verrucose surface, sometimes tetrahedral or cross-shaped, with central hole [68]. Animals colorless. Size 1-4 mm. In sand. Rare.

Taxonomy. Only one described species in the genus, but worldwide distribution indicated. So far no records from N Europe.

Literature

Arnaud, P. M., Poizat, C. L., & Salvini-Plawen, L. v. (1986). Marine-interstitial Gastropoda (including one freshwater interstitial species). In *Stygofauna Mundi. A Faunistic, Distributional, and Ecological Synthesis of the World Fauna inhabiting Subterranean Waters (including the Marine Interstitial)*: 153-165. Botosaneanu, L. (Ed.). Leiden: E.J. Brill/Dr. W. Backhuys.

Brenzinger, B., Wilson, N. G., & Schrödl, M. (2010). 3D microanatomy of a gastropod "worm": *Rhodope rousei* n. sp. (Heterobranchia) from Southern Australia. *J Moll Stud* **77**: 375-387.

Brenzinger, B., Haszprunar, G. & Schrödl, M. (2013). At the limits of a successful body plan – 3D microanatomy, histology and evolution of *Helminthope* (Mollusca: Heterobranchia: Rhodopemorpha), the most worm-like gastropod. *Front Zool* **10**: 37.

Delamare-Deboutteville, C. (1960). Biologie des eaux souterraines littorales et continentales. Hermann Montpellier (ed.)/ Laboratoire Arago Université de Paris. Paris: Causse, Graille et Castelnau.

Eder, B., Schrödl, M., & Jörger, K. M. (2011). Systematics and redescription of the European meiofaunal slug *Microhedyle glandulifera* (Kowalevsky, 1901)(Heterobranchia: Acochlidia): evidence from molecules and morphology. *J Molluscan Stud* **77:** 388-400.

Gascoigne, T., & Todd, C. D. (1977). A description of a specimen of *Calliopaea bellula* d'Orbigny, 1857 found at Robin Hood's Bay, North Yorkshire (Opisthobranchia, Sacoglossa). *Journal of Molluscan Studies*, **43**(3): 290-295.

Haszprunar, G. & Heß, M. (2005). A new *Rhodope* from the Roscoff area (Bretagne), with a review of *Rhodope* species (Gastropoda: Nudibranchia?). *Spixiana* **28:** 193-197.

Higgins, R. P., & Thiel, H. (1988). *Introduction to the study of meiofauna*. Smithsonian Institution Press.

Jörger, K. M., Kristof, A., Klussmann-Kolb, A., & Schrödl, M. (2010b). Redescription of the meiofaunal gastropod *Parhedyle cryptophthalma* (Acochlidia, Panpulmonata), with focus on nervous system and sensory organs. *Spixiana* **33:** 161-288.

Jörger, K. M., Neusser, T. P., Brenzinger, B., & Schrödl, M. (2014a). Exploring the Diversity of Mesopsammic Gastropods: How to Collect, Identify, and Delimitate Small and Elusive Sea Slugs? *Amer Malac Bull* **32**(2): 290-307.

Jörger, K. M., Neusser, T. P., Haszprunar, G., & Schrödl, M. (2008). Undersized and underestimated: 3D visualization of the Mediterranean interstitial acochlidian gastropod *Pontohedyle milaschewitchii* (Kowalevsky, 1901). *Org Divers Evol* **8:** 194-214.

Jörger, K. M., Stöger, I., Kano, Y., Fukuda, H., Knebelsberger, T., & Schrödl, M. (2010a). On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. *BMC Evol Biol* **10:** doi:10.1186/1471-2148-10-323.

Jörger, K. M., Stoschek, T., Migotto, A. E., Haszprunar, G., & Neusser, T. P. (2014b). 3D-microanatomy of the mesopsammic *Pseudovermis salamandrops* Marcus, 1953 from Brazil (Nudibranchia, Gastropoda). *Mar Biodiv* **44**(3): 327-341.

