MORPHOLOGICAL, ECOLOGICAL AND MOLECULAR CHARACTERIZATION OF THE ENIGMATIC PLANISPIRAL SNAIL GENUS *ADEUOMPHALUS* (VETIGASTROPODA: SEGUENZIOIDEA)

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ABSTRACT

Adeuomphalus Seguenza, 1876 is a little known genus among the skeneimorph vetigastropods, with very few specimens previously reported alive from the deep sea. We examined newly collected and museum-stored specimens from upper to lower bathyal depths in the Atlantic, Mediterranean, Pacific and Indian Oceans and recognize seven recent species in the genus: *A. ammoniformis* Seguenza, 1876, *A. densicostatus* (Jeffreys, 1884), *A. trochanter* Warén & Bouchet, 2001, *A. sinuosus* (Sykes, 1925) n. comb., *A. guillei* n. sp., *A. elegans* n. sp. and *A. collinsi* n. sp., along with a fossil species, *A. bandeli* (Schröder, 1995) from the Lower Cretaceous, Poland. These species are characterized by a minute and colourless shell with almost perfectly planispiral whorls, an orthocline aperture, distinct radial ribs and a deeply concave apex and base. At least three species are confirmed to be radula-less, while *A. guillei* n. sp. has a simplified (3–2–1–2–3) rhipidoglossate radula. Anatomical investigations of *A. collinsi* n. sp. and *A. trochanter* revealed the following traits: a monopectinate ctenidium, blunt and tapering cephalic tentacles with sensory papillae, a cylindrical snout, a simple right neck lobe, a large foot with the anterior corners drawn out into finger-like projections, a smooth ESO-tentacle and a single, micropapillate epipodial tentacle on each side of the foot; absence of pigmented eyes, eye lobes, cephalic lappets and subocular peduncles. Three species collected by submersibles in the vicinity of hydrothermal vents co-occurred with carnivorous sponges of the family Cladorhizidae; a parasitic mode of life is suggested based on the lack of the radula and the peculiar, tube-like shape of the snout. Separate and combined phylogenetic analyses of mitochondrial (COI and 16S rRNA) and nuclear (histone H3 and 18S rRNA) gene sequences revealed six monophyletic groups in Seguenzioidea: Seguenziidae, Chilodontidae, Calliotropidae, Cataegidae, *Spinicalliotropis* and skeneimorph seguenzioids. Three included skeneimorphs (*A. elegans* n. sp., *Xyloskenea* sp. and *Ventsia tricarinata*) were ambiguously grouped together with long branches and low statistical supports, possibly suggesting a vast, undiscovered phylogenetic diversity of the group. Taxonomic composition, morphological characteristics and evolutionary history are discussed for the skeneimorphs and five other groups in the superfamily.

INTRODUCTION

Vetigastropoda are an archaic and diverse group of Gastropoda, comprising several thousand living species. Traditional classifications recognized some 20 Recent families in the group, mainly based on the morphology of the shell, operculum, radula and ctenidium (e.g. Knight *et al*., 1960; Hickman 1998), but the systematic scheme has changed considerably in the last few years through increased knowledge of anatomy and the application of molecular phylogenetics (Warén *et al*., 2003; Bouchet *et al*., 2005; Geiger & Thacker, 2005; Williams & Ozawa, 2006; Kano, 2008; Williams, Karube & Ozawa, 2008). The phylogenetic trees indicate that our concept of some traditional families is polyphyletic or paraphyletic and that they consist of more than one independent evolutionary unit.

'Skeneidae' are probably the most infamous case of a polyphyletic family in Vetigastropoda. This family included hundreds of described and more undescribed species, classified in dozens of genera and subgenera with minute, variously shaped, usually colourless, shells (Thiele, 1929; Wenz, 1938–44; Marshall, 1988b; Hickman & McLean, 1990). Although most 'skeneid' species were described from empty shells and almost nothing is known about their anatomy, the subsequent finding of many fundamentally different radular plans among the taxa has led some authors to suggest that they are polyphyletic (Warén, 1992; Warén & Bouchet, 1993; Hickman, 1998). The core members of the family, the type species of *Skenea* Fleming, 1925 and some similar taxa from the North Atlantic, have been shown to share a unique propodial 'penis' and turbinid-like radular morphology with a flat, broad central tooth (Warén, 1991, 1992, 1993; Warén & Bouchet, 1993). Molecular phylogenies (Heß *et al*., 2008; Kano, 2008; Williams *et al*., 2008) have confirmed five unrelated lineages in the traditional 'Skeneidae' (*Dillwynella* Dall, 1889; *Munditiella* Kuroda & Habe, 1954; *Bathyxylophila* Marshall, 1988; *Xyloskenea* Marshall, 1988 + *Ventsia* Warén & Bouchet, 1993; and *Leptogyra* Bush, 1897 + *Leptogyropsis* Marshall, 1988). This supports the idea that the family is a miscellany of little-known minute vetigastropods, often mixed up even with caenogastropods and heterobranchs. Such *Skenea*-like snails have therefore been termed 'skeneimorphs' (Warén, 1992;

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Kano, 2008) or 'skeneiforms' (Hickman, 1998). *Skenea* and the subfamily Skeneinae have been classified in the family Turbinidae based on the phylogenetic position of the morphologically similar genera *Protolira* (Warén *et al*., 2003) and *Dillwynella* (Kano, 2008; Williams *et al*., 2008). However, most skeneimorphs remain inadequately studied and are provisionally placed in Skeneinae or Skeneidae and many other suprageneric taxa including Vitrinellidae (Caenogastropoda), therefore constituting a significant gap in the knowledge of gastropod phylogeny.

Adeuomphalus Seguenza, 1876 is a little known and puzzling taxon among the skeneimorphs and less than five specimens have previously been documented alive (Warén, 1991; Warén & Bouchet, 2001). Shells of this deep-sea genus can be described as 'miniature ammonites', having almost perfectly planispiral whorls, radial ribs and an orthocline aperture (Seguenza, 1876; Norfroni & Sciubba, 1985). The digestive system of previously known *Adeuomphalus* species seems to lack a radula (Warén & Bouchet, 2001), the most practical morphological character in the higher classification of gastropods. As a result, it had not been possible to assign the genus to a family or a higher taxon within Vetigastropoda, until a molecular phylogenetic study was conducted using a recently collected specimen (Kano, 2008); two independent gene trees unanimously showed its close relationship to the Seguenziidae, Eucyclinae and Cataeginae of the polyphyletic 'Trochidae' (*sensu* Hickman & McLean, 1990) and two other skeneimorph genera (*Ventsia* Warén & Bouchet, 1993 and *Xyloskenea* Marshall, 1988). These taxa were assigned to the redefined superfamily Seguenzioidea in Vetigastropoda (Bouchet *et al*., 2005; Kano, 2008). Shell and radular characteristics suggest that the superfamily includes many more skeneimorph genera, mostly from the deep sea (Kano, 2008; see also Warén, 1991, 1992).

In contrast to the robust support for the monophyly of Seguenzioidea, the internal relationships within the superfamily are uncertain and phylograms show basal polytomies. This leaves all remaining seguenzioids unassigned to families except for the Seguenziidae (*sensu* Marshall, 1991; Quinn, 1991), which are characterized by unique anatomical features including the presence of presumed copulatory organs in both sexes (Quinn, 1983; Sasaki, 1998). Among other taxa, *Adeuomphalus* may play an important role in reconstructing the internal phylogeny of the superfamily. A Bayesian tree inferred from the mitochondrial COI gene sequences identified the genus as the first offshoot among seguenzioids studied, although statistical support for this topology was not significant (Kano, 2008: fig. 1A).

In this paper, we describe the sequenced specimen of *Adeuomphalus* from Lau Basin, off Tonga in the South Pacific (Kano, 2008) as a new species, along with two other new species collected alive from Manus Basin (off Papua New Guinea) and off Reunion Island (Indian Ocean), respectively. Morphological, taxonomic and ecological information is also provided for the genus based on newly obtained or museum-stored material and a literature survey. In addition, we examine the phylogenetic position of *Adeuomphalus* in the superfamily Seguenzioidea by analysing DNA sequences from the 16S rRNA (18 newly determined sequences), COI, Histone H3 and 18S rRNA genes and by reconstructing independent and concatenated gene trees.

MATERIAL AND METHODS

Sampling and preparation of new Adeuomphalus

A single specimen of *Adeuomphalus elegans* was obtained in the YK04-09 SWEEP VENTS Expedition cruise to the Lau Basin and Kermadec Ridge in the South Pacific, on the research vessel *Yokosuka* with the submersible *Shinkai 6500* from September to November 2004. The specimen was collected at the Vai Lili hydrothermal vent field in the Lau Basin during the dive #837. Vai Lili was discovered in 1989 at a depth of *c*. 1,700 m in the northern section of the central Valu Fa Ridge with vigorous hydrothermal activity and fluid temperatures exceeding 340°C (Fouquet *et al*., 1993). However, the vent activity appeared to have declined significantly in the YK04-09 dives, with water temperatures around the vent of 88°C and diffuse flows associated with yellow patches of iron oxides (Ishibashi *et al*., 2006).

The specimen was collected during this dive in association with unidentified carnivorous sponges of the genus *Abyssocladia* Topsent, 1901 (family Cladorhizidae). It was collected in the vicinity of 'shimmering' water, resulting from the confluence of warm vent fluid and cooler sea-water, with a temperature of 35°C (22°12.866′S, 176°36.484′W, 1,737 m depth). The sponges were found on black volcanic rocks and were sampled by grabbing and breaking the rocks with the manipulator arm of the Shinkai 6500. In the course of sorting out the sponges from broken rock fragments on board the mother ship *Yokosuka*, Y.K. found the *Adeuomphalus* specimen attached to the flat head of one of the sponges. However, it was uncertain whether the snail was found *in situ* or if it was stuck accidentally to the mucous head of *Abyssocladia* by the movements of the sample box. No other mollusc specimen was collected in the same dive.

The snail was very shy in a dish filled with seawater at room temperature and did not extend out of its shell. To prevent retraction of the head-foot deep inside the shell, the specimen was relaxed in 7.5% magnesium chloride, then preserved in pure ethanol and stored at −20°C. After removing a small piece of foot tissue for DNA extraction, the shell and operculum were prepared for SEM observation using standard techniques: cleaned with an ultrasonic cleaner, dried, mounted on stubs and coated with gold. The specimen has been deposited in the National Science Museum, Tokyo (NSMT).

A single slightly damaged specimen of *Adeuomphalus collinsi* was collected by Patrick Collins in an environmental survey of hydrothermal vents, in the Manus Basin off New Guinea. Biological samples from the same site also contained specimens of cladorhizid sponges (C.L. Van Dover, personal communication). The snail specimen was fixed in formalin, transferred to 80% ethanol and forwarded to A.W. for identification. The last 0.5 whorl of the partly broken shell was removed and the head-foot was extracted and critical-point dried; the shell was cleaned with commercial bleach and both were afterwards examined with SEM. It then turned out that the specimen was infested by a parasitic copepod, which had damaged the gill. The copepod body was inside the host and the developing eggs of the parasite filled the pallial cavity. The eggs had to be removed in several instalments with SEM examination between, since the gastropod and parasite were too small to be properly examined under the dissecting scope (Wild M5A APO). After finishing the SEM, the body was dissolved in KOH but no radula was found. The specimen has been temporarily deposited in the Swedish Museum of Natural History (SMNH).

Eleven specimens of *Adeuomphalus guillei* in the Muséum National d'Histoire Naturelle, Paris, France (MNHN), had been sorted from a preserved sediment sample, collected on 24 August 1982 from west of Reunion Island, Indian Ocean in the Marion Dufresne Cruise (MD 32, station DS78) with Sanders' epibenthic sled. They had been dried at the time of examination, and only the shell, operculum and radula were studied.

Taxonomic sampling for molecular phylogeny

We used 17 ingroup operational taxonomic units (OTUs) listed in Table 1 in COI, 16S and H3 data sets to effectively use the existing DNA sequence data. Partial sequences of the COI and/or H3 genes were determined in Kano (2008) for 16 species of Seguenzioidea including the new *Adeuomphalus*. They represented a wide variety of seguenzioid families and subfamilies, including four seguenziids, four calliotropine, one cataegine and four chilodontine 'trochids' (*sensu* Hickman & McLean, 1990), and three skeneimorph seguenzioids, while one of the two genes was not available for three species owing to difficulties with PCR. In the present phylogenetic reconstruction, the same 16 species were used as OTUs with the missing COI and H3 data obtained by employing different primers (see below). In addition, sequences of the hydrothermal-vent species *Bathymargarites symplector* Warén & Bouchet, 1989 were obtained from the DDBJ/EMBL/GenBank with accession numbers shown in Table 1. *Bathymargarites* is one of the most puzzling taxa in seguenzioid phylogeny, with an unknown familial position and a unique male copulatory organ (Warén & Bouchet, 1989; Kano, 2008). We also included two vetigastropod species, *Margarites olivaceus* (Brown, 1827) and *Conradia* sp., for outgroup comparison in the data sets of the three genes. *Conradia* Adams, 1863 constituted a moderately supported clade with seguenzioids in a previous Bayesian analysis of the COI gene (Kano, 2008).

A different set of OTUs was used for analyses of near-complete 18S rRNA sequences. This slowly evolving gene generally shows little variation in Vetigastropoda, and therefore the ingroup Seguenzioidea was represented by only six species, assuming that no significantly better results could have been obtained with all 17 species. On the other hand, Pleurotomarioidea and several other groups had long branches in previously reconstructed phylogenetic trees (e.g. Williams & Ozawa, 2006; Kano, 2008; Williams *et al.*, 2008). Nine sequences for outgroup comparison were obtained from the DDBJ/EMBL/GenBank repository, representing a wide

Table 1. Species used in the present analysis, arranged systematically, with DDBJ/EMBL/GenBank accession numbers and collection sites of specimens.

Species	COI	16S	H3	18S	Locality, depth and habitat
Seguenzioidea					
'Seguenzioid skeneimorphs'					
Adeuomphalus elegans n. sp.	AB365257	**AB481177**	AB365299	**AB481195**	Lau Basin; 1,737 m, HV
Xyloskenea sp. cf. *costulifera* Marshall, 1988	AB365249	**AB481178**	AB365291	–	Solomon Islands; 1,100 m, SW
Ventsia tricarinata Warén & Bouchet, 1993	AB365248	**AB481179**	AB365290	AB365311	Lau Basin; 1,817 m, HV
Seguenziidae Verrill, 1884					
Fluxinella sp. cf. *polita* Marshall, 1991	AB365250	**AB481180**	AB365292	AB365312	off Amami I., Japan; 340 m
Hadroconus sp. cf. *altus* (Watson, 1879)	AB365251	**AB481181**	AB365293	–	Malakula, Vanuatu; 600 m
Seguenzia sp. A cf. *levii* Marshall, 1991	AB365252	**AB481182**	AB365294	–	off Amami I., Japan; 580 m
Seguenzia sp. B cf. *eidalima* Marshall, 1991	AB365253	**AB481183**	AB365295	–	Malakula, Vanuatu; 600 m
Bathymargarites symplector Warén & Bouchet, 1989	DQ093521	DQ093477	DQ093503	DQ093433	
Calliotropidae Hickman & McLean, 1990					
Calliotropis pagodiformis (Schepman, 1908)	AB365229	**AB481184**	AB365275	AB365307	off Honiara, Solomon Islands; 700 m
Calliotropis sp. cf. *abyssicola* Rehder & Ladd, 1973	AB365230	**AB481185**	**AB481197**	–	off Amami I., Japan; 580 m
Ginebis argenteonitens (Lischke, 1872)	AB365231	**AB481186**	AB365277	–	Misaki, Kanagawa, Japan; 80 m
Turcica coreensis Pease, 1860	AB365234	**AB481187**	AB365279	–	Misaki, Kanagawa, Japan; 80 m
Cataegidae McLean & Quinn, 1987					
Cataegis sp. cf. *finkli* (Petuch, 1987)	AB365235	**AB481188**	AB365280	AB365308	Malakula, Vanuatu; 780 m
Chilodontidae Wenz, 1938					
Agathodonta nortoni McLean, 1984	AB365228	**AB481189**	AB365274	–	Panglao, Philippines; 300 m
Granata lyrata (Pilsbry, 1890)	AB365232	**AB481190**	AB365278	–	Ibusuki, Kagoshima, Japan; IN
Herpetopoma pauperculus (Lischke, 1872)	AB365233	**AB481191**	**AB481198**	–	Ibaraki, Japan; IN
Incretae sedis					
Spinicalliotropis chalkeie (Vilvens, 2007)	**AB481196**	**AB481192**	AB365276	–	Malakula, Vanuatu; 600 m
Outgroup taxa					
Margarites olivaceus (Brown, 1827)	AB365222	**AB481193**	AB365269	–	Hinlopen St., Svalbard, Arctic; 292 m
Conradia sp. cf. *clathrata* Adams, 1860	AB365239	**AB481194**	AB365285	–	Izu, Japan; IN
Dillwynella planorbis Hasegawa, 1997	–	–	–	AB365310	Kochi, Japan; 150 m, SW
Calliostoma sakashitai (Sakurai, 1994)	–	–	–	AB365306	Misaki, Kanagawa, Japan; 80 m
Liotina semiclathratula (Schrenck, 1862)	–	–	–	AB365305	Bonotsu, Kagoshima, Japan; IN
Sinezona confusa Rolán & Luque, 1994	–	–	–	AF120512	
Haliotis tuberculata Linnaeus, 1758	–	–	–	AF120511	
Lepetodrilus elevatus McLean, 1988	–	–	–	AY145381	
Tegula argyrostoma (Gmelin, 1791)	–	–	–	AF165311	
Turbo cornutus Lightfoot, 1786	–	–	–	AF165311	
Gibbula cineraria (Linnaeus, 1758)	–	–	–	AY340430	

Nomenclature for suprageneric ranks reflects results from Kano (2008) and present phylogenetic analyses. Accession numbers of newly obtained sequences are given in bold. Abbreviations: IN, intertidal; HV, hydrothermal vent; SW, sunken wood.

phylogenetic range of Vetigastropoda with supposedly low evolutionary rates (Table 1).

