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New species from a 'lost world': *Sulawesidrobia* (Caenogastropoda, Tateidae) from ancient Lake Matano, Sulawesi, Indonesia

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Abstract. Five new species of freshwater gastropods of the tateid genus *Sulawesidrobia* are described from the ancient Lake Matano on Sulawesi, Indonesia: *S. wilsoni* sp. nov., *S. carsonae* sp. nov., *S. ehrlichi* sp. nov., *S. crutzeni* sp. nov., and *S. dinersteini* sp. nov. The descriptions were based on shell morphology, anatomy as well as phylogenetic analysis using DNA sequence data of a fragment of the mitochondrial *cytochrome oxidase I*. All three suits of characters were included into the diagnoses. The new species formed a clade with two species from Lake Towuti, but separate from already known species from Lake Matano. The species were discovered between 2003 and 2005. However, not a single specimen of *Sulawesidrobia* was found when several sites were revisited in 2018 and 2019. This may be a consequence of the release of South American flowerhorn cichlid fish into the lake, in combination with heavy eutrophication of the once ultra-oligotrophic lake. It seems likely that several populations or even entire species of *Sulawesidrobia* in Lake Matano may be extinct. The species names given reflect this by acknowledging important conservationists.

Keywords. Cryptic species, DNA taxonomy, extinction, integrative taxonomy, invasive species.

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Introduction

The vast majority of the small-sized freshwater species of the snail family Tateidae Thiele, 1925, which occurs in Austral Asia, on a number of Pacific islands, and has one representative genus in South America, dwell in springs, small streams, and the groundwater (Ponder 2019). The radiations of lake species living in the ancient lakes of Sulawesi are exceptional (Bouchet 1995). So far, 16 species have been described from Lake Poso (Abbott 1945; Ponder & Haase 2005; Haase & Bouchet 2006) and 10 from the Malili Lake system (Zielske *et al.* 2011). Whether these radiations originated and diversified exclusively in the lakes cannot be judged at this point as flowing waters, in particular springs, have hardly been surveyed for tateids in Sulawesi. The much larger pachychilids of the speciose *Tylomelania* Sarasin & Sarasin, 1897 are of fluviatile origin and have colonized the lakes several times independently. These and the similarly spectacular species flocks of fishes, shrimps and crabs have caught the attention of taxonomists and evolutionary biologists. These lakes provide a range of heterogeneous habitats and are ideal natural laboratories to study adaptation, parallel, and co-evolution. The degree of endemism is high in all of these groups (von Rintelen *et al.* 2010, 2012).

Discriminating species among small organisms such as tateid gastropods has always been contentious as small species tend to have simplified morphologies and the taxonomic significance of small differences is difficult to assess. This has been amply discussed in the context of cryptic species by Horsáková *et al.* (2018) and is also why integrative approaches combining several suites of characters are to be advocated (Dayrat 2005; Haase *et al.* 2007; Padial & de la Riva 2010; Padial *et al.* 2010). This also means that no single type of character outweighs all other types. Young species, for example, will not differ considerably in their mitochondrial DNA sequences but may be morphologically well differentiated and these can be considered genetically cryptic species (where morphological as well as genetic only refer to the particular characters respectively sequences investigated; e.g., Haase *et al.* 2007). Theoretically, we adhere to the differential fitness species concept of Hausdorf (2011). Operationally, we recognize two populations as different species if any kind of character suggests that differences are fixed and that they have a more complex genetic basis than being a simple polymorphism (e.g., due to alternative alleles) so that genetic isolation can be inferred (modified from Haase & Bouchet 2006).

Among Sulawesi's ancient lakes, only Lake Poso and Lake Matano are of tectonic origin. Lake Matano is with ca 590 m the deepest and in terms of area – 164 km^2 – the third largest (von Rintelen 2012) (Fig. 1). Lake Matano has received less attention regarding tateid gastropods so far, as the focus of previous accounts lay on Lakes Poso (Haase & Bouchet 2006) and Towuti (Zielske *et al.* 2011). Only three species have been described from Lake Matano so far (Zielske *et al.* 2011). We have now surveyed all samples collected during three expeditions from 2003 to 2005. Integrating shell morphology, anatomy and mitochondrial COI sequences, we describe five new species of *Sulawesidrobia* Ponder & Haase, 2005. All three suites of characters were considered for the diagnoses (Kühn & Haase 2020; Verhaegen & Haase 2021).

Material and methods

Collection

Snails were collected by hand-picking from rocks and partly macrophytes, mostly in shallow water (< 1 m) (Table 1). We also included three samples of *S. anceps* Zielske, Glaubrecht & Haase, 2011, deposited at the Museum für Naturkunde Berlin (ZMB) [ZMB 107086, 107087, 191640 (paratypes)] and one of *S. bicolor* Zielske, Glaubrecht & Haase, 2011 (ZMB 107088), into the morphological comparisons, because of the similarity of these species to one of the new ones.

All material was deposited in the Museum Zoologicum Bogoriense (MZB; Bogor/Sulawesi) and the Museum für Naturkunde Berlin.

Morphology and anatomy

Adult shells characterized by a thickened, continuous apertural lip (Verhaegen *et al.* 2018) were measured from digital photographs using the program AxioVision40 ver. 3.8 (Zeiss). The photographs were taken with a Zeiss Axio Cam MR3 on a Zeiss SteREO Discovery microscope. The shell dimensions – shell height and width, aperture height and width, and width of the body whorl – were measured parallel or perpendicular to the coiling axis. The number of whorls was counted to the nearest eighth (Kerney & Cameron 1979). For statistical comparisons of the measurements we conducted a principal component analysis (PCA) and a multivariate analysis of variance (MANOVA) followed by paired Hotelling's T^2 tests in PAST ver. 4.10 (Hammer *et al.* 2001).

Anatomical dissections of each 2–3 females and males per population – if available – were made under the same microscope. Shells, radulae and penes were also investigated by scanning electron microscopy (SEM) using a Zeiss EVO LS10 SEM. For this, shells and radulae had to be cleaned in ca 2.5% sodium

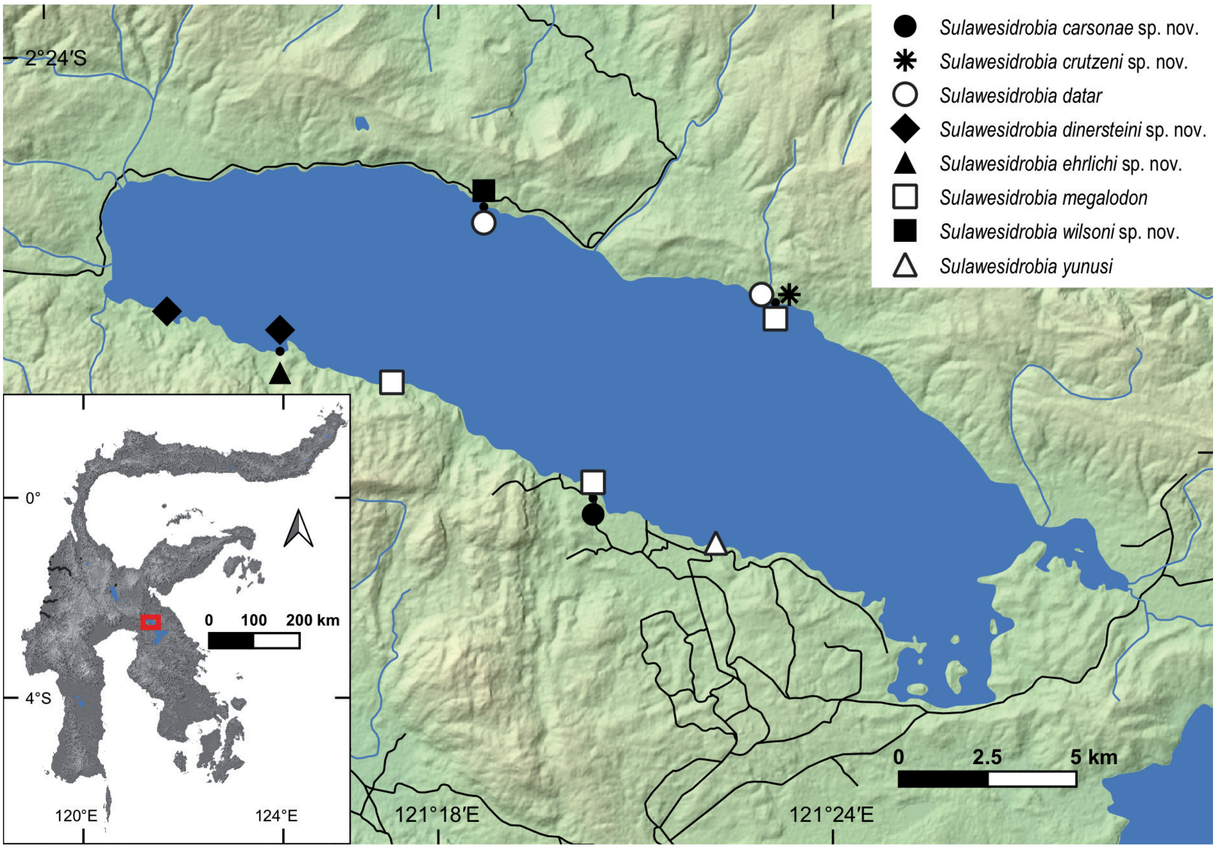

Fig. 1. Map of Lake Matano with the sampling sites of *Sulawesidrobia* Ponder & Haase, 2005. Black symbols for new species, white for known ones. The red frame on the map of Sulawesi in the left-bottom insert shows the location of Lake Matano on the island. Black lines indicate roads. When several species occur at one locality, the central black dot marks the actual sampling site.

Table 1. Locality data of newly sequenced species/populations. New species in order of description.

Species	Catalogue#	Locality	Latitude	Longitude	Collectors/Date
S. wilsoni sp. nov.	Gst. 12117 191842	N shore, NW of Nuha	2°26′15.66″ S	121°18′41.52″ E	Glaubrecht 24 Oct. 2005
S. carsonae sp. nov.	Gst. 12119 107079	S shore, INCO boathouse, below guesthouse	2°30′41.76″ S	121°20′21.12″ E	Glaubrecht, von Rintelen, Zitzler 10 Sep. 2003
S. ehrlichi sp. nov.	Gst. 12121 107095	S shore	2°28′27.66″ S	121°15′35.46″ E	von Rintelen, Zitzler 24 Jul. 2004
S. crutzeni sp. nov.	Gst. 12123 191838	N Shore, SE of Nuha	2°27′43.26″ S	121°23′07.50″ E	Glaubrecht 24 Oct. 2005
S. dinersteini sp. nov.	Gst 12125 107092	S shore	2°27′51.00″ S	121°13′52.20″ E	von Rintelen. Zitzler 1 Aug. 2004
S. dinersteini sp. nov.	Gst 12126 107094	S shore	2°28′27.66″ S	121°15′35.46″ E	von Rintelen, Zitzler 24 Jul. 2004
S. datar	/ 191835	N shore, SE of Nuha	2°27′43.26″ S	121°23′07.50″ E	Glaubrecht 24 Oct. 2005
S. megalodon	/ 191819	S shore, NW of Soroako Limestone drop-off	2°28′56.04″ S	121°17′17.34″ E	Glaubrecht 24 Oct. 2005
S. megalodon	/ 106823	S shore, INCO boathouse, below guesthouse	2°30′41.76″ S	121°20′21.12″ E	Glaubrecht, von Rintelen, Zitzler 10 Sep. 2003

hypochlorite. Anterior bodies with heads and penes were dried in hexamethyldisilazane (Nation 1983). All objects were coated with palladium/platinum with a Fisons Polaron SC7640 sputter coater.

