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- Abstract
- Introduction
- Materials and Methods
- Results
- Discussion
- Acknowledgements
- References
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In Focus

The cover picture shows *Triphoris albidus* A. Adams, 1851

See paper of **Albano PG et al.** Annotated catalogue of the types of Triphoridae (Mollusca, Gastropoda) in the Natural History Museum of the United Kingdom, London

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A new species of *Bungona* in Turkey (Ephemeroptera, Baetidae): an unexpected biogeographic pattern within a pantropical complex of mayflies

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Abstract

By using an integrative approach, we describe a new species of mayfly, *Bungona* (*Chopralla*) *pontica* **sp. n.**, from Turkey. The discovery of a representative of the tropical mayfly genus *Bungona* in the Middle East is rather unexpected. The new species shows all the main morphological characters of the subgenus *Chopralla*, which has its closest related species occurring in southeastern Asia. Barcoding clearly indicated that the new species represents an independent lineage isolated for a very long time from other members of the complex. The claw is equipped with two rows of three or four flattened denticles. This condition is a unique feature of *Bungona* (*Chopralla*) *pontica* **sp. n.** among West Palaearctic mayfly species. Within the subgenus *Chopralla,* the species can be identified by the presence of a simple, not bifid right prostheca (also present only in *Bungona* (*Chopralla*) *liebenauae* (Soldán, Braasch & Muu, 1987)), the shape of the labial palp, and the absence of protuberances on pronotum.

Introduction

The Middle East is regarded as a transitory region containing elements of Western and Eastern Palaearctic faunas (Heller 2007). This explains why also the mayfly fauna of Turkey is very diversified, comprising 157 species reported in the most recent checklist (Salur et al. 2016, with some later comments by Kazancı and Türkmen 2016). Regarding biogeographic patterns of Turkish mayflies, a large proportion of species exhibits a broad Palaearctic or West Palaearctic distribution. A large part of the fauna is composed of European species with ranges extending into the Middle East (see Bauernfeind and Soldán 2012 for distributional ranges of all European species). Another major group represents strictly Middle East species, including those described and known from only Turkey. Caucasian species also frequently occur, particularly in Eastern Turkey (Kazancı 2009, Türkmen

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and Kazancı 2013). However, mayfly taxa usually showing preferences for tropical regions but occur in Turkey outside the tropical realm (and in the Middle East in general) at the same time are extremely rare.

In the present contribution, we describe such a taxon occurring in the Anatolian Peninsula, specifically a new species from the genus *Bungona* Harker, 1957, subgenus *Chopralla* Waltz & McCafferty, 1987. This subgenus currently encompasses seven species and is distributed in Borneo, Vietnam, Hong Kong, and Sri Lanka (Marle et al. 2016). *Bungona* is one of the four genera of the *Cloeodes*-complex (sensu Salles et al. 2016), this complex containing *Cloeodes* Traver, 1938, *Potamocloeon* Gillies, 1990, and *Crassolus* Salles, Gattolliat & Sartori, 2016. This complex is distributed in the Neotropical, Nearctic, Afrotropical, Oriental, and Australasian regions but is most diversified in the Pantropical area. Only a few species are reported from the Nearctic (Waltz and McCafferty 1987) and none from the Palaearctic. Consequently, the discovery of this lineage in Asia Minor is extremely surprising, and thus, we discuss the relationships of the new species with other members of the *Cloeodes*-complex together with the evolutionary and biogeographic implications of this discovery. To achieve this goal, we use an integrative approach combining evaluation of morphological characteristics with a molecular analysis of mtDNA sequences. We also provide information on the evolutionary history of the new species and a review of tropical mayfly lineages reported from the Middle East up to now.

Material and methods

Taxon sampling

A new species of mayflies *Bungona* (*Chopralla*) *pontica* sp. n. was collected in northern Turkey in 2011 (Fig. 8). Herein, we describe the new taxon including both, morphological and molecular techniques. To analyze the affinities of the new species based on the molecular data, we built a dataset comprising sequences of several mayfly taxa, as summarized in Table 1.

