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Towards a sound definition of Skeneidae (Mollusca, Vetigastropoda): 3D interactive anatomy of the type species, *Skenea serpuloides* (Montagu, 1808) and comments on related taxa

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Abstract The family Skeneidae, originally characterized by their minute size, lack of nacre and a rhipidoglossate radula, is an example of a polyphyletic assemblage. Most 'skeneimorph' species are based on the shell, sometimes the radula and rarely features of the external body. Data on internal anatomy are almost entirely lacking. In order to provide a complete anatomical data set with histological information, we applied serial semithin sectioning and 3D reconstructions to describe and visualize the anatomy of the type species of Skeneidae, *Skenea serpuloides* (Montagu, 1808). In addition, comparative data are provided for three other Skeneidae, *Skenea profunda* Friele, 1879; *Dillwynella lignicola* Marshall, 1988 and *Dillwynella voightae* Kunze, 2011 as well as for a tiny turbinid-like species, *Lodderena minima* (Tenison-Woods, 1887). We diagnose Skeneidae as trochoidean vetigastropods with combined epipodial sense organs (ESOs), neck lobes, eyes with a closed vesicle and the diagnostic propodial penis. Other features include simultaneous hermaphroditism with distinct testis/vas deferens and ovary/oviduct, a urogenital opening with the right kidney and a distinct seminal receptacle. Several features of Skeneidae are explained by dwarfing through progenesis, and accordingly, we interpret paedomorphosis of various characters. In contrast, *L. minima* has a true hermaphroditic gland, but lacks of propodial penis and a receptaculum. Also, molecular data support an exclusion of *Lodderena* from the Skeneidae.

Keywords Microgastropods · Systematics · Progenesis · Paedomorphosis

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Introduction

Fleming (1825) created the genus *Skenea* for *Helix serpuloides* Montagu, 1808 and Clark, (1851a: 472 Skeneadae as nomen nudum, 1851b: 44ff with diagnosis) designated *Skenea serpuloides* as the type species for the vetigastropod family Skeneidae, a concept stood for more than 120 years. Keen and McLean 1971) summed up the diagnosis of the family as follows: 'No other family combines the features of rhipidoglossate radula, lack of nacre, and multispiral operculum'. Some authors have speculated that there may be hundreds of described and many more undescribed species of Skeneidae (e.g. Marshall 1988; Kano et al. 2009). However, with increasing data, it is clear that many small snails share these characters, especially inhabitants of deep water or of chemosynthetic habitats like sunken wood or hydrothermal vents and these have proved to belong to different subgroups (e.g. Marshall 1988; Warén and Bouchet 1993, 2001; Hasegawa 1997). It is now obvious that the accepted diagnosis is not sufficient to reflect a monohyletic clade. Indeed, most recent authors assumed the family to be polyphyletic (Marshall 1988; Hickman and McLean 1990; Warén 1992; Warén and Bouchet 1993; Hickman 1998, 2013; Kano et al.

2009). Accordingly, several authors have named these gastropods informally ‘skeneimorph’ or ‘skeneiform’ (Warén 1992; Kano 2008; Hickman 1998, 2013). Herein, we follow this tradition, calling gastropods having the features described above skeneimorph, and restrict Skeneidae for those species forming a clade including the type species, *Skenea serpuloides* (Montagu, 1808) (Table 1). The respective taxon has been assigned both, family status as Skeneidae (e.g. Clark 1851a, b; Wenz 1938; Fretter and Graham 1977; Keen and McLean 1971; Marshall 1988; Hickman and McLean 1990; Warén 1991, 1992, 1993; Warén and Bouchet 1993, 2001; Williams and Ozawa 2006; Williams 2012) ocae (e.g. Thiele 1929; Bouchet et al. 2005; Williams et al. 2008; Nye et al. 2013).

Several molecular studies revealed Skeneidae as part of Turbinidae (Williams and Ozawa 2006; Williams et al. 2008; Kano 2008; Aktipis and Giribet 2012), but the most recent ones (Williams 2012; Nye et al. 2013) again resolved Skeneidae as a separate clade, a point of view we followed herein. Skeneidae and Turbinidae are incorporated together with the families Calliostomatidae, Liotiidae, Margaritidae, Solariellidae and Trochidae as Trochoidea (Williams et al. 2008; Williams 2012). In contrast, the ‘trochoid’ Phasianelloidea and Angarioidea as well as Seguenzioidea (see Kano 2008; Kano et al. 2009) are currently accepted as separate vetigastropod clades.

Concerning the content of Skeneidae sensu stricto, Warén (1991, 1992) first assumed the presence of a propodial penis

Table 1 Size and volume of the inner organs of *Skenea serpuloides* (specimens SMSN 98643/98644)

Organs	Size (μm)	Volume (10^6 μm^3)	% of soft body
Soft body	l: 880/860, w: 350/370,	77/79.9	100/100
Operculum	h: 710/700, d: 550/550	–	
Mantle cavity			
Hypobranchial gland	l: 210/–, w: 175/–, h: 100/–	1.53/–	1.987/–
Anterior pedal gland	l: 110/–, w: 105/–, h: 230/–	1.09/–	1.416/–
Ctenidium	l: 150/–, w: 290/–, h: 80/–	1.29/–	1.675/–
Vascular and excretory system			
Pericardium	l: 225/190, w: 145/105	0.77/0.49	1.00/0.61
Auricle	l: 75/–, h: 100/–	0.16/–	0.21/–
Ventricle	l: 70/–, h: 120/–	0.24/–	0.31/–
Right kidney	l: 180/260, w: 240/260, h: 75/55	0.88/0.69	1.14/0.86
Left kidney	l: 205/230, w: 65/60, h: 55/30	0.66/0.69	0.86/0.86
Urogenital duct	l: 50, w: 65	–	–
Genital system			
Ovary	l: 260/245, w: 135/125, h: 150/130	4.46/3.92	5.79/4.91
Oviduct	l: 200/100, w: 60/60	–	–
Testis	l: 300/285, d: 80/70	0.75/0.72	0.97/0.90
Vas deferens	l: 35/20, w: 40/50	–	–
Seminal receptacle	l: 195/185, w: 125/175, h: 90/145	1.10/1.57	1.43/1.97
Bursa copulatrix	l: 115/80, d:60/45	0.26/0.07	0.34/0.09
Alimentary tract			
Radula incl. caecum	l: 450/450	–	–
Radular cartilage	l: 60/75, w: 90/60, h: 95/160	0.29/0.57	0.38/0.71
Anterior oesophagus	l: 420/430, w: 200/170, h: 130/135	4.09/3.82	5.31/4.78
Posterior oesophagus	l: 300/325, d: 45/50	–	–
Stomach	l: 420/380, w: 160/145, h: 185/180	6.96/5.54	9.04/6.93
Intestine	l: 2350/2150, w: 60–70/55–70	8.34/5.45	10.83/6.82
Midgut gland	l: 700/890, w: 110/150	6.12/5.31	7.95/6.65
Nervous system		–/3.59	–/4.49
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	–/0.07
Eyes	d: 55/50	0.09/0.10	0.12/0.13

as diagnostic and included, aside from *Skenea* Clark, 1851, also the genera *Lissospira* Bush, 1897; *Pseudorbis* Monterosato, 1884; *Lodderena* Iredale, 1924 (but see below); *Dikoleps* Høisæter, 1968 and *Skeneoides* Warén, 1992. Later on also *Dillwynella* Dall, 1889 and *Protolira* Warén & Bouchet, 1993 from the hot-vent habitat were integrated (Marshall 1988; Warén and Bouchet 1993). About 130 genus names have been assigned to Skeneidae (Hickman 2013). The current (access 5 December 2015) WoRMS-webpage still lists more than 40 genera among Skeneidae, the Worldwide Mollusc Species Data Base only 32, but in both cases, many of these 'skeneimorphs' are still doubtful members of Skeneidae. Recently Hickman (2013) assigned *Conjectura* Finlay, 1926; *Conradia* A. Adams, 1860; *Crossea* A. Adams, 1865 and *Crosseola* Iredale, 1924 to the newly erected family Crosseolidae Hickman 2013, but according to A. Warén (pers. comm.) *Conjectura* belongs to Tornidae and has a taenioglossate radula.

Recent studies using molecular and micromorphological methods excluded a good number of genera originally assigned to Skeneidae: Among the vetigastropods *Akritogyra* Warén, 1992; *Anekes* Bouchet & Warén, 1979; *Granigyra* Dall, 1889; *Ventsia* Warén & Bouchet, 1993; *Xyloskenea* Marshall, 1988 and *Adeuomphalus* Seguenza, 1876 that were transferred to Seguenzioidea (Kano 2008; Kunze et al. 2008, 2016; Kano et al. 2009). *Bathyxylophila* Marshall, 1988 is now classified among Scissurelloidea (Kano 2008; Kunze et al. 2008). Some genera have been assigned to Neomphalina, these being *Leptogyra* Bush, 1897 and *Leptogyropsis* Marshall, 1988 (Heß et al. 2008; Kunze et al. 2008). *Hyalogyra* Marshall, 1988; *Hyalogyrina* Marshall, 1988 and *Xenoskenea* Warén & Gofas, 1993 are now included in the heterobranch Hyalogyrinidae (Warén and Bouchet 1993; Warén et al. 1993; Kunze et al. 2008; Haszprunar et al. 2011). Whereas a number of recent reports and descriptions on skeneimorphs (e.g. Aartsen and van Bogi 1988; Ponder 1990; Rubio-Salazar 1991; Rubio and Rodriguez-Babio 1991; Rubio and Rolán 1991, 2013a, b, 2015; Warén 1991, 1992, 1993, 1996; Engl 1996, 2001; Moolenbeek 1996; La Perna 1998; Rubio et al. 1998a, 2004, 2015; Rolán and Ryall 2000; Carrozza and van Aartsen 2001; de Barros et al. 2002; Redfern and Rolán 2005; Hoffman et al. 2008, 2010; Kunze 2011; de Lima et al. 2011; Romani et al. 2015) provided extensive SEM-data on shell, protoconch and radula, there is a severe lack of anatomical and molecular data (Tables 2 and 3). Indeed, head–foot data are scarce and skeneid anatomy is known from only two species (Table 3). Because the only known diagnostic character of Skeneidae is the presence of a propodial penis (Warén 1992; Kunze et al. 2008; Hickman 2013), most species are only tentatively assigned to Skeneinae.

Based on serial semi-thin sectioning, 3D reconstructions and their interactive embedding in PDFs, we provide the first detailed anatomical description with histological data for a skeneid, although some preliminary data have been published by Brückner et al. (2004), and Kunze et al. (2008). Together with the SEM-data of the head-foot recently provided by Rubio and Rolán (2013a), the anatomical data of the type species of Skeneidae allow us to define the family morphologically. To show variability of characters we also provide relevant data on the internal anatomy of three other skeneids.