Kano, Y., Neusser, T. P., Fukumori, H., Jörger, K. M., & Schrödl, M. (2015). Sea-slug invasion of the land. *Biol J Linn Soc*, doi:10.1111/bij.12578.

Karling, T. G. (1966). *Rhodope veranyi* (Gastropoda, Euthyneura) von der norwegischen Küste. *Sarsia* **24**(1): 33-35.

Langegger-Weinbauer, C. & Salvini-Plawen, L. v. (2013). Anatomical redescription of two species of Philinoglossidae (Gastropoda, Cephalaspidea). *Spixiana* **36:** 21-41.

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

Marcus, Er. & Marcus, Ev. (1954). Über Philinoglossacea und Acochlidiacea. *Kieler Meeresforsch* **10:** 215-223.

Marcus, Ev. & Marcus, Er. (1955). Über Sand-Opisthobranchia. *Kieler Meeresforsch* **11:** 230-243.

Marcus, Ev. & Marcus, Er. (1958). Opisthobranchia aus dem Schill von Helgoland. *Kieler Meeresforsch* **14:** 91-96.

Neusser, T. P., Martynov, A. V., & Schrödl, M. (2009). Heartless and primitive? 3D reconstruction of the polar acochlidian gastropod *Asperspina murmanica*. *Acta Zool* **90:** 228-245.

Odhner, N. H. (1937). *Hedylopsis suecica* n.sp. und die Nacktschneckengruppe Acochlidiacea (Hedylacea). *Zool Anz* **120**: 51-64.

Ohnheiser, L. T., & Malaquias, M. (2013). Systematic revision of the gastropod family Philinidae (Mollusca: Cephalaspidea) in the north-east Atlantic Ocean with emphasis on the Scandinavian Peninsula. *Zool J Linn Soc* **167**(2), 273-326.

Oskars, T. R., Bouchet, P., & Malaquias, M. A. E. (2015). A new phylogeny of the Cephalaspidea (Gastropoda: Heterobranchia) based on expanded taxon sampling and gene markers. *Mol Phylo Evol* **89:** 130-150.

Poizat, C.L. (1978). Recherches des paramètres écologiques favorables à l'existence du gastéropode opisthobranche Acochlidiacea *Platyhedyle* Salvini-Plawen 1973, dans des sédiments marins des environs de Marseille (France). *Haliotis* **7:** 31–38.

Poizat, C. L. (1981a). Gasteropodes mesopsammiques de la mer du nord (Robin Hood's Bay, U.K.). Ecologie et distribution. *J Molluscan Stud* **47:** 1-10.

Poizat, C. L. (1981b). Signification écologique de quelques Gastéropodes Opisthobranches mésopsammiques des côtes de Provence. *Haliotis* **11:** 201-212.

Poizat, C. L. (1985). Interstitial opisthobranch gastropods as indicator organisms in sublittoral sandy habitats. *Stygologia* **1:** 26-42.

Poizat, C. L. (1991). New data on an interstitial opisthobranch assemblage and other meiofauna from the Skagerrak, Sweden. *J Moll Stud* **57:** 167-177.

Riedl, R. (1959). Beiträge zur Kenntnis der *Rhodope veranii*, Teil I. Geschichte und Biologie. *Zool Anz* **163:** 107-122.

Rieger, R. M. & Sterrer, W. (1975). New spicular skeletons in Turbellaria, and the occurrence of spicules in marine meiofauna. Part II. *Z f zool Syst u Evol.-forsch.* **13:** 249-278.

Salvini-Plawen, L. v. & Sterrer, W. (1968). Zur Kenntnis der mesopsammalen Gattung *Pseudovermis* (Gsatropoda, Nudibranchia). *Helgoländer wiss Meeresunters* **18:** 69-77.

Salvini-Plawen, L. v. (1973). Zur Kenntnis der Philinoglossacea und der Acochlidiacea mit Platyhedylidae fam. nov. (Gastropoda, Cephalaspidea). *Z f zool Systematik u Evol.-forsch.* **11:** 110-133.