DNA sequencing

DNA was extracted using the DNeasy Blood & Tissue kit (QIAGEN). We amplified a fragment of the mitochondrial *cytochrome oxidase I* (COI) using the primers LCO1490 and H1298 of Folmer *et al.* (1994), the latter modified at position 12 where the original G was replaced by an A (Zielske *et al.* 2011). Polymerase chain reactions (PCR) were performed in a total volume of 25 µl and comprised 2.25 µl 10X BH4 buffer (Bioline), 4.5 mM $MgCl_2$, each primer at 0.3 µM, 0.2 mM dNTP, 1 µl BSA (1%), 0.5 U DNA polymerase (Bioline), and 20–100 µg DNA. The cycling profile was 5 min denaturation at 94°C followed by 40 cycles of denaturation at 94°C for 1 min, annealing at 48°C for 1.5 min and extension at 72°C for 1 min. The reaction ended with a final extension at 72°C for 7 min. The amplification products were cleaned using exonuclease I and shrimp alkaline phosphatase. For cycle sequencing, Big Dye Terminator Ready Reaction Mix ver. 3.1 (Thermo Fisher) was used with the PCR primers. Products were sequenced on an ABI 3130xl Genetic Analyzer. Sequences were edited in BioEdit ver. 7.0.5.3 (Hall 1999) and aligned with ClustalW (Thompson *et al.* 1994) implemented in BioEdit. The final alignment comprised 658 bp. All new sequences were submitted to GenBank under the accession numbers ON969101–ON969125.

Phylogenetic analyses

All sequences published by Zielske *et al.* (2011) were included in the phylogenetic analyses. Sequences of *Edgbastonia alanwillsi* Ponder, 2008 (EU580440; Ponder *et al.* 2008), *Jardinella tumorosa* Ponder, 1991 (AY622455; Perez *et al.* 2005), *Tatea huonensis* (Tenison Woods, 1876) (JX970619; Wilke *et al.* 2013), and *Trochidrobia punicea* Ponder, Hershler & B. Jenkins, 1989 (AY622459; Perez *et al.* 2005), all Australian tateids, were added from GenBank as outgroup taxa. Tree reconstructions were conducted in both a Bayesian (BA) and a maximum likelihood (ML) framework. The best fitting substitution model – HKY + Γ – was identified by jModeltest ver. 2.1.4 (Darriba *et al.* 2012). Bayesian analyses were performed in MrBayes ver. 3.2.2 (Ronquist *et al.* 2012). Every 100th tree was sampled over 5 M generations after a burnin of 12 500 (25%). Other settings were default. Convergence of parameter estimates and effective sample sizes were controlled by the diagnostics provided in MrBayes. ML analyses were conducted in Garli ver. 2.01 (Zwickel 2006) with 500 replicates for both optimal search and bootstrapping. A 50% bootstrap consensus tree was assembled with PAUP* ver. 4.10b (Swofford 2003).

DNA taxonomy

In order to extend diagnoses to incorporate diagnostic DNA alignment positions, we used the R package QUIDDICH (Kühn & Haase 2020). We searched for diagnostic characters of types 1–3. Type 1 characters are fixed in a particular species, type 2 characters exhibit a polymorphism unique for a taxon, and type 3 characters distinguish at least some individuals of a particular species from all other ones (Kühn & Haase 2020). These positions were identified in the clade containing all new species as well as *S. anceps* and *S. bicolor*. The alignment of these taxa in fasta format is given in Supp. file 2.

Results

Systematic descriptions

For the diagnosis of the genus we refer to Ponder & Haase (2005), Haase & Bouchet (2006) and Zielske *et al.* (2011). Shell measurements are given in Table 2. In the descriptions we do not repeat the detailed measurements. All diagnostic molecular characters were either of type 1 or 3. There were no type 2 characters. They are summarized in Table 3.

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Family Tateidae Thiele, 1925
Genus *Sulawesidrobia* Ponder & Haase, 2005

Sulawesidrobia wilsoni sp. nov.

urn:lsid:zoobank.org:act:06EBD388-C63B-4C22-BB74-4FC6970B6CAE
Figs 2A, 3A–B, 5A, 6A–C, 7A–B, 8A–B

Diagnosis

Sulawesidrobia wilsoni sp. nov. is characterized by the combination of the unique egg-shaped shell with very weakly depressed sutures, a white subsutural band and an enlarged denticle close to the base of the inner marginal radular tooth. Only two alignment positions are diagnostic, one of type 1 and one of type 3 (Table 3).

Etymology

Sulawesidrobia wilsoni sp. nov. is named after the American naturalist Edward Osborn Wilson (1929–2021), who not only contributed significantly to the ecological theory of biogeography as an important aspect of conservation biology, but coined biodiversity as an important agenda for our and the next generation.

Material examined

Holotype (Fig. 2A)
INDONESIA • Sulawesi, Lake Matano, N-shore, NW of Nuha, on rocks; 02°26.261′ S, 121°18.692′ E; 24 Oct. 2005; Glaubrecht leg.; MZB Gst. 12116.

Paratypes (Fig. 3A–B)
INDONESIA • 27 specs; same collection data as for holotype; MZB Gst. 12117 • 27 specs; same collection data as for holotype; ZMB 191842.

Description

Shell (Figs 2A, 3A–B). Egg-shaped, height of whorls increasing allometrically, sutures hardly incised, height of body whorl about four fifths of total height, total shell about 1.5 times as high as wide, brown-translucent with white subsutural band, periostracum light brown; protoconch comprising ca 0.9 whorls; entire shell with 3.5 to 3.875 whorls without structure apart from growth lines; umbilicus at best a narrow slit; aperture orthocline, only slightly higher than wide, outer lip hardly extends beyond body whorl.

Operculum. Very pale yellow, thin, paucispiral, nucleus eccentric.

External features. Epidermis black except for mantle edge and areas over distal genital glands and stomach; tentacles black with median white stripe and patch of cilia (Fig. 5A).

Mantle cavity (N = 3). 16–19 ctenidial filaments; osphradium ovate-elongate lying centrally under ctenidium along 75% of its length.

Digestive system. The radula has the formula R 4-5 1 4-5/2-3 2-3, L 3 1 6-7, M1 24-25, M2 23-26, two rhachidial basal cusps were only rarely observed, the first marginal tooth has proximally an enlarged denticle (Fig. 6A–C); stomach without caecum and pigment; intestine follows distal genital glands, in females closer than in males.

Table 2. Shell morphometrics. Measurements in mm. Abbreviations: AH = aperture height; AW = aperture width; BWW = width of body whorl; cv = coefficient of variation corrected for unequal sample sizes; max = maximum; min = minimum; N = sample size; sd = standard deviation; SH = shell height; SW = shell width; W = number of whorls.

Species		**SH**	**SW**	**AH**	**AW**	**BWW**	**SH/SW**	**W**
S. wilsoni sp. nov.	holotype	2.22	1.53	1.08	0.94	1.34	1.45	3.750
N = 20	min	1.99	1.38	0.96	0.88	1.24	1.39	3.500
	max	2.40	1.60	1.11	0.99	1.45	1.53	3.875
	mean	2.20	1.50	1.07	0.95	1.35	1.46	3.706
	sd	0.10	0.06	0.04	0.03	0.05	0.04	0.117
	cv	4.77	3.76	3.43	3.42	4.10	2.74	3.187
S. carsonae sp. nov.	holotype	1.97	1.29	0.92	0.75	1.14	1.52	3.875
N = 17	min	1.71	1.18	0.79	0.71	1.02	1.36	3.750
	max	2.00	1.36	1.01	0.80	1.16	1.54	4.125
	mean	1.91	1.27	0.90	0.76	1.09	1.50	3.882
	sd	0.08	0.04	0.05	0.02	0.04	0.04	0.112
	cv	4.46	3.23	5.48	3.15	3.65	2.99	2.938
S. ehrlichi sp. nov.	holotype	2.83	1.75	1.26	1.03	1.54	1.61	4.750
N = 20	min	2.49	1.55	1.07	0.95	1.36	1.46	4.125
	max	3.02	2.01	1.32	1.20	1.83	1.68	4.750
	mean	2.74	1.73	1.19	1.05	1.51	1.59	4.388
	sd	0.16	0.12	0.07	0.07	0.11	0.05	0.194
	cv	5.98	6.82	6.11	6.40	7.19	3.36	4.479
S. crutzeni sp. nov.	holotype	2.89	1.91	1.41	1.21	1.67	1.51	4.000
N = 11	min	2.81	1.85	1.31	1.21	1.62	1.42	3.875
	max	3.31	2.17	1.52	1.38	1.86	1.55	4.375
	mean	3.03	2.01	1.42	1.27	1.74	1.51	4.091
	sd	0.16	0.10	0.06	0.06	0.08	0.03	0.126
	cv	5.38	5.28	4.58	4.59	4.53	2.21	3.122
S. dinersteini sp. nov. ZMB 107092	holotype	1.94	1.23	0.86	0.76	1.10	1.59	3.750
N = 20	min	1.74	1.11	0.76	0.70	1.00	1.52	3.500
	max	2.39	1.46	1.00	0.85	1.28	1.69	4.125
	mean	1.99	1.25	0.86	0.76	1.11	1.60	3.769
	sd	0.17	0.10	0.07	0.05	0.08	0.05	0.178
	cv	8.76	7.85	7.91	6.29	7.32	3.05	4.783
S. dinersteini sp. nov. ZMB 107094	min	1.69	1.06	0.77	0.63	0.93	1.54	3.500
N = 20	max	2.21	1.28	0.89	0.76	1.12	1.80	4.250
	mean	1.95	1.19	0.81	0.70	1.06	1.64	3.950
	sd	0.13	0.05	0.03	0.03	0.05	0.07	0.179
	cv	6.88	4.59	4.25	4.68	4.50	4.21	4.579

Female genitalia (N = 2; Fig. 7A–B). Ovary starts 1–1.5 whorls below apex, comprises about 0.5 whorls and overlaps proximal stomach chamber; renal oviduct simple, first coiling 180° clockwise, then 270° counter-clockwise; no receptaculum seminis; bursa copulatrix broadly pear-shaped, behind albumen gland, bursal duct entering subcentrally; albumen gland with opaque-white anterior and milky-white posterior section, anterior capsule gland white, posterior one yellowish.