Material and methods

1. *S. serpuloides* (Montagu, 1808): Collected on maërl off Roscoff, Bretagne, France, by E.C. Rodriguez-Babio (see Rodriguez-Babio and Thiriot-Quievreux 1975: 172) and determined by Anders Warén (Naturhistoriska Riksmuseet, Stockholm: SMNH). Section series SMNH: 98643, 98644, 98645, and 98646 were used for histological examination. 3D reconstructions were compiled based on of the section series: SMNH-98643 and 98644 body and inner organs; SMNH-98643 and 98645 body and tentacles. Measurements of the organ systems (size and volume) were taken for both specimens (Table 1). Both have almost the same size and arrangement of organs, but the retraction grade is different. Respiratory and circulatory systems were better preserved 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. In addition, five sections series are based on specimens collected in 2005 by GH on the surface of 'amphioxus-sand' dredged at 48° 43′ 532 N, 3° 50′ 712 W, 20–25 m (Zoologische Staatssammlung Munich, molluscan section, SNSB-ZSM-Moll 20140452 to 20140456). The shell (1.5 mm) and protoconch of *S. serpuloides* are described and figured via SEM by several authors (Rodriguez-Babio and Thiriot-Quievreux 1975; Fretter and Graham 1977; van Aartsen et al. 1984; Rubio-Salazar 1991; Warén 1991).
2. *Skenea profunda* Friele, 1879 is a deep-water species, originally described from sunken wood in 2400 m west of Svalbad (Friele 1879). The present sample is the host of an epibiotic nematode described by Holovachov et al. (2011) discovered at a large wood fall found during an expedition with RV 'G.O. Sars' in the northeast East Atlantic in June 2007 at 2830 m depth using the ROV 'Bathysaurus' at 73° 833.19′ N 08° 816.900′ E (Swedish Museum of Natural History in Stockholm, SMNH 99624). SEM images of shell, protoconch and radula were provided by Warén (1991).
3. *Dillwynella lignicola* Marshall, 1988 represents the genus *Dillwynella* Dall, 1889, which is supposed to be closely

Table 2 Molecular data (GenBank accession numbers) on Skeneidae and possibly related forms (marked by *)

Species	18S	28S	16S	H3	12S	COI	References
Cirsonella extrema Thiele, 1912	HE800798	HE800714	HE800754	–	HE800663	HE800615	Williams 2012
Cirsonella spC (Chiba 260 m, Hota, Japan)	–	–	–	–	–	AB365247	Kano 2008, Williams 2012
Cirsonella spA (Chiba 90 m,Tateyama, Japan)	–	–	–	–	–	AB365245	Kano 2008, Williams 2012
Cirsonella spB (Panglao, Philippines)	–	–	–	AB365289	–	AB365246	Kano 2008, Williams 2012
Dillwynella planorbis Hasegawa, 1997	AB365310	–	–	AB365285	–	AB365240	Kano 2008
–“–	AB365310	–	–	–	–	AB365240	Williams et al. 2008
–“–	–	–	–	–	–	AB365240	Williams 2012
Dillwynella sp1 (Bohol Sea, Philippines)	–	–	HE800755	–	HE800664	HE800616	Williams 2012
Dillwynella sp1 (Bohol/Sulu Sea, Philippines)	HE800799	HE800715	HE800756	–	HE800665	HE800716	Williams 2012
Dillwynella spA (Panglao 300 m, Philippines)	–	–	–	–	–	AB365241	Kano 2008, Williams 2012
Dillwynella spB (Panglao 70 m, Philippines)	–	–	–	–	–	AB365242	Kano 2008, Williams 2012
Dillwynella vitrea Hasegawa, 1997	AM048641	AM048701	AY153406	–	–	AM049336	Williams 2012
–“–(Owase City, Japan)	AM048641	AM048701	–	–	–	AM049336	Williams & Ozawa 2006
–“–(Owase City, Japan)	AM048641	EU530046	–	–	–	EU530143	Williams et al. 2008
–“–(Owase City, Japan)	AM048641	AM048701	HE800757	–	HE800666	AM049336	Williams et al. 2008
–“–(Off Tashi, Taiwan)	–	HE800716	–	–	HE800667	HE800618	Williams 2012
–“–(Owase City, Japan)	AM048641	AM048701	AY153406	–	–	AM049336	Aktipis & Giribet 2012
Dillwynella cf. *vitrea* (Owase City, Japan)	–	–	AY153406	–	–	–	Nye et al. 2013
Iheyspira bathycodon Nye, 2012 *	–	–	JQ306327	–	–	–	Nye et al. 2013
Lodderena sp. (Izu, Japan) *	–	–	–	AB365287	–	AB365243	Kano 2008, Williams 2012
Protolira sp. (Lost City, Mid–Atlantic)	–	GQ160652	GQ160698	–	–	–	Williams 2012
–“–	GQ160803	GQ160652	GQ160698	GQ160738	–	–	Aktipis & Giribet 2012
–“–	–	–	GQ160698	–	–	–	Nye et al. 2013
Protolira thorvaldssoni Warén, 1996	–	HE800717	–	–	HE800668	–	Williams 2012
Protolira valvatoides Warén & Bouchet, 1993	–	–	AY163405	–	–	–	Williams 2012, Nye et al. 2013
Skeneidae sp. (Balicosag, Philippines)	–	HE800718	HE800758	–	HE800669	HE800619	Williams 2012

related to *Skenea* (Kano 2008) and has been included in several molecular analyses concerning phylogeny (Williams and Ozawa 2006; Kano 2008; Williams et al. 2008; Aktipis and Giribet 2012; Nye et al. 2013). Paratypes (M.75290, BS931, 42° 47.1′–48.2′ S, 175° 45.6′–47.2′ W, NE of Chatham Is., 1174–1180 m, 22 July 1984, FV *OtagoBuccaneer*, stn B01/102/84 (773)). Marshall (1988: 953–955, Figs. 1a–e, j, 9a, 10c–e, Table 1) provided SEM photos of the shell, protoconch and radula, description and a sketch of the external morphology of the head-foot (two section series in the ZSM-Molluscan section).

4. *Dillwynella voightae* Kunze, 2011. Paratypes (North Atlantic, Gulf of Mexico, Louisiana, USA (27° 44.090′ N, 91° 14.490′ W), natural wood fall, 610 m depth). Kunze (2011) provided data on shell, radula and external morphology (section series have in Field Museum of Natural History, Chicago).
5. *Lodderena minima* Tenison-Woods, 1887, the type species of *Lodderena* Iredale, 1924, is still included in Skeneidae by most current authors, although the available molecular data (Table 3) on a not named *Lodderena* species, do not support this assumption. Shells have been depicted and an actual description of proto- and teleoconch is provided at http://seashellsofnsw.org.au/Skeneidae/Pages/Lodderena_minima.htm and http://www.gastropods.com/8/Shell_16378.shtml The specimen under investigation (DLG706, shelly beach at low tide, collected at 2001-11-14 by rock washing, Manly Beach, Sidney, NSW, Australia, collected by Daniel Geiger) were originally preserved in seawater-buffered formalin and embedded in Epon resin. A resin block and two section series have been deposited in the ZSM-Molluscan section, and the remaining specimens of the original sample is still housed in the Swedish Museum of Natural History.

Table 3 Previous data on the soft bodies of Skeneidae

Species	Method	Structures described/depicted	References
Dikoleps cutleriana (Clark, 1849)	SEM	Head and foot, mantle edge	Fretter and Graham 1977: 88
–"–	SEM	Head and foot, all tentacles, propodial penis	Rubio et al. 1998a: 83, 86
Dikoleps marianae (Rubio et al., 1998)	SEM	Head and foot, all tentacles, propodial penis	Rubio et al. 1998b: 88–89
'*D. nitens*'	Text, drawing	Head and foot	Rubio-Salazar 1991: 192–193
Dikoleps nitens (Philippi, 1844)	SEM	Head and foot, neck lobe, propodial penis	Warén and Bouchet 1993: 27[a])
–"–	SEM	Head and foot, all tentacles, propodial penis	Rubio et al. 1998a: 90–92
Dikoleps pruinosa (Chaster, 1896)	SEM	Head and foot, all tentacles, mantle, propodial penis	Rubio et al. 2004: 126, 129
Dikoleps rolani (Rubio et al., 1998)	SEM	Head and foot, all tentacles, mantle, propodial penis	Rubio et al. 2004: 117, 119
Dikoleps templadoi (Rubio et al., 2004)	SEM	Head and foot, all tentacles, mantle, propodial penis	Rubio et al. 2004: 120,122,124
Dikoleps umbilicostriata (Brugnone in Gaglini, 1987)[b])	SEM	Head and foot, all tentacles, mantle, propodial penis	Rubio et al. 2004: 125, 127
Dillwynella fallax (Hasegawa, 1997)	SEM text, sketch	Head and foot, eye conditions head and foot	Hasegawa 1997: 98–99, Fig. 23A–B
Dillwynella lignicola (Marshall, 1988)	SEM SEM SEM SEM	Head and foot, eye conditions Head and foot,	Marshall 1988: 954, 992, 1001.
Dillwynella lignicola (Hasegawa, 1997)		eye conditions Head and foot, eye conditions	Hasegawa 1997: 92–93, Fig. 23C–D
Dillwynella planorbis (Hasegawa, 1997)		Head and foot, mantle edge	Hasegawa 1997: 96, Fig. 23E–F
Dillwynella seishinmaruae (Hasegawa, 1997)			Hasegawa 1997: 102, Fig. 23G–H
Dillwynella voightae (Kunze, 2011)			Kunze 2011: 38–39
Lissospira sp.	Text (SEM)	Propodial penis	Warén 1992: 152
Protolira valvatoides (Warén & Bouchet, 1993)	SEM	Head and foot, propodial penis, mantle cavity	Warén and Bouchet 1993: 22–25[a])
Pseudorbis sp.	Text (SEM)	Propodial penis	Warén 1992: 152
Pseudorbis granulum (Brugnone, 1873)	Text (SEM)	Propodial penis	Rubio and Rolán 2013b: 90
Skenea basistriata (Jeffreys, 1877)	SEM	Head and foot	Warén 1993: 169
Skenea catenoides (Monterosato, 1877)	Text (SEM)	Propodial penis	Warén 1992: 152, 156 (as *Lodderena*)
Skenea serpuloides (Montagu, 1808)	Text, sketch	Head and foot from below	Clark 1851a: 45–46
–"–	Text only	Head, foot and mantle edge	Fretter and Graham 1977: 82–83
–"–	Text, drawing	Head and foot	Rubio-Salazar 1991: 188–190
–"–	SEM	Head and foot, tentacles, mantle edge, propodial penis	Rubio and Rolán 2013b: 88–90
–"–	Histology	Epipodium, egg, propodial penis, head and foot	Kunze et al. 2008: 121–122, 125, 128
Skenea trochoides (Friele, 1874)	SEM		Warén 1993: 169
Skenoides sp.	Text (SEM)	Propodial penis	Warén 1992: 152, 156
Skenoides exilissima (Philippi, 1844)	Text (SEM)	Propodial penis	Rubio and Rolán 2013b: 90

[a] The online version of Warén and Bouchet (1993) paper (DOI: 10.1111/j.1463-6409.1993.tb00342.x) shows identical Fig. 20 (A–F) on *Protolira valvatoides* and Fig. 21 on *Bruceiella globulus* (A–C) and *Skenea* [*Dikoleps*] *nitens* (D–F), the labelling of Fig. 20 is the correct one according to the descriptions. In contrast, the printed version shows both correct figures

[b] According to Warén (1992: 158), the taxon *Skenea umbilicostriata* Brugnone in Gaglini, 1987 is based on a specimen of *Dikoleps nitens* (Philippi, 1844)

Specimens of *S. serpuloides*, *S. profunda* and *D. voightae* were preserved and stored in 70 % ethanol. Shells were decalcified by postfixation with Bouin's fluid (picric acid, acetic acid and concentrated (i.e. 36 %) formaldehyde in a ratio of 15:1:5) and after dehydration in a graded ethanol series the bodies were embedded in araldite resin. Semi-thin section series were performed with 'Ralph'-glass knifes with the glue-method according to Ruthensteiner (2008), stained with a 1:1 mixture of methylene blue and Azur II for approx. 5 s at 80 °C (Richardson et al. 1960) and sealed with araldite resin.