DNA extraction, amplification and sequencing

DNA was extracted with Qiagen DNeasy kit from the preserved foot or shell muscle tissue. Voucher material of 16 ingroup and 5 outgroup OTUs (Table 1) was deposited at the Department of Biological Production and Environmental Science, University of Miyazaki, Japan, or MNHN. Most shells, opercula and radulae were kept undamaged for future taxonomic studies. Photographs of shells are available from Y.K. upon request.

A portion of the mitochondrial 16S rRNA gene was amplified using the primer pair 16Sar-L (5′-CGCCTGTTTATC AAAAACAT-3′) and 16Sbr-H (5′-CCGGTCTGAACTCAGA TCAYGT-3′) designed by Palumbi *et al.* (1991). PCRs were carried out in a final volume of 25 μl [2.5 μl genomic DNA template (*c.* 100 ng), 17.5 μl ddH_2O, 2.5 μl Takara ExTaq buffer, 2 μl dNTPs, 0.2 μl of each primer (20 μM stock) and 0.1 μl Takara ExTaq enzyme]. After an initial denaturation for 3 min at 94°C, the reaction solution was run for 35 cycles with the following parameters: denaturation for 40 s at 94°C, annealing for 40 s at 45–50°C, followed by extension for 60 s at 72°C. PCR products were visualised by electrophoresis on 1.5% TBE agarose gel, which was stained with ethidium bromide, and photodocumented. If amplification was unsuccessful under this condition, either or both of the primers were replaced with the modified 16Sar-veti (5′-GCCTGTTTAG CAAAAACA-3′) and 16Sbr-veti (5′-GATCACGTAAGATTT TAATGGTCG-3′). Successful PCR products were cleaned using ExoSAP-IT (USB) following the described protocol. Sequences were directly determined using the amplification primers with a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) on an ABI 310 automated sequencer at University of Miyazaki.

Kano (2008) reported partial sequences of the COI and H3 genes for the majority of seguenzioids used in the present phylogeny, but either of the two genes was not successfully amplified from three OTUs (*Spinicalliotropis chalkeie*, *Calliotropis* sp. cf. *abyssicola* and *Herpetopoma pauperculus*), presumably due to mismatches of primer(s) in PCR. For these difficult taxa, the modified primers LCOmod (Kano, 2008) and H3MRI (5′-GGCATGATTGTTACACGCTTGGCGTG-3′) were employed in combination with the respective 'universal' primers HCO2198 (Folmer *et al.*, 1994) and H3MF (Kano, 2008). Annealing temperature of 40°C was used for COI amplification and 48°C for histone amplification. A near-complete 18S rRNA sequence was also determined for the new *Adeuomphalus* using 18A1 and 1800r primers (Steiner & Dreyer, 2003). PCR was carried out with following modifications: an annealing temperature of 54°C and extension time of 90 s. Purified PCR products were sequenced with the two amplification primers and four internal primers shown in Kano (2008). All sequences have been deposited in the DDBJ/EMBL/GenBank with accession numbers in Table 1.

Sequence analysis and phylogenetic reconstruction

Sequences of the two rRNA genes (16S and 18S) were aligned by ProAlign ver 0.5 (Löytynoja & Milinkovitch, 2003) with the band-width set to 500. Regions with posterior probabilities (PPs) <60% were regarded as alignment-ambiguous sites and were excluded in the following analyses of the 18S data set. Two data sets were created for the 16S sequences, both with and without the alignment-ambiguous sites. The COI and H3 sequences were aligned by eye in MacClade 4.08 (Maddison & Maddison, 2005). All alignments are available upon request from Y.K.

Phylogenetic trees were reconstructed from six data sets using the Bayesian inference and maximum likelihood (ML) methods. The first four data sets were analysed for all ingroup species listed in Table 1 and consisted of the independent COI, H3 and 16S gene sequences (two data sets for 16S, with and without alignment-ambiguous sites). The fifth data set concatenated sequences from the three genes; the ambiguous 16S sites were excluded in this data set. The sixth data set consisted of the 18S sequences from representative species. In the Bayesian analyses performed with MrBayes 3.1.1 (Ronquist & Huelsenbeck, 2003), the general time-reversible model was used for all the data sets with invariant site frequency and γ-shape parameter estimated from the data (GTR + I + G). The shape, proportion of invariant sites, state frequency and substitution rate parameters were estimated for each codon position separately in the amino acid coding COI and H3 genes. Each gene was allowed to have different parameters in concatenated data sets, hence the fifth data set involving all COI, H3 and 16S genes had seven partitions of parameters. Two parallel runs were made for 5,000,000 generations (with a sample frequency of 100) using default value of four Markov chains. The first 20,000 trees for each run were discarded to ensure the four chains reached stationarity. The consensus tree and PPs were computed from the remaining 60,000 trees (30,000 trees × 2 runs). Posterior probabilities ≥95% were considered significant support.

The ML analysis was performed using heuristic searches in PAUP* 4.0b10 (Swofford, 2002) with parameter settings identified by the Akaike Information Criterion (AIC, implemented in Modeltest 3.06; Posada & Crandall, 1998). The robustness of tree topology was assessed by a nonparametric bootstrap ML analysis using Garli 0.951 (Zwickl, 2006). Bootstrap runs consisted of 300 pseudoreplicates with the Modeltest parameters. Bootstrap probabilities (BPs) ≥75% were considered significant support. Congruence between individual gene trees was assessed by looking for conflicting branches with PP and BP support.

SYSTEMATIC DESCRIPTIONS

Superfamily Seguenzioidea Verrill, 1884

Family uncertain

Genus *Adeuomphalus* Seguenza, 1876

Adeuomphalus Seguenza, 1876: 10 (type species *Adeuomphalus ammoniformis* Seguenza, 1876, by monotypy; Upper Pliocene to Lower Pleistocene, Sicily, Italy; Recent in Mediterranean?).

Transomalogyra Palazzi & Gaglini, 1979: 33 (type species *Ammonicerina simplex* sensu Palazzi & Gaglini, 1979, not Costa, 1861 = *Homalogyra densicostata* Jeffreys, 1884).

Diagnosis: Shell minute, up to 2.95 mm in diameter, colourless, almost perfectly planispiral with deeply concave apex and base. Protoconch paucispiral, *c.* 0.2 mm in diameter. Teleoconch whorls ornamented with straight or slightly flexuous axial ribs, often keeled at both apical and basal sides; suture deeply impressed; aperture simple, nearly or perfectly orthocline, trapezoidal to horseshoe-shaped to nearly round with a thin edge. Operculum transparent, multispiral with a central nucleus. Animal colourless, cephalic and epipodial tentacles with sensory papillae, simple right neck lobe present, gill small and monopectinate, foot anteriorly bifurcated with a pair of epipodial sense organs (ESOs) and epipodial tentacles. Pigmented eyes, eye lobes, cephalic lappets and subocular peduncles all lacking. Radula absent or 3–2–1–2–3 in formula.

Distribution: Indo-Pacific, Atlantic and Mediterranean in upper to lower bathyal zone (300–2,000 m); Early Cretaceous to Recent.

Remarks: We will here discuss some features directly connected to the species we have included in *Adeuomphalus*; the phylogenetic results for the genus are discussed in the Discussion section. The genus includes five previously named species: (1) *A. ammoniformis* Seguenza, 1876 from Plio-Pleistocene deposits in Italy and in the Mediterranean; (2) *A. densicostatus* (Jeffreys, 1884) from northeastern Atlantic and fossil in the Mediterranean; (3) *A. sinuosus* (Marshall, 1925) (new combination) from northeastern Atlantic; (4) *A. bandeli* (Schröder, 1995) from the Early Cretaceous of Poland; and (5) *A. trochanter* Warén & Bouchet, 2001 from a hydrothermal vent site on Juan de Fuca Ridge in northeastern Pacific. Three new species are named here: (1) *A. elegans* from a vent site in Lau Basin off Tonga; (2) *A. collinsi* from a vent in Manus Basin off New Guinea; and (3) *A. guillei* from off Reunion Island, Indian Ocean.

The species of *Adeuomphalus* closely resemble those of *Eudaronia* Cotton, 1945 and *Palazzia* Warén, 1991 in having an almost perfectly planispiral shell with a deeply concave apex and base and a perfectly or nearly orthocline aperture. *Eudaronia* and *Palazzia* are also rare inhabitants of the deep sea of unknown familial placement (Warén, 1991; Rex, 2002; Kano, 2008). The three genera are probably closely related, and *Adeuomphalus* has characteristics of both *Eudaronia* and *Palazzia*.

The shell of *Eudaronia* species, including the type *E. jaffaensis* (Verco, 1909), *E. aperta* (Sykes, 1925), *E. biconcava* (Thiele, 1925) and *E. pusilla* (Gründel, 2000), is rather uniformly smooth without axial ribs. The whorls are keeled both apically and basally; hence the aperture has a typical trapezoidal outline as in the type species of *Adeuomphalus* (Warén, 1991: fig. 14A–E; Kaim, 2004: fig. 2A–C). Indeed, *E. aperta* was once described as a new species of *Adeuomphalus* (*A. laevis*) by Rindone (1990), who was apparently unaware of Sykes's name (Warén, 1991). *Palazzia* contains at least five species (Warén, 1991; Warén & Hain, 1996): the type *P. ausonia* (Palazzi, 1988), *P. planorbis* (Dall, 1927), *P. nautiliformis* (Powell, 1927), *P. ramosa* (Powell, 1940) and *P. andersi* Palazzi & Villari, 1996. The shells of *Palazzia* are smaller and more sturdily built than those of *Adeuomphalus* and *Eudaronia*, superficially approaching *Ammonicera* Vayssière, 1893 of the heterobranch family Omalogyridae (Warén, 1991). *Palazzia* species have axial ribs that frequently branch dichotomously and then disappear abruptly towards the periphery of the shell, in contrast to the continuous and unbranched ones in *Adeuomphalus* species. The ribs of *Palazzia* are also broad and rounded instead of narrow and sharp as in *Adeuomphalus*. The apical and basal spiral keels are absent in adult *Palazzia*, present only in the first teleoconch whorl, and the aperture is perfectly round with a continuous peristome.

However, these differences are not always clear-cut and there are intermediate forms, especially between *Adeuomphalus* and *Eudaronia*. For example, the aperture is nearly round and only very slightly indented by the preceding whorl in *A. sinuosus*, *A. collinsi* and *A. guillei*. The spiral keels are completely lacking in *A. sinuosus* and *A. collinsi*. The axial ribs of *A. sinuosus* almost disappear at the periphery in the last adult whorl. The assignment of the study taxa to *Adeuomphalus* is therefore possible only by a combination of the shell characters, not by a clearly defined synapomorphy, because of the lack of anatomical and molecular data for most species of the three genera.

Another problem for the generic concept and classification is that *A. guillei* has a radula, whereas *A. densicostatus*, *A. trochanter* and *A. collinsi* evidently lack this organ (confirmed by serial sectioning of *A. trochanter*; Warén & Bouchet, 2001). Presence and absence of a radula would normally suggest the use of two genera, but this should not be done automatically as the loss of an organ does not necessarily imply a great phylogenetic distance. Furthermore, it is not known if the type species *A. ammoniformis* has a radula, since only shells are known, and therefore we have preferred tentatively to place all these species of similar shell morphology under a single generic heading. Two examined species of *Eudaronia* have a radula similar to that of *A. guillei*, while no radula has been found in four species of *Palazzia* (Warén, 1991: fig. 8A; A.W., personal observation).

Adeuomphalus has a subjective junior synonym, *Transomalogyra*. Palazzi & Gaglini (1979: pl. 2, fig. 1) figured '*Omalogyra simplex* (O.G. Costa, 1861)' from bathyal water off Bonifacio, southern Corsica, Mediterranean, and proposed *Transomalogyra* as a new subgenus in *Omalogyra* Jeffreys, 1860 (Omalogyridae). We consider the identification erroneous and that the subgenus is based on a shell of *A. densicostatus* (see also Warén, 1991). The identity of *Ammonicerina simplex* Costa, 1861 from the 'zone of coralline algae off Sardinia' still remains unconfirmed, but it seems unlikely that a true member of *Adeuomphalus* is involved.

Warén & Hain (1996: 319) suggested that '*Zerotula*' *crenulata* Powell, 1937 described from an upper-bathyal (260 m) depth in New Zealand might also belong to the genus *Adeuomphalus*, because it shares the planispiral teleoconch with spiral keels at apical and basal sides (Powell, 1937: pl. 54, figs 6, 7). Indeed, the paucispiral protoconch of the species with a clear demarcation line and a granular sculpture (A.W., personal observation) indicates a systematic position within Vetigastropoda, while true members of *Zerotula* Finlay, 1926 (Zerotulidae) belong to Littorinoidea in the Caenogastropoda (Warén & Hain, 1996). However, its teleoconch characteristics including many spiral ridges show some discrepancies from the eight species of *Adeuomphalus* treated herein. Not having had the opportunity to examine soft parts, we refrain from assigning this species to a genus although *Microcarina* Laseron, 1954 is a possibility.

***Adeuomphalus ammoniformis* Seguenza, 1876**
(Fig. 1F–I)

Adeuomphalus ammoniformis Seguenza, 1876: 10 (Plio-Pleistocene deep-sea deposit near Messina, southern Italy; types unknown).

Type material: The collection of Seguenza was destroyed by the Messina Earthquake in 1908. Only a minor collection survived in Florence (Bertolaso & Palazzi, 2000), except scattered specimens that Seguenza had sent to his correspondents. A.W. has not recognized any types of *Adeuomphalus* among such material.

Material examined: Three empty shells from off Capraia I. (near Corsica), Italy, Mediterranean (*c.* 43°N, 10°E), *c.* 400 m depth, SMNH. One fossil shell from Vallone Catrica, Reggio Calabria, southern Italy, Plio-Pleistocene deep-sea deposit (see Vazzana, 1996), SMNH.