Male genitalia (N = 2; Fig. 8A–B). Testis lobate, starts about one whorl below apex, comprises ca 1.25 whorls, extends over stomach; vesicula seminalis coils along anterior two thirds of testis; proximal and distal vasa deferentia insert closely in about middle of kidney-shaped prostate; penis with broad base and slender, parallel-sided elongate distal end.

Remarks

The white subsutural band is shared with *S. crutzeni* sp. nov. described below. An enlarged denticle close to the base of the inner marginal radular tooth is seen in two other species, *S. megalodon* Zielske, Glaubrecht & Haase, 2011 (Zielske *et al.* 2011) and *S. bulat* Haase & Bouchet, 2006 (Haase & Bouchet 2006). All three are morphologically very different from *S. wilsoni* sp. nov., though. *Sulawesidrobia crutzeni* is much larger and has a conical shell (see below) while *S. megalodon* is trochiform (Zielske *et al.* 2011), and *S. bulat* globular (Haase & Bouchet 2006). In addition, *S. crutzeni* lacks a bursa copulatrix. In the phylogenetic trees (Figs 9–10, Supp. file 1), *S. wilsoni* received high support although there were only two diagnostic alignment positions, one of type 1 and one of type 3 (Table 3).

Sulawesidrobia carsonae sp. nov.

urn:lsid:zoobank.org:act:1E37CB23-9233-4A75-810F-C6109B54C098

Figs 2B, 3C–D, 4A–B, 5B, 6D, 7C–D, 8C–D

Diagnosis

The new species has a small, short-conical shell with a unique protoconch structure where the fine pits are distally rearranged as irregular longitudinal striae. It is the only short-conical species combining a single large inner denticle on the lateral radular tooth and a penis with broad base and slender, parallel-sided distal end. A single position of type 1 characterizes this new species (Table 3).

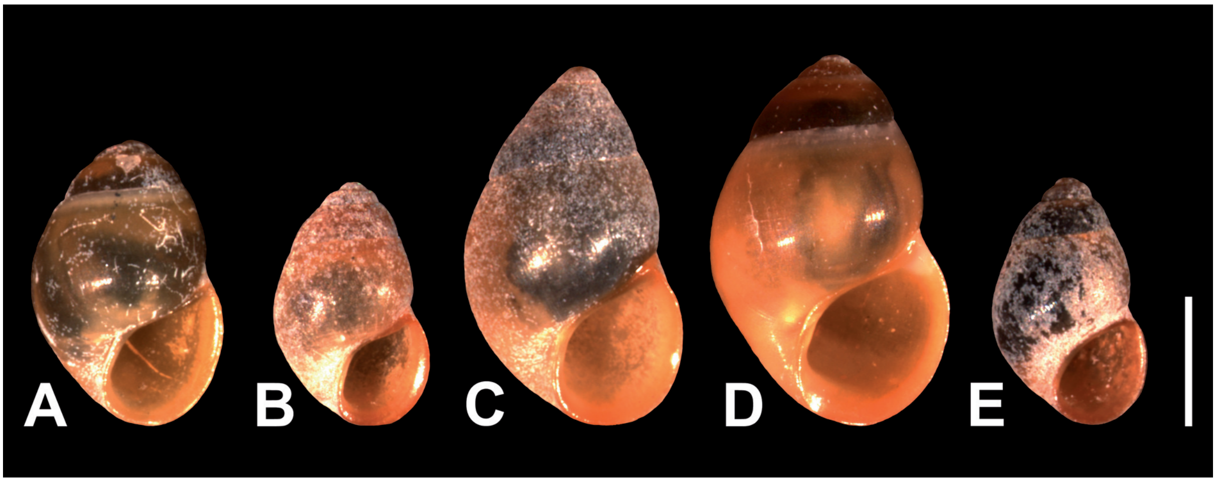

Fig. 2. Holotypes. **A**. *Sulawesidrobia wilsoni* sp. nov. (MZB Gst. 12116). **B**. *S. carsonae* sp. nov. (MZB Gst. 12118). **C**. *S. ehrlichi* sp. nov. (MZB Gst. 12120). **D**. *S. crutzeni* sp. nov. (MZB Gst. 12122). **E**. *S. dinersteini* sp. nov. (MZB Gst. 12124). Scale bar = 1 mm.

Table 3. Diagnostic alignment positions of the new species as well as *Sulawesidrobia anceps* Zielske, Glaubrecht & Haase, 2011 and *S. bicolor* Zielske, Glaubrecht & Haase, 2011 relative to each other. Characters are either of type 1, i.e., fixed in a particular species (bold) or 3, i.e., unique in only some individuals of a particular species (italic). Positions refer to the alignment of COI in Supp. file 2.

Species	Position/State																			
S. wilsoni sp. nov.	**206** **C**	*304* *C*																		
S. carsonae sp. nov.	**268** **G**																			
S. ehrlichi sp. nov.	*331* *G*	**502** **G**	**550** **G**																	
S. crutzeni sp. nov.	*187* *C*	*307* *A*	*436* *G*	*532* *C*																
S. dinersteini sp. nov.	**061** **G**	**082** **A**	**250** **C**	*290* *C*	*295* *C*	*353* *G*	**403** **G**	**454** **G**	**472** **G**											
S. anceps	**034** **G**	*046* *G*	*055* *C*	*074* *T*	**088** **G**	*092* *C*	*118* *C*	*133* *C*	*157* *T*	**181** **A**	*190* *G*	**235** **C**	*244* *G*	**265** **G**	**289** **G**	*319* *C*	**343** **A**	**379** **T**	*538* C	*539* C
S. bicolor	**028** **G**	**040** **C**	**043** **A**	*154* *C*	**223** **G**	**229** **G**	*241* *G*	*277* *C*	*301* *T*	**316** **G**	*340* *C*	**370** **G**	**382** **G**	**400** **C**	**412** **C**	**457** **C**	**460** **C**	**490** **G**	**541** **G**	**559** **G**

Etymology

Sulawesidrobia carsonae sp. nov. is dedicated to the American zoologist and writer Rachel Carson (1907–1964) whose influential 1962 book *Silent Spring* had a lasting effect on the global environmental movement.

Material examined

Holotype (Fig. 4C)

INDONESIA • Sulawesi, Lake Matano, S-shore, Inco boat house, below guest house, on rocks; 02°30.696′ S, 121°20.352′ E; Sep. 2003; Glaubrecht, von Rintelen and Zitzler leg.; MZB Gst. 12118.

Paratypes (Figs 4D, 5B–C)

INDONESIA • 11 specs; same collection data as for holotype; MZB Gst. 12119 • 10 specs; same collection data as for holotype; ZMB 107079.

Description

Shell (Figs 2B, 3C, 4A–B). Short-conical, sutures very shallow, about 1.5 times as high as wide, shell and priostracum light brown; protoconch initially with fine pits rearranging to irregular longitudinal striae and ca 0.75 whorls; entire shell with 3.75 to 4.125 whorls, teleoconch without structure apart from growth lines; umbilicus a narrow slit; aperture orthocline, only slightly higher than wide.

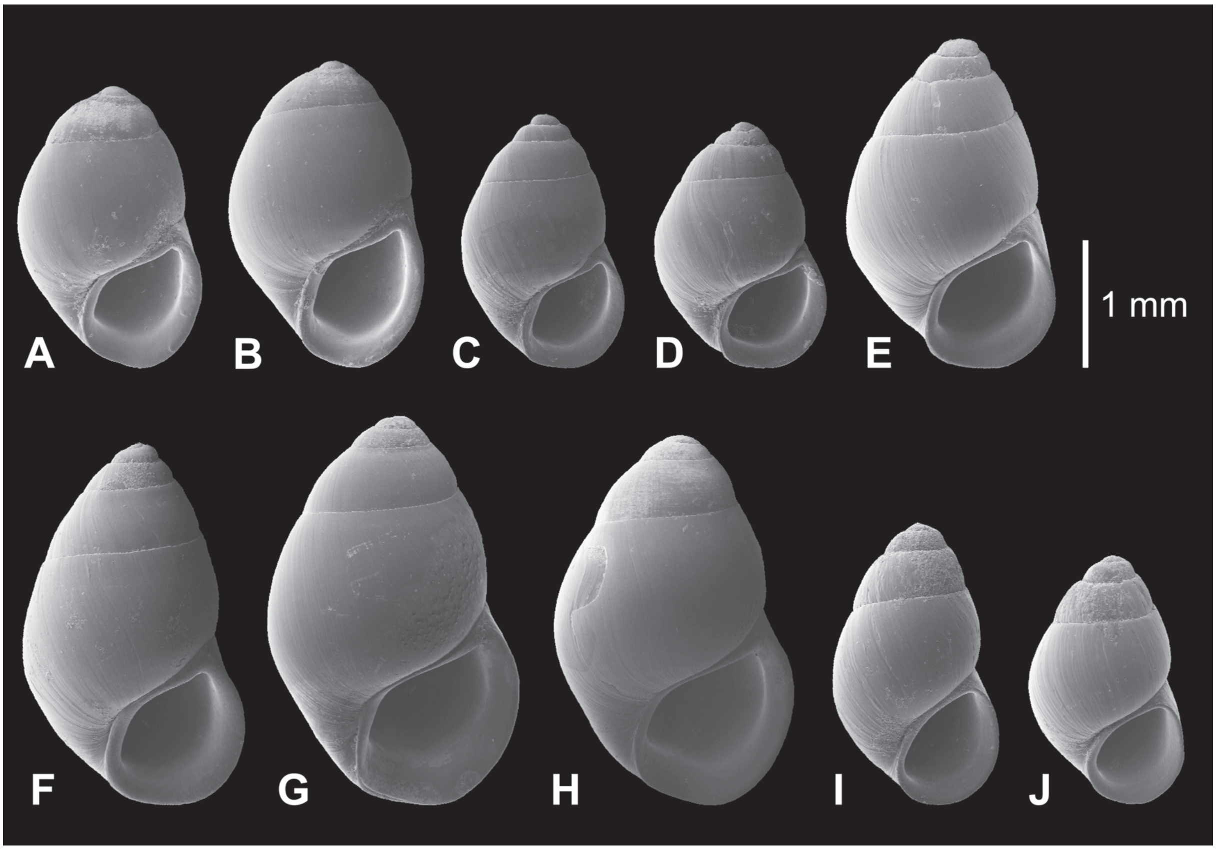

Fig. 3. SEM micrographs of paratypes, all from type localities. **A–B**. *Sulawesidrobia wilsoni* sp. nov. (MZB Gst. 12117). **C–D**. *S. carsonae* sp. nov. (MZB Gst. 12119). **E–F**. *S. ehrlichi* sp. nov. (MZB Gst. 12121). **G–H**. *S. crutzeni* sp. nov. (MZB Gst. 12123). **I–J**. *S. dinersteini* sp. nov. (MZB Gst. 12125).