Specimens of *D. lignicola* were originally frozen in situ, later on preserved in alcohol causing a suboptimal histological condition in particular of the external epithelia. The shell was again decalcified by postfixation with Bouin's fluid and after dehydration in a graded ethanol series the body was embedded in paraplast. Histological section series (á 5 μm) were done with a regular microtome, and the sections were stained by Hainhain's Azan trichrome method or by the more robust haematoxylin-eosin protocol (Mulisch and Welsch 2015). Unfortunately, many sections are folded or partly disrupted so that only certain characteristics could be verified.

The sections of *S. serpuloides* were photographed with a digital camera (Olympus Camedia 5060) mounted on a light microscope (Olympus CX 41, objective Plan C 10×). 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 Heß et al. 2008; Haszprunar et al. 2011), 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 and Heß (2008).

Specimens of *S. profunda* and *D. voightae* were fixed and treated as with *S. serpuloides*, but the analyses were restricted to observe the histological sections in order to detect any differences from the type species.

Results

The anatomical and histological data of *S. serpuloides*, *S. profunda* and the two *Dillwynella* species are nearly identical; thus, we provide a common description mainly based on *S. serpuloides*, from which measurements were taken (Table 1) for future comparison.

Head

Recently, Rubio and Rolán (2013b) provided an excellent series of SEM-photos on the external morphology of *S. serpuloides*. We agree on their results and add the histological details of the respective structures.

Caused by the retraction of the animal into the shell, the foot and the tentacles of *S. serpuloides* were compressed. The visceropallium is located on the right side of the median plane and is comprise of 1.5 whorls (height 350 μm; Fig. 1a). The operculum is circular and multispiral (SEM-photos by Warén 1992: Fig. 4b and Rubio and Rolán 2013b: Figs. 1 and 2) and located on the dorso-posterior portion of the foot. The snout is long and broad, distinct oral lappets are however lacking.

The paired cephalic tentacles are long (contracted 350 μm) with a circular profile and a diameter of 30–40 μm (Fig. 1a–c). The tentacles are filled with longitudinal and diagonal muscles forming a complex grid. The distal parts of the cephalic tentacles are provided with sensory papillae (not shown in the 3D reconstructions, but beautifully depicted by Rubio and Rolán 2013b).

An eye lobe is located dorsal to each eye at the base of the cephalic tentacle. While the left one is small (length 30 μm, diameter 5 μm) and inconspicuous, the right eye lobe 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 ciliated neck lobe (Fig. 1a–c), originating on the level of the mouth cavity and leading backward. The right one is 130-μm long, while the left one has a length of 90 μm (diameter of both neck lobes 25 μm). They are innervated by the right/left pedal ganglion.

Marshall (1988: 954) described the head conditions of *D. lignicola*: 'Two small, smooth, narrowly tapered right suboptic tentacles. One smooth, bifid left suboptic tentacle, below which is a tight cluster of 2 or 3 tentacles'.

Foot and shell muscles

The epipodium bears three pairs of epipodial tentacles (Fig. 1a–c: et1–3). The tentacles are strongly retracted (length 90–140 μm, diameter 25–50 μm). All of these tentacles are distally covered with sensory papillae (Fig. 3d; also Rubio and Rolán 2013b). The most anterior pair of epipodial tentacles (Fig. 1: et1) is short, situated on the level of the pedal ganglia, and slightly anterior to the operculum. The second and third pair is located beyond the operculum. The epipodial sense organs (ESOs) are small, smooth knobs with the sensory epithelium lying distally (Fig. 3d). They are attached ventrally to the first pair of epipodial tentacles in both, *S. serpuloides* and *D. voightae*, whereas in *S. profunda* ESOs are attached to the second epipodial tentacle. In *D. lignicola*, the large epipodial tentacles have strongly ciliated edges, there are 3 on left side and 3 or 4 on the right side (Marshall 1988).

In all Skeneidae investigated, the large foot has a broad sole and a prominent propodium. In *S. serpuloides*, the right, frontal edge of the propodium forms a thick, smooth, cyclindrical-shaped penis, which 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 deep channel (seminal groove) is formed by a fold and leads from a latero-proximal to a dorsal position along the entire penis. The apical channel of the penis is ciliated, and the interior of the penis has large haemocoel spaces (Fig. 3b). Whereas the penis of *S. profunda* is identical, *D. voightae* and *D. lignicola* both have a quite small propodial penis at the right frontal edge of the foot with just an outer ciliated rim.

The pedal gland is mainly situated in the dorsal part of the propodium, but reaches far back into the foot. The cells of the gland are quite voluminous (Fig. 2b, c, g). The pedal gland opens via a ciliated channel at the dorso-anterior tip of the propodium.

There are two shell muscles made up of smooth muscle fibres, which spread into the foot and form the muscular wall of the head. The right shell muscle has its attachment zone at the line where the posterior oesophagus begins. The attachment area of the left shell muscle is situated beneath the osphradial ganglion.

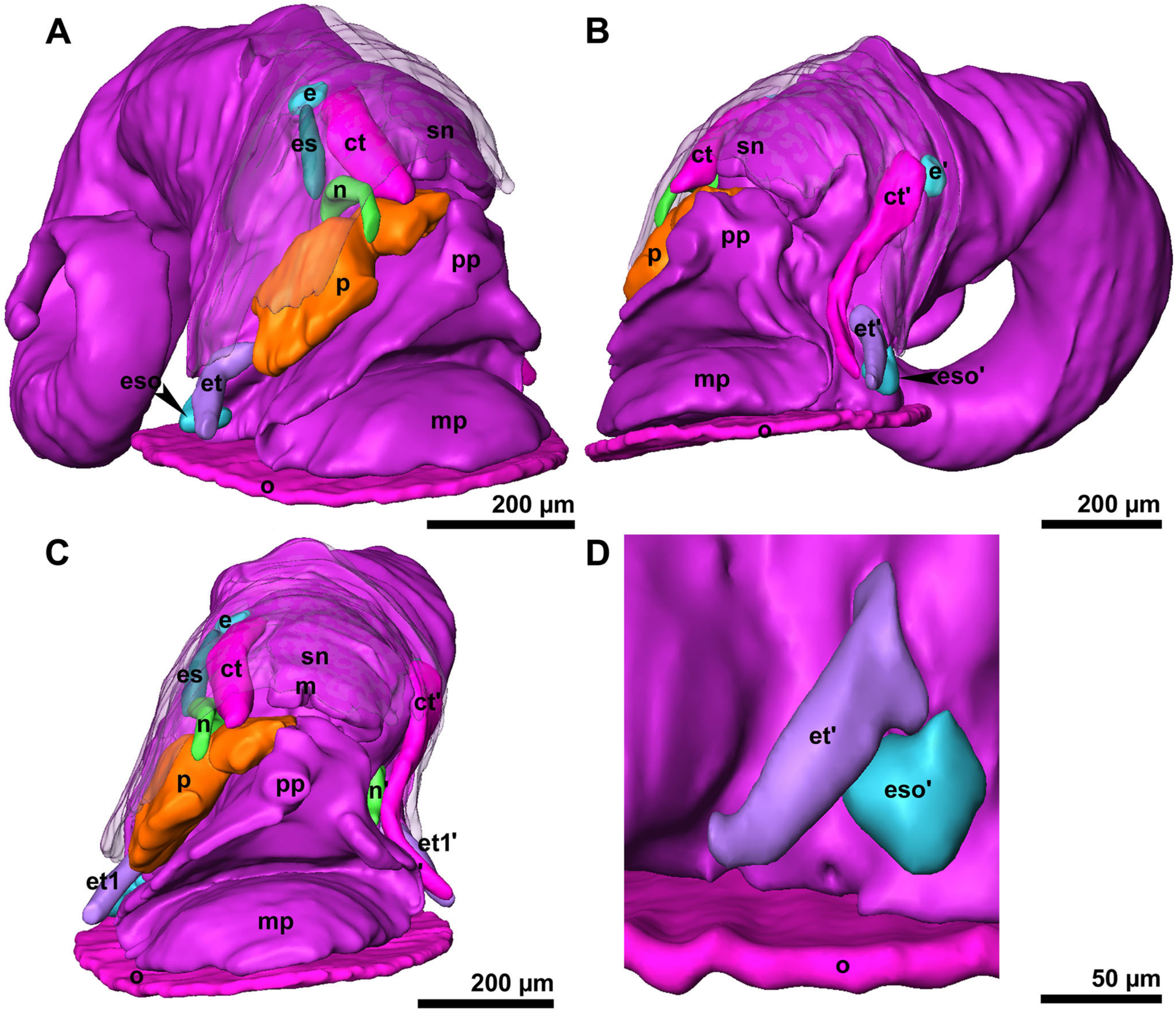


Fig. 1 3D reconstructions of the body and tentacles of *Skenea serpuloides*. **a** Latero-frontal view on the right side, mantle roof transparent. **b** Latero-frontal view on the left side, mantle roof transparent. **c** Frontal view, mantle roof transparent. **d** Right side view onto epipodial tentacle and epipodial sense organ, mantle roof removed. **a**, **b** SMNH-98645; **c**, **d** SMNH-98644. *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

Mantle cavity

The mantle rim itself is smooth in *S. serpuloides* and *S. profunda*, but papillate like the cephalic tentacles in *D. voightae* (no data on *D. lignicola*).

The mantle cavity of *S. serpuloides* extends around a quarter whorl of the body. The epithelium of the mantle roof is very thin and underlain by haemolymph sinuses. The central portion of the mantle roof is largely occupied by the rectum, which performs two semi-circular loops. The osphradium and ctenidium are located at the anterior left site (Fig. 2c). To the right the hypobranchial gland, the left kidney and the rectum are present. The centre of the posterior end of the mantle roof hosts the seminal receptacle (interactive Fig. 2). At the posterior left end of the mantle cavity, the seminal receptacle opens dorsally into the mantle cavity, 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 along the right neck towards the base of the penis. The opening of the penis channel is ciliated (Fig. 3b).

The single (left) monopectinate ctenidium has eight leaflets. The ctenidial axis, which is equipped with a skeletal rod, is attached along 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. The epithelium of the ctenidial leaflets is built up by cuboidal to high-prismatic and densely ciliated cells. A zone with flat epithelium is lacking; accordingly, there is no distinct respiration area at the ctenidium. Also, the ctenidial leaflets are supported by paired skeletal rods. A bursicle occupies the anterior, efferent part of each leaflet, showing a slit-like channel about 30-µm long. In the larger *D. lignicola*, the monopectinate ctenidium consists of 12 leaflets, each with a (small but distinct) respiratory area in the proximal part.

The single (left) hypobranchial gland occupies the central right side of the mantle cavity, between the gill and left kidney (interactive Fig. 2). Three different parts can be distinguished histologically: the cells of the anterior part stain darkly, showing granular secretion. Posteriorly, the largest section follows with large, voluminous cells. The third portion 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 and 3i–k), while the urogenital opening is placed more ventrally.

In several specimens of *S. serpuloides*, we found a parasite (Fig. 3e), which was located in the right portion of the mantle cavity. The cuticularized parasite was attached anterio-laterally of the hypobranchial gland to the epithelium of the mantle cavity. Its anatomy was highly simplified, but histology suggests it is a crustacean (probably copepod).