In the selection of taxa, we wanted to include all major clades within the *Cloeodes*-complex, as inferred based on morphological data by Salles et al. (2016). Specifically, the sampling included the genus *Potamocloeon* Gillies, 1990 with the subgenera *Potamocloeon* and *Aquaediva* Salles et al. 2016, which together constitute a monophyletic group sister to all the rest of the *Cloeodes*-complex. We also included the genus *Crassolus* Salles et al. 2016, forming a sister lineage to the clade comprising the genera *Cloeodes* and *Bungona*. These latter two taxa were also included in the analysis, in case of the genus *Bungona*, all three subgenera (*Bungona*, *Centroptella* Braasch & Soldán, 1980 and *Chopralla* Waltz & McCafferty, 1987) were sampled. Therefore, we achieved a comprehensive set of sequences from all major phylogenetic lineages within the *Cloeodes*-complex. We also included some taxa outside of the complex, considered related to the ingroup based on previous morphological investigations (Salles et al. 2016). These encompass the genera *Crassabwa* Lugo-Ortiz & McCafferty, 1996, *Cheleocloeon* Wuillot & Gillies, 1993, *Dabulamanzia* Lugo-Ortiz & McCafferty, 1996 and *Centroptilum* Eaton, 1869.

A part of the sequences used for the analysis were obtained from the public databases, the rest was newly sequenced within the framework of the present study (see Table 1 for details including sources of data and accession numbers). We also searched in BOLD and GenBank databases for other existing similar sequences. However, no sequences more similar than 84% (and therefore potentially informative for the analysis) were found except those already included in the dataset.

Voucher specimens of the new species, as specified in Results, is deposited in the collection of the Biology Centre of the Czech Academy of Sciences, Institute of Entomology, České Budějovice, Czech Republic (IE CAS: holotype larva, three paratype larvae) and in the Musée cantonal de zoologie, Lausanne, Switzerland (MZL: two paratype larvae).

Morphological study

Two paratype specimens of *Bungona* (*Chopralla*) *pontica* sp. n. were mounted on slides, using HydroMatrix (MicroTech Lab, Graz, Austria), Canada balsam, or Euparal. Drawings were made using an Olympus SZX7 stereomicroscope and an Olympus BX41 microscope, both equipped with a drawing attachment (camera lucida). Photographs were made using a Leica M205 C stereomicroscope with a Canon EOS 1200D digital camera. All photographs were subsequently enhanced using Adobe Photoshop CS5. For scanning electron microscopy (SEM), the samples in 96% ethanol were transferred in three mixtures of graded series ethanol : acetone (2:1, 1:1 and 1:2) with 15 minutes in each mixture and dried by means of a critical point dryer CPD 2 (Pelco TM). The samples were mounted on an aluminium target by means of carbon tape, coated with gold using a sputter coater Baltec SCD 050. Finally, the samples were examined in a FE-SEM JSM 7401-F scanning electron microscope (JEOL Ltd, Tokyo, Japan) at low accelerating voltage of 4 kV using GB-low mode. The accomplished topographic images provided a resolution of 1.5 nm by an efficient semi-in-lens detector. The morphological terminology follows Salles et al. (2016).

Molecular study

DNA extraction, amplification and sequencing. Genomic DNA was extracted from whole specimens or legs using the NucleoSpin 96 (Macherey-Nagel, Düren, Germany) tissue kit, the BioSprint 96 extraction robot (Qiagen), or the Wizard SV Genomic DNA Purification System Kit (Promega, California, USA), following the manufacturer's protocol. We analyzed the 658 bp fragment of the mitochondrial DNA barcoding gene cytochrome *c* oxidase subunit 1 (*cox1*). Standard polymerase chain reaction (PCR) amplifications were performed with the primer pair: LCO1490 + HCO2198 (Folmer et al. 1994) or C1-J-1718 (Simon et al. 1994) + HCO2198 (for the Neotropical material, see Table 1). The PCR products were pu-

Table 1. Taxa used in the molecular dataset.