Operculum. Very light yellow and thin, paucispiral, nucleus eccentric.

External features. Epidermis entirely black with the exception of mantle rim and areas over distal genital glands and stomach; tentacles with ciliated field (Fig. 5B).

Mantle cavity (N = 4). 13–16 ctenidial filaments; osphradium elongate lying centrally under ctenidium along 75% of its length.

Digestive system. The radula has the formula R 5 1 5/2-3 2-3, L 1-2 1 5-6, M1 18-24, M2 23-27, denticles of central tooth pointed and basally fused, two rhachidial basal cusps were only rarely observed, the same holds for a second small inner denticle on the lateral tooth, mostly there is only a single, very large one (Fig. 6D); stomach without caecum, black; intestine follows pallial genital glands, in females closer than in males.

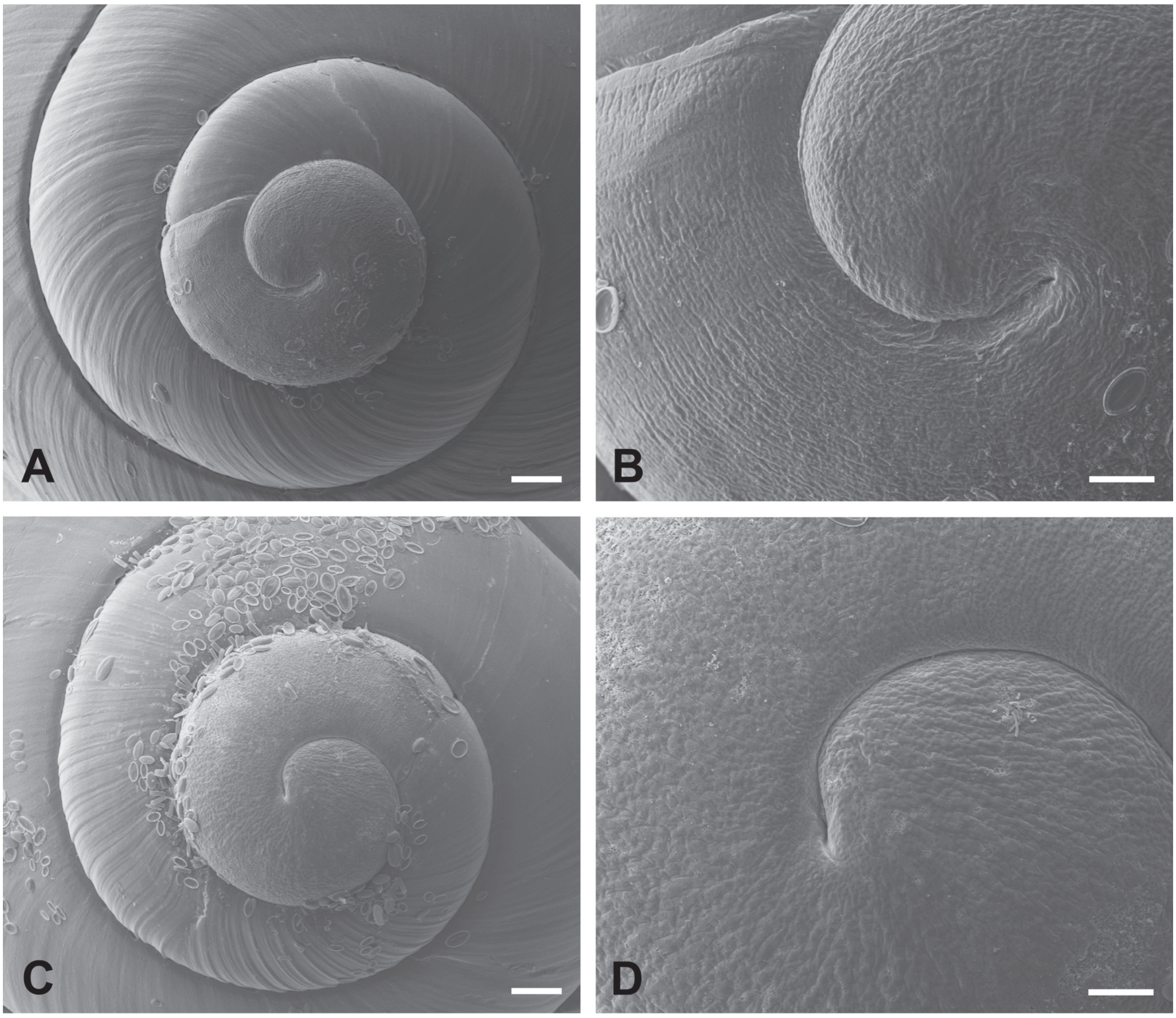

Fig. 4. SEM micrographs of protoconchs. **A–B**. *Sulawesidrobia carsonae* sp. nov. (MZB Gst. 12119). **C–D**. *S. ehrlichi* sp. nov. (MZB Gst. 12121). Scale bars: A, C = 50 µm; B, D = 20 µm.

Female genitalia (N = 2; Fig. 7C–D). Ovary starts 1–1.25 whorls below apex, comprises 0.5–0.7 whorls and covers the posterior stomach chamber; renal oviduct first coiling 180° clockwise, then 270° counter-clockwise; no receptaculum seminis; bursa copulatrix spherical, behind albumen gland, bursal duct entering anteriorly; albumen gland milky-white, capsule gland bipartite, opaque-white.

Male genitalia (N = 2; Fig. 8C–D). Testis a lobate sac, starts 0.5–0.75 whorls below apex, comprises ca 1.25 whorls, anteriorly overlapping stomach; vesicula seminalis coils along anterior quarter of testis; proximal and distal vasa deferentia insert close to middle of kidney-shaped prostate; penis with broad base and slender, parallel-sided distal end.

Remarks

There is only one other short-conical congener with a single large inner denticle on the lateral radular tooth, viz *S. crutzeni* sp. nov. The latter is 1.6 times larger and has a penis with very broad base and continuously tapering long distal end, though. In addition, it lacks a bursa copulatrix (see below). *Sulawesidrobia carsonae* sp. nov. was highly supported in the phylogenetic trees (Figs 9–10, Supp. file 1) although it had only a single diagnostic alignment position of type 1 (Table 3).

Sulawesidrobia ehrlichi sp. nov.

urn:lsid:zoobank.org:act:329722EB-1CD2-4441-AFC1-4C69C9203758
Figs 2C, 3E–F, 4C–D, 6E, 7E–F, 8E–F

Diagnosis

This new species is a larger conical *Sulawesidrobia* with a characteristic radula in which the denticles of the central tooth are fused, the central denticles of both central and lateral teeth have rounded tips, and the denticles on the lateral teeth are comparatively large and reduced in number. It is the only larger conical species with a broad based penis and slender, parallel-sided distal end. There are three diagnostic positions, two of type 1 and one of type 3 (Table 3).

Etymology

Named in honor for the American biologist Paul Ralph Ehrlich (born 1932), best known for his early warnings of the devastating effects of overpopulation depleting natural resources in his 1968 book *The Population Bomb*, coauthored with his wife Anne.

Material examined

Holotype (Fig. 2C)

INDONESIA • Sulawesi, Lake Matano, S shore, on rocks and macrophytes; 02°28.461′ S, 121°15.591′ E; 24 Jul. 2004; von Rintelen and Zitzler leg.; MZB Gst. 12120.

Paratypes (Fig. 3E–F)

INDONESIA • 70 specs; same collection data as for holotype; MZB Gst. 12121 • 69 specs; same collection data as for holotype; ZMB 107095.

Description

Shell (Figs 2C, 3E–F, 4C–D). Short-conical, sutures very shallow, about 1.6 times as high as wide, shell and periostracum light brown; protoconch with fine pits and ca 0.8 whorls; entire shell with 4.125 to 4.750 whorls, teleoconch without structure apart from growth lines; umbilicus a narrow slit; aperture orthocline, only slightly higher than wide.

Operculum. Light yellow and thin, paucispiral, nucleus eccentric.

External features. Epidermis entirely black with the exception of mantle rim and areas over distal genital glands and stomach; tentacles with ciliated field.

Mantle cavity (N = 4). 17–20 ctenidial filaments; osphradium elongate lying under posterior two thirds of ctenidium.

Digestive system. The radula has the formula R 4-5 1 4-5/3 3, L 2 1 2-4, M1 10-12, M2 18-24, denticles of central tooth basally fused, central denticles of both central and lateral teeth with rounded tip, denticles of lateral tooth comparatively large but reduced in number, innermost cusp of lateral tooth may be very small (Fig. 6E); stomach black without caecum; intestine follows pallial genital glands, in females closer than in males.

Female genitalia (N = 2; Fig. 7E–F). Ovary starts 1–1.25 whorls below apex, comprises 0.5 whorls and covers the stomach chambers; renal oviduct first coiling 180° clockwise, then 270° counter-clockwise;