Circulatory and excretory system

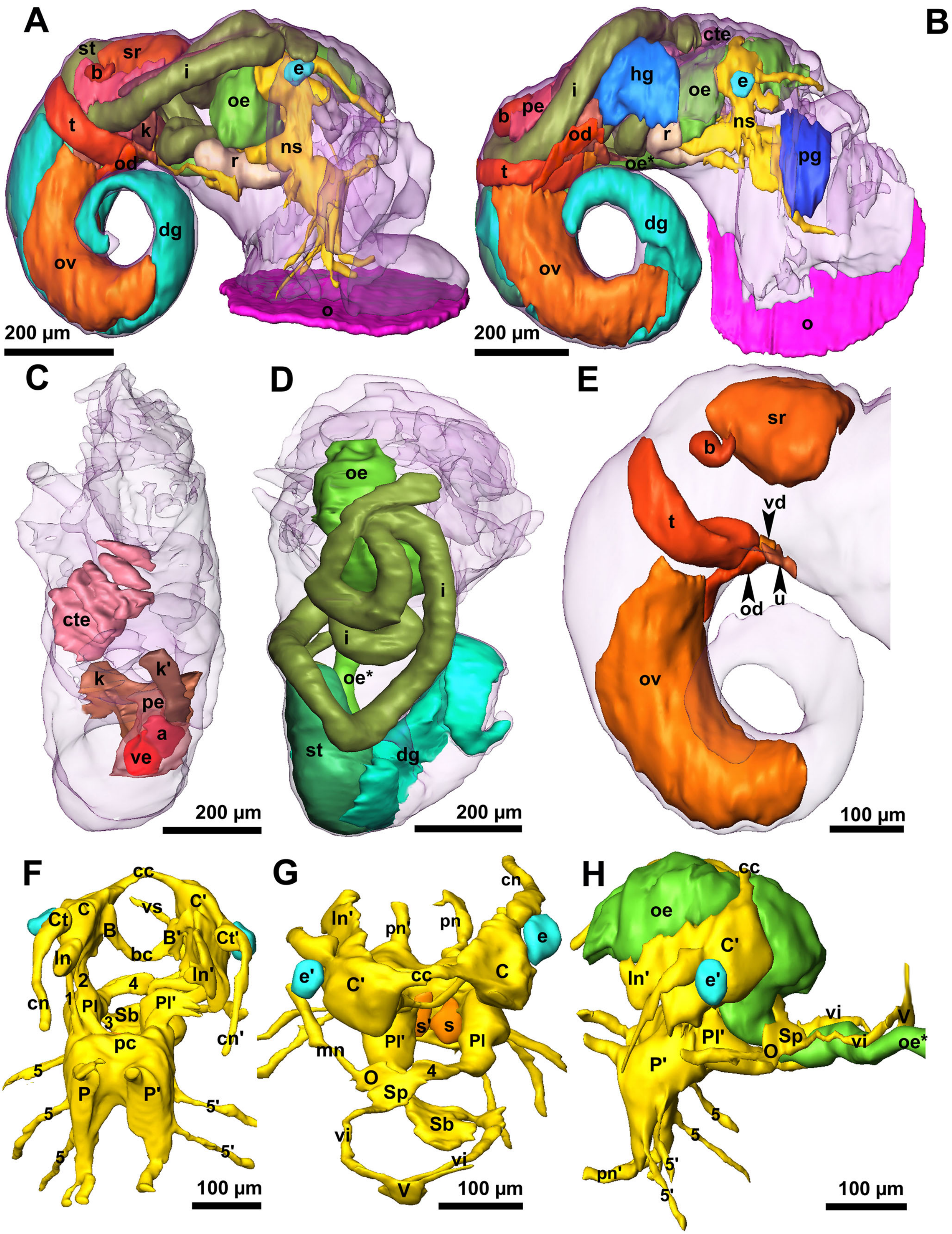
The monotocardian heart is located just behind the mantle cavity on the right side of the visceral body (Fig. 2c) and consists of a single (left) auricle and a (thicker) ventricle, both being surrounded by a pericardium (Fig. 3k). The irregular shape of the heart results from being wedged between the intestine, seminal receptacle and both kidneys. The wall of the pericardium is very thin. The auricle and ventricle are both oval (only preserved in specimen SMNH-98643). The auricle is located anterio-dorsally and it is connected ventrally with the ventricle. The heart is always close to the intestine: In *S. serpuloides* and *D. voightae*, the heart does not completely encircle the rectum, whereas this is the case in *S. profunda* (no data on *D. lignicola*).

Unfortunately, the preservation of the blood sinuses was not sufficient for complete reconstruction. Small blood sinuses from the gill leaflets merge into the efferent gill sinus, which proceeds on the left part of the mantle roof and leads backwards into the auricle. A second efferent sinus from the left kidney opens into the auricle at its ventral side. The anterior aorta emerges posterior-ventrally from the ventricle and runs in the same direction.

Fig. 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 onto the nervous system. **g** Dorsal view onto the nervous system. **h** Left side view onto the nervous system and oesophagus. **a**, **d**–**h** Specimen SMNH-98644; **b**, **c** specimen SMNH-98643. *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 sac, *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 *S. 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.)

All skeneids studied have two kidneys, both located at the right side of the animal (Fig. 2c). The left kidney lies ventro-laterally left of the rectum (Figs. 2a and 3j: k'). It borders 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, papillary tube with a diameter of about 50 µm (Fig. 3j: k'). Its anterio-dorsal part lies close to the pericardium and is connected to the pericardium via a ciliated 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 ramifies with irregular lobes between the viscera and has a large lumen (Fig. 3i, j: k). The epithelial cells are small and weakly stained. A renopericardial duct connects the right kidney with the ventral side of the pericardium. Anterior-ventrally, both the oviduct and the vas deferens open into the distal part of the right kidney.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From here, the very short urogenital duct opens into the mantle cavity.

Genital system

The hermaphroditic genital apparatus of all species investigated consists of separate ovary with oviduct and testis with vas deferens and is also equipped with a seminal receptacle, a bursa copulatrix and a propodial penis (Fig. 2e; see also external morphology: Fig. 1a–c). Ovary and testis are fully mature in the examined specimens with sperm and eggs in all stages of development.

The large ovary together with the digestive gland occupies the uppermost whorl of the shell. The various developmental stages of the eggs (Fig. 3l) are not sorted by size. Yolky, mature eggs have diameters of about 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 and 3l). The anterior part of the testis is filled with fibrous spermatids, whereas the posterior testis contains spermatogonia (diameter 4 μm) stuffed with small granules. Anteriorly, the testis merges into the vas deferens. This tube is very short and opens into the right kidney close to the opening of the oviduct.

The large and oval seminal receptacle is located posteriorly in the ventral portion of the mantle roof (Fig. 2e). The opening into the mantle cavity is at the anterio-ventral end of the seminal receptacle, containing sperm cells in its frontal 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. *S. profunda* and the two *Dillwynella* species lack a bursa copulatrix.

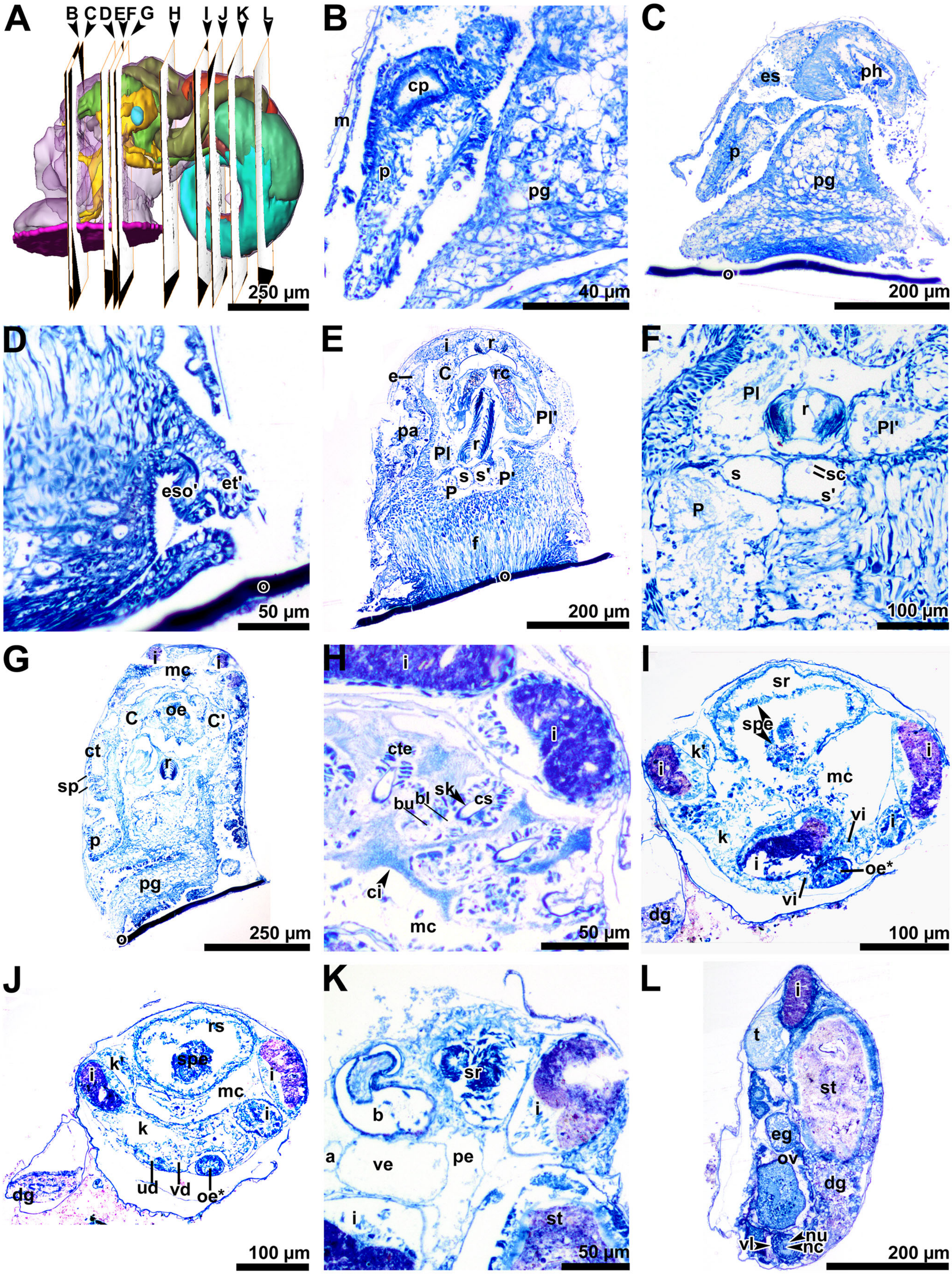
Alimentary tract

The blunt snout is retracted far inside the mantle cavity (Fig. 1a–c). The mouth opening lies fronto-dorsally and has a small fold 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 detected.

Fig. 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 propodeal 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). *a* auricle, *b* bursa copulatrix, *bl* bursicle lumen, *bu* bursicle, *C*/*C*' right/left cerebral ganglion, *ci* cilia, *cp* penis channel, *cs* ctenidial 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 and 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 ganglia, *r* radula and radular sac, *rc* radular cartilage, *s*/*s*' right/left statocyst, *sc* statoconia, *sk* ctenidial skeletal rods, *sp* sensory papillae, *spe* sperm, *sr* seminal receptacle, *st* stomach, *t* testis, *ud* urinogenital duct, *vd* vas deferens, *ve* ventricle, *vi* visceral loop, *vl* vitteline layer of egg

The delicate, paired jaws are fused dorsally and consist of small rod-like elements. The radula of *S. serpuloides* is located latero-dorsal of the jaws, is of the rhipidoglossate type (see the SEM photos provided by Ponder 1990; Rubio-Salazar 1991 and Warén 1991, 1992), and lacks a radular caecum. 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 is thickened at its posterior end. Contrary to the smooth shell muscles and head musculature, all buccal muscles are cross striated. The odontohore has two pairs of slender radular cartilages. The drop-shaped anterior pair of cartilages is located anterio-ventral of the radula, and the left and right cartilages contact each other closely proximally (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 posterior-dorsal of the other pair. It is quite small and the separation from the anterior pair is so inconspicuous, that they could not be individualized in the reconstructions. A subradular organ is lacking.