Salvini-Plawen, L. v. (1984). Notes on molluscan meiofauna from Plymouth. *J Mar Biol Assoc U. K.* **64:** 497-502.

Salvini-Plawen, L. v. (1991). The status of the Rhodopidae (Gastropoda: Euthyneura). *Malacologia* **32:** 301-311.

Schrödl, M. & Neusser, T. P. (2010). Towards a phylogeny and evolution of Acochlidia. *Zool J Linn Soc* **158:** 124-154.

Swedmark, B. (1964). The interstitial fauna of marine sand. *Biol Rev* **39:** 1-42.

Swedmark, B. (1968a). The biology of interstitial Mollusca. *Symp Zool Soc London* **22:** 135-149.

Swedmark, B. (1968b). Deux espèces nouvelles d'acochlidiacées (mollusques opisthobranches) de la faune interstitielle marine. *Cah Biol Marine Roscoff* **9:** 175-186.

Thompson, T.E. (1976) Biology of opisthobranch molluscs. Volume I. The Ray Society, London.

Thompson, T. E. (1988). *Molluscs: benthic opisthobranchs: Mollusca, Gastropoda: keys and notes for the identification of the species* (Vol. 8). Brill.

Todd, C. D. (1982). Further observations on the ascoglossan opisthobranch *Calliopaea bellula* d'Orbigny. *J Moll Stud* **48** (1): 101-102.

Urgorri, V., Cobo, F., & Besteiro, C. (1991). *Pseudovermis artabrensis* (Nudibranchia: Aeolidoidea), a new species from Galicia, Spain. *J Moll Stud* **57**(Supplement Part 4)**:** 189-197.

Wawra, E. (1989). Zur Kenntnis der interstitiellen Opisthobranchierart *Hedylopsis spiculifera* (Kowalevsky) (Mollusca, Gastropoda). *Zool Scr* **18:** 397-403.

Wägele, H., Klussmann-Kolb, A., Verbeek, E., & Schrödl, M. (2013). Flashback and foreshadowing - a review of the taxon Opisthobranchia. *Org Divers Evol***:** 1-17.

Westheide, W. (1987). Progenesis as a principle in meiofauna evolution. *J Nat Hist* **21:** 843-854.

Westheide, W., & Wawra, E. (1974). Organisation, Systematik und Biologie von *Microhedyle cryptophthalma* nov. spec.(Gastropoda, Opisthobranchia) aus dem Brandungsstrand des Mittelmeeres. *Helgoländer Wiss Meeresunters* **26**(1)**:** 27-41

Appendices

Legends to graphical keys

Graphical key to Group A

Graphical key to Group B

Graphical key to Groups C+D

Legend to graphical key A

[1-2] *Philinoglossa helgolandica*, dorsal and ventral views of live specimen, and first lateral tooth of radula (after Salvini-Plawen, 1973). [3-4] *Philinoglossa praelongata*, dorsal and ventral views of live specimen, and first lateral tooth of radula (after Salvini-Plawen, 1973 and own photograph). [5] *Abavopsis latosoleata*, dorsal and ventral views of live specimens (after Salvini-Plawen, 1973). [6] *Philinoglossa praelongata*, preserved specimens, right lateral view. [7] *Philinoglossa* sp., preserved specimen, right and ventral view [8] *Abavopsis latosoleata*, preserved specimen. [9] *Philine catena*, dorsal view (after Arnaud et al., 1986). [10] *Philine catena*, apertural view of shell, with detail of shell sculpture (chain-like connected pits). [11] *Philine scabra*, dorsal view (after Ohnheiser & Malaquias, 2013). [12] *Philine scabra*, apertural view of shell, with detail of shell sculpture (rounded pits) (after Ohnheiser & Malaquias, 2013). [13] *Philine* sp., right lateral view of preserved specimen (after Ohnheiser & Malaquias, 2013). [14] *Philine* sp., ventral view of preserved specimen (after Ohnheiser & Malaquias, 2013). [15] *Philine* sp. cf. *catena*, dorsal view. Preserved specimen. [16] *Runcina coronata*, live specimen, dorsal and ventral views. [17] *Runcina ferruginea*, dorsal and ventral view. After live photograph. [18-19] *Runcina* sp. juv., right lateral and dorsal views. Preserved specimen.