Description: Shell minute, up to 1.66 mm in diameter, 0.77 mm in height (Fig. 1F–H). Protoconch sculptured by irregularly shaped granules that are interconnected to form several indistinct spiral ridges, demarcated from teleoconch by a simple and clear line (Fig. 1I); maximum diameter of exposed area 160 μm in both apical and basal views. Teleoconch whorls 2.9 in number, ornamented with very strong apical and basal spiral keels and up to 119 straight to very slightly flexuous axial ribs. Axial ribs 5–20 μm in width, wider near periphery; 22–29 present on first whorl, 36–43 on second whorl; straight

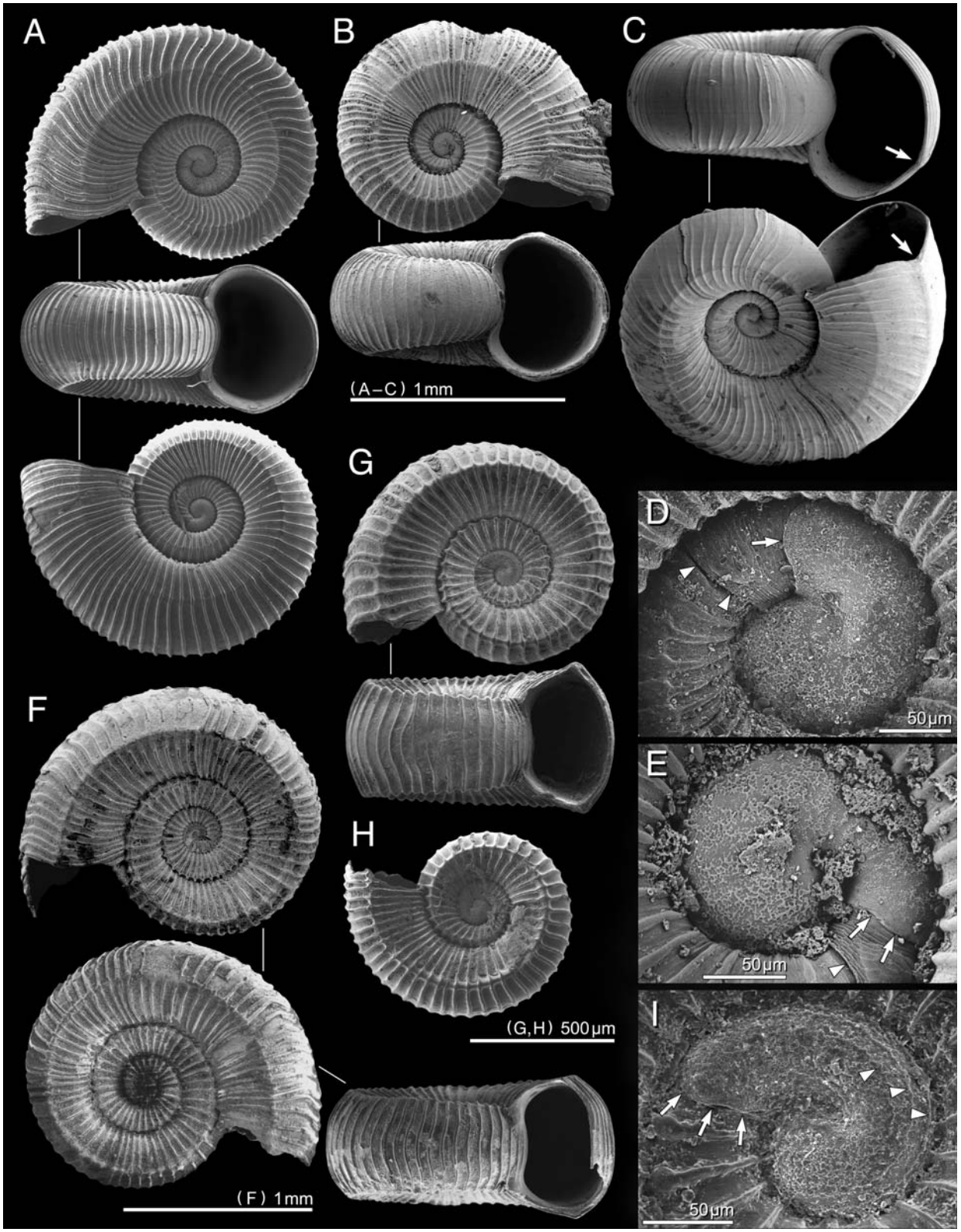

Figure 1. A–E. *Adeuomphalus densicostatus* (Jeffreys, 1884). **A.** Empty shell from off southern Portugal, 305–320 m, SMNH. **B.** Plio-Pleistocene fossil from Ponte Cellantoni, southern Italy, SMNH. **C.** Empty shell from Rockall Trough, northwest of Ireland, 2,175 m, SMNH 94951; arrows point to a blunt corner or third keel between periphery and basal keel. **D, E.** Apical (**E**) and basal (**D**) views of protoconch, same specimen as **A**; arrows and arrowheads indicate protoconch/teleoconch boundary and end of lamellate section of teleoconch, respectively. **F–I.** *Adeuomphalus ammoniformis* Seguenza, 1876. **F, G.** Empty shells from off Capraia I., Corsica, Italy, *c*. 400 m, SMNH. **H.** Plio-Pleistocene fossil from Vallone Catrica, Calabria, southern Italy, SMNH. **I.** Basal view of protoconch, same specimen as **G**; arrows and arrowheads indicate protoconch/teleoconch boundary and spiral ridges, respectively.

and radial on first two whorls, slightly flexuous on third whorl with two weak inflections between periphery and keels (Fig. 1F); interspaces at periphery twice rib width on first whorl, three times on succeeding whorls. Keels run along subsequent suture lines on early whorls, located closer to periphery than to suture on third whorl in apical and basal views, with distances from suture to keels being 60–65% to periphery; two keels reach to aperture with approximately same strength. Aperture orthocline, simple, up to 0.56 mm in width; peristome trapezoidal or almost pentagonal with peripheral part evenly curved between keels, without a clear indentation by preceding whorl.

Remarks: *Adeuomphalus ammoniformis* was described from Upper Pliocene to Lower Pleistocene deep-sea mollusc assemblages in the vicinity of Messina, southern Italy. The species was not figured by Seguenza, but his original description mentioned its characteristically quadrangular aperture (Seguenza, 1876), making species identification possible. Empty shells of this species have been found in 300–900 m depths in the Tyrrhenian Sea of the Mediterranean (Norfroni & Sciubba, 1985; Cecalupo, 1986; Palazzi, 1988; Smriglio, Mariottini & Gravina, 1988). However, these specimens might also be fossils, since they are often worn with their apertures filled with sediment, and no living animal has been discovered. It is therefore uncertain if this Tyrrhenian species represents a living member of the genus. However, since the shells occur with an accompanying fauna well known from the Italian Uppermost Pliocene to Pleistocene deposits, with *A. densicostatus* and many other taxa known also as extant species, there is a good possibility that it is still living.

***Adeuomphalus densicostatus* (Jeffreys, 1884)**
(Fig. 1A–E)

Homalogyra densicostata Jeffreys, 1884: 129, pl. 10, fig 1 [lectotype (Palazzi; 1990) BMNH 1885.11.5.1922–3; off southern Portugal, eastern Atlantic, Porcupine Expedition 1870, stations 16 and 17a, 1,000–2,000 m depth]

Material examined: Lectotype. Three live and one dead specimens from Rockall Trough, northwest of Ireland, eastern Atlantic (Challenger II, station ES218, 57°22′N, 10°24′W), 2,175 m depth, SMNH 94951. One shell from off southern Portugal (36°33.7′N, 11°30.1′W), 305–320 m depth, MNHN. One fossil shell from Ponte Cellantoni (near Terreti), 3 km northeast of Reggio Calabria, southern Italy (38°07′N, 15°43′E), Plio-Pleistocene deep-sea deposit (see Gaetani & Saccà, 1984), SMNH.

Description: Shell small, up to 2.25 mm in diameter (Fig. 1A–C). Protoconch sculptured by small, irregular, somewhat star-shaped granules that often connect to form net-like pattern (Fig. 1D, E); maximum dimensions of exposed area 180–185 μm and 165–180 μm in apical and basal views, respectively. Teleoconch whorls up to 2.5 in number, consists of two parts with different ornamentation. First 0.1 whorl after clear demarcation line of protoconch bears 15–17 irregularly lamellate growth lines. Succeeding teleoconch whorls ornamented with apical and basal spiral keels and up to 110 flexuous axial ribs. Axial ribs 10–15 μm in width, wider near periphery; 30–40 present on first whorl, 59–70 on second whorl; only slightly flexuous on first two whorls, clearly flexuous on third whorl with a conspicuous point of inflection between periphery and basal keel; interspaces at periphery twice rib width on first whorl, three times on succeeding whorls. Keels relatively strong on early whorls, quite weak or evanescent on third whorl; basal keel slightly stronger and longer than apical one; both located halfway between suture and periphery on third whorl in apical and basal views, with distances from suture to keels being 44–49% to periphery. A blunt corner or third keel may be formed near aperture at inflection between periphery and basal keel (Fig. 1C). Aperture slightly prosocline, simple, up to 0.9 mm in width; peristome horseshoe- or round D-shaped, very slightly indented by preceding whorl.

Radula absent (three specimens with dried soft parts were examined, with no result).

Remarks: *Adeuomphalus densicostatus* was described by Jeffreys (1884) in the genus *Homalogyra* (= *Omalogyra*) based on two empty shells from a deep water (1,000–2,000 m) off Portugal, eastern Atlantic. A lectotype was designated by Palazzi (1990) because the figures of the two syntypes in the original description seemed to include two different species and the paralectotype could have represented a specimen of *A. ammoniformis* (*seusu* Palazzi, 1990). In the lectotype the spiral keels on the teleoconch are weak and disappear on the third whorl (Jeffreys, 1884: pl. 10, fig. 1), while in the smaller paralectotype they are much stronger and approach those of *A. ammoniformis* (Jeffreys, 1884: pl. 10, fig. 1a). Warén (1991: 74) instead synonymized the two species after examining the types of *A. densicostatus* (Warén, 1991: fig. 15A, B), considering that the difference in development of the keel was simply the result of ontogenetic change.

Now, after examination of more specimens, it seems clear that *A. densicostatus* is distinct from *A. ammoniformis*, and that the smaller, partly crushed paralectotype is a young specimen of the former species before the shape of the whorls has changed from keeled to round. The different strength of the apical and basal keels in *A. densicostatus* also contributes to the different appearance of the two types. Because the basal keel is more obvious than the apical one in this species (Fig. 1A), the paralectotype glued upside down to cardboard shows a stronger keel than the lectotype, which is also glued but with the apical surface uppermost.

Besides the weaker keels, *A. densicostatus* is readily distinguished from the type species by more loosely coiled whorls. At a diameter of 1 mm, a normal size for *A. ammoniformis*, that species has 2.2 whorls, while *A. densicostatus* has only 1.6 teleoconch whorls at the same size. Other discrepancies of the two species include (1) the relative positions of the two teleoconch keels, (2) position of inflection(s) in the axial ribs, (3) sculpture of the protoconch and (4) presence or absence of a short lamellate zone on the early teleoconch (Table 2). The teleoconch keels are located more peripherally in *A. ammoniformis* than in *A. densicostatus*, resulting in different shapes of the aperture: trapezoidal in the former species and round D-shape in the latter. The axial ribs have two, equally developed inflections between the periphery and keels in the former species, while there is only one inflection in the ribs of the latter species, which is apparent between the periphery and basal keel in the aperture (Fig. 1C). The protoconch surface bears several indistinct spiral ridges in the former and a net-like pattern in the latter (Fig. 1D–I).

The present species has (while the type species lacks) a short section with fine and close-set axial lamellae between the protoconch and teleoconch, obviously different in structure from the protoconch but not fully conforming with the succeeding part of the teleoconch. The significance of this section remains unknown, but it might represent a short period of a pelagic, lecithotrophic veliger larva or a settled but not fully transformed pediveliger. Similar but obviously analogous modifications of the protoconch/teleoconch boundary have been found in many deep-sea vetigastropods, including two seguenzioid species, *Bathymargarites symplector* and *Ventsia tricarinata* (Hickman, 1992: fig. 5G; Warén & Bouchet, 1993: 82; Marshall, 1995b: 385; A.W., personal observation).

Table 2. Morphological characteristics of seven living species of genus *Adeuomphalus*.

Species	*A. ammoniformis*	*A. densicostatus*	*A. elegans*	*A. trochanter*	*A. sinuosus*	*A. collinsi*	*A. guillei*
Max. shell diameter	1.7 mm	2.3 mm	3.0 mm	2.7 + mm*	1.4 mm	2.3 mm	1.1 mm
Max. shell height	0.8 mm	1.1 mm	1.4 mm	1.2 + mm*	0.6 mm	No data	0.5 mm
No. of teleoconch (T) whorls	2.9	2.5	2.8	2.7 + *	1.8	2.3	1.5
Shell diam. at 2 whorls	0.9 mm	1.4 mm	1.4 mm	1.7 mm	NA	1.7 mm	NA
Apical keel	2.9 whorls	2.2 whorls	2.5 whorls	No data	Absent	Absent	1.1 whorls
Basal keel	2.9 whorls	2.2+ whorls†	2.8 whorls	1.3 whorls	Absent	Absent	1.2 whorls
No. of axial ribs on 1st whorl	22–29	30–40	27	21	18	21	17
Apertural shape	Trapezoid	Round-D	Round-D	Round-D	Circular	Circular	Circular
Peristome	Interrupted	Interrupted	Interrupted	Interrupted	Continuous	Continuous	Interrupted
Protoconch (P) sculpture	Spiral ridges	Net-like	Net-like	Net-like	Net-like	Net-like	Granules
P apical dimension‡	160 μm	180–185 μm	165 μm	No data	185 μm	185 μm	245 μm
P basal dimension‡	160 μm	165–180 μm	185 μm	175 μm	No data	155 μm	230 μm
P/T lamellae§	Absent	Present	Present	Present	Absent	Present	Absent
Radula	No data	Absent	No data	Absent	No data	Absent	Present

*Largest specimen (holotype) partly broken and cannot be measured precisely.
†Based on second largest specimen; largest lectotype is glued to a cardboard and its base cannot be observed.
‡Maximum dimension of exposed area of protoconch, encircled by first teleoconch whorl.
§Irregularly lamellated section after demarcation line of protoconch and teleoconch.

The two species co-occur in the same Plio-Pleistocene deposits in southern Italy (A. Vazzana, personal communication). Occurrence of fossil *A. densicostatus* has already been reported from Bocche di Bonifacio, southern Corsica, Italy (Gaglini & Palazzi, 1979: fig. 1).

Adeuomphalus trochanter Warén & Bouchet, 2001
(Fig. 2D–F)

Adeuomphalus trochanter Warén & Bouchet, 2001: 132, figs 8f, 15l, 16d [holotype MNHN 21051, one paratype SMNH 5083 (both serially sectioned), Beard Chimney Source hydrothermal-vent site, Juan de Fuca Ridge, Coaxial Segment, Eastern Pacific, 46°09.3′N, 129°48.4′W; 2,060 m depth].

Description: Shell small, holotype with partly broken last whorl measures 2.7 mm in diameter and 1.2 mm in height (Fig. 2E). Protoconch sculptured with a fine, irregular net-like pattern (Fig. 2F); maximum dimension of exposed area 175 μm in basal view. Teleoconch whorls 2.7+ in number, ornamented with apical and basal spiral keels and 90 flexuous axial ribs. Axial ribs 10–30 μm in width, wider near periphery; 21 present on first whorl, 47 on second whorl; only slightly flexuous on first whorl, clearly winding on second and third whorls with a conspicuous inflection between periphery and basal keel; interspaces at periphery twice rib width on first whorl, two to three times on succeeding whorls. Basal keel very strong on first whorl, abruptly disappearing after around 1.3 whorls. Aperture rounded D-shaped, very slightly indented by preceding whorl.

Operculum corneous, transparent but sturdy, multispiral with a central nucleus and >6.5 whorls, sculptured by faint, irregular growth lines; diameter 1.07 mm, nearly the same as that of peristome; width of whorls gradually increases, with last whorl only very slightly wider than previous whorl and occupying 25% of opercular radius.