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

The oval stomach is slightly curved (Figs. 2d and 3l), and its epithelium is quite thin in the anterior part (10 μm). The cells have long cilia (8 μm) and are also entirely covered 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 stomach. 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 epithelial cells (Fig. 3j, l) suggest intense secretion.

The intestine emerges in the most anterior part of the stomach. The epithelium is ciliated and a longitudinal deep rim is present. 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. In *S. serpuloides* and *D. voightae*, the heart it encircling the rectum only partly (interactive Fig. 2b), while in *S. profunda* and many other vetigastropods, the rectum is encircled completely (no clear data in *D. lignicola*). 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 and sensory organs

The central nervous system consists of four paired ganglia (cerebral, buccal, pleural and pedal ganglia) and four unpaired ganglia (osphradial, sub- and supraoesophageal and visceral ganglion). Due to contraction and the poor preservation, 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 base of a cephalic tentacle flanking the transition zone of pharynx and oesophagus latero-distally. Both ganglia are interconnected by the cerebral commissure (Fig. 2f–h). Each cephalic tentacle nerve forms a small cephalic tentacle ganglion at its base in front of the eyes. The short and thin buccal-cerebral connectives emerge at the ventral side of the cerebral ganglia. The buccal ganglia are located proximally to the cerebral ganglia and ventral to the pharynx (Fig. 2f). The buccal ganglia are interconnected via the buccal commissure, which forms a ventral loop and marks the beginning of the anterior oesophagus.

The pedal ganglia (Figs. 2f and 3e) 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, posterior pedal commissures were not detected. The flat (squashed?) statocysts (see also sense organs) were attached posterior to the pedal ganglia (Figs. 2g and 3e). Neural cords with many nerve cells emerge from the pedal ganglia and innervate the foot and epipodial tentacles. A nerve emerges from the right pedal ganglion leading into the right parts of the body and mantle roof, whereas a left counterpart of this nerve could not be found. The cerebro-pedal connectives are located in front of the cerebro-pleural connectives. The long, conical pleural ganglia are located close to the pedal ganglia (hypoathroid condition; Fig. 2h). 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 connective emerges from the posterior right pleural ganglion, crosses the anterior oesophagus dorsally and leads to the supraoesophageal ganglion at the left side (interactive Fig. 2). This ganglion is located dorso-laterally above the posterior oesophagus. From there, the quite short 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 suboesophageal 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 (Fig. 2g) 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 reach 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.

Cephalic and epipodial tentacles have been described above. The eyes lie somewhat embedded in the body surface (Figs. 2f–h and 3e), lack a lens, but the vesicle is filled with a vitreous body. In the section series available, the eyes vesicles are always devoid of pigment, a known bleaching artefact of the alcohol storage (pers. comm. A. Warén). A closed and pigment-less eye vesicle is also present in *D. lignicola*. The depressed (squashed?) statocysts are located adjacent to the pedal ganglia (Figs. 2g and 3e). Each statocyst contains several to many (*D. lignicola*) statoconia (Fig. 3f). Bursicles of the ctenidial leaflets have been described above. The single and densely ciliated osphradium (diameter 30 μm) is located on the left side of the mantle roof and is directly underlain by the large osphradial-ganglion.

Anatomy of *L. minima* (Tenison-Woods, 1887)

The anatomy of this species resembles those of the true skeneids; thus, only a short description with a focus on differences is provided.

As in the skeneid species, the ESOs are attached to the ventral basis of the first papillate epipodial tentacle. There are two shell muscles. The mantle cavity is provided with a monopectinate ctenidium, and the leaflets of which lack respiratory zones, but are equipped with skeletal rods and bursicles. Right of the rectum, there is a large hypobranchial glands consisting of several types of large mucous cells. Two kidneys are present; the right one also releases the gametes via a urogenital opening.

However, the genital system shows significant differences to the skeneid species: there is a true hermaphroditic gland and the large and yolky eggs are provided with a thin vitelline layer. A copulatory organ is absent and a receptaculum is lacking.

The gut resembles that of skeneids. The jaws with rod-like elements are delicate, the long radular sheath shows a large loop and the two pair of radular cartilages are slender. The anterior oesophagus lacks significant oesophageal pouches, shows torsion and enters ventrally into the large stomach, which is equipped with toothed gastric shield and tooth and two separated digestive glands. The intestine again shows a longitudinal rim, and the rectum runs through the heart and makes a large loop along the mantle roof.

Conditions of the nervous system do not differ from those of the skeneid species. However, the eyes show closed vesicles and pigment. The osphradium is large, and the statocysts contain several tiny statoconia.

Discussion

General remarks

In the following discussion, only genera with a propodial penis (see Table 3 for data) are referred as Skeneidae. Descriptions of internal conditions are so far restricted to *S. serpuloides* and concern either an unpublished thesis (Brückner 2003) or preliminary data (Brückner et al. 2004; Kunze et al. 2008). In addition, Warén and Bouchet (1993: 22ff) provided sketchy anatomical information on *Protolira valvatoides*.

The considerable degree of homoplasy of many phenotypic characters in basal 'archaeo-' gastropods (reviewed in detail e.g. by Haszprunar 1988b; 1993; Ponder and Lindberg 1997; Sasaki 1998) limits the application of these data to infer relationships. Although the molecular data are far from being entirely non-homoplasious, they are usually more suitable concerning phylogenetics. Nevertheless, since we also want to infer also evolutionary trends and environmental adaptations, an evaluation of morphological characters concerning the systematic position of Skeneidae is desirable. Assis et al. (2011), Richter and Wirkner (2014), Lee and Palci (2015) and Giribet (2015) have provided general points of view on the subject.

Character analysis

The small teleoconch lacking nacre cannot be used to define Skeneidae. However, protoconchs of skeneid species studied by SEM are generally smooth or finely granular; most of them also show few longitudinal fine cordlets, which might be a useful character (Hoffman et al. 2008). Accordingly, we regard all species with a sculptured pattern of the protoconch as doubtful members of Skeneidae.

The papillate condition of the cephalic and epipodial tentacles and the mantle edge reflect the vetigastropod nature of Skeneidae (von Salvini-Plawen and Haszprunar 1987; Haszprunar 1988b; Ponder and Lindberg 1997). TEM-details of these papillae have been provided by Crisp (1981) and Künz and Haszprunar (2001).

The two ciliated necklobes (Fig. 1a) of *S. serpuloides* were also reported by Fretter and Graham (1977), Rubio-Salazar (1991), Warén and Bouchet (1993) and Rubio and Rolán (2013b). As the right eyestalk is much larger than the small and inconspicuous left one (Fig. 1a, b), it was interpreted originally as a penis by Fretter and Graham (1977), but SEM and our histological data identify it as an enlarged eyestalk.

In living animals, the epipodial tentacles are quite long (Clark 1851b; Rubio-Salazar 1991; Rubio and Rolán 2013b), but because the specimens under investigation were heavily retracted in the shell, these tentacles appear short and stumpy in the reconstructions (Fig. 1a, b). Fretter and Graham (1977) did not mention the presence of epipodial sense organs (ESOs) in *S. serpuloides*, whereas Rubio-Salazar (1991: Fig. 1) described three ESOs: one ventral to the first right epipodial tentacle and two ESOs associated with the first 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 and 3d). Our data corroborate the SEM data by Rubio and Rolán (2013b), who described nominally 'four epipodial tentacles', the first, third and fourth pair is papillate (true epipodial tentacles), but the second one much shorter and non-papillate (ESO). The available data on further skeneids (Table 3 and own observations) show considerable variation in number of epipodial tentacles and ESOs. ESOs of all skeneid species examined are located at the ventral base of an epipodial tentacle, a condition generally found in Haliotidae, Trochoidea and Phasianelloidea (Crisp 1981; TK pers. obs.). In contrast, species of Seguenzioidea (in the concept of Kano 2008 and Kano et al. 2009 including several skeneimorph taxa) have separated ESO tentacles (Kunze et al. 2016).

The retention of both shell muscles is a plesiomorphic character of Gastropoda (Haszprunar 1985b, 1988b). Whereas this condition in found in many Vetigastropoda, it is rare among Trochoidea, where usually only the left adult shell muscle is retained (e.g. Bandel 1982).

The single left ctenidium is monopectinate in all Skeneidae, which might be a matter of small size or paedomorphosis, since this condition is also known in early juveniles of taxa with bipectinate conditions as adults. As typical for most Vetigastropoda and several Neomphalida each ctenidial leaflet is equipped with a bursicle and skeletal rods (Szal 1971; Haszprunar 1987, 1988b; Heß et al. 2008; Kunze et al. 2008).

Retention of two asymmetric kidneys with different structure and functions is diagnostic for the Vetigastropoda and Patellogastropoda (Andrews 1985; von Salvini-Plawen and Haszprunar 1987; Haszprunar 1988b, 1993; Ponder and Lindberg 1997; Sasaki 1998). The structure of the left kidney as a papillary tube is typical for Vetigastropoda as is the release of the gametes via visceral gonoducts proper and a urogenital opening with the right kidney.

Simultaneous hermaphroditism with separated ovary/oviduct and testis/vas deferens has been observed in all Skeneidae studied so far. Similar conditions occur in lepetelloidean Vetigastropoda (Haszprunar 1988a, 1998) and also in the heterobranch Architectonicidae (Haszprunar 1985a) and Omalogyridae (Bäumler et al. 2008), although the latter have a common distal and glandular gonoduct.

The most striking feature of the species investigated is the propodial penis (Figs. 1a and 3c, g), which was until now the only diagnostic morphological synapomorphy for the Skeneidae (Warén 1991, 1992; Warén and Bouchet 1993). There is little doubt that copulatory organs have repeatedly evolved among gastropods in general and also among Vetigastropoda, in particular, in species which are small or inhabit deep-sea or chemosynthetic habitats, but a propodial penis remains unique. However, it should be noted that such a propodial penis may be quite small and inconspicuous as in the *Dillwynella* species studied. Indeed, the penis was not mentioned in the descriptions of the head-foot of *Dillwynella* species by Marshall (1988), Hasegawa (1997) or Kunze (2011) and can only be detected in serial sections.

The yolky eggs of all species under investigation have a vitelline layer, a diagnostic character for Vetigastropoda (Ponder and Lindberg 1997). In addition, all three skeneid species investigated have a separated seminal receptacle in the left and central mantle roof; a bursa copulatrix is present only in *S. serpuloides* (Fig. 3k). Similar conditions occur in a number of other vetigastropod taxa, namely within the Lepetelloidea (Haszprunar 1988a; 1998) and the Seguenzioidea (Kano 2008; Kano et al. 2009; Kunze et al. 2016).