Species	Location	GBIF or institutional code	GenBank acc. number	Sources
Bungona (*Chopralla*) *pontica* sp. n.	Turkey	GBIFCH00272819	MH969424	Present study
Bungona (*Chopralla*) *pontica* sp. n.	Turkey	GBIFCH00272820	MH969425	Present study
Bungona (*Bungona*) *narilla* Harker, 1957	Australia	See Fig. 9	HM017831 to HM017836	Webb and Suter 2010
Bungona (*Bungona*) *illiesi* (Lugo-Ortiz & McCafferty, 1998)	Australia	295442100	HM017842	Webb and Suter 2010
		295442098	HM017842	
Bungona (*Centroptella*) *soldani* (Müller-Liebenau, 1983)	India	–	LC061855	Selvakumar et al. 2016
Bungona (*Centroptella*) sp.	Brunei	GBIFCH00517514	MH969410	Present study
		GBIFCH00517515	MH969411	
Bungona (*Chopralla*) *ceylonensis* (Müller-Liebenau, 1983)	India	–	LC061854	Selvakumar et al. 2016
Bungona (*Chopralla*) sp.	Sumatra	MG0535	MH969418	Present study
		MG0539	MH969419	
		MG0544	MH969420	
		MG0561	MH969421	
		MG0588	MH969422	
		MG1083	MH969423	
Centroptilum elongatum Suter, 1986	Australia	JWA766	HM017830	Webb and Suter 2010
Cheleocloeon soldani Gattolliat & Sartori, 2008	Saudi Arabia	–	HG935111	Salles et al. 2014
Cloeodes aymore Massariol & Salles, 2011	Brazil	Ep2743B	MH969407	Present study
Cloeodes barituensis Nieto & Richard, 2008	Argentina	EP6756B	MH969405	Present study
Cloeodes ioachimi Salles, Massariol & Angeli, 2015	Brazil	Ep6536B	MH969408	Present study
Cloeodes itajara Massariol & Salles, 2011	Brazil	Ep2715C	MH969406	Present study
Cloeodes sp.	Costa Rica	Ep7015A	MH969409	Present study
Crassabwa flava (Crass, 1947)	South Africa	GBIFCH00517544	MH969417	Present study
Crassolus sp.	South Africa	GBIFCH00517535	MH969415	Present study
Dabulamanzia improvida Lugo-Ortiz & McCafferty, 1997	Madagascar	GBIFCH00517533	MH969413	Present study
		GBIFCH00517534	MH969414	
Potamocloeon (*Aquaediva*) *pseudogladium* (Gattolliat, 2001)	Madagascar	GBIFCH00517532	MH969412	Present study
Potamocloeon (*Potamocloeon*) *dentatum* (Kimmins, 1956)	Republic of Guinea	GBIFCH00517540	MH969416	Present study

rified using the QIAquick PCR purification kit (Qiagen) or with ExoSAP-IT PCR Product Cleanup (Affymetrix, Ohio, USA), and customary sequenced from both directions by Macrogen (Amsterdam, The Netherlands) or Microsynth (Balgach, Switzerland). Forward and reverse sequences were assembled and edited using Geneious R7 v.7.1.3 (Biomatters Ltd).

Analyses of molecular data. To get an overview of the phylogenetic position of the here newly described species and its closely related species, we reconstructed a Bayesian phylogenetic tree. The molecular analysis comprised sequences of 70 specimens, including 21 newly sequenced specimens (Table 1). A multiple sequence alignment was obtained by using MAFFT v.7.050b (L-INS-i algorithm with default settings; Katoh and Standley 2013). The alignment was checked for the occurrence of stop codons and indels using Mesquite v.2.75 (Maddison and Maddison 2011). Identical haplotypes were removed using collapsetypes_v.4.5.pl (Chesters 2013). An ultrametric gene tree was reconstructed using a coalescent prior sensu Monaghan et al. (2009) and Rutschmann et al. (2014, 2017) in BEAST v.2.4 (Bouckaert et al. 2014). We applied the HKY + Γ model of molecular evolution as this has been shown to fit well *cox1* data sets of mayflies (e.g. Rutschmann et al. 2017, Gattolliat et al. 2018). Moreover, more complex partitioning-schemes resulted in very low effective sample sizes (ESS) for preliminary tree inferences (see also Gattolliat et al. 2018). Three independent tree inferences each with 50 mio generations were performed in order to check consistency among runs. The convergence of each run and between runs was checked using Tracer v.1.7 (Rambaut et al. 2018), considering effective sample sizes > 200. We summarized the trees using LogCombiner v.2.4 (Bouckaert et al. 2014), discarding 10 % of each tree as burnin and obtained a maximum clade credibility tree using TreeAnnotator v.2.4 (Bouckaert et al. 2014).

Results

Taxonomy

Bungona (*Chopralla*) *pontica* Sroka, Godunko & Gattolliat, sp. n.

http://zoobank.org/78B55194-D8FC-422C-A0C1-5715400FEEAE

Figures 1–6

Type material. *Holotype.* Male mature larva (IE CAS), TURKEY, Dipsiz Önü Stream, Gemiciler village, 500 m upstream from the village, in forest near Inebolu–Ayancık road, 50 m a.s.l., 41°57.641'N, 33°53.026'E; 06.vii.2011, Sroka & Godunko leg. [locality code: TUR11/52].