The serially sectioned paratype had no trace of a radula, radular sac or radular cartilages. Anterior end of foot bifurcated with corners drawn out to form tentacle-like projections. Cephalic tentacles blunt, cylindrical and slightly longer than large snout. Pigmented eyes absent. Gill monopectinate, a simple series of ridges fused to pallial roof.

Remarks: *Adeuomphalus trochanter* resembles *A. densicostatus* in its relatively large size, wavy axial ribs and a rounded, D-shaped aperture in the teleoconch and a net-like sculpture in the protoconch (Table 2). However, the spiral keels of the teleoconch of *A. trochanter* are much shorter than those of *A. densicostatus*; the basal keel of the former species is very strong on the first whorl and abruptly disappears early on the second whorl (Fig. 2E), while that of the latter species gradually decreases in strength and always reaches the early third whorl (Fig. 1A, C). Moreover, the present species has a little looser coiling of teleoconch whorls than does the latter species (Table 2). The presence (in *A. densicostatus*) or apparent absence (in *A. trochanter*) of the short lamellate zone between the protoconch and teleoconch seems to be a further difference between the two species (Figs 1D, 2F).

The two type specimens were found in an area where cladorhizid sponges were commonly observed (V. Tunnicliffe, personal communication).

Adeuomphalus elegans new species
(Fig. 3)

Type material: Holotype (NSMT-Mo76859) collected alive from the Vai Lili hydrothermal vent field, Lau Basin, South Pacific (22°12.866′S, 176°36.484′W; 1,737 m depth).

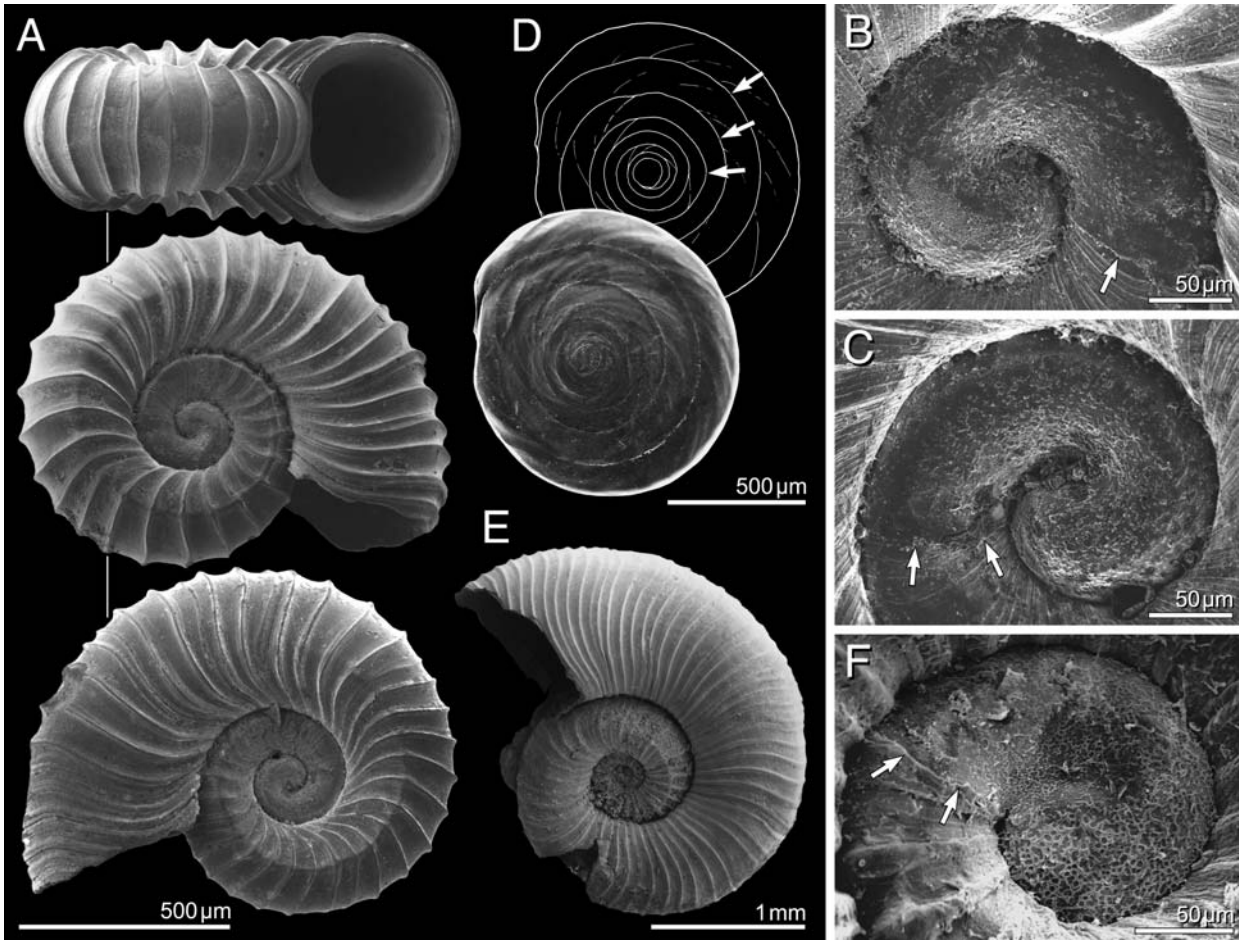

Figure 2. A–C. *Adeuomphalus guillei* n. sp., holotype, collected alive from west of Reunion Island, Indian Ocean, 1,175–1,200 m, MNHN 21052. **A.** Teleoconch. **B, C.** Apical (**B**) and basal (**C**) views of protoconch; arrows indicate protoconch/teleoconch boundary. **D–F.** *Adeuomphalus trochanter* Warén & Bouchet, 2001, holotype, collected alive from Juan de Fuca Ridge, Eastern Pacific, 2,060 m, MNHN 21051. **D.** Operculum, exterior view; trace of outline and sutures (arrows) shows gradual increase of whorls. **E.** Teleoconch, basal view. **F.** Protoconch, basal view; arrows indicate protoconch/teleoconch boundary.

Etymology: Referring to the elegantly sculptured shell of the new species.

Diagnosis: Shell 2.95 mm in diameter, largest for genus. Protoconch with an irregular net-like sculpture; exposed area larger basally than apically. Teleoconch with 2.8 whorls, including a short, irregularly lamellate section immediately after protoconch; first teleoconch whorl with 27 fine axial ribs, second with 46; apical keel weaker than basal one, disappearing near horseshoe-shaped aperture. Last whorl of operculum three times as wide as previous whorl.

Description: Shell small, 2.95 mm in diameter, 1.44 mm in height, semitransparent, thin but not fragile (Fig. 3A, J). Apical face is slightly more concave than basal face or umbilicus. Protoconch sculptured by small, irregular, somewhat star-shaped granules that often interconnect to form net-like pattern (Fig. 3F, G, I); maximum dimensions of exposed area 165 and 185 µm in apical and basal views, respectively. Teleoconch whorls 2.8 in number, consists of two clearly demarcated parts. First 0.1 whorl after demarcation line of protoconch bears 15 irregularly lamellate growth lines. Succeeding teleoconch whorls ornamented with apical and basal spiral keels and 145 flexuous axial ribs. Whole surface covered by numerous, randomly scattered pores of 0.5–3 µm diameter (Fig. 3C). Axial ribs thin, 7–15 µm in width; 27 present on first whorl (first six or seven of these rather faint), 46 on second whorl; only slightly flexuous on first two whorls, clearly wavy on last whorl with a weak inflection between periphery and basal keel (Fig. 3B); interspaces at periphery twice rib width on first whorl, four to six times on last whorl except last 0.2 of this whorl with more densely packed ribs. Incremental lamellae on first part of teleoconch gradually become less distinct and disappear after 0.8 whorl (Fig. 3F, I). Keels strong and located close to subsequent sutures on early whorls, becoming weaker towards aperture and located halfway between suture and periphery on last whorl in apical and basal views, with distances from suture to keels being 45% to periphery; basal keel stronger than apical one, clearly reaching aperture; apical keel lacking on last 0.3 whorl. Cross-section of whorls thus gradually changes from tall (twice as high as wide) and keeled near protoconch to almost round near aperture. Aperture slightly prosocline, simple, with no dentition or flare or thickening, sharp along margin, 1.15 mm in width; peristome horseshoe-shaped, indented by preceding whorl.

Operculum corneous, transparent but sturdy, multispiral with a central nucleus and >3 whorls, sculptured by faint, irregular growth lines; diameter nearly same as that of peristome; last whorl disproportionately wide, occupying half

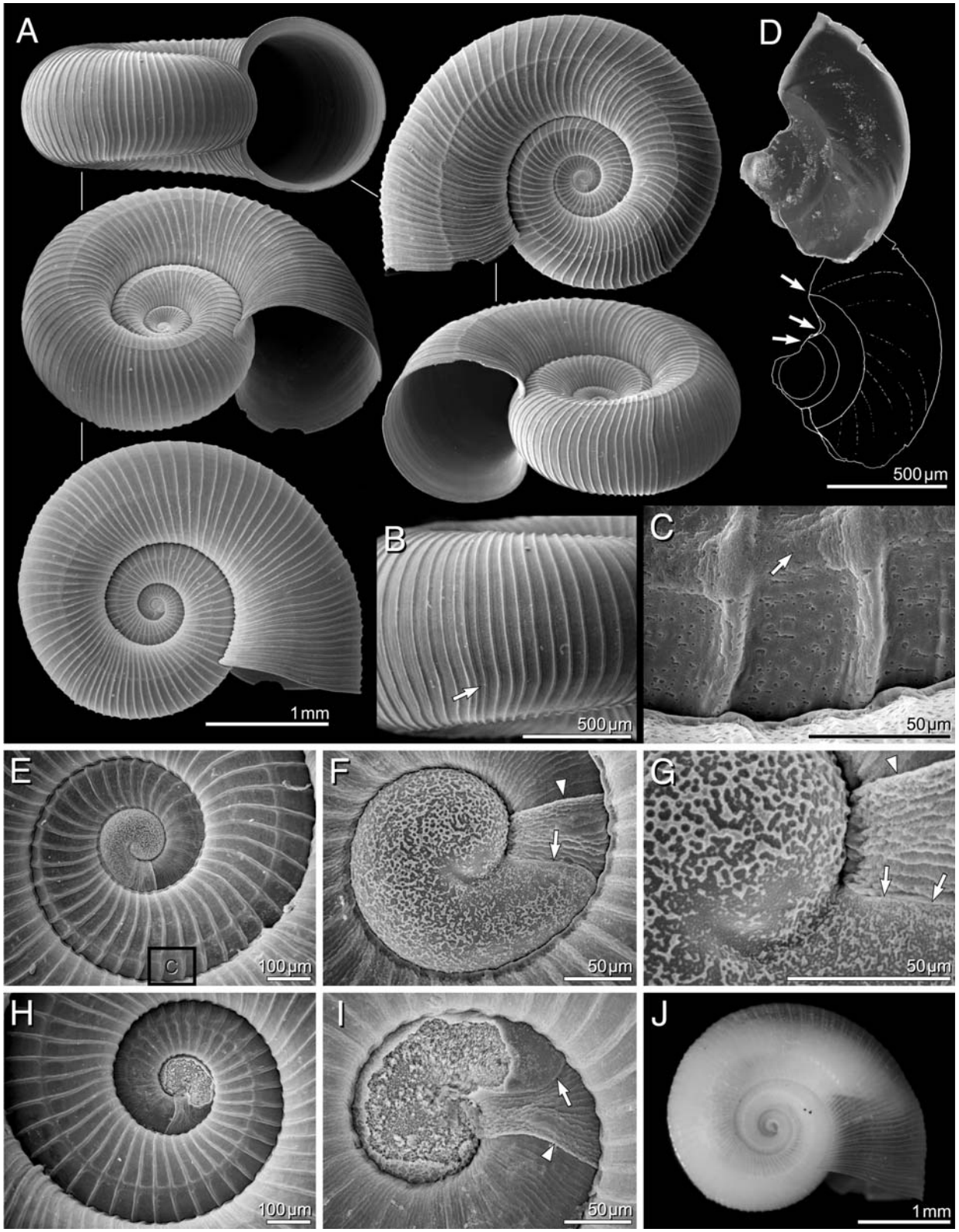

Figure 3. *Adeuomphalus elegans* n. sp., holotype, collected alive from Lau Basin, South Pacific, 1,737 m, NSMT Mo-76859. **A.** Teleoconch. **B.** Close-up of frontal view in **A**, showing inflection of axial ribs (arrow) between periphery and basal keel. **C.** Close-up of **E**, showing scattered microscopic pores and details of basal keel (arrow) and 30th and 31st axial ribs. **D.** External view of operculum, largely broken; trace of outline and sutures (arrows) illustrates disproportionally wide last whorl. **E–I.** Protoconch and early teleoconch whorls in basal (**E–G**) and apical (**H, I**) views; arrows and arrowheads indicate protoconch/teleoconch boundary and end of lamellate section of teleoconch, respectively. **J.** Light micrograph of teleoconch, taken before dehydration and metal coating.

opercular radius and three times wider than previous whorl. Animal entirely colourless; pigmented eyes absent.

Remarks: The present new species is nearly identical to *A. densicostatus* in shell shape (Table 2). This suggests a close phylogenetic relationship between them, despite their remote occurrences in the South Pacific and eastern Atlantic. However, their mature sizes seem to be different; the single specimen of *A. elegans* is 2.95 mm in diameter, while the largest of *A. densicostatus* attains only 2.25 mm (Table 2). They also differ in the dimensions of the exposed areas of the protoconch. In *A. elegans*, the protoconch is less widely exposed in the apical concavity of the teleoconch (165 μm) than in the umbilicus (185 μm), while this is reversed in *A. densicostatus* (180–185 μm in the apex and 165–175 μm in the umbilicus). The difference seemingly arises from dissimilar formation of the first teleoconch whorl, which is slightly hyperstrophic in the former species and orthostrophic (not perfectly planispiral but slightly displaced downwards) in the latter.

Adeuomphalus elegans was found attached to the flat head of a carnivorous, 'lollipop' sponge of the genus *Abyssocladia* in the vicinity of 'shimmering' water of a hydrothermal vent. However, it was uncertain whether the snail was in its natural position or accidentally stuck to the slimy head of the sponge after collection.