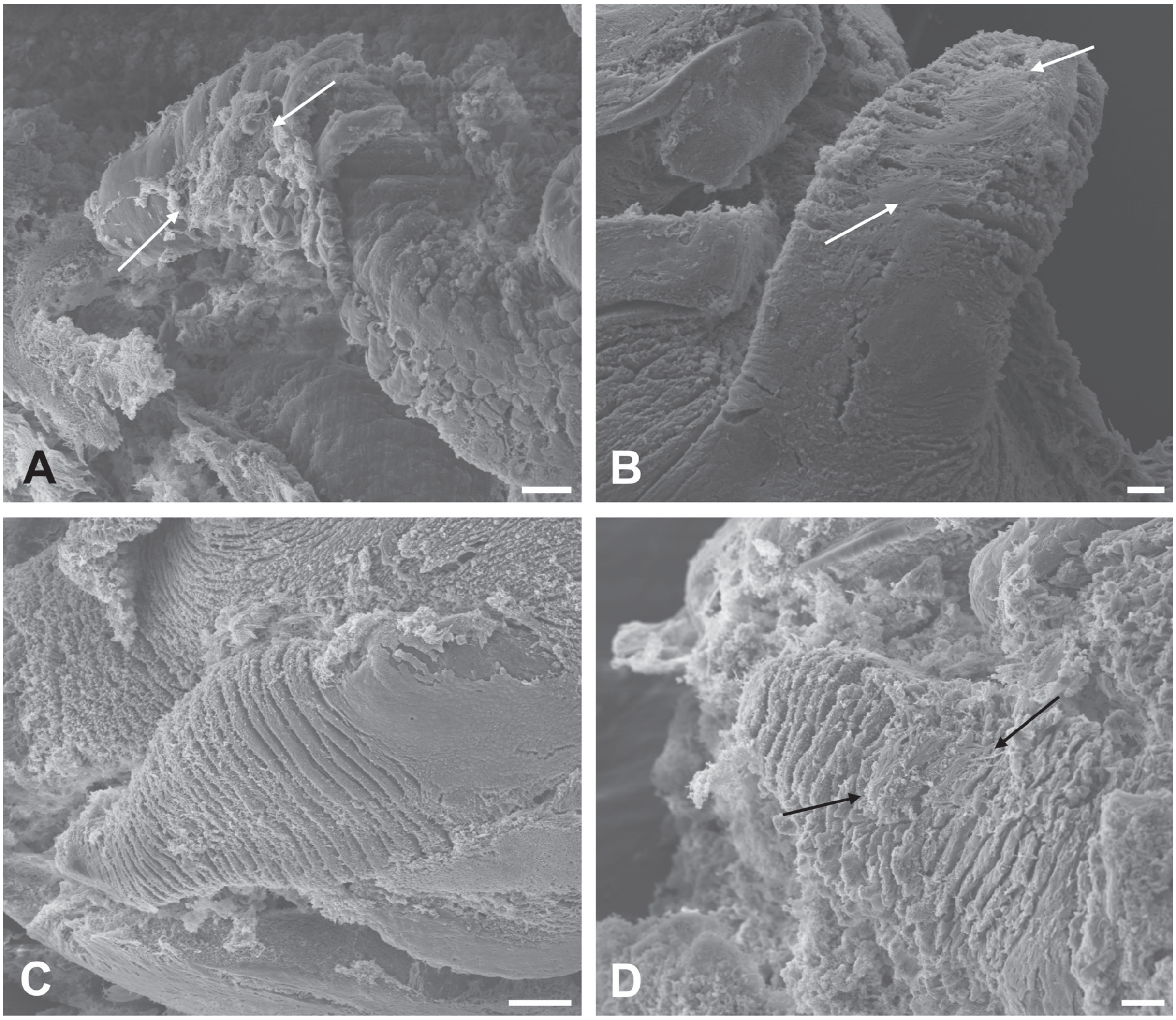

Fig. 5. SEM micrographs of cephalic tentacles. **A**. *Sulawesidrobia wilsoni* sp. nov. (ZMB 191842). **B**. *S. carsonae* sp. nov. (ZMB 107079). **C**. *S. crutzeni* sp. nov. (ZMB 191838). **D**. *S. dinersteini* sp. nov. (ZMB 107092). Arrows indicate field of cilia. Scale bars: A–B, D = 20 µm; C = 50 µm.

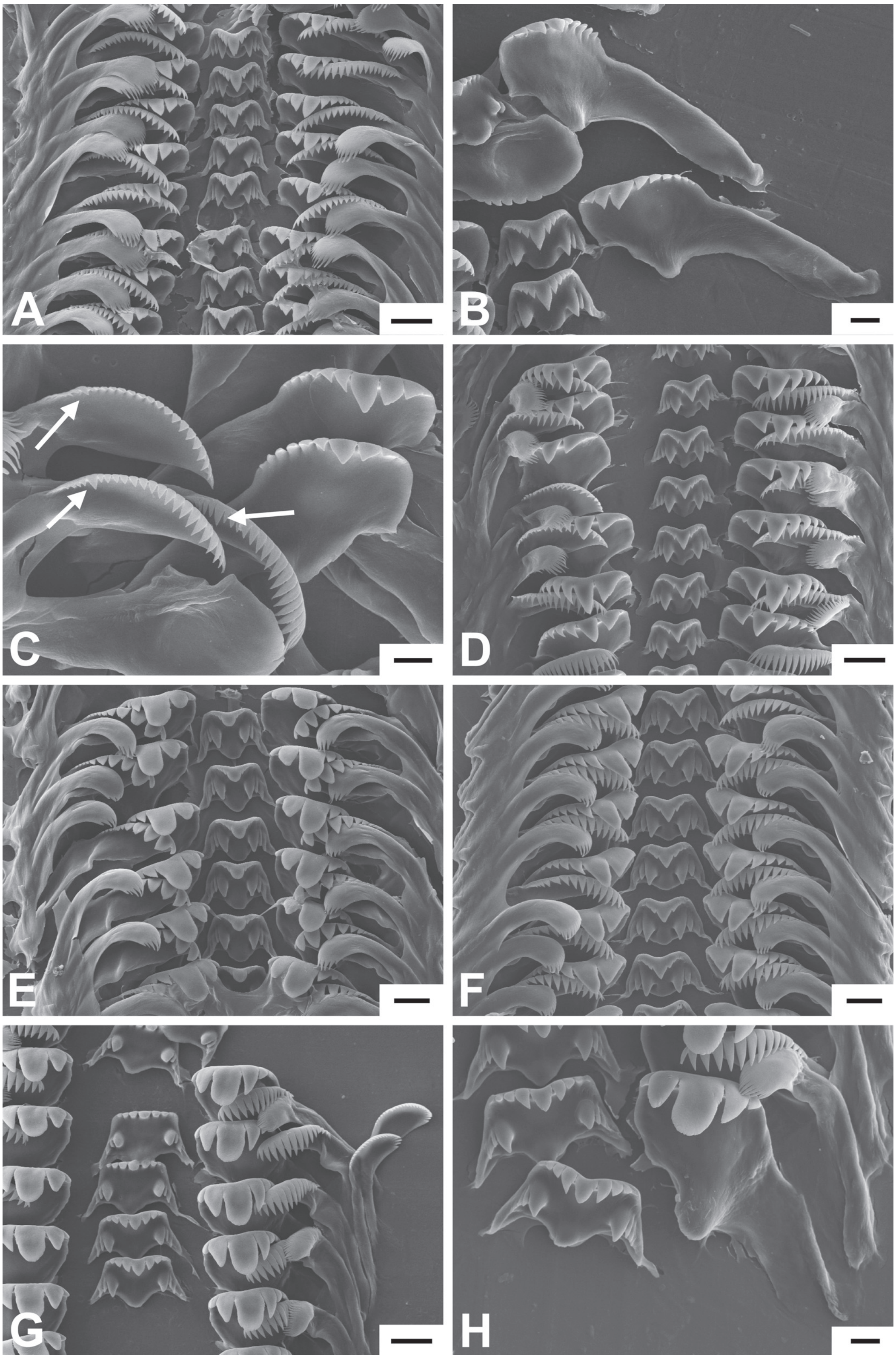

Fig. 6. Radula. **A–C**. *Sulawesidrobia wilsoni* sp. nov. **D**. *S. carsonae* sp. nov. **E**. *S. ehrlichi* sp. nov. **F**. *S. crutzeni* sp. nov. **G–H**. *S. dinersteini* sp. nov. Note different shapes of denticles on central and lateral teeth across species. Arrows indicate enlarged denticle on marginal tooth 1 in *S. wilsoni* sp. nov. Scale bars: A, C–G = 10 µm; B, H = 5 µm.

no receptaculum seminis; bursa copulatrix egg-shaped behind albumen gland, bursal duct entering anteriorly; albumen gland milky-white, capsule gland with smaller anterior white and larger posterior yellow portion.

Male genitalia (N = 2). Testis lobate, starts 0.75–1 whorls below apex, comprises ca 1.25 whorls, covers stomach chambers; vesicula seminalis coils along anterior half of testis; vasa deferentia insert close to middle of kidney-shaped prostate; penis with slightly broadened base and long, slender, parallel-sided distal end (Fig. 8E–F).

Remarks

The unresolved relationships with *S. crutzeni* sp. nov., possibly due to incomplete lineage sorting, suggest a close relationship (Figs 9–10, Supp. file 1) reflected also by the low number of diagnostic alignment positions, two of which were of type 1 and one of type 3 (Table 3). Yet, radular and genital features clearly indicate that both are distinct. Lateral and both marginal teeth have considerably less denticles in *S. wilsoni* sp nov. than in *S. crutzeni*. The latter lacks a bursa copulatrix and its penis is broad-based with a long, tapering distal end (see below). *Sulawesidrobia dinersteini* sp. nov. shares the lateral tooth morphology seen in this species (see below).

Sulawesidrobia crutzeni sp. nov.

urn:lsid:zoobank.org:act:D1E8AE3D-C211-4CAC-B4E8-16623EEA9853
Figs 2D, 3G–H, 5C, 6F, 7G–H, 8G

Diagnosis

This new species is a large conical *Sulawesidrobia* and the only one in which no bursa copulatrix was seen. The single inner denticle of the lateral tooth is very large. The four diagnostic alignment positions are all only of type 3 (Table 3).

Etymology

Sulawesidrobia crutzeni sp. nov. is named after the Dutch meteorologist, atmospheric chemist and 1995 Nobel Prize winner Paul J. Crutzen (1933–2021) who not only studied the effect of mankind on climate change but also coined (together with the freshwater biologist Eugene F. Stoermer) and popularized the term and concept of the Anthropocene, a proposed new epoch in the Quaternary period.

Material examined

Holotype (Fig. 2D)

INDONESIA • Sulawesi, Lake Matano, N shore, SE of Nuha, on rocks; 02°27.721′ S, 121°23.125′ E; 24 Oct. 2005; Glaubrecht leg.; MZB Gst. 12122.

Paratypes (Fig. 3G–H)

INDONESIA • 15 specs; same collection data as for holotype; MZB Gst. 12123 • 13 specs; same collection data as for holotype; ZMB 191838.

Description

Shell (Figs 2D, 3G–H). Conical with convex outline, appearance fairly massive, sutures shallow, about 1.5 times as high as wide, periostracum and translucent shell brown with white subsutural band; protoconch structure not verified due to corosion, comprises ca 0.8 whorls; entire shell with 3.875 to 4.375 whorls, teleoconch without structure apart from growth lines; umbilicus a narrow slit; aperture slightly higher than wide, outer lip orthocline.