Paratypes. 2 mature male larvae (IE CAS: 1 larva in EtOH with some body parts mounted on a slide: mouthparts, legs,

Figure 1. *Bungona* (*Chopralla*) *pontica* sp. n., habitus. **A** Dorsal. **B** Lateral.

gills, tergum X, paraprocts, cerci; 1 larva dried and gilded as a SEM sample), same data as holotype; 1 mature male larva (IE CAS: in EtOH), TURKEY, Ilişi Stream, Inebolu–Ayancık road, Yakaören village, vicinity of Abana town, 50 m a.s.l., 41°56.244'N, 34°13.360'E; 06.vii.2011, Sroka & Godunko leg. [locality code: TUR11/53]; 2 female larvae (MZL: 1 larva in EtOH: GBIFCH00272819 [FREDIE SR24E11] and 1 larva on a slide GBIFCH00272820 [FREDIE SR24E12]), same data as holotype.

Diagnosis. The prostheca of right mandible simple (not bifid) with several minute denticles apically; setae on the dorsal margin of the femur reaching 1/4 of the femur width; the surface of pronotum without tubercles. A detailed comparison with related species is presented in the Discussion.

External morphology of the larva. Body length approx. 4.5 mm–4.7 mm ($n = 2$). Length of cerci ca 1.5–2.0 mm (0.3 × body length), paracercus equal in length to cerci (Fig. 1A).

Head. Labrum (Fig. 2A) ca 1.3× wider than long, broadly rounded distally, with shallow medial emargination. Dorsal surface of labrum (Fig. 2A, right) with one long seta submedially (sI in Fig. 2A), apicolateral arc of three slightly shorter setae (sII in Fig. 2A); and with few short hair-like setae scattered on surface. Dense row of short branched setae present along anterior margin of labrum, longer setae anteromedially. Ventral surface of labrum (Fig. 2A, left) with group of fine hair-like setae near anterior margin.

Hypopharynx with trilobed lingua apically, slightly longer than superlingua. Distal parts of lingua and superlingua covered with short, hair-like setae.

Right mandible (Fig. 2C) with two partially fused incisor groups (outer incisor group (oig) in Fig. 2C, and inner incisor group (iig) in Fig. 2C), each equipped with three denticles. Right prostheca (prs in Fig. 2C) simple, not bifid, with several minute denticles apically. Numerous short setae present between prostheca and mola.

Left mandible (Fig. 2B) with two mostly fused incisor groups, outer incisor group with four denticles (oig) in Fig. 2B, and inner incisor group with three denticles (iig) in Fig. 2B. Left prostheca (prs in Fig. 2B) robust, with about three short rounded denticles and comb-shaped structure apically. Numerous short setae present between prostheca and mola.

Maxilla (Fig. 2H) with two-segmented maxillary palp. Segment II 1.8 × longer than segment I, narrowing distally, and pointed at apex.

Labium (Figs. 2D–2G) with glossa slightly longer than paraglossa, inner margin of glossa with row of setae increasing in length apically. Second row of shorter setae present submarginally on ventral surface of glossa. Outer margin of glossa mostly without setation except for subapical part.

Paraglossa along outer margin with row of setae, increasing in length apically. Groups of similar setae in subapical region present on both, dorsal and ventral surface. Along inner margin, short rows consisting of ca five setae submarginally also present on both, dorsal and ventral surface.