The shell shape of the present species somewhat resembles to that of *A. trochanter*, also collected from a vicinity of hydrothermal-vent activity. However, their opercula are quite different. In the present species, the operculum has <4 whorls that rapidly

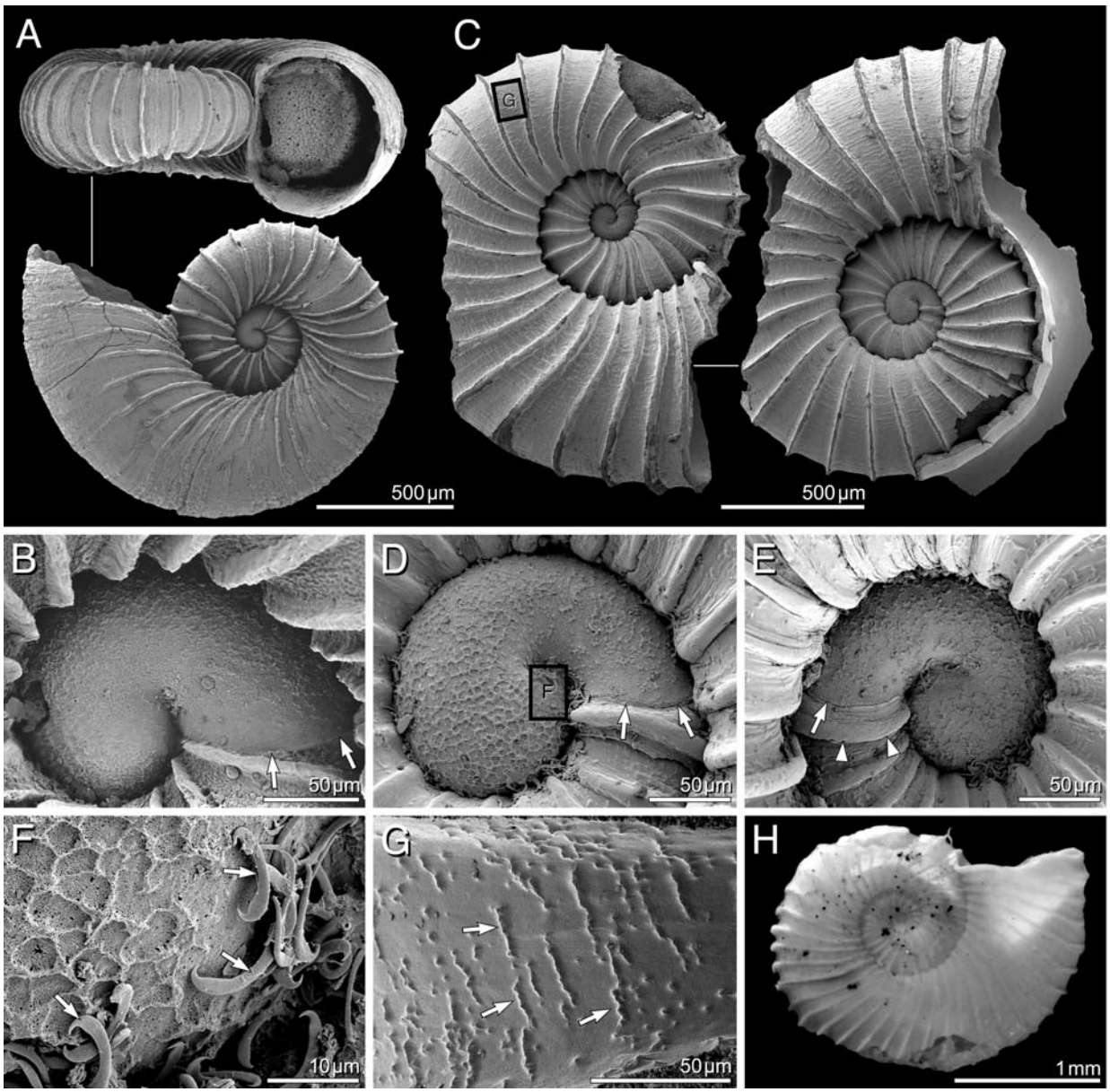

Figure 4. A, B. *Adeuomphalus sinuosus* (Sykes, 1925), syntype from southern Portugal, 1,990 m, BMNH. **A.** Teleoconch with a foraminiferan stuck in aperture. **B.** Protoconch, apical view; arrows indicate protoconch/teleoconch boundary. **C–H.** Holotype of *Adeuomphalus collinsi* n. sp., collected alive from Manus Basin, off Papua New Guinea, 1,440 m, SMNH 5539. **C.** Teleoconch; last 0.5 and 0.2 whorl broken off in basal (left) and apical (right) shots, respectively. **D, E.** Protoconch in apical (**D**) and basal (**E**) views; arrows and arrowheads indicate protoconch/teleoconch boundary and end of lamellate section of teleoconch, respectively. **F.** Close-up of **D**, showing sigmancistra spicules of cladorhizid sponges (arrows) attached to suture of protoconch. **G.** Close-up of **C**, between 30th and 31st axial ribs; minute, conical tubercles are interconnected to form spiral ridges (arrows). **H.** Light micrograph of near-intact teleoconch, taken before dissection and dehydration.

increase in width (Fig. 3D), whereas that of the latter species is more tightly and evenly coiled with >6 whorls (Fig. 2D).

Adeuomphalus sinuosus (Sykes, 1925) new combination
(Fig. 4A, B)

Homalogyra sinuosa Sykes, 1925: 192, pl. 9, fig 8 (two syntypes BMNH unregistered; off southern Portugal, eastern Atlantic, Porcupine Expedition 1870, station 17; 39°42′N, 09°43′W, depth 1,095 fathoms or 1,990 m)

Description: Shell minute; figured syntype 1.41 mm in diameter and 0.60 mm in height (Fig. 4A). Protoconch sculptured with a fine, irregular net-like pattern (Fig. 4B); maximum dimensions of exposed area 185 μm in apical view. Protoconch/teleoconch boundary simple without a lamellate section. Teleoconch whorls 1.8 in number, ornamented with 46 axial ribs (18 in first whorl and 28 in second); spiral keels completely lacking; surface covered with fine, irregularly shaped granules. Axial ribs thin but strong, dome-shaped in cross-section, 10–15 μm in width, with interspaces four to nine times wider than ribs at periphery; first 12 ribs nearly straight while later ones strongly curved backward near sutures; last 20 ribs being faint towards periphery. Aperture orthocline with a protruding outer lip; peristome complete, not indented by preceding whorl, nearly circular except a short, flattened inner lip.

Remarks: This species has not been reported or hardly mentioned since the description by Sykes (1925) based on two empty shells from a bathyal depth off Portugal. Although it was originally placed in the genus *Homalogyra*, we do not hesitate in the present assignment to *Adeuomphalus*. In addition to a general resemblance in teleoconch shape, the fine, irregular net-like sculpture of the protoconch (Fig. 4B) is shared by four species of *Adeuomphalus* (Table 2).

On the other hand, *A. sinuosus* is readily distinguished from the four congeneric species mentioned above in completely lacking the apical and basal spiral keels. It somewhat resembles the sympatric *A. densicostatus*, but the axial ribs of the present species are stronger, more sinuous and more widely spaced than those of the latter.

Adeuomphalus collinsi new species
(Figs 4C–H, 5)

Type material: Holotype (temporary register number SMNH 5539, awaiting a permanent storage solution in Papua New Guinea), collected alive from South Su, Manus Basin, off Papua New Guinea (03°48.76′S, 152°06.24′E; *c.* 1,440 m depth) in the Luk Luk Cruise 2007, Dive #29.

Etymology: Named after Patrick Collins, who found the specimen.

Diagnosis: Shell small, 2.29 mm in diameter. Protoconch with an irregular net-like sculpture; exposed area larger apically than basally. Teleoconch with 2.3 whorls, including an indistinct lamellate section after protoconch; no trace of spiral keels; 73 axial ribs evenly strong, of which 21 present on first whorl and 37 on second; interspaces of ribs bear numerous minute projections that are interconnected in a spiral direction; aperture nearly circular.

Description: Shell small, 2.29 mm in diameter, opaque, thin but not especially fragile (Fig. 4H). Protoconch with numerous pits of 2–6 μm diameter, together forming a net-like sculpture (Fig. 4D, F), ventrally less dense and obvious (Fig. 4E); exposed areas of entire protoconch measure 185 and 155 μm in diameter, apically and basally, respectively. Teleoconch whorls 2.3 in number, ornamented with 73 axial ribs (21 on first whorl and 37 on second); no trace of spiral keels. Immediately after a thin demarcation line of protoconch, several lamellate growth lines appear ventrally on an axial rib, together giving an impression of a thickened lip to protoconch (Fig. 4E). Axial ribs relatively thick and strong throughout, 15–35 μm in width; interspaces at periphery two to four times wider than ribs on first whorl, four to eight times on succeeding whorls; first 10 ribs nearly straight while later ones are sinuous basally. Interspaces of ribs ornamented with numerous, minute conical tubercles of 1–2 μm diameter, often being connected with one another to give rise to fine spiral ridges (Fig. 4G). Aperture simple, orthocline, of nearly circular cross-section, not indented by preceding whorl.

Operculum very thin and fragile (Fig. 5B, C; accidentally damaged); last whorl wide, occupying 35–40% of radius. Radula absent.

Soft parts partly deformed and obscured by an egg mass of a parasitic copepod, possibly of family Chitonophilidae (Fig. 5A, B), with the female seemingly inside the snail body. Snout small and slender, not expanded at distal end; mouth partly ciliated at periphery (Fig. 5D); it can probably be expanded to a funnel. Cephalic tentacles with sensory papillae, basally of similar width as snout, twice as long and tapering (Fig. 5G). Right neck lobe simple, apparently lacking a subocular peduncle. Left neck lobe, cephalic lappets, pigmented eyes and eyelobes absent. Foot large, very wide and flat, posteriorly rounded (Fig. 5C); anterior part drawn out to form two finger-like, ciliated projections (Fig. 5E); propodium not demarcated by anterior pedal groove. Left side of foot with a single epipodial tentacle with sensory papillae and a smooth tentacle with an ESO shortly in front of it (Fig. 5F); ESO-tentacle bears an apical depression from which arose a tuft of cilia; right side of foot similarly equipped. Pallial cavity deep and spacious; gill concealed and inseparably stuck to parasite egg mass.

Remarks: This new species from a hydrothermal vent field in the Manus Basin (off northeastern Papua New Guinea) most closely resembles the preceding *A. sinuosus* from off Portugal in lacking the apical and basal spiral keels, which are conspicuous in most species of the genus (Table 2). However, *A. collinsi* can readily be distinguished from the preceding species by its uniformly strong radial ribs and by a fine spiral sculpture in the interspaces of the ribs (Fig. 4C, G); in *A. sinuosus*, the ribs are faint towards the periphery on the last whorl, and their interspaces are covered with fine, irregularly shaped granules (Fig. 4A, B). Other differences include a larger average size of protoconch pits and the presence of a lamellate section of the teleoconch in the present new species (Fig. 4B, D, E). A fine spiral sculpture has also been described for *A. bandeli* from the early Cretaceous, but the spiral threads of the latter are continuous (Kaim, 2004: fig. C4), not made of interconnected tubercles as in *A. sinuosus*.

No associated sponge was noticed by Patrick Collins, but SEM examination showed cladorhizid spicules to be stuck in the suture of the protoconch. The spicules are 11–13 μm in length, slightly curved and equipped with a hook at each end (Fig. 4F). These characteristics perfectly conform in size to the descriptions for the sigmancistra-2 spicule of *Abyssocladia* species, especially *Abyssocladia dominalba* Vacelet, 2006 (Vacelet, 2006: fig. 14F).

Adeuomphalus guillei new species
(Figs 2A–C, 6)

Type material: Holotype and four paratypes (MNHN 21052, 21053) and five paratypes (SMNH 5540), all collected alive from west of Reunion Island, Indian Ocean (cruise MD32, station DS78, 21°13′S, 55°04′E; 1,175–1,200 m depth).

Etymology: Named after the late Alain Guille (1937–2001) who was the leader of the MD 32 cruise and a specialist on

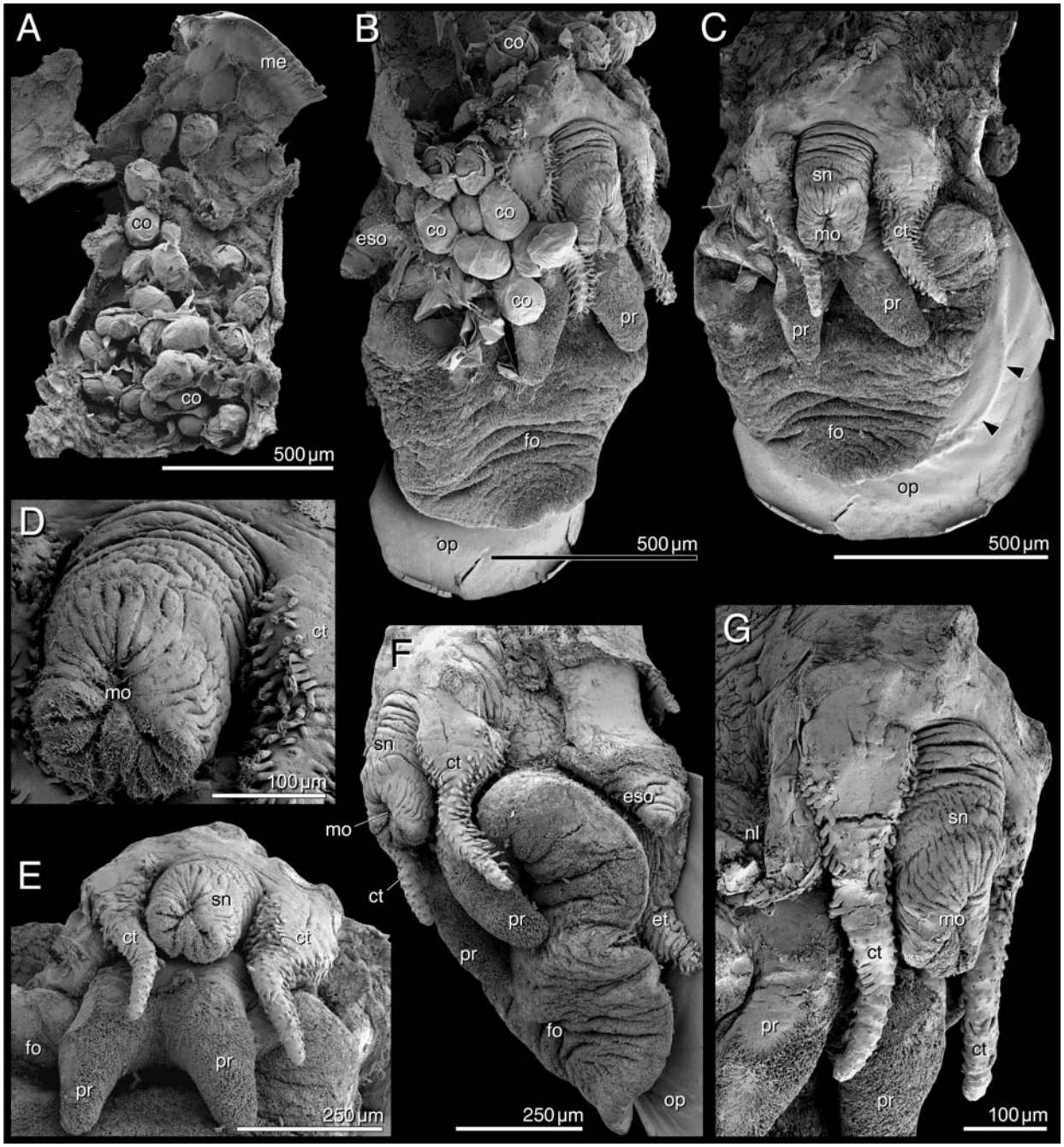

Figure 5. *Adeuomphalus collinsi* n. sp., critical point-dried animal of holotype. **A.** Ventral view of detached mantle roof with an egg mass of a parasitic copepod. **B–G.** Frontal (**C–E**) and lateral (**B, F, G**) views of head foot with removed mantle; copepods removed in **C–G**; arrowheads in **C** indicate suture line of operculum. Abbreviations: co, copepod; ct, cephalic tentacle; eso, tentacle with epipodial sense organ; et, epipodial tentacle; fo, foot; mo, mouth; nl, right neck lobe; op, operculum, pr, propodium or anterior projections of foot; sn, snout.

ophiuroids at MNHN, later director of the Marine Biological Station in Banyuls.

Diagnosis: Shell minute, up to 1.06 mm in diameter. Protoconch large with randomly scattered small tubercles; exposed apical area 245 µm in maximum dimension. Teleoconch whorls up to 1.5 in number; axial ribs strong and flexuous, triangular in cross-section, up to 37 in number, of which *c*. 17 present on first whorl; interspaces of ribs with faint growth lines only; keels present on first 1.1 whorls apically and 1.2 basally; aperture almost circular. Radula present, with formula 3–2–1–2–3.