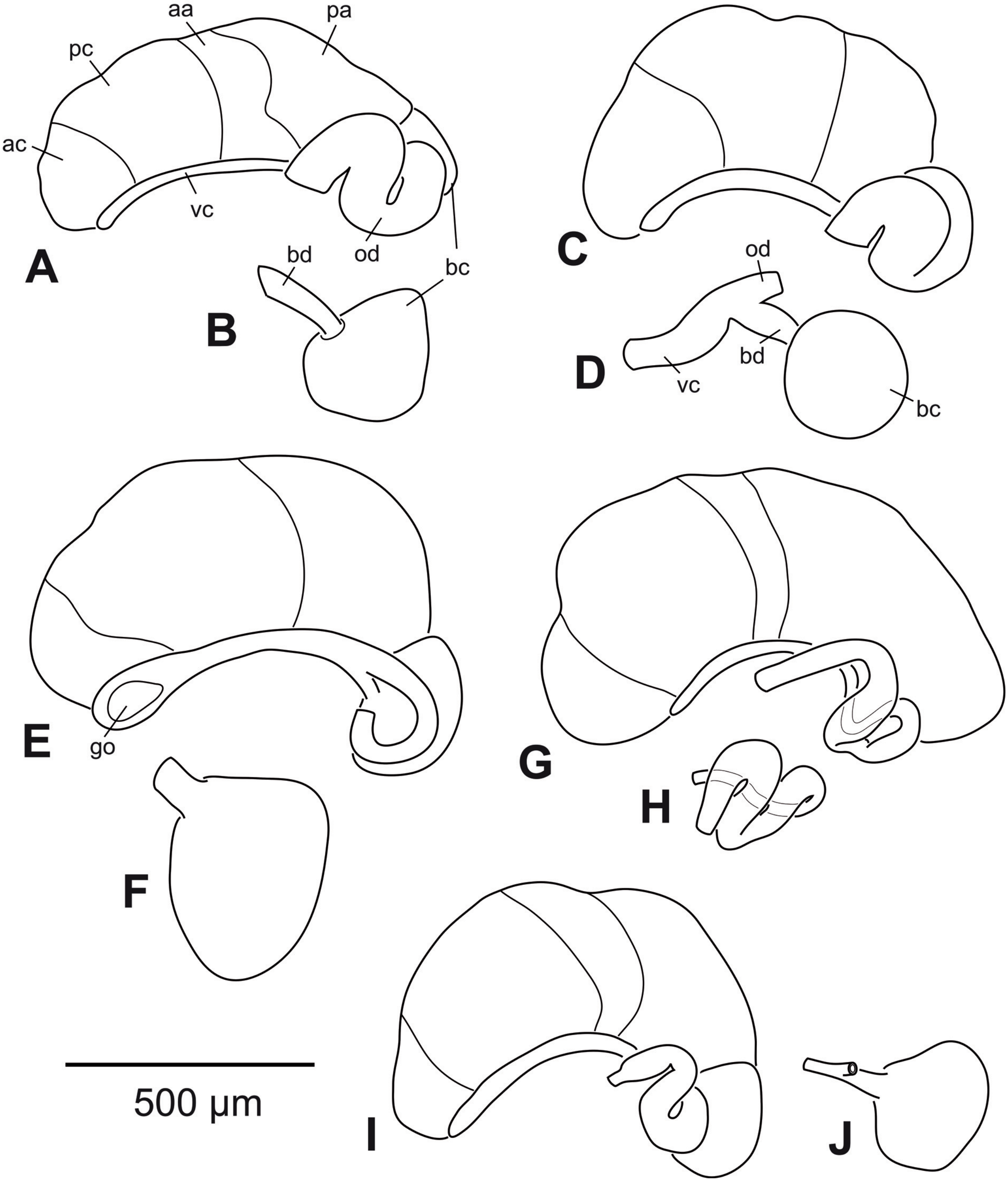

Fig. 7. Distal female genitalia. **A–B**. *Sulawesidrobia wilsoni* sp. nov. **C–D**. *S. carsonae* sp. nov. **E–F**. *S. ehrlichi* sp. nov. **G–H**. *S. crutzeni* sp. nov. **I–J**. *S. dinersteini* sp. nov. Abbreviations: aa = anterior albumen gland; ac = anterior capsule gland; bc = bursa copulatrix; bd = bursal duct; od = oviduct; pa = posterior albumen gland; pc = posterior capsule gland; vc = ventral channel.

Operculum. Very light yellow and thin, paucispiral, nucleus eccentric.

External features. Epidermis entirely black with the exception of mantle rim and areas over distal genital glands and stomach; tentacles with small ciliated field (Fig. 5C).

Mantle cavity (N = 3). 20–23 ctenidial filaments; osphradium elongate underneath central two thirds of gill.

Digestive system. The radula has the formula R 3-4 1 3-4/3 3, L 1 1 4-5, M1 14-18, M2 23-26, inner denticle of lateral tooth very large (Fig. 6F); stomach without caecum and pigment; intestine follows pallial genital glands, in females closer than in males.

Female genitalia (N = 2; Fig. 7G–H). Ovary starts ca 1.25 whorls below apex, comprises 0.5–0.7 whorls, covers stomach chambers; renal oviduct first coiling 180° clockwise, distal part more variable, in one individual coiling then 270° counter-clockwise and again 180° clockwise (Fig. 7G), in the second female dissected 180° counter-clockwise and then 270° counter-clockwise (Fig. 7H); no receptaculum seminis; no bursa copulatrix seen; albumen gland anteriorly opaque-white merging gradually into a milky-white posterior portion, capsule gland with a smaller anterior white and a larger posterior yellow portion.

Male genitalia (N = 1; Fig. 8G). Lobate testis starts ca 1 whorl below apex, comprises ca 1 whorl, covers stomach; vesicula seminalis coils along anterior half of testis; vasa deferentia insert close to middle of relatively small, almost rectangular prostate; penis with massive, broad base and long, slender and tapering distal end, distally grey.

Remarks

This is the only species of *Sulawesidrobia* apparently lacking a bursa copulatrix. It would be desirable, though, to check this characteristic in well-fixed material as here the preservation was far from ideal and only few specimens were available. Mosaic similarities with all three above described species are discussed under their respective Remarks. As *S. crutzeni* sp. nov. was paraphyletic (see below, Figs 9–10, Supp. file 1), it was not surprising that the four diagnostic alignment positions were all only of type 3 (Table 3).

Sulawesidrobia dinersteini sp. nov.

urn:lsid:zoobank.org:act:5AD928D7-232F-4D7E-AB84-FE9BA9D471F4

Figs 2E, 3I–J, 5D, 6G–H, 7I–J, 8H (all from type locality)

Diagnosis

In the new species, the penis tapering continuously from a broadened base with triangular lobe in about the middle on the right side is unique within the genus. Six diagnostic positions are of type 1 and three of type 3 (Table 3).

Etymology

Sulawesidrobia dinersteini sp. nov. is named after the American conservation biologist Eric Dinerstein (born 1952) for his influential contributions in identifying representative and biologically important ecoregions which help to develop a global safety net aiming to at least protect 30 percent of Earth's surface in order to save a considerable fraction of biodiversity.

Material examined

Holotype (Fig. 2E)

INDONESIA • Sulawesi, Lake Matano, S shore, on rocks and macrophytes; 02°27.850′ S, 121°13.870′ E; 1 Aug. 2004; von Rintelen and Zitzler leg.; MZB Gst. 12124.

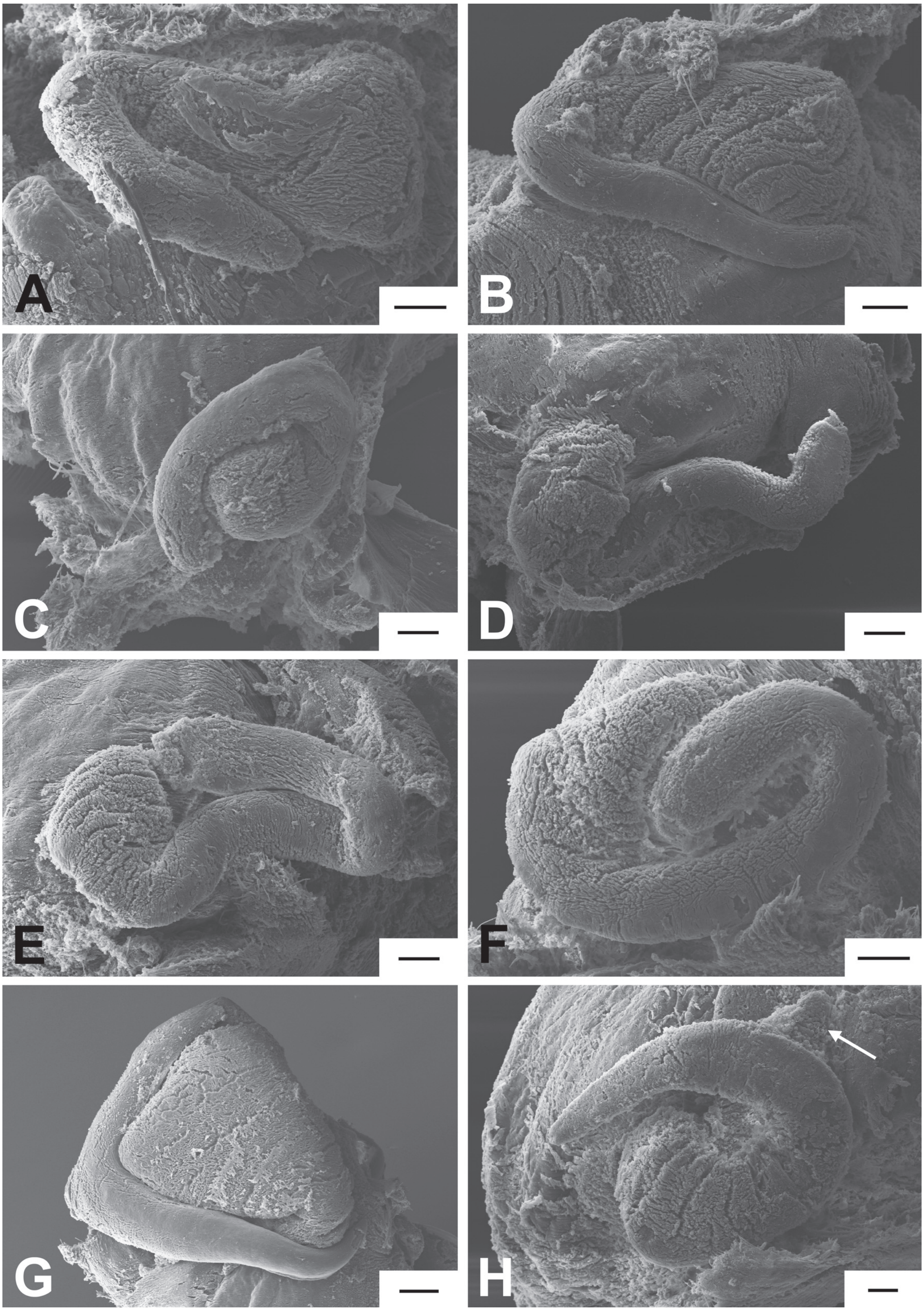

Fig. 8. Penis. **A–B**. *Sulawesidrobia wilsoni* sp. nov. (ZMB 191842). **C–D**. *S. carsonae* sp. nov. (ZMB 107079). **E–F**. *S. ehrlichi* sp. nov. (ZMB 107095). **G**. *S. crutzeni* sp. nov. (ZMB 191838). **H**. *S. dinersteini* sp. nov. (ZMB 107092). Arrow indicates lobe in H. Scale bars: A–F, H = 50 µm; G = 100 µm.