Paired jaws with rod-like elements are typical for Neomphalida and Vetigastropoda, but occur also in hyalogyrinid and many other Heterobranchia (Haszprunar et al. 2011). Many skeneimorph species show a quite similar radular type. However, Warén (1990) showed that juvenile turbinids or trochids have a very similar rhipidoglossate radula, even if the radula type substantially differs in adults. This similarity of the radulae might be due to similar food being targeted in juveniles, namely grazing on biofilms on various substrates (Warén 1990), and thus might be a matter of convergence. Alternatively, it might be a homologous structure, if so probably a vetigastropod plesiomorphy or the radular type of the vetigastropod (plus neomphalidan) stem species, respectively. Finally (and most likely), the radular structures of these small species are due to paedomorphosis and thus again a matter of parallelism. In any case, the skeneid radula type cannot be used to infer systematic relationships.

Two pairs of radula cartilages and a papillate oesophagus were found in many vetigastropod clades (e.g. Sasaki 1998; Katsuno and Sasaki 2008), whereas the conditions of the stomach with its gastric shield and two digestive glands reflect basic gastropod conditions. Often, it is difficult to determine whether the rectum is encircled by the heart completely, because this region is often damaged by hardened haemolymph during fixation and the pericardial wall is very thin and fragile. A complexly coiled rectum has been also reported in *Turbo stenogyrum* (Sasaki 1998), in certain Seguenzioidea (e.g. *Carenzia carinata*; GH pers. obs.) and in ectobranch (valvatoidean) Heterobranchia (Haszprunar et al. 2011).

Conditions of the skeneid hypoathroid and streptoneuran central nervous system reflect plesiomorphic gastropod conditions.

S. serpuloides has pigmented eyes, which are black in living animals (Jeffreys 1865; Fretter and Graham 1977; Rubio-Salazar 1991). The eyes are closed vesicles with a vitreous body (sensu Sasaki 1998) like those found in the Scissurellidae (Bourne 1910; Strasoldo 1991), Fissurellidae (Boutan 1885; Illingworth 1902) or Phasianellidae (Marcus and Marcus 1960).

Marshall (1988: 953) constituted ‘eyeless optic tentacles’ in the diagnosis of the genus *Dillwynella*. However, Hasegawa (1997: 89) reported black eyes in *Dillwynella vitrea* and *Dillwynella planorbis*, pigment-less eyes in *Dillwynella fallax* and total lack of eye and optic tentacle in *Dillwynella seishinmaruae*. Kunze (2011) did not mention an eye in *D. voightae*; thus, it is likely that they are devoid of pigment also in the living animal. The same is certainly true for the deep-water *D. lignicola* and very likely for *S. profunda*. Accordingly, eye conditions are quite variable in *Dillwynella* and generally in Skeneidae.

Conditions of the statocysts with several statoconia reflect again vetigastropod relationships.

Ecology of Skeneidae

Skeneid species are found in various marine habitats from intertidal gravels or shallow coastal waters down to the bathyal plane, but for many locations detailed data about the habitat or bottom structure are not available (e.g. Høisæter 1968; Bouchet and Warén 1979). *S. serpuloides* is known from infra- and circalitoral amphioxus sand and maërl in depths between 15 to 145 m (Fretter and Graham 1977; Rubio-Salazar 1991; Rubio and Rolán 2013b; herein), whereas *S. profunda* lives on sunken wood in deep waters beyond 2000 m. Other *Skenea* species live in depths between 50 and 3500 m on algae, rock, sunken wood, sand and silty bottoms (Rubio-Salazar 1991; Warén 1991, 1993; pers. comm. C. Schander; pers. obs. TK). *Dikoleps* and *Skeneoides* species live in intertidal gravel, in shallow water from 0 to up to 160 m on different bottoms like sand, maërl and also on stones, algae and corals (Rubio-Salazar 1991; Warén 1992). Both known species of *Protolira*, *Protolira thorvaldssoni* Warén, 1996 and *Protolira valvatoides* live in depths between 850 and 3700 m in hydrothermal vent habitats, among mussels in sediments and also on whale bone (Warén and Bouchet 1993, 2001). All species of the genus *Dillwynella* inhabit deep-water sunken wood and algal holdfasts (Marshall 1988; Hasegawa 1997; Kunze 2011). Thus, skeneids occur in most benthic habitats.

According to WMSDB, most *Skenea*, *Dikoleps* and *Skeneoides* species have been described and recorded from the European Atlantic coast, from Spain to Svalbard and around Iceland, while many *Dillwynella* species were exclusively found in the Pacific Ocean. However, there is little doubt that many species still remain to be discovered, rendering biogeographic data highly preliminary.

Constraints of small size

Skeneidae are small. Based on various similarities with the related (see below for systematics) trochid or turbinid juveniles, we assume that the small size probably is a secondary condition probably been reached by progenesis, i.e. acceleration of sexual maturation into a juvenile stage (e.g. Raff 1996). Accordingly, skeneid gastropods (and other skeneimorph species as well) show several special conditions and circumstances:

A nacreous layer of the teleoconch is typical for trochoid and seguenzioid Vetigastropoda, but is often missing in small species (Hickman 1983).

Most of the larger (>5 mm) trochoidean species have an ESO at the ventral bases of each epipodial tentacle (e.g. Crisp 1981). In contrast, skeneids often have only a single ESO attached to the first or second epipodial tentacle pair; occasionally, there is a scattered distribution of ESOs at the epipodial tentacles.

All vetigastropods have yolky eggs and show lecithotrophic development. Thus, to provide enough yolk for the developing embryo and larva, the size of mature eggs cannot be reduced. With a decreasing body size, the number of ripe eggs decrease dramatically (assuming the same overall shape 50 % body length equals only 12.5 % of volume, 20 % body length 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) seguenzioid species *Putilla porcellana* (Tate & May, 1900) and the even smaller *L. minima* (<2 mm) neither have any copulatory organ nor receptacula (pers. obs. TK). The same is true for certain small Scissurellidae such as *Incisura lytteltonensis* (Smith, 1894) (about 1 mm; cf. Bourne 1910) or *Scissurella jucunda* (about 2 mm; cf. Strasoldo 1991; Baborka 2007). In these cases, fertilization success of the few eggs might be enhanced by special reproductive behaviour or spermatophores.

A monopectinate gill is also found in other minute vetigastropod species (Kano 2008; Geiger et al. 2008), and this condition might reflect paedomorphosis, since a monopectinate condition occur during early ontogeny of bipectinate species (e.g. Crofts 1937; Strasoldo 1991). However, there are small species with bipectinate ctenidia like *Leucorhynchia caledonica* (2 mm) and several scissurellids, and relatively large species like *D. voightae* (5.8 mm) with a monopectinate ctenidium; so this is not a strict rule. In addition, the ctenidia of many small gastropods do not show distinct respiratory areas but probably use their lateral cilia as ventilators of the mantle cavity: In these cases, respiration is mainly provided by the thin mantle roof and (in limpets) the subpallial epithelia.

The nervous system of skeneids appears more concentrated and more voluminous than those of larger vetigastropods. Again, this reflect both size constraints (the number of neurons cannot be reduced below a certain point and the size of neurons remains constant) and paedomorphic conditions.

Systematics

The vetigastropod nature of Skeneidae is beyond doubt and well supported by all molecular studies and morphological data including: papillate conditions of tentacles and mantle rim, ctenidium with skeletal rods and bursicles, two different kidneys, the left one a papillary tube, the right one ramifying between the viscera and forming an urogenital opening, eggs with a vitelline layer, paired and rod-like jaws, a rhipidoglossate radula and papillate anterior oesophagus, a hypoathroid and streptoneuran nervous system and statocysts with several statoconia.

xThe recent molecular studies support inclusion of the Skeneidae among Trochoidea close to the Turbinidae.

Morphologically, this is supported by the epipodial conditions with attached ESOs, which separate Trochoidea (and Phasianellidae and Haliotidae) from Seguenzioidea (sensu Kano 2008; Kano et al. 2009) with separated ESOs (Kunze et al. 2016), the latter conditions also occurs in Scissurellidae, Clypeosectidae and Lepetodrilidae (TK pers. obs.).

It is more difficult to define monophyletic Skeneidae by phenotypic characteristics. At our current stage of knowledge, the genital apparatus appears to be the most promising character set. All skeneid species investigated are true hermaphrodites with separated ovary/oviduct and testis/vas deferens and show a unique propodial penis. The current concept based on the presence of a propodial penis includes the genera (alphabetic order):

Dikoleps Høisæter, 1968 with type species *Margarita pusilla* Jeffreys, 1847
Dillwynella Dall, 1889 with type species *Teinostoma* (*Dillwynella*) *modesta* Dall, 1889
Lissospira Bush, 1897 with type species *Cyclostrema proxima* Tryon, 1888
Protolira Warén and Bouchet, 1993 with type species *P. valvatoides* Warén & Bouchet, 1993
Pseudorbis Monterosato, 1884 with type species *Fossarus granulum* Brugnone, 1873
Skenea Fleming, 1824 (type genus) with type species *H. serpuloides* Montagu, 1808
Skeneoides Warén, 1992 with type species *Delphinula exilissima* Philippi, 1844

However, most of these genera need to be studied also anatomically to confirm inclusion. Based on consistent molecular data (Kano 2008; Williams 2012), we tentatively add here *Cirsonella* Angas, 1877 (syn. *Tharsiella* Bush, 1897) with type species *Cirsonella australis* Angas, 1877 (currently considered as a synonym of *Cyclostrema weldii* Tenison-Woods, 1877; see Rosenberg 2015), although this should be confirmed by checking the type species for a propodial penis.

Soft part characters of *Iheyaspira lequios* (Okutani et al. 2000); the type species of its genus, in particular, a tentacle-like right neck lobe; the separated ESO-tentacle and the lack of a propodial penis (Okutani et al. 2000; Nye et al. 2013) suggest seguenzioid affinities of *Iheyaspira* rather than the stated classifications among Trochidae or Skeneidae. The molecular analysis of Nye et al. (2013) inferred *Iheyaspira bathycodon* in a clade together with Skeneidae, but is not sufficient to prove inclusion, because in particular seguenzioid taxa have not been considered in that study. Most recently, however, Chen et al. (2015) showed that *I. lequios* Okutani et al. 2000 is composed of four lineages belonging to both, Vetigastropoda—Skeneidae and Neomphalina.

The record of a propodial penis in *Lodderena catenoides* by Warén (1992) and thus for *Lodderena* in general is misleading, because *L. catenoides* is now accepted as *Skenea catenoides* (Monterosato, 1877) (WoRMS). The current data on the type species of *Lodderena*, *L. minima* (Tenison-Woods, 1878), revealed significant differences in the genital system, namely a true hermaphroditic gland, lack of propodial penis and lack of a receptaculum. In addition, molecular data (H3 + COI) group *Lodderena* with Trochidae/Turbinidae rather than with Skeneidae (Kano 2008; Williams 2012). Therefore, *Lodderena* Iredale, 1924 should be excluded from the Skeneidae.

The type species of *Leucorhynchia* Crosse, 1867, *L. caledonica* Crosse, 1867, also shows papillate conditions, but a bipectinate ctenidium, a true hermaphroditic gland with a common gonoduct and a propodial penis on the left side (pers. obs. TK). Accordingly, we also exclude *Leucorhynchia* Crosse, 1867 from Skeneidae.

For the numerous other genera, which have been assigned to Skeneidae or Skeneinae, molecular or soft part studies (ideally both) are required for in- or exclusion, hard part characters alone clearly are not sufficient, although a protoconch with few spiral cordlets (e.g. *Haplocochlias* Carpenter, 1864; cf. e.g. Rubio & Rolan 2015) raises the probability of inclusion. Representatives of only two genuine skeneid genera with confirmed propodial penis, *Dillwynella* (Warén 1992: 152) and *Protolira*, and the tentatively assigned *Cirsonella*, were included in molecular analyses (Table 2).