Description: Shell minute, up to 1.06 mm in diameter, 0.47 mm in height, semitransparent, thin but not fragile (Fig. 2A). Protoconch with randomly scattered small tubercles, of variable shape, size around 1–5 µm in diameter (Fig. 2B, C); maximum dimensions of exposed area 245 and 230 µm in apical and basal views, respectively. Protoconch/teleoconch boundary simple without a lamellate section. Teleoconch with 1.5 whorls, apical and basal spiral keels and up to 37 flexuous axial ribs; first 0.3 whorl sculptured only by faint growth lines. Axial ribs on succeeding whorls triangular in cross-section, 5–20 µm in width, wider near periphery; 17 present on first whorl (first 6 or 7 of them rather faint), 20 on second whorl; interspaces sculptured

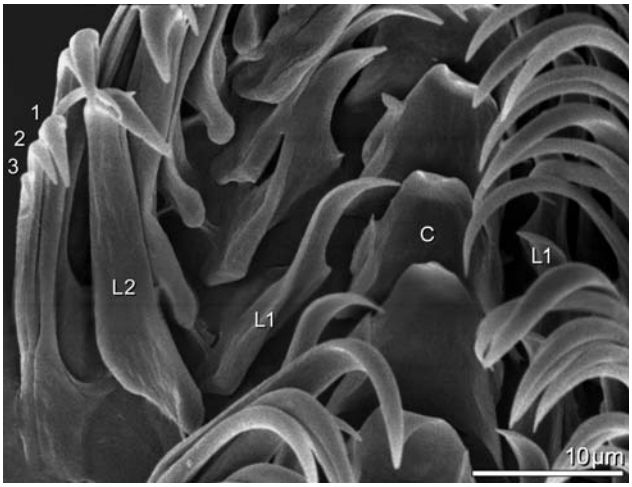

Figure 6. *Adeuomphalus guillei* n. sp., radula of a paratype. Abbreviations: 1–3, first to third marginal teeth; C, central tooth; L1, inner lateral tooth; L2, outer lateral tooth.

only by faint growth lines, two to four times wider than ribs at periphery, except on last 0.3 whorl where ribs are placed more densely and irregularly. Keels strong and located close to subsequent suture in first whorl, but becoming weaker towards aperture; apical keel more prominent than basal one, present on first 1.2 whorls (apical one on first 1.1 whorls). Aperture orthocline, simple, of roughly circular cross-section, 0.36 mm in width, 0.44 mm in height; peristome not continuous, very slightly indented by preceding whorl.

Radula present, of seguenzioid type, formula 3–2–1–2–3 (Fig. 6). Central tooth membranaceous and triangular, *c.* 12 µm in width, interlocking with inner lateral tooth for about half its height. Inner lateral tooth flat, *c.* 18 µm in length, with a poorly set off apical cusp; outer lateral tooth *c.* 1.5 times larger than inner tooth, equipped with a well-defined apical hook. Marginals unusually few in number, similar to outer lateral but slightly smaller, much more slender; innermost one bears a flat base, somewhat similar to 'lateromarginal plate' in calliotropid seguenzioids.

Remarks: This is the only species in the genus known to have a radula, although presence or absence has not been examined in the type *A. ammoniformis* and some other species. The radula is fairly close to that of *Eudaronia biconcava* in having the same formula and similar shapes of teeth (Warén, 1991: fig. 8A), but the presence of prominent axial ribs in the teleoconch seems to justify the assignment of this new species to the genus *Adeuomphalus*. Unfortunately, nothing is known about the biology of *A. guillei*.

Adeuomphalus guillei bears some resemblance to young specimens of *A. densicostatus*. However, the axial ribs are more clearly sinuous, the spiral keels are much shorter and the cross-section of the whorls is more rounded in *A. guillei* than in the latter species. Its protoconch is the largest among the species of the genus and is uniquely sculptured with small, randomly scattered tubercles (Table 2). The small size of *A. guillei* may indicate that the specimens all are juveniles, and no specimens have the weaker sculpture of the last whorl, which seems to be characteristic of large specimens of most species of *Adeuomphalus*.

MOLECULAR PHYLOGENY

Sequence data

Nineteen sequences of the partial 16S gene used in this study range from 499 bp in *Seguenzia* sp. B to 563 bp in *Cataegis* sp. (595 bp in the outgroup *Conradia*) in length, excluding 42 bp of the conserved sequences of the amplification primers 16Sar-L and 16Sbr-H. Ambiguous sites at the 3′ end were trimmed prior to the ProAlign alignment. The aligned data set had 609 sites, of which 298 (48.9%) were variable and 211 (34.6%) were parsimony informative. AIC selected the GTR + I + G model for the ML analyses of the data set. Pairwise divergence among seguenzioid species ranged from 3.6% to 51.9% in the ML distance (3.4–24.3% in uncorrected p-distance). Mean sequence divergence between the ingroup seguenzioids and outgroup vetigastropods was 45.2% in the ML distance and 22.1% in the uncorrected distance.

In addition to this first data set, the second set was created for the 16S sequences by excluding 220 alignment-ambiguous sites that received PP of <60% in the ProAlign analysis. Of the 389 remaining sites, 159 (40.9%) were variable and 105 (27.0%) were parsimony informative. The GTR + G model was selected for the ML analyses and pairwise divergence among seguenzioids ranged from 1.7% to 40.3% in the ML distance (1.6–19.0% in uncorrected distance). Mean sequence divergence between the ingroup seguenzioids and outgroup vetigastropods was 28.8% in the ML distance and 14.8% in the uncorrected distance.

The amplified COI sequence of *Spinicalliotropis chalkeie* was 655 bp in length excluding the regions of two primers (LCOmod and HCO2198). One ambiguous site at the 5′ end was trimmed. The alignment with 18 other COI sequences from the DDBJ had no indels, resulting in 654 available sites for the succeeding analyses. Of these, 339 characters (51.8%) were variable and 300 (45.9%) parsimony informative. Significant substitution saturation was observed in this gene region. Pairwise distances among seguenzioids ranged from 18.4% to 344.3% under the selected TrN + I + G model (10.2–29.7% in uncorrected distance). Mean divergence between the ingroup and outgroup was 199.8% and 26.2% in the ML and uncorrected distances, respectively.

The length of two amplified sequences of the histone H3 gene was 314 bp with the H3MF and H3MR1 primers. The alignment of the H3 data set had no indels; an ambiguous site at each end was trimmed and 312 sites were included in the final alignment, of which 79 (25.3%) were variable and 63 (20.2%) were parsimony informative. Pairwise distances among seguenzioids ranged from 1.3% to 19.5% under the selected TIM +I + G model (1.3–12.5% in uncorrected distance). Distances between ingroup and outgroup OTUs averaged 21.4% in the ML distance and 12.1% in the uncorrected distance. The concatenated three-gene (COI, H3 and 16S) data set consisted of 19 OTUs and unambiguously aligned 1355 sites, which included 577 variable and 468 informative characters. The GTR + I + G model was selected for the ML analyses of this concatenated data set.

The complete 18S rRNA sequence of *Adeuomphalus elegans* amplified in this study was 1924 bp in length, including 44 bp of the conserved primer regions. This is the longest known sequence of the vetigastropod 18S gene except those of Pleurotomariidae (*c.* 2050 bp). Fourteen sequences obtained from the DDBJ had lengths of 1855–1863 bp. The initial alignment generated by ProAlign had 1879 characters after the exclusion of poorly determined sites near the amplification primers. Alignment-ambiguous regions (PP < 60%) were also excluded in the subsequent analyses; more than half of the excluded 181 sites were long insertions in *Adeuomphalus*, which were not found in other taxa. The final alignment had 15 OTUs and 1698 sites, of which 384 (22.6%) were variable and 123 (7.2%) were parsimony informative. The 18S sequence of *Adeuomphalus* differed greatly from those of other taxa, including outgroup vetigastropods, and yet it was closest

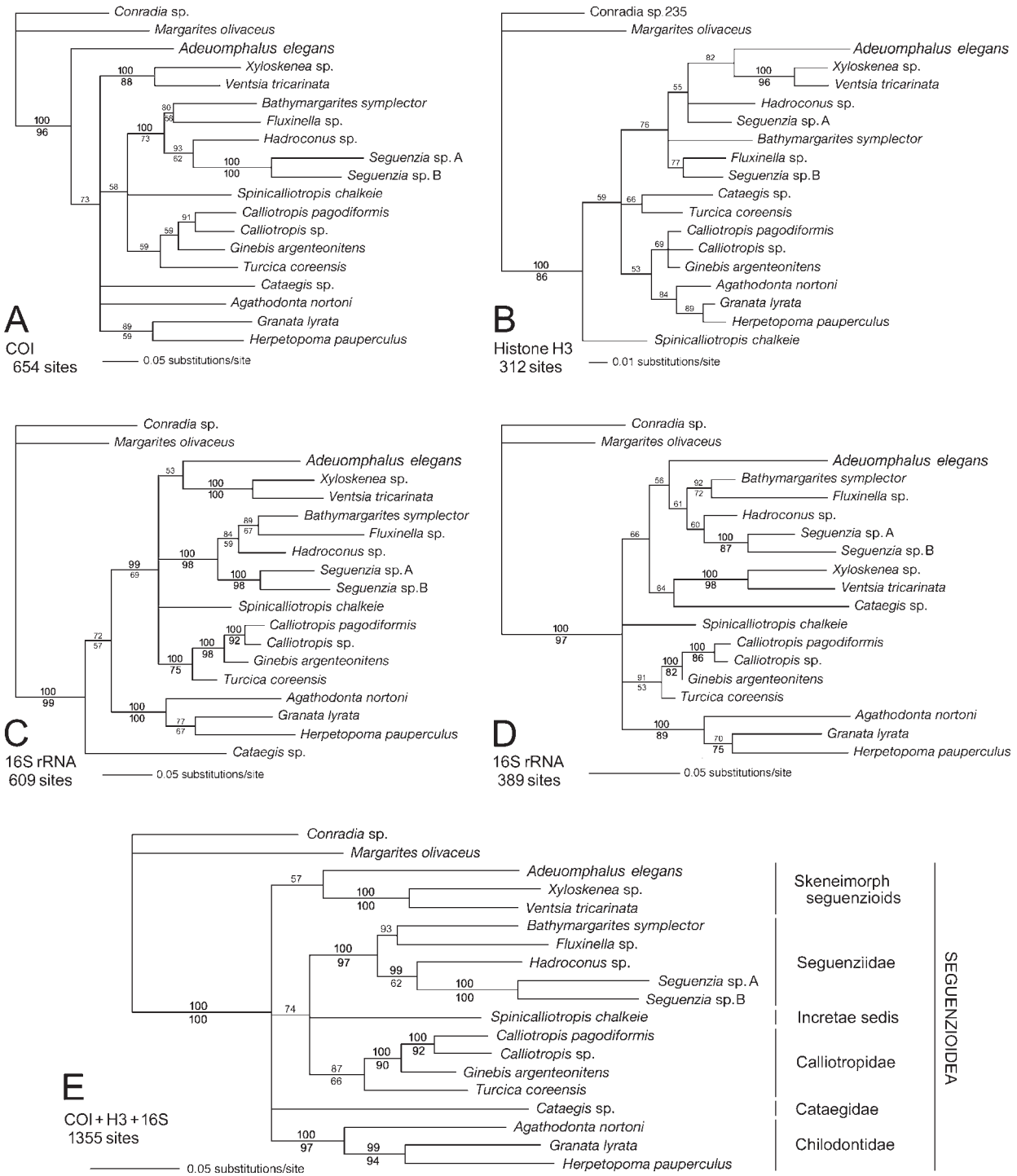

Figure 7. Bayesian phylogenies of Seguenzioidea. Numbers above branches denote PPs and below branches are BPs calculated by ML analyses; significant support (PP $\geq$ 95%, BP $\geq$ 75%) in bold. **A–D.** Trees based on single gene analyses of nuclear histone H3, mitochondrial COI and 16S rRNA genes. 16S trees were reconstructed with or without 220 alignment-ambiguous sites detected by ProAlign analysis (**C** and **D**, respectively). **E.** Concatenated-gene tree of histone H3, COI and 16S. New familial classification of superfamily is introduced based on present phylogenies.

to the ingroup species *Calliotropis pagodiformis*. Pairwise distances between *Adeuomphalus* and other OTUs ranged from 29.5% to 32.2% in the TrN + I + G distance selected by AIC (15.1–15.9% in uncorrected distance), whereas mean divergence between the ingroup and outgroup species was only 9.9% and 6.4% in the ML and uncorrected distances, respectively.

Phylogenetic analyses

Bayesian analyses of six data sets yielded the consensus trees shown in Figures 7 and 8. The ML analyses produced tree topologies very similar to those of the Bayesian trees, retrieving all clades with significant PP support ($\geq$95%), and therefore the ML trees are not shown here. Seguenzioidea were

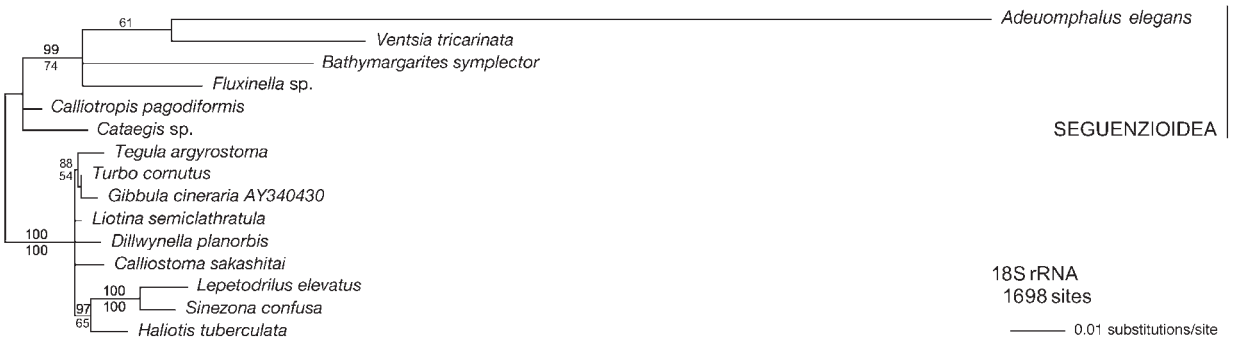

Figure 8. Bayesian phylogenies of Seguenzioidea, based on near-complete sequences of nuclear 18S rRNA gene. Numbers above branches denote PPs and below branches are BPs calculated by ML analyses; significant support (PP $\geq$ 95%, BP $\geq$ 75%) in bold.

recovered as a robust monophyletic clade in all data sets (PP = 100%, BP $\geq$ 86%). No conflicting clades with significant support were identified among the trees inferred from the six data sets.

The COI data set yielded the Bayesian tree shown in Figure 7A. Three ingroup clades received significant statistical support under either or both of the Bayesian and ML criteria: *Xyloskenea* + *Ventsia* (PP = 100%, BP = 88%), two species of *Seguenzia* (PP, BP = 100%) and *Bathymargarites* + *Fluxinella* + *Hadroconus* + *Seguenzia* (PP = 100%, BP = 73%). *Adeuomphalus* appeared as the first offshoot in Seguenzioidea, but with low support values (PP = 73%, BP < 50%). Short sequences of the H3 gene yielded a poorly resolved tree by the Bayesian analysis (Fig. 7B). Only one clade, *Xyloskenea* + *Ventsia*, received significant support in Seguenzioidea (PP = 100%, BP = 86%), and these skeneimorphs appeared as the possible sister group of *Adeuomphalus* (PP = 82%, BP < 50%).

The 16S data set with alignment-ambiguous sites recovered a number of highly supported clades (Fig. 7C), although some doubt remains as to character homologies at those sites; such signals might have significant effects leading to reconstruction of erroneous tree topologies. All three clades recovered unambiguously in the COI trees also received high support values in this 16S reconstruction (PP = 100%, BP $\geq$ 98%). The following clusters were additionally recognized with significant PP (100%) and BP ($\geq$75%): *Agathodonta* + *Granata* + *Herpetopoma* (BP = 100%), two *Calliotropis* (92%), *Calliotropis* + *Ginebis* (98%) and *Calliotropis* + *Ginebis* + *Turcica* (75%). All ingroup OTUs excluding *Agathodonta*, *Granata*, *Herpetopoma* and *Cataegis* constituted a large clade with a high PP (99%) and a moderate BP (69%). *Adeuomphalus* equivocally clustered with *Xyloskenea* and *Ventsia* (PP = 53%, BP < 50%). The exclusion of 220 alignment-ambiguous sites resulted in less resolved trees for the 16S-gene phylogeny (Fig. 7D). Deep nodes were collapsed or supported only by insignificant PP and BP values, whereas five shallower nodes were consistently retrieved with high PP and BP (100% and $\geq$82%, respectively): *Agathodonta* + *Granata* + *Herpetopoma* (BP = 89%), *Calliotropis* (86%), *Calliotropis* + *Ginebis* (82%), *Seguenzia* (87%) and *Xyloskenea* + *Ventsia* (98%). The exclusion of the ambiguous sites moved the position of *Adeuomphalus* close to *Bathymargarites* and seguenzioids, but with negligible statistical support (PP = 56%, BP < 50%).