Paratypes (Fig. 3I–J)
INDONESIA • 40 specs; same collection data as for holotype; MZB Gst 12125 • 38 specs; same collection data as for holotype; ZMB 107092 • 11 specs; Sulawesi, Lake Matano, S shore, on rocks and macrophytes; 02°28.461′ S, 121°15.591′ E; 24 Jul. 2004; von Rintelen and Zitzler leg.; MZB Gst 12126 • 11 specs; same collection data as for preceding; ZMB 107094.

Description

SHELL (Figs 2E, 3I–J). Short-conical, sutures very shallow, about 1.6 times as high as wide, shell and priostracum light brown; protoconch structure not verified, ca 0.8 whorls; entire shell with 3.500 to 4.250 whorls, teleoconch without structure apart from growth lines; umbilicus a narrow slit; aperture orthocline, only slightly higher than wide.

OPERCULUM. Light yellow and thin, paucispiral, nucleus eccentric.

EXTERNAL FEATURES. Epidermis entirely black except mantle edge, eventually pigment less dense over distal genital glands; tentacles with small, central field of cilia (Fig. 5D).

MANTLE CAVITY (N = 4 from each locality). 16–18 (type locality) and 14–17 (2nd locality) ctenidial filaments, respectively; osphradium ovate-elongate, underneath middle or slightly behind middle of gill, half to two thirds of length of gill.

DIGESTIVE SYSTEM. The radula has the formula R 3-4 1 3-4/3-4 3-4, L 2 1 2-3, M1 15-20, M2 23-28, central denticle of lateral tooth with rounded tip (Fig. 6G–H); stomach without caecum, without pigment at type locality, pigmented at locality 2; intestine follows pallial genital glands, in females closer than in males.

FEMALE GENITALIA (N = 2 from each locality; Fig. 14I–J). Ovary starts ca 1.25 or slightly more whorls below apex, comprises ca 0.5 whorls, covers stomach chambers; renal oviduct first coiling 180° clockwise, then 270° counter-clockwise; no receptaculum seminis; bursa copulatrix more or less globular, bursal duct enters anteriorly; albumen gland with opaque-white anterior and milky-white posterior section, capsule gland with small opaque white and large yellow posterior portion.

MALE GENITALIA (N = 2 from each locality; Fig. 8H). Testis lobate, starts 0.75 (type locality) to 1 whorl (locality 2) below apex, comprises ca 1.25 whorls, covers stomach; vesicula seminalis coils along distal half to 0.75 whorls of testis; vasa deferentia insert close to middle of kidney-shaped prostate, which is much longer (almost twice as long) in locality 2 than at type locality; penis tapering continuously from broadened base, with triangular lobe in about middle on right side, can be considerable longer than in Fig. 8H, distal end subterminally grey.

Remarks

In the phylogenetic trees, *S. dinersteini* sp. nov. received high support. Its penis is unique as it is considerably shorter than the similar one of *S. megalodon* (see Zielske *et al*. 2011). Some similarity of the radula with that of *S. ehrlichi* sp. nov. has already been mentioned above. *Sulawesidrobia dinersteini* had the highest number of diagnostic alignment positions (Table 3) among the new species which clearly reflects the well-supported position in the phylogenetic analyses (see below, Figs 9–10, Supp, file 1).

Phylogenetic analyses

Maximum likelihood and Bayesian analyses found the same major groupings of species, however, differed in relationships at deeper nodes and resolution (Figs 9–10, Supp. file 1). The monophyly of *Sulawesidrobia* was well supported and a clade comprising *S. anceps*, *S. bicolor* – both from Lake Towuti –

and all newly described species from Lake Matano was found to be sister group to all other species in both analyses. The support was moderate [Bayesian posterior probability (BPP) = 0.94, bootstrap support (BS) < 50], though. *Sulawesidrobia wilsoni* sp. nov., *S. carsonae* sp. nov. and *S. dinersteini* sp. nov. were monophyletic and highly supported (BPP = 1 in all cases, BS = 95, 82, 88, respectively). *Sulawesidrobia ehrlichi* sp. nov. and *S. crutzeni* sp. nov. had paraphyletic relationships. In this clade, the species from Lake Towuti were paraphyletic with respect to the clade uniting the new species.

The species from Lake Poso were either sister group to or paraphyletic with respect to the remaining species from Lakes Mahalona, Matano, and Towuti. The entire clade as well as the three-lakes subclade

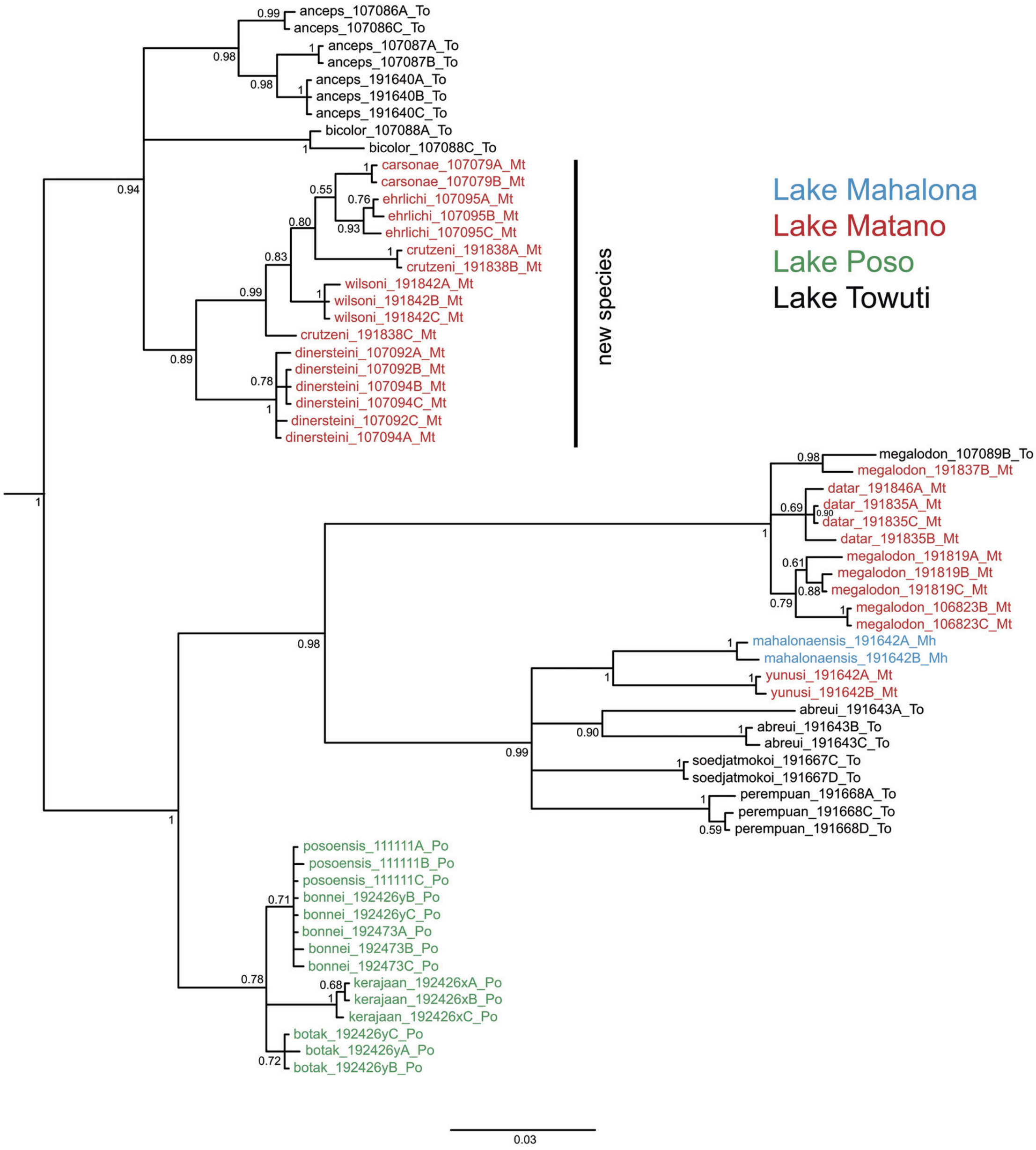

Fig. 9. Bayesian phylogenetic analysis. Outgroup pruned from tree. Taxa represented by "species name_ZMB catalogue number and specimen_abbreviation of lake". Numbers at nodes are posterior probabilities > 0.50. Scale in substitutions per site.

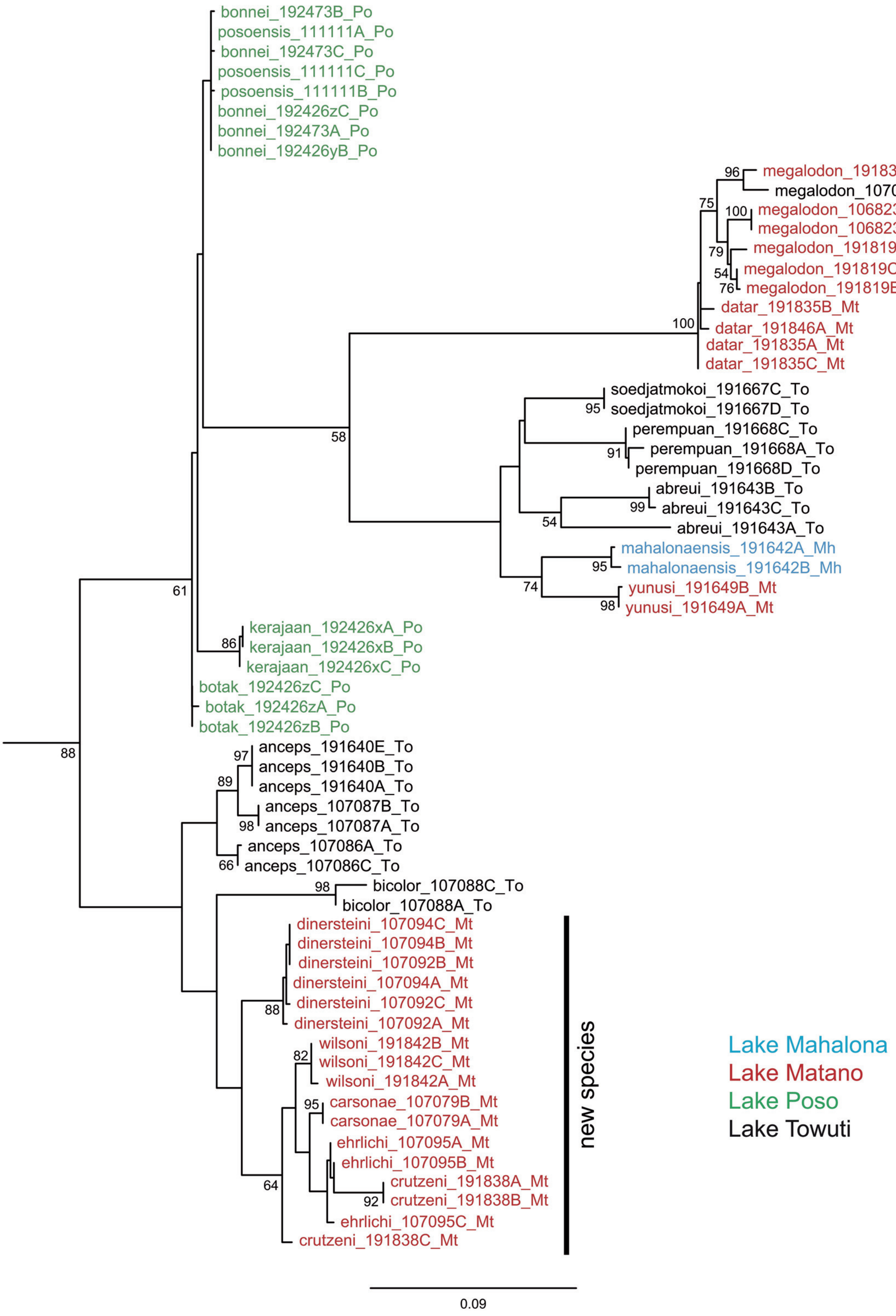

Fig. 10. Maximum likelihood phylogenetic analysis. Outgroup pruned from tree. Taxa represented by "species name_ZMB catalogue number and specimen_abbreviation of lake". Numbers at nodes are bootstrap support values > 50. Scale in substitutions per site.