Legend to graphical key B

[20-23] *Hedylopsis spiculifera*, dorsal views of head, juvenile, dorsal and ventral views of adult specimen, and spicules (22 after Odhner, 1937). [24-26] *Asperspina brambelli*, dorsal view, spicules, and head (after Swedmark, 1968). [27] *Asperspina murmanica*, dorsal view of head (after Neusser et al., 2009). [28] *Asperspina loricata*, dorsal view of head (after Swedmark, 1968). [29] *Asperspina murmanica*, right lateral view of living specimen (after Neusser et al., 2009). [30-31] *Hedylopsis spiculifera*, right lateral views of preserved specimens. [32] *Asperspina loricata*, ventral and right lateral view of typical preserved, retracted specimen (after Swedmark, 1968). [33-36] *Microhedyle glandulifera*, dorsal views of head, adult specimens, and juvenile, spicules (34, 36 after Eder et al., 2011). [37-40] *Parhedyle cryptophthalma*, dorsal views of head, adult specimens, and juvenile, spicules (after Jörger et al., 2010; 39 after Westheide & Wawra, 1974). [41-44] *Pontohedyle milaschewitchii*, dorsal and ventral views of head, adult specimens, spicules (42 after Jörger et al., 2008). [45-46] *Microhedyle*/*Parhedyle* sp., right lateral views of typical preserved specimens. [47] *Pontohedyle milaschewitchii*, right lateral view of preserved specimen [after Jörger et al., 2008]. [48] *Pontohedyle milaschewitchii*, ventral view of retracted, preserved specimen (after Jörger et al., 2014a). [49-50] *Platyhedyle denudata*, dorsal view of head and live specimen (after Jörger et al., 2014a). [51-52] *Platyhedyle denudata*, ventral view and right lateral views (after Poizat, 1976). [53] *Platyhedyle*, view of preserved specimen.

Legend to graphical key C+D

[53] *Calliopaea bellula*, dorsal view of live specimen (after Todd, 1982). [54] *Calliopaea bellula*, ventral view of live specimen (after Gascoigne & Todd, 1977). [55] *Embletonia pulchra*, dorsal view of live specimen (after Delamare-Deboutteville, 1960). [56] *Embletonia pulchra*, dorsal view of head (after photograph by Bernard Picton/habitas.org.uk). [57] *Calliopaea bellula*, dorsal view of typical preserved specimen. [58] *Embletonia pulchra*, dorsal views of typical preserved specimens. [59] *Embletonia pulchra*, right lateral view of damaged, preserved specimen with cerata torn off. [60] *Pseudovermis schulzi*, dorsal view of live specimen (after description in Marcus & Marcus, 1955). [61] *Pseudovermis boadeni*, dorsal view of live specimen (after description in Salvini-Plawen & Sterrer, 1968). [62] *Pseudovermis artabrensis*, dorsal view of live specimen (after Urgorri et al., 1991). [63] *Pseudovermis* sp., right lateral view of typically contracted specimen (after Jörger et al., 2014b). [64-65] *Rhodope roskoi*, dorsal view of live specimen and spicules (after Haszprunar & Heß, 2005). [66] *Rhodope* sp., dorsal view of specimen (after description by Karling, 1966). [67-68] *Helminthope* sp., dorsal view of live specimen and spicules. [69-70] *Rhodope* sp., right lateral views of typical preserved specimens (after Brenzinger et al., 2010). [71] *Helminthope* sp., right lateral view of typical preserved specimen.