We cannot exclude the possibility that Skeneidae in the present diagnosis is only a subclade within a broader clade of trochoid vetigastropods which may also include taxa without a propodial penis (or with a left one as in *L. caledonica* Crossé, 1867; Anders Warén pers. comm.). On the other hand, we prefer a clear diagnosis of Skeneidae instead of continuous usage of a family name as a lumping pot for small vetigastropods, which are better assigned as ‘Vetigastropoda *incertae sedis*’. Such a diagnosis now is available, and there is little doubt that many skeneid-like species need to be excluded from Skeneidae characterized in this way. This is also a plea to study microgastropods more intensively than up to now. Aside from shell, protoconch and radula, the soft body (by SEM and/or 3D-morphology) also needs consideration, and ideally molecular data also (see e.g. Chen et al. 2015 as a tale of caution) should be added in order to proceed in our understanding of ‘what [else] is Skeneidae?’ To conclude, ‘Before we came here we were confused about this subject. Having done our work we are still confused—but on a higher level’ [modified from Enrico Fermi, nuclear physicist] (Mackey 1991: 90).

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References

Aartsen, J. J., & van Bogi, C. (1988). *Anekes gittenbergeri* and *Anekes nofronii*, two new gastropods from the Mediterranean. *Bolletino Malacologico, 24*, 27–32.

Aktipis, S. W., & Giribet, G. (2012). Testing relationships among the vetigastropod taxa: a molecular approach. *Journal of Molluscan Studies, 78*, 12–27.

Andrews, E. B. (1985). Structure and function in the excretory system of archaeogastropods and their significance in the evolution of gastropods. *Philosophical Transactions of the Royal Society of London B, 310*, 383–406.

Assis, L. C. S., De Carvalho, M. R., & Wheeler, Q. D. (2011). Homoplasy: from detecting pattern to determining process in evolution, but with a secondary role for morphology? *Zootaxa, 2984*, 67–68.

Baborka, C. (2007). Computergestützte 3D-Rekonstruktion und vergleichende Anatomie scissurellider Mikrogastropoden an *Scissurella jucunda* Smith, 1910 und *Larochea miranda* Finlay, 1927. Unpublished Diploma Thesis. Ludwig-Maximilians-University Munich, Biological Faculty, 72 pp.

Bandel, K. (1982). Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies (Erlangen), 7*, 1–198. **pls. 1–22**.

Bäumler, N., Haszprunar, G., & Ruthensteiner, B. (2008). 3D interactive microanatomy of *Omalogyra atomus* (Philippi,1841) (Gastropoda, Heterobranchia,Omalogyridae). In Geiger, D., & Ruthensteiner, B. (Eds.), *Micromolluscs: Methodological Challenges - Exiting Results. Zoosymposia, 1*, 108–116.

Bouchet, P., & Warén, A. (1979). The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. *Sarsia, 64*, 211–243.

Bouchet, P., Rocroi, J.-P., Frýda, J., Hausdorf, B., Ponder, W. F., Valdés, Á., & Warén, A. (2005). Classification and nomenclator of gastropod families. *Malacologia, 47*, 1–397.

Bourne, G. C. (1910). On the anatomy and systematic position of *Incisura* (*Scissurella*) *lytteltonensis*. *Quarterly Journal of Microscopical Science, 55*, 1–47. **pls. 1–5**.

Boutan, L. (1885). Recherches sur l'anatomie de le développement de la Fissurelle. *Archive de Zoologie Expérimentale et Génerale, Serie 2, 3 Supplement, 4*, 1–173. **pls. 31–44**.

Brückner, M. (2003). Vergleichende Morphologie und Anatomie zweier Microgastropoda: *Skenea serpuloides* (Montagu, 1808) und *Cyclostremiscus ornatus* Olsson & McGinty, 1958 (Mollusca: Vetigastropoda: "Skeneidae"). Unpublished Diploma Thesis. Ludwig-Maximilians-University Munich, Biological Faculty, 78 pp.

Brückner, M., Ruthensteiner, B., & Haszprunar, G. (2004). What is Skeneidae? *Organisms, Diversity and Evolution, Supplement, 4*, 73 **[poster]**.

Carrozza, F., & van Aartsen, J. J. (2001). *Skenea divae* sp. nov., a new skeneimorph gastropod from the Mediterranean. *Conchiglia, 33*, 37–38.

Chen, C., Watanabe, H., Ward, A., Taylor, M.L., Rogers, A.D., & Takai, K. (2015). Cryptic diversity of skeneiform gastropods in the hydrothermal vent fields of Okinawa Trough, Japan. *Book of Abstracts of the Systematic Association Biennial Meeting, Oxford 2015,* 104. Available online at: http://systass.org/biennial2015/.

Clark, W. (1851a). On the classification of the British marine testaceous Mollusca. *Annals and Magazine of Natural History, serie 2, 7*(47), 469–481.

Clark, W. (1851b). On the Skeneadae [sic!]. *Annals and Magazine of Natural History, serie 2, 8*(42), 44–48.

Crisp, M. (1981). Epithelial sensory structures of trochids. *Journal of the Marine Biological Association of the U.K., 61*, 95–106.

Crofts, D. R. (1937). The development of *Haliotis tuberculata*, with special reference to the organogenesis during torsion. *Philosophical Transactions of the Royal Society of Londong, B, 228*, 219–268. **pls. 21–27**.

de Barros, J. C. N., dos Santos, F. N., do Carmo Ferrão Santos, M., Cabral, E., & Acioli, F. D. (2002). Sobre duas espécies novas de *Haplocochlias* Carpenter, 1864 (Prosobranchia, Archaeogastropoda) da costa do Brasil. *Boletim Técnico-Científico do CEPENE, 10*, 39–53.

de Lima, S. F. B., Barros, J. C. N., Francisco, J. A., & Oliveira, P. S. (2011). New records of Caribbean Gastropods (Skeneidae, Tornidae, Orbitestellidae and Omalogyridae) for Saint Peter and Saint Paul Archipelago (Brazil). *Tropical Zoology, 24*, 87–106.

Engl, W. (1996). A new skeneomorph species from Lanzarote. *La Conchiglia, 28*, 21–23.

Engl, W. (2001). *Parviturbo rolani* n. sp. (Gastropoda: Skeneidae) from the Canary Islands. *Novapex, 2*, 141–143.

Fleming, J. (1825). On the British testaceous annelids. *The Edinburgh Philosophical Journal, 12*, 238–248.

Fretter, V., & Graham, A. (1977). The prosobranch molluscs of Britain and Denmark. 2. Trochacea. *Journal of Molluscan Studies, Supplement, 3*, 39–100.

Friele, H. (1879). Catalog der auf der norvegischen Nordmeer-Expedition bei Spitzbergen gefunden Mollusken. *Jahrbücher der Deutschen Malacozoologischen Gesellschaft, 6*, 264–286.

Geiger, D. L., Nützel, A., & Sasaki, T. (2008). Vetigastropoda. In W. F. Ponder & D. R. Lindberg (Eds.), *Phylogeny and evolution of the Mollusca* (pp. 295–328). Berkley: University of California Press.

Giribet, G. (2015). Morphology should not be forgotten in the era of genomics—a phylogenetic perspective. *Zoologischer Anzeiger, 256*, 96–103.

Hasegawa, K. (1997). Sunken wood-associated gastropods collected from Suruga Bay, Pacific side of the Central Honshu, Japan, with descriptions of 12 new species. *National Science Museum Monographs, 12*, 59–123.

Haszprunar, G. (1985a). Zur Anatomie und systematischen Stellung der Architectonicidae (Mollusca, Allogastropoda). *Zoologica Scripta, 14*, 25–43.

Haszprunar, G. (1985b). On the innervation of gastropod shell muscles. *Journal of Molluscan Studies, 51*, 309–314.

Haszprunar, G. (1987). The fine structure of the ctenidial sense organs (bursicles) of Vetigastropoda (Zeugobranchia, Trochoidea) and their functional and phylogenetic significance. *Journal of Molluscan Studies, 53*, 46–51.

Haszprunar, G. (1988a). Comparative anatomy of cocculiniform gastropods and its bearing on archaeogastropod systematics. In: W.F. Ponder (Ed.): *Prosobranch Phylogeny. Malacological Reviews, Supplement 4,* 64–84.

Haszprunar, G. (1988b). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies, 54*, 367–441.

Haszprunar, G. (1993). The Archaeogastropoda: a clade, a grade or what else? *American Malacological Bulletin, 10*, 165–177.

Haszprunar, G. (1998). Superorder Cocculiniformia. In P. L. Beesley, G. J. B. Ross, & A. Wells (Eds.), *Mollusca: the Southern Synthesis. Fauna of Australia, 5B* (pp. 653–664). Melbourne: CSIRO Publishing.

Haszprunar, G., Speimann, E., Hawe, A., & Heß, M. (2011). Interactive 3D anatomy and affinities of the Hyalogyrinidae, basal

Heterobranchia (Gastropoda) with a rhipidoglossate radula. *Organisms, Diversity & Evolution, 11*, 201–236.

Heß, M., Beck, F., Gensler, H., Kano, Y., Kiel, S., & Haszprunar, G. (2008). Microanatomy, shell structure and molecular phylogeny of *Leptogyra*, *Xyleptogyra* and *Leptogyropsis* (Gastropoda: Neomphalina: Melanodrymiidae) from sunken wood. *Journal of Molluscan Studies, 74*, 383–401.

Hickman, C. S. (1983). Radular patterns, systematics, diversity, and ecology of deep-sea limpets. *The Veliger, 26*, 73–92.

Hickman, C. S. (1998). Superfamily Fissurelloidea; Superfamily Trochoidea; Superfamily Seguenzioidea. In P. L. Beesley, G. J. B. Ross, & A. Wells (Eds.), *Mollusca: the Southern Synthesis. Fauna of Australia, 5B* (pp. 669–693). Melbourne: CSIRO Publishing.

Hickman, C. S. (2013). Crosseolidae, a new family of skeneiform microgastropods and progress toward definition of monophyletic Skeneidae. *American Malacological Bulletin, 31*, 1–16.

Hickman, C. S., & McLean, J. H. (1990). Systematic revision and suprageneric classification of trochacean gastropods. *Los Angeles County Museum Science Series, 35*, 1–169.

Hoffman, L., van Heugten, B., & Lavaleye, M. S. S. (2008). A new genus with four new species in the family Skeneidae (Gastropoda) from the Rockall Bank, northeastern Atlantic Ocean. *Miscellanea Malacologica, 3*, 39–48.

Hoffman, L., van Heugten, B., & Lavaleye, M. S. S. (2010). Skeneimorph species (Gastropoda) from the Rockall and Hatton Banks, northeastern Atlantic Ocean. *Miscellanea Malacologica, 4*, 47–61.

Høisæter, T. (1968). Taxonomic notes on the Nkeorth-European species of «*Cyclostrema*» sensu Jeffreys 1883 (Prosobranchia, Diotocardia). *Sarsia, 33*, 43–58.

Holovachov, O., Bostrøm, S., Reid, N., Warén, A., & Schander, C. (2011). *Endeolophos skeneae* sp. nov. (Chromadoridae)—a free-living marine nematode epibiotically associated with deep-sea gastropod *Skenea profunda* (Skeneidae). *Journal of the Marine Biological Association of the U.K., 92*, 387–394.

Illingworth, J. F. (1902). The anatomy of *Lucapina crenulata* Gray. *Zoologische Jahrbücher*, *Abt. Anatomie, 16*, 449–490. **pls. 31–33**.