Figure 7E shows a Bayesian tree reconstructed from the concatenated COI, H3 and 16S sequences (excluding the alignment-ambiguous sites). As the independent gene trees were congruent in terms of robust clades, support for various nodes was increased in this concatenated data set. The above-mentioned robust clades were all recovered with PP of 100% (BP $\geq$ 90%), except two in the 16S phylogeny with ambiguous sites. Of these, the clade *Calliotropis* + *Ginebis* + *Turcica* received relatively high support (PP = 87%, BP = 66%), while the other large clade with 13 OTUs (see Fig. 7C) was collapsed to a basal polytomy in the three-gene Bayesian tree. Two clusters were newly recognized with significant statistical values: *Granata* + *Herpetopoma* (PP = 99%, BP = 94%) and *Hadroconus* + *Seguenzia* (PP = 99%, BP = 62%). The position of *Adeuomphalus* was still unclear; the new species formed an ambiguous clade with *Xyloskenea* and *Ventsia* (PP = 57%, BP < 50%).

The near-complete sequences of 18S were used to investigate phylogenetic relationships among six ingroup genera, including *Adeuomphalus*, *Ventsia*, *Bathymargarites*, *Fluxinella*, *Calliotropis* and *Cataegis* (Fig. 8). Only one clade received significant PP support: *Adeuomphalus* + *Ventsia* + *Bathymargarites* + *Fluxinella* (PP = 99%, BP = 74%). *Adeuomphalus* clustered with *Ventsia* in both Bayesian and ML analyses, albeit with insignificant support values (PP = 61%, BP < 50%).

DISCUSSION

Shell and radular characteristics of Adeuomphalus

The present morphological investigation supports previous assumptions that *Adeuomphalus* is related to *Eudaronia* and *Palazzia*, two little-known genera from the deep sea. The latter two taxa share many characteristics with *Adeuomphalus*, including an almost perfectly planispiral shell, a deeply concave apex and base, apical and basal spiral keels, and a protoconch surface with star-shaped granules that are often interconnected to each other to form a net-like pattern (Figs 1–4; Warén, 1991: figs 14–18). The radula of *Adeuomphalus*, which has been found only in *A. guillei*, also shows a fair resemblance to that of *Eudaronia* species. Their radulae have the same number of teeth in the transverse row and are similar in the shape of each tooth, with some modification in the size of the outer lateral and marginal teeth that are a little longer in *E. biconcava* than in *A. guillei* (Fig. 6; Warén, 1991: fig. 8A). The fact that the seven species of *Adeuomphalus* are morphologically so diverse and that they have characteristics intermediate between the type species of *Eudaronia* and *Palazzia* may pose a question as to the monophyly of the present genus. However, it is impossible at present to demarcate the genera based rigorously on phylogenetic relationships among all species of the three groups. The external soft-part morphology is known only for *A. collinsi*, some anatomical details are known in *A. trochanter*, and ethanol-preserved material useful for DNA extraction has been available only for *A. elegans* among the species of these rare genera.

Although the monophyly of the three genera together is almost unquestionable, the sister group of this clade cannot be easily identified based on morphological characteristics. The

radulae of *A. guillei* and *E. biconcava* show seguenzioid affinity in the reduced number of teeth and the triangular central tooth with an interlocking structure (Kano, 2008). However, somewhat similar radulae have been found in various, presumably unrelated, genera of Seguenzioidea. These genera include the members of the family Seguenziidae [*Ancistrobasis* Dall, 1889, *Asthelys* Quinn, 1987, *Basilissa* Watson, 1879, *Calliobasis*, Marshall, 1983, *Carenzia* Quinn, 1983, *Fluxinella* Marshall, 1983, *Guttula* Schepman, 1908, *Halystes* Marshall, 1988, *Halystina* Marshall, 1991, *Quinnia* Marshall, 1988 (= *Seguenziella* Marshall, 1983), *Seguenzia* Jeffreys in Seguenza, 1876 and *Sericogyra* Marshall, 1988; see Knudsen, 1964; Quinn, 1983; Marshall, 1983, 1988a, 1991; Hickman 1998] and 'skeneimorph seguenzioids' of unknown familial affinity (e.g. *Akritogyra* Warén, 1992, *Anekes* Bouchet & Warén, 1979, *Benthobrookula* Clarke, 1961, *Retigyra* Warén, 1989, *Trenchia* Knudsen, 1964, *Ventsia*, *Vetulonia* Dall, 1913 and *Xyloskenea*; see Knudsen, 1964; Marshall, 1988b; Warén & Bouchet, 1989, 1993; Hickman & McLean, 1990; Warén, 1992, 1993, 1996; Zelaya, Absalão & Pimenta, 2006). The similarity of their radula may partly be due to convergence during the process of simplifying the teeth associated with the reduction of body size (Warén, 1991; Kano, 2008).

A protoconch sculpture similar to the net-like pattern found in most species of *Adeuomphalus*, *Eudaronia* and *Palazzia* is present in *Benthobrookula*, but the protoconch of the latter genus is more globose and inflated with a shorter, less marked suture line (Zelaya *et al*., 2006: figs 4–8). The heterogeneity of protoconch sculptures within *Adeuomphalus* (Table 2) and also within many other vetigastropod genera (e.g. Marshall, 1988b, 1991; Warén, 1992, 1993) suggests that only very similar patterns of the same size and structure should be used to infer close relationships and that great differences do not necessarily indicate distant relationships. Similar, but seemingly analogous, protoconch sculptures such as spiral threads or reticulate patterns have been reported in distantly related genera of Vetigastropoda (e.g. spiral threads in *Carenzia*, *Collonista* Iredale, 1918, *Seguenzia*, *Skenea* and *Xyloskenea*; reticulate patterns in *Lepetella* Verrill, 1880 and *Calliostoma* Swainson, 1840; see Marshall, 1988b, 1991; Warén, 1991; Hickman, 1992).

Variations in external anatomy of seguenzioids

External anatomy also gives rather little information about the phylogenetic affinity of *Adeuomphalus* within Seguenzioidea. This is mainly because of our limited knowledge of the anatomy of seguenzioids, but probably also because structures have become simplified in association with reduced body size and specialized ecology (see below). The two species of the genus for which some soft-part information is available, *A. collinsi* and *A. trochanter*, share several of the few characters known. They have blunt and tapering cephalic tentacles with sensory papillae, a simple right neck lobe and a large foot with the anterior corners drawn out into finger-like projections; pigmented eyes, eye lobes, cephalic lappets and subocular peduncles are all lacking (Fig. 5). The gill was not successfully observed in *A. collinsi* due to an inseparably stuck egg mass of a parasitic copepod, but it was found to be monopectinate and composed of ten leaflets in *A. trochanter* (Warén & Bouchet, 2001: 132). Details of epipodial appendages were first observed in the present study (in *A. collinsi*). Each side of the foot similarly bears a smooth 'ESO-tentacle' anteriorly and an epipodial tentacle with sensory papillae posteriorly (Fig. 5B, F). The ESO was first described by Crisp in trochids as a small knob with a central depression from which arises a tuft of long cilia (Crisp, 1981: fig. 5A), but a more elaborate tentacular structure in *Clypeosectus* McLean, 1989 and *Pseudorimula* McLean, 1989 (Lepetodriloidea), with an ESO at the tip was described as an ESO-tentacle (Haszprunar, 1989: fig. 8B).

Besides *Adeuomphalus*, scattered details of the soft-part morphology have been reported for only 18 genera among over 60 living ones in Seguenzioidea. They include *Calliotropis* Seguenza, 1903 and *Bathybembix* Crosse, 1893 of Calliotropidae (see below for familial classification), *Danilia* Brusina, 1865, *Euchelus* Philippi, 1847, *Granata* Cotton, 1957, *Herpetopoma* Pilsbry, 1889 and *Hybochelus* Pilsbry, 1889 of Chilodontidae, *Cataegis* McLean & Quinn, 1987 of Cataegidae, *Seguenzia*, *Bathymargarites*, *Guttula* and *Sericogyra* of Seguenziidae, and *Akritogyra*, *Anekes*, *Granigyra* Dall, 1889, *Ventsia*, *Vetulonia* and *Xyloskenea* of skeneimorph seguenzioids (Beu & Climo, 1974; Quinn, 1983, 1991; McLean & Quinn, 1987; Marshall, 1988a, b; Warén & Bouchet, 1989, 1993; Hickman & McLean, 1990; Warén, 1991, 1993; Sasaki, 1998; Kano, 2008).

Of these, genera in two common, large-sized families, namely Calliotropidae and Chilodontidae, all have well-developed eyes and eye lobes, right subocular peduncle(s), cephalic lappets, right and left neck lobes with fringing tentacles, several pairs of micropapillate epipodial tentacles, and a large bipectinate ctenidium with a short afferent membrane and a long free tip (Hickman & McLean, 1990; Kano, 2008). *Cataegis* has somewhat similar soft-part characteristics, but it lacks the cephalic lappets and right subocular peduncle, and its bipectinate ctenidium has a long afferent membrane and a relatively short free tip (McLean & Quinn, 1987; Hickman & McLean, 1990; Warén & Bouchet, 1993). Both *Seguenzia* and *Bathymargarites* have the right subocular peduncle and lack the cephalic lappets, but otherwise they are quite different from each other in external anatomy. Pigmented eyes, eye lobes and neck lobes are present only in *Bathymargarites*; the epipodium is equipped with three pairs of micropapillate tentacles in *Seguenzia* and dozens of pairs in *Bathymargarites*; the mantle margin bears numerous small projections with an apical tuft of cilia in the former, while the margin is simple and smooth in the latter; the ctenidium is simple and monopectinate in the former, whereas it is bipectinate with a short afferent membrane in the latter; the subocular peduncle is modified and hypertrophied to function as a penis in male *Bathymargarites*, while a penis of different morphology is present in male *Seguenzia* posterior to the peduncle, along with another projection called the 'accessory cephalic process' with an unknown function (Quinn, 1983; Warén & Bouchet, 1989; Sasaki, 1998; T. Sasaki, personal communication).

The six genera of skeneimorph seguenzioids for which anatomical information is available (*Akritogyra*, *Anekes*, *Granigyra*, *Ventsia*, *Vetulonia* and *Xyloskenea*) collectively have simplified organization of the soft parts, including a short monopectinate gill and absence of the cephalic lappets, perhaps associated with reduction of body sizes. However, significant differences also exist in their cephalic and epipodial regions. *Akritogyra* and *Granigyra* retain the right and left neck lobes, a small right subocular peduncle and several pairs of epipodial tentacles, although they lack sensory papillae in all tentacles (Warén, 1992: 162, 1993: fig. 20). *Anekes* is also peculiar in having an anteriorly and posteriorly bifid foot; it otherwise bears pigmented eyes in lobes, neck lobes on both sides, right subocular peduncles, three pairs of papillate epipodial tentacles and one pair of possible ESO-tentacles (Warén, 1992: 166). *Vetulonia* is rather similar to calliotropids and chilodontids in retaining large eyes in lobes, both neck lobes and seven pairs of epipodial tentacles; a possible subocular peduncle is also seen below the right cephalic tentacle in an SEM photograph (Warén & Bouchet, 1993: fig. 9C).

In soft part morphology, *Xyloskenea* and *Ventsia* are fairly similar to each other. According to Marshall (1988b) and Warén & Bouchet (1993), these snails have degenerate eye

lobes, two fairly large right subocular peduncles and two pairs of epipodial appendages. Pigmented eyes and left neck lobe are lacking in both genera. Interestingly, the two pairs of epipodial appendages of the two genera are very similar to those of *Adeuomphalus*. The anterior ESO-tentacles are characterized by a smooth surface and a round tip with a crown of cilia, and the posterior epipodial tentacles by a tapering shape and sensory papillae (Marshall, 1988b: 968; Warén & Bouchet, 1993: fig. 25A, B; Kunze *et al*., 2008: fig. 1A). Moreover, they share the anterior, finger-like projections of the foot with *Adeuomphalus* (Marshall, 1988b: fig. 9D; Warén & Bouchet, 1993: fig. 25C). These similarities might suggest a phylogenetic position of *Adeuomphalus* close to *Xyloskenea* and *Ventsia*, but other morphological characters do not particularly support such a relationship. The right subocular peduncles and laterally expanded oral disk are found only in *Xyloskenea* and *Ventsia*; a low-spired teleoconch and a spirally ribbed protoconch also distinguish these two genera from *Adeuomphalus*, as does the radula (Warén & Bouchet, 1993: figs 23, 24; see below). More anatomical information on skeneimorph seguenzioids is clearly needed for a rigorous assessment of the phylogenetic implications of these characters.

Molecular phylogeny and systematics of skeneimorph seguenzioids

The present molecular phylogeny based on the concatenated three-gene sequences suggest, although rather ambiguously, that *Adeuomphalus* constitutes a clade with the above-mentioned *Xyloskenea* and *Ventsia* (Fig. 7E). As they are the only skeneimorph seguenzioids included in the analyses, it does not necessarily suggest a close relationship between *Adeuomphalus* and the latter two genera. Rather, it confirms the phylogenetic position of *Adeuomphalus* among some skeneimorph seguenzioids. The monophyly of the three genera was not supported in the independent trees of the COI gene and the small data set of the 16S rRNA gene; *Adeuomphalus* was equivocally retrieved as the sister group of either the family Seguenziidae or all the ingroup OTUs (Fig. 7A, D). However, the former, the earliest branching of *Adeuomphalus* among seguenzioids, was clearly rejected by the analyses of the complete sequences of the 18S rRNA gene, where the genus constitutes a robust clade with *Ventsia*, *Bathymargarites* and *Fluxinella* (Fig. 8, PP = 99%; but see below). Two included skeneimorphs constituted a clade (*Adeuomphalus* + *Ventsia*), again suggesting close relationships among those groups of minute snails.

Xyloskenea and *Ventsia* are undoubtedly closely related to each other, with high support values in all independent and concatenated gene trees. *Ventsia* is a monotypic genus and its type *Ventsia tricarinata* is from a hydrothermal vent in the Lau Basin, South Pacific (Warén & Bouchet, 1993). *Xyloskenea* comprises numerous species from sunken pieces of wood in the worldwide deep-sea (Marshall, 1988b; Warén, 1996). As briefly mentioned above, they are morphologically similar to each other and also to a third genus, *Trenchia*, from the Kermadec Trench off New Zealand, in the teleoconch shape and protoconch sculpture (Warén & Bouchet, 1993). On the other hand, the radula of *Xyloskenea* displays a major modification from the typical seguenzioid arrangement with sharply serrated teeth in *Ventsia* and *Trenchia* (Knudsen, 1964: fig. 6; Warén & Bouchet, 1993: fig. 24; Warén, 1996: figs 5, 6). The present molecular data thus verify that the radular morphology may be surprisingly different in closely related skeneimorph genera; this may be driven by paedomorphic evolution or different feeding ecology. Therefore, suprageneric classification should not be based uncritically on this often overvalued character (see Warén, 1990; Warén & Gofas, 1996).

The present phylogeny involves only a very small part of the vast diversity of skeneimorph seguenzioids, which are only vaguely grouped by derived characters including a minute size, simplified anatomy and radula, and lack of a nacreous shell layer (Kano, 2008). We therefore refrain from classifying these skeneimorphs into a family or (sub-) families such as Eudaroniinae proposed by Gründel (2004), until more material becomes available for molecular and anatomical studies. The following 17 skeneimorph genera are confirmed or probable members of Seguenzioidea: *Adeuomphalus*, *Aequispirella* Finlay, 1924, *Akritogyra*, *Anekes*, *Benthobrookula*, *Eudaronia*, *Granigyra*, *Microcarina*, *Notosetia* Iredale, 1915, *Trenchia*, *Palazzia*, *Putilla* Adams, 1867, *Retigyra*, *Ventsia*, *Vetulonia*, *Wanganella* Laseron, 1954 and *Xyloskenea*. Four more taxa, *Brookula* Iredale, 1912, *Lissotesta* Iredale, 1915, *Lissotestella* Powell, 1946 and *Moelleriopsis* Bush, 1897 (= *Abyssogyra* Clarke, 1961) are plausible members of the group (see Warén, 1989, 1991, 1992, 1993, 1996 for descriptions of their morphology).