were highly supported in the BA (BPP = 1, 0.98), less so by ML (BS = 61, 58). Of the species from Lake Poso, only *S. kerajaan* Haase & Bouchet, 2006, received high support (BPP = 1, BS = 86). In the three-lakes clade, all species were found to be monophyletic except *S. datar* Zielske, Glaubrecht & Haase, 2011, and *S. megalodon*. The newly sequenced specimens of these two species sorted correctly to the older sequences.

Shell morphometry

The PCA (Fig. 11) shows the morphological variation among the newly described species as well as three populations of *S. anceps* and one of *S. bicolor* included because of their similarity to *S. carsonae* sp. nov. Principal component (PC) 1 already explained 96.94% of the total variation and was, as usual, dominated by size where shell height had the highest loading. Shell height had also the highest loading on PC2, albeit with a negative sign. Thus, shell size increased along PC1 from the left to the right and along PC2 from top to bottom. The MANOVA (Wilks $\lambda = 0.0045$; $df1 = 45$, $df2 = 557.8$; $F = 29.1$, $p < 0.0001$) was highly significant and after sequential Bonferroni correction for multiple testing only *S. anceps* (ZMB 107086) and *S. carsonae* were not significantly distinguished in pairwise Hotelling's tests.

Discussion

As seen in some other radiations of tateid gastropods (Haase 2008; Zielske & Haase 2014a, 2014b; Zielske *et al.* 2017), morphological, anatomical and COI differentiation were not congruent among the species from Lake Matano indicating that these suites of characters evolve independently, in a mosaic-like fashion (de Beer 1954). COI within-species differentiation was low and although three of the new species were highly supported, the number of diagnostic alignment positions was low except in the case of *S. dinersteini* sp. nov. The low level of COI differentiation was also expressed in the paraphyly of *S. crutzeni* sp. nov. and possibly also *S. ehrlichi* sp. nov., probably due to incomplete lineage sorting (Funk & Omland 2003). In general, extant species of *Sulawesidrobia* appear to be young although their ancestor reached Sulawesi possibly about 10 Ma (Zielske *et al.* 2017).

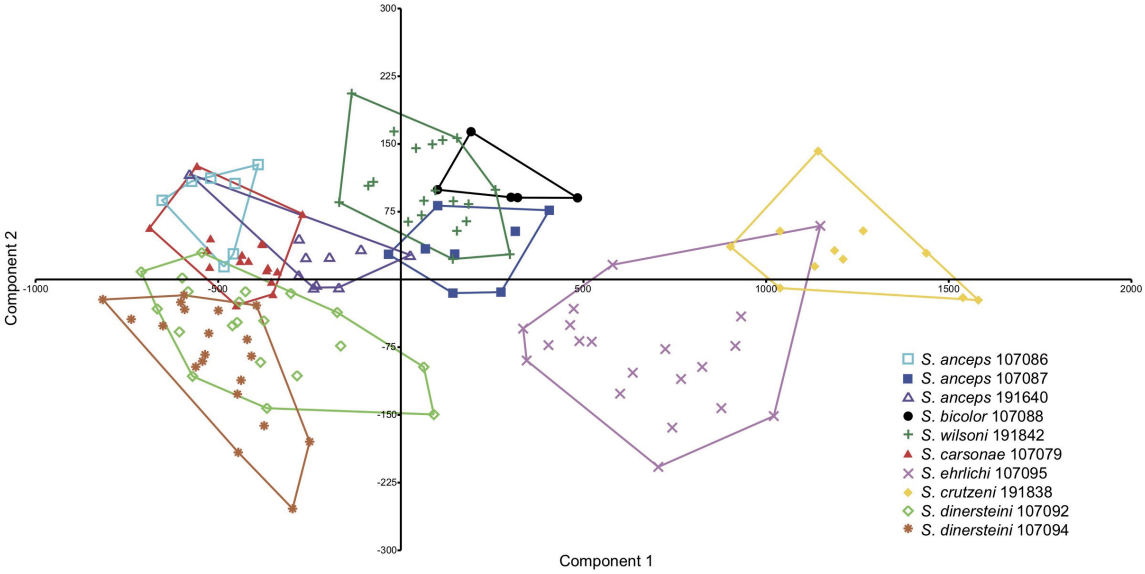

Fig. 11. Principal component analysis based on five shell measurements. Numbers are ZMB catalogue numbers.

The female genitalia, fairly variable among the species from Lakes Poso and Towuti (Haase & Bouchet 2006; Zielske *et al.* 2011) were quite conservative among the new species, only *S. crutzeni* sp. nov. had somewhat more complex oviduct loops. Similarly, the penes of *S. wilsoni* sp. nov., *S. carsonae* sp. nov., and *S. ehrlichi* sp. nov. were very similar. Those of *S. crutzeni* and *S. dinersteini* sp. nov. were more derived with a very broad base and slender distal end in the former and a lobe in the latter. Radular features and shell morphology had to be considered as well for an unambiguous species discrimination.

Despite the close relationships, the radulae differed substantially among species, especially with regards to the number, size and shape of the denticles of the lateral teeth. Particularly large denticles in low numbers were encountered in *S. dinersteini* sp. nov. Here, they were rounded, like in *S. ehrlichi* sp. nov. In all other species, they were pointed. Other conspicuous features were the fusion of the denticles of the central teeth in *S. carsonae* sp. nov. and *S. ehrlichi* and an enlarged basal denticle on the first marginal teeth in *S. wilsoni* sp. nov. All these features are shared with other, mostly unrelated species from other lakes (Ponder & Haase 2005; Haase & Bouchet 2006; Zielske *et al.* 2011) as already pointed out in the species descriptions. This probably indicates parallel evolution although the intraspecific variation observed in *S. bonnei* (Abbott, 1945) and *S. posoensis* Ponder & Haase, 2005, may suggest phenotypic plasticity (Ponder & Haase 2005). Most likely, the radular diversity is linked to different food sources and substrates they are rasped off from. Unfortunately, we lack detailed data on those to be able to make meaningful inferences such as for example in *Tylomelania* occurring in the same lake system (von Rintelen *et al.* 2004, 2010; Glaubrecht *et al.* 2008).

Lake Matano has undergone significant environmental change during the last decade. Between 2005 and 2010, South American flowerhorn cichlids, which constitute a man-made hybrid complex involving three genera, were released into the lake, either accidentally or intentionally, and this invasive species had spread to the entire lake by 2012 (Herder *et al.* 2012) and has more recently also been found to be widespread in Lake Mahalona and Lake Towuti in 2019 (TvR and Werner Klotz pers. obs.). In Lake Matano, flowerhorns are now certainly the dominant fish species in both shallow and deeper (ca 15 m, limit of exploration) water. At the same time, the invertebrate communities in Lake Matano have declined dramatically. During visits by TvR in 2017, 2018, and 2019 to nine sites in total, the number of living specimens of previously ubiquitous species of *Tylomelania*, was found to be much reduced and no small specimens or species were found at all. In 2018 and 2019, particular attention was paid to *Sulawesidrobia*, but not a single individual was found. This is perhaps not surprising, as these small snails seem to form an important part of the diet of flowerhorns (Herder *et al.* 2012; Hilgers *et al.* 2018). However, the sampling for the flowerhorn diet analyses was done in 2012 (Herder *et al.* 2012) and 2013 (Hilgers *et al.* 2018), so it would be interesting to see whether any *Sulawesidrobia* turn up in recent samples, which we predict to be unlikely.

Several sites around the lake were also heavily overgrown with algae, which was previously not the case in this ultra-oligotrophic lake. A link between the invasive flowerhorns and the apparent eutrophication, which yet remains to be quantified, is speculative at present, as Lake Matano is subjected to other anthropogenic changes as well. Its water level is to some degree regulated by a weir at its outflow by the Nickel mining company operating at the Malili lakes and the human population around the lake is increasing. In combination, these might also be contributing factors here. Whatever the exact causes, it seems unfortunately very likely that the populations or species of *Sulawesidrobia* in Lake Matano must be considered extinct, victims to some of the main threats to freshwater molluscs in general (Böhm *et al.* 2021). The species names given in this paper reflect this by acknowledging important conservationists. Their work has obviously not led to the necessary actions, as sadly driven home by our findings.

Acknowledgements

We thank Christel Meibauer for producing the COI sequences. Stefan Bock from the Imaging Centre of the University of Greifswald is acknowledged for taking the SEM images. Kristina von Rintelen assisted in parts of the field work conducted in 2003 and 2004. Field work at the central lakes in Sulawesi was financed through grants to MG (DFG GL 297/7-1, 7-2, and 7-3), which is thankfully acknowledged here. The Indonesian Institute of Sciences (LIPI) kindly issued the research permits (5209/SU/KS/2003, 4059/SU/KS/2004, 5263/SU/KS/2005) for the fieldwork in Indonesia.

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Supplementary material

Supp. file 1. Bayesian phylogenetic analysis including outgroup. Taxa represented by "species name_ZMB catalogue number and specimen_abbreviation of lake". Numbers at nodes are posterior probabilities > 0.50. Scale in substitutions per site. https://doi.org/10.5852/ejt.2022.864.2089.8747

Supp. file 2. Alignment (COI, 658 bp) of new species as well as *Sulawesidrobia anceps* Zielske, Glaubrecht & Haase, 2011 and *S. bicolor* Zielske, Glaubrecht & Haase, 2011 for identification of diagnostic positions. https://doi.org/10.5852/ejt.2022.864.2089.8749

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