Jeffreys, J. G. (1865). *British conchology or an account of the Mollusca which now inhabit the British Isles and the surrounding seas. Volume III. Marine shells, comprising the remaining Conchifera, the Solenogastres, and Gastropoda as far as Littorina. 1–393, pls. 1–8.*. London: John van Voorst.

Kano, Y. (2008). Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. *Zoologica Scripta, 37*, 1–21.

Kano, Y., Chikyu, E., & Warén, A. (2009). Morphological, ecological and molecular characterisation of the enigmatic planispiral snail *Adeuomphalus* (Vetigastropoda: Seguenzioidea). *Journal of Molluscan Studies, 75*, 397–418.

Katsuno, S., & Sasaki, T. (2008). Comparative histology of radula-supporting structures in Gastropoda. *Malacologia, 50*, 13–45.

Keen, K., & McLean, J. H. (1971). *Sea shells of Tropical West America. Marine mollusks from Baja California to Peru* (2nd ed.). Stanford: Stanford University Press. **1004 pp**.

Künz, E., & Haszprunar, G. (2001). Comparative ultrastructure of gastropod cephalic tentacles: Patellogastropoda, Neritaemorphi and Vetigastropoda. *Zoologischer Anzeiger, 240*, 137–165.

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.

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

Kunze, T., Heß, M., & Haszprunar, G. (2016). 3D-interactive microanatomy of *Ventsia tricarinata* Warén & Bouchet, 1993 (Vetigastropoda: Seguenzioidea) from Pacific hydrothermal vents. *Journal of Molluscan Studies* (in press).

La Perna, R. (1998). A new Mediterranean *Skeneoides* (Gastropoda : Skeneidae) from a shallow-water cave. *Journal of Conchology, 36*, 21–27.

Lee, M. S. Y., & Palci, A. (2015). Morphological phylogenetics in the genomic age. *Current Biology, 25*(19), R922–R929.

Mackey, A. L. (1991). *A dictionary of scientific quotations*. Bristol and Philadelphia: Institute of Physics Publishing. **297 pp**.

Marcus, E. V. B. R., & Marcus, E. (1960). On *Tricolia affinis cruenta. Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo. Zoologia 23, 260*, 171–198. **6 pls**.

Marshall, B. (1988). Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History, 22*, 949–1004.

Montagu, G. (1808). *Supplement to Testacea Britannica. Pp. i-v, 1–183, pls. 17–30*. London: White.

Moolenbeek, R. G. (1996). New skeneiform species of the genus *Lodderena* Iredale, 1924 from the Sultanate of Oman (Gastropoda: Skeneidae). *Vita Marina, 44*, 21–28.

Mulisch, M. & Welsch, U. (2015). *Romeis Mikroskopische Technik*. 19th edition. ISBN 978-3-642-55189-5. Xii + 545 pp. Springer Spektrum.

Nye, V., Copley, J., Linse, K., & Plouviez, S. (2013). *Iheyaspira bathycodon* new species (Vetigastropoda: Trochoidea: Turbinidae: Skeneinae) from the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean. *Journal of the Marine Biological Association of the U.K., 93*, 1017–1024.

Okutani, T., Fujikura, K., & Kojima, S. (2000). New taxa and review of vesicomyid bivalves collected from the Northwest Pacific by deep sea research systems of Japan Marine Science & Technology Center. *Venus (Japanese Journal of Malacology), 59*, 83–1001.

Ponder, W. F. (1990). A gravel beach shelled micro-gastropod assemblage from Ceuta, Strait of Gibraltar, with the description of a new truncatelloidean genus. Bulletin du Muséum National d'Histoire Naturelle, 4ème série, section A. *Zoologie, Biologie et Écologie Animals, 12*, 291–311.

Ponder, W. F., & Lindberg, D. R. (1997). Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society of London, 119*, 83–265.

Raff, R. A. (1996). *The shape of life* (Genes, development, and the evolution of animal form). Chicago: University of Chicago Press. **xix + 520 pp**.

Redfern, C., & Rolán, E. (2005). A new species of *Lodderena* (Gastropoda: Skeneidae) from the Bahamas. *Iberus, 23*, 1–6.

Richardson, K. C., Jarett, L., & Finke, E. H. (1960). Embedding in epoxy resins for ultrathin sectioning in electron microscopy. *Stain Technology, 35*, 313–323.

Richter, S., & Wirkner, C. S. (2014). A research program for evolutionary morphology. *Journal of Systematic Zoology and Evolutionary Research, 52*, 338–350.

Rodriguez-Babio, C. E., & Thiriot-Quievreux, C. (1975). Trochidae, Skeneidae et Skeneopsidae (Mollusca, Prosobranchia) de la région de Roscoff. Observation *au microscope electronique à balayage. Cahiers de Biologie Marine, 16*, 521–530.

Rolán, E., & Ryall, P. (2000). A new species of the genus *Notosetia* (Mollusca, Skeneidae) from Ghana. *Argonauta, 14*, 39–41.

Romani, L., Bogi, C., & Bartolini, S. (2015). A new *Skenea* species from Mediterranean Sea, with notes on *Skenea serpuloides* (Montagu, 1808) (Gastropoda, Vetigastropoda, Skeneidae). *Iberus, 33*, 159–165.

Rosenberg, G. (2015). *Cirsonella australis* Angas, 1877. In: MolluscaBase (2015). Accessed on 2015-08-21 through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=598300.

Rubio, F., & Rodriguez-Babio, C. (1991). Sobre la posición sistemática de *Pseudorbis granulum* Brugnone, 1873 (Mollusca, Archaeogastropoda, Skeneidae) y descripción de *Pseudorbis jameoensis* n. sp., procedente de las Islas Canarias. *Iberus, 9*, 203–207.

Rubio, F., & Rolán, E. (1991). Aportaciones a los conocimentos sobre les micromoluscos de Africa Occidental. 1. Archaeogastropoda de Sao Tome y Principe. *Iberus, 9*, 209–219.

Rubio, F., & Rolán, E. (2013a). Some new species of Skeneinae (Prosobranchia, Turbinidae). *Iberus, 31*, 1–9.

Rubio, F., & Rolán, E. (2013b). New images of the soft parts of *Skenea serpuloides* (Prosobranchia, Turbinidae). *Iberus, 31*, 87–91.

Rubio, F., & Rolán, E. (2015). The species of *Haplocochlias* (Gastropoda, Skeneidae) from Guadeloupe Island (Caribbean Sea) collected in the KARUBENTHOS expedition. *Novapex, 15*, 1–12.

Rubio, F., Dantart, L., & Luque, A. A. (1998a). Two new species of *Dikoleps* (Gastropoda, Skeneidae) from the Mediterranean coast of Spain. *Iberus, 16*, 81–93.

Rubio, F., Rolán, E., & Redfern, C. (1998b). The genus *Lodderena* Iredale, 1924 (Archaeogastropoda, Skeneidae) in the Caribbean. *Argonauta, 11*, 39–48.

Rubio, F., Dantart, L., & Luque, A. A. (2004). El género *Dikoleps* (Gastropoda, Skeneidae) en las costas Ibéricas. *Iberus, 22*, 115–132.

Rubio, F., Rolán, E., & Fernándes-Garcés, R. (2015). Revision of the genera *Parviturbo* and *Pseudorbis* (Gastropoda, Skeneidae). *Iberus, 33*, 167–259.

Rubio-Salazar, F. (1991). Skeneidos infra y circalitorales de las costas del sur y Levante Espanol. *Iberus, 9*, 187–202.

Ruthensteiner, B. (2008). Soft part 3D visualization by serial sectioning and computer reconstruction. *Zoosymposia, 1*, 63–100.

Ruthensteiner, B., & Heß, M. (2008). Embedding 3D models of biological specimens in PDF publications. *Microscopic Research and Technique, 71*, 778–786.

Sasaki, T. (1998). Comparative anatomy and phylogeny of the recent Archaeogastropoda (Mollusca: Gastropoda). *University Museum, The University of Tokyo, Bulletin, 38*, 1–223.

Strasoldo, M. (1991). Anatomie und Ontogenie von *Scissurella jucunda* (Smith, 1890) und Anatomie von *Anatoma* sp. *Dissertation.* Zoologisches Institut der Universität Wien, pp. i-iii, 1–145, **pls. 1–37.**

Szal, R. A. (1971). New sense organ of primitive gastropods. *Nature (London), 229*, 490–492.

Thiele, J. (1929). *Handbuch der Systematischen Weichtierkunde. Erster Teil. Loricata, Gastropoda. 1. Prosobranchia (Vorderkiemer)* (pp. 1–778). Jena: Gustav Fischer.

van Aartsen, J. J., Menkhorst, H. P. M. G., & Gittenberger, E. (1984). The marine Mollusca of the Bay of Algeciras, Spain, with general notes on Mitrella, Marginellidae and Turridae. *Basteria Supplement, 2*, 3–135.

von Salvini-Plawen, L., & Haszprunar, G. (1987). The Vetigastropoda and the systematics of streptoneurous Gastropoda (Mollusca). *Journal of Zoology, 211*, 747–770.

Warén, A. (1990). Ontogenetic changes in the trochoidean (Archaeogastropoda) radula, with some phylogenetic interpretations. *Zoologica Scripta, 19*, 179–187.

Warén, A. (1991). New and little known Mollusca from Iceland and Scandinavia. *Sarsia, 76*, 53–124.

Warén, A. (1992). New and little known "skeneimorph" gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. *Bolletino di Malacologico, 27*, 149–248.

Warén, A. (1993). New and little known Mollusca from Iceland and Scandinavia. Part 2. *Sarsia, 78*, 159–201.

Warén, A. (1996). New and little known Mollusca from Iceland and Scandinavia. Part 3. *Sarsia, 81*, 197–245.

Warén, A., & Bouchet, P. (1993). New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrothermal seeps. *Zoologica Scripta, 22*, 1–90.

Warén, A., & Bouchet, P. (2001). Gastropoda and Monoplacophora from hydrothermal vents and seeps, new taxa and records. *The Veliger, 44*, 116–231.

Warén, A., Gofas, S., & Schander, C. (1993). Systematic position of three European heterobranch gastropods. *The Veliger, 36*, 1–15.

Wenz, W. (1938). Gastropoda, Teil 1: Allgemeiner Teil und Prosobranchia. In O. H. Schindeworf (Ed.), *Handbuch der Paläozoologie, 6* (pp. 241–480). Berlin: Gebrüder Bornträger.

Williams, S. T. (2012). Advances in molecular systematics of the Vetigastropod superfamily Trochoidea. *Zoologica Scripta, 41*, 571–595.

Williams, S. T., & Ozawa, T. (2006). Molecular phylogeny suggests polyphyly of both the turban shells (family Turbinidae) and superfamily Trochoidea (Mollusca: Vetigastropoda). *Molecular Phylogenetics & Evolution, 39*, 33–51.

Williams, S. T., Karube, S., & Ozawa, T. (2008). Molecular systematics of Vetigastropoda: Trochidae, Turbinidae and Trochoidea redefined. *Zoologica Scripta, 37*, 483–506.

WMSDB—Worldwide Mollusc Species Data Base—Skeneidae available from www.bagniliggia.it/WMSD/PDFFamily/SKENEIDAE.pdf Accessed 2015-12-08.

WoRMS—World Register of Marine Species. Skeneidae Clark, W., 1851 (2015). Available from www.marinespecies.org/aphia.php?p=taxdetails&id=558146 .Accessed 2015-12-08.