As the radula is an easily available morphological character for distinguishing a seguenzioid or a trochoid affinity of skeneimorph snails (Kano, 2008), many radula-less taxa remain unassigned to either of these superfamilies. However some, if not most, of these radula-less skeneimorphs show resemblances to the plausible seguenzioids listed above in shell morphology. They include *Lissomphalia* Warén, 1992 and *Mikro* Warén, 1996. Species of *Mikro* resemble *Lissotesta* species in having a globose teleoconch with smooth, strongly convex whorls and a wide umbilicus, although their protoconchs are different (Warén, 1996: fig. 1). *Lissomphalia* might have a close relationship to *Akritogyra* or *Moelleriopsis*, which have somewhat similar teleoconch and protoconch morphology (Warén, 1992: figs 39, 40).

Here it is interesting to note that *Trochaclis* Thiele, 1912 has shell characteristics similar to those of *Moelleriopsis*. They both have conspicuous keels on the shoulder of early teleoconch whorls and in the umbilicus (Warén, 1992: figs 31A–C, 36). *Trochaclis* is the type genus of another enigmatic family Trochaclididae Thiele, 1929, which is diagnosed exclusively by numerous feather-like teeth in a transverse row of the radula (Warén, 1989; Marshall, 1995a). However, such a highly apomorphic condition does not provide a phylogenetic signal in assigning the family to a vetigastropod superfamily. Specialised feeding ecology may explain the unique radular morphology; association with sponges has been observed in trochaclidids (Warén, 1992; Marshall, 1995a).

The extremely high evolutionary rate of the nuclear small-subunit rRNA gene in *Adeuomphalus*, and in *Ventsia*, *Bathymargarites* and *Fluxinella* to lesser extent (Fig. 8), may possibly have affected the topology of the gene tree and erroneously clustered the four genera due to the long-branch attraction (LBA) artefact. We do not think this is likely, because the Bayesian and likelihood methods are less sensitive, to LBA than simple parsimony, although not immune to its effects (Bergsten, 2005), and because two other genes (nuclear Histone H3 and mitochondrial 16S rRNA) yielded similar tree topologies (Fig. 7B, C). However, too high an evolutionary rate in an rRNA gene is problematic as it prevents a rigorous sequence alignment and sequence comparisons with short-branched OTUs. Extraordinarily high rates are also observed in the large-subunit (28S) rRNA gene sequences of skeneimorph seguenzioids (Y.K., unpubl.). Exploitation of different genes would be highly valuable in future phylogenetic studies of the group.

New classification of seguenzioid families

In contrast to the limited resolution of the suprageneric classification of skeneimorphs, the present molecular data provide an improved phylogenetic basis for the familial classification of other seguenzioid taxa. In the superfamily Seguenzioidea, we

recognize four extant families, namely Seguenziidae Verrill, 1884, Chilodontidae Wenz, 1938, Calliotropidae Hickman & McLean, 1990 and Cataegidae McLean & Quinn, 1987 and one unclassified genus *Spinicalliotropis* Poppe, Tagaro & Dekker, 2006, in addition to the above skeneimorphs (Table 1, Fig. 7E).

One of the most interesting findings in the present phylogeny is the inclusion of *Bathymargarites* in Seguenziidae (Fig. 7E, PP = 100%, BP = 97%). *Bathymargarites* is a medium-sized snail from hydrothermal vents on the East Pacific Rise (Warén & Bouchet, 1989, 1993). It has a large and complicated penis in males and lacks the cephalic lappets, while otherwise similar to calliotropids and chilodontids, but not to *Seguenzia*, in external anatomy as well as in radular morphology (Kano, 2008). The previous taxonomic position of *Bathymargarites* in Eucyclinae of Trochidae (*sensu* Hickman & McLean, 1990; Calliotropidae and Chilodontidae in the present classification) was primarily based on the radula with a hooded central and laterals, a lateromarginal plate and numerous marginals in each transverse row. However, such a radula most probably represents a plesiomorphic condition for the entire Seguenzioidea, which is retained only in large or medium-sized taxa, as is also the case for the bipectinate ctenidium (Kano, 2008). An intriguing fact is that the penes in *Bathymargarites* and *Seguenzia* are rather different in shape and position (see above) and may possibly have been acquired independently (Kano, 2008). The homology or analogy of the copulatory organs could probably be revealed by future anatomical studies of various seguenziids, especially *Fluxinella*, which was clustered with *Bathymargarites* in the COI, 16S and concatenated gene trees (Fig. 7A, C–E).

Semi-internal fertilization in the female mantle cavity is strongly suspected in all seguenziids and also in many, if not all, skeneimorph seguenzioids (previously exemplified in *Microcarina* and *Ventsia*; see Kano, 2008; Kunze *et al*., 2008). Interestingly, Seguenziidae and three included skeneimorphs constituted a clade in the present H3 and 18S gene trees as well as in those from the small 16S data set (PP = 99% in the 18S data). The three-gene data set yielded a different topology (Seguenziidae + Calliotropidae + *Spinicalliotropis*), but with low PP and bootstrap values (PP = 74%, BP < 50%). Regardless of the homology or analogy of the penes and seminal receptacles in these groups, copulation and semi-internal fertilization may have evolved only once in the superfamily. Even the least known (semi-) internal fertilization of Pendromidae (Warén, 1991; Kano, 2008) may suggest a phylogenetic placement of the family in this possible monophylum.

We classify most genera of Eucyclinae *sensu* Hickman & McLean (1990) in Chilodontidae and Calliotropidae. The two families were treated previously as sister tribes in the trochid subfamily Eucyclinae (Hickman & McLean, 1990; Hickman, 1996, 1998) or as two subfamilies in Chilodontidae (Bouchet *et al*., 2005; Williams *et al*., 2008). However, species of the two groups did not constitute a clade in any of the present trees; rather, calliotropids were found to be more closely related to seguenziids and skeneimorphs than to chilodontids (Fig. 7A, C, E). Conchological resemblances between *Calliotropis* and some seguenziids have also been pointed out (Bouchet *et al*., 2005; Kano, 2008). We therefore consider that Chilodontini and Calliotropini (*sensu* Hickman & McLean, 1990) are better regarded as two independent family groups. Included genera of the two families largely correspond to those listed in Hickman & McLean (1990: 77–86) for the two respective tribes, but *Turcica* Adams, 1854 is here reallocated from Chilodontidae to Calliotropidae based on tree topologies (e.g. Fig. 7C; PP = 100%, BP = 75%). Characters discriminating the Chilodontini from the Calliotropini included a smaller and thicker shell and the presence of columellar denticles and a thickened outer lip in the shell aperture (Hickman & McLean, 1990). However, these characters do not clearly separate the two groups. Species of *Turcica* including the type *T. monilifera* and sequenced *T. coreensis* combine conchological features of both groups: large (>30 mm) but relatively thin shell, one or two columellar teeth and slightly thickened outer lip (e.g. Knight *et al*., 1960: fig. 163.12; Hickman & McLean, 1990: fig. 40A). Columellar teeth and thickened outer lip can be found in some species of *Calliotropis*, the type genus of Calliotropidae (e.g. Vilvens, 2007). Rigorous synapomorphies of the two families may be found in anatomical characters, which have not yet been adequately investigated in spite of the common occurrences of these snails in the intertidal to upper bathyal depths of temperate to tropical seas of the world.

The fourth family Cataegidae was originally described as a new subfamily of Trochidae with a peculiar radular configuration. *Cataegis*, so far the only genus of the family, is a group of medium-sized turbiniform snails from bathyal, soft-bottom environments in the Western Pacific and the Western Atlantic. The radulae of two species examined in the original description lacked the central tooth and possess a fused first pair of laterals (McLean & Quinn, 1987). Warén & Bouchet (1993) and Bouchet *et al*. (2005) later found less modified radulae in two other species of the genus that bear the hooded and interlocking central and lateral teeth of typical, large-sized, probably plesiomorphic seguenzioids, exemplified by Chilodontidae and Calliotropidae. Based on the less modified radulae, they included *Cataegis* within the Chilodontidae, while maintaining the subfamily Cataeginae in their classification (Bouchet *et al*., 2005). Our concatenated three-gene analysis placed the genus in an unresolved position alongside five other main clades in basal polytomies, and none of the independent gene trees firmly clustered it with other seguenzioids (Figs 7, 8). We therefore tentatively treat it as an independent family; this familial status may be justified by its anatomical uniqueness including the relatively long afferent membrane of the ctenidium as well as the lack of the right subocular peduncles and cephalic lappets (McLean & Quinn, 1987; Warén & Bouchet, 1993: fig. 15; see above).

Another evolutionary branch with an ambiguous phylogenetic position is represented by *Spinicalliotropis chalkeie* (new combination) from a bathyal soft-bottom in Vanuatu, South Pacific. *Spinicalliotropis* was originally proposed as a subgenus of *Calliotropis* by emphasizing the presence of spiny or scale-like projections at the intersections of the axial and spiral ribs in the teleoconch of the type species '*Calliotropis* (*Spinicalliotropis*)' *spinosa* (Poppe *et al*., 2006). On the other hand, its gross shell shape resembles that of small-sized species of *Calliotropis s. s.* and the subgeneric name was not referred to in the description of the very similar '*Calliotropis*' *chalkeie* (Vilvens, 2007). Neither radula nor anatomy has previously been investigated in *Spinicalliotropis*, but the sequenced specimen of *S. chalkeie* revealed a number of diagnostic characters in its external anatomy, and they might prove a long independent evolutionary history of the genus. It has two right subocular peduncles, a few pairs of epipodial appendages, a laterally expanded oral disk, a bipectinate ctenidium and a possible seminal receptacle, and lacks the cephalic lappets, pigmented eyes, eye lobes and right and left neck lobes; the cephalic tentacles are very large with peculiarly adjoining bases near the midline of the head (Y.K., personal observation). However, we refrain from establishing a new family or other taxonomic ranks until a full anatomical description for the genus and a better-resolved molecular phylogeny are available. *Spinicalliotropis* can be distinguished conchologically from other seguenzioids in having a small (<7 mm in height), conical, thin and nacreous shell with a cancellate and spiny surface and an almost perfectly circular aperture. We allocate the following species to *Spinicalliotropis*:

C. spinosa Poppe *et al.*, 2004, *Trochus clavatus* Watson, 1879, *C. chalkeie*, *C. ericius* Vilvens, 2006, *C. lamellifera* Jansen, 1994 and *C. solariellaformis* Vilvens, 2006.

The fossil record of Seguenzioidea dates back to the Middle Triassic, some 240 million years ago (Mya) (Hickman & McLean, 1990). The extinct family Eucyclidae Koken, 1897 was the only recognized Triassic representative of the superfamily, but this does not exclude the existence of unrecognized members. The morphological and taxonomic diversity apparently increased in the Middle and Late Jurassic around 150–170 Mya. The Jurassic seguenzioids include almost unmistakable members of Chilodontidae, Calliotropidae and the skeneimorph *Eudaronia* (Knight *et al.*, 1960; Hickman & McLean, 1990; Kaim, 2004). The first known appearances of Seguenziidae and Cataegidae were much later, in the Late Cretaceous and Cenozoic, respectively (Hickman & McLean, 1990; Hickman, 1998), but their apparent absence in older sediments can probably be attributed to difficulties in determining phylogenetic positions of some of these seguenzioids solely by shell characters. Williams *et al.* (2008) estimated the divergence of Seguenzioidea from Scissurellidae + Lepetodrilidae + Fissurellidae to have taken place 124–221 Mya, based on their multi-gene molecular data and several calibration points from various vetigastropod fossils. The same data also suggested that the first split among *Granata* (Chilodontidae), *Bathymargarites* (Seguenziidae) and *Ginebis* Taki & Otuka, 1942 (Calliotropidae) occurred 72–158 Mya. As discussed by Williams *et al.* (2008), these divergence dates are younger than those apparent in the fossil record of Seguenzioidea, possibly due to such errors as the use of an incorrect tree, inadequate calibration points and highly variable rates of molecular evolution.

Ecology of Adeuomphalus *species*

Among the five species of *Adeuomphalus* collected alive, three were captured by submersibles in the surroundings of active hydrothermal vents. Interestingly, all the three species were found more or less associated with carnivorous sponges of the family Cladorhizidae. *Adeuomphalus elegans* was stuck to the flat head of an unidentified, lollipop-shaped sponge of the genus *Abyssocladia*; the holotype of *A. collinsi* was collected in an area rich in cladorhizid sponges and indeed spicules that probably belong to a species of *Abyssocladia* were attached to its shell (Fig. 4F); *A. trochanter* was also found with lollipop sponges (V. Tunnicliffe, personal communication). These co-occurrences seem to be more than coincidence, but we cannot determine the type of association between *Adeuomphalus* and sponges with the limited information available. Cladorhizid sponges are exclusively carnivorous and capture small invertebrates by means of sticky substance and hook-like spicules (Vacelet, 2006; Watling, 2007). Their prey is mainly pelagic microcrustaceans, and polychaete worms might be caught opportunistically (Vacelet & Duport, 2004). Considering this feeding ecology, it is apparent that shelled molluscs are less easily captured than soft, setose invertebrates. Instead, *Adeuomphalus* may feed on the sponges or possibly microcrustaceans accumulated on their surface. The lack of the radula in at least three species of the genus as well as the cylindrical snout documented in *A. collinsi* (Fig. 5B–G) indicate a highly specialized diet and feeding mode for the genus, rather than the deposit feeding widespread in Seguenzioidea that is often accompanied by numerous radular teeth and a laterally expanded oral disk (Hickman, 1981, 1998). Radula-less gastropods, including parasitic eulimids, pyramidellids and coral-dwelling muricids, use the snout (or proboscis) and buccal cavity as a pump to suck the body fluid or soft tissue of their prey; other radula-less snails including some terebrids engulf prey items such as polychaete worms (Kay, Wells & Ponder, 1998). The snout of *A. collinsi* may similarly function as a suctorial device in sponge feeding.

Two nonvent species (*A. densicostatus* and *A. guillei*) were caught in deep trawls and their associated faunas could not be determined. However, the conchological resemblance between *A. densicostatus* and *A. elegans* (Figs 1A–E, 3) suggest that these species have a similar anatomical configuration and feeding ecology. *Adeuomphalus guillei* with a radula possibly has different ecological characteristics.

It is not clear whether the three species of *Adeuomphalus* associated with cladorhizid sponges are obligate dwellers of hydrothermal vents. Vacelet (2006) noted that the sponges of *Abyssocladia* have not been found in the rich animal communities that thrive in the immediate environment of the active smokers and thus they cannot be considered as true members of the vent fauna. They occur at some distance from the active vents, in areas where sessile macrofauna is still very poor but more stable; the sponges may therefore benefit from a general organic enrichment around the vent sites, or they may simply take advantage of the presence of relatively recent basaltic lava that is still thinly covered by sediment (Vacelet, 2006). *Adeuomphalus elegans* with its presumed host *Abyssocladia* was also collected on a bare volcanic rock in the vicinity of 'shimmering' water with a temperature of 35°C, where no macrobenthos was otherwise observed from the submersible.

Parasites are rare in hydrothermal vents (de Buron & Morand, 2004; Tunnicliffe *et al.*, 2008). This is especially true for gastropods. Not a single species of the two large families of parasitic snails, Eulimidae and Pyramidellidae, is known from vents (e.g. Warén & Bouchet, 1989, 1993, 2001), although they are common in the surrounding deep sea and their hosts (echinoderms, annelids and molluscs) also occur there. The apparent absence or scarcity of parasites in general may be explained simply by neglect by vent biologists (de Buron & Morand, 2004), but this does not apply to these two gastropod families. We think that the rarity is due, at least in part, to the presumably small probability of finding the hosts by the larvae of parasites. The parasite larvae do not only have to find the hydrothermal vents, but also the right host species. The supposed parasitic mode of life in the three *Adeuomphalus* species and the finding of an endoparasitic copepod in *A. collinsi* may perhaps be taken as indications that none of them belong to the true hydrothermal vent fauna.

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