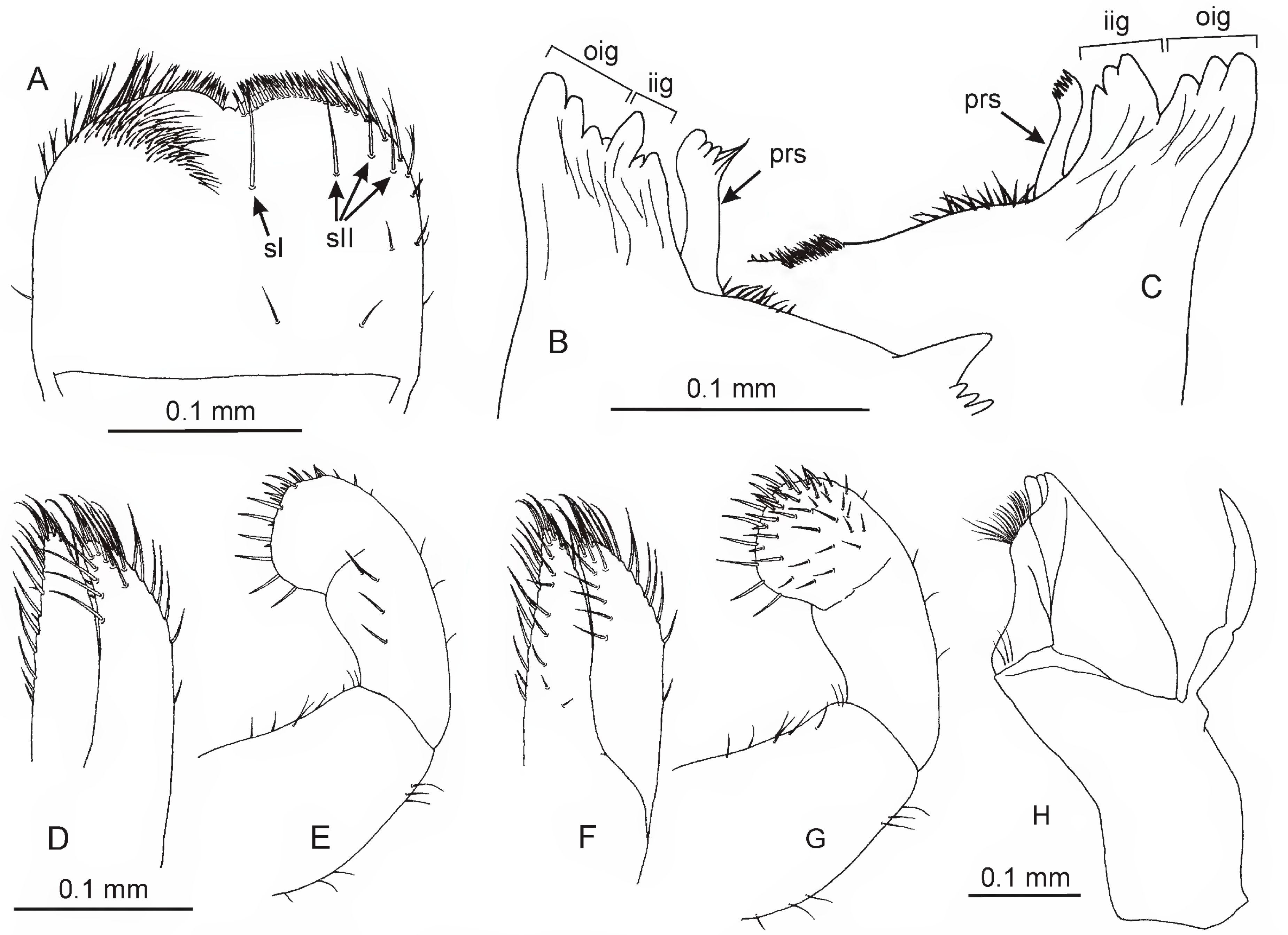

Figure 2. *Bungona* (*Chopralla*) *pontica* sp. n., mouthparts. **A** Labrum (right side dorsal, left side ventral). **B** Incisors of left mandible (dorsal, same scale bar for **B** and **C**). **C** Incisors of right mandible (dorsal). **D** Glossa and paraglossa (dorsal, same scale bar for **D–G**). **E** Labial palp (dorsal). **F** Glossa and paraglossa (ventral). **G** Labial palp (ventral). **H** Maxilla. Abbreviations: oig–outer incisor group, iig–inner incisor group, prs–prostheca, sI–submedial seta, sII–apicolateral arc of setae.

Labial palp with segment I slightly longer than segments II and III combined. Segment I equipped with sparse short hair-like setae. Segment II with ca four stout setae in central part of dorsal surface, not expanded distoventrally. Segment III quadrangular, slightly distally expanded, with numerous setae on ventral surface, increasing in length and thickness distally.

Thorax. Colour whitish with distinct dark brown pattern (Fig. 1A, B). Surface of pronotum with short minute scales and without any protuberance (Fig. 6A).

Legs whitish, tarsi slightly darker (Fig. 1B). Scales abundant on surface of femora, tibiae, and tarsi (Fig. 4A).

Femur in all leg pairs with dorsal and ventral margin subparallel, ca 4 × longer than wide. Dorsal margin with sparse row of 8 or 9 long, apically rounded setae, slightly widened apically (Fig. 3A, C, E). Length of setae ca 0.25 × femur width. Occasional short setae present along anterior margin of femur.

Tibia with patella-tibial suture (middle and hind leg; pts in Figs 3D, F, 4C, D) which is absent on foreleg (Fig. 3B, 4B). Position of patella-tibial suture at middle of tibia length in hind leg, and slightly more distally in middle leg (Fig. 3D, F). Length of row of long setae on anterior surface of tibia extending for ca 0.5 × length of tibia in all legs. Width of row of long setae on posterior surface of tibia extends ca 0.5 × width of tibia in fore- and middle leg. In hind leg, row of long setae on posterior surface of tibia running parallel to outer margin of tibia, for same distance as row of setae on anterior surface. Angle between rows of setae on anterior and posterior margin of tibia more acute on hind leg compared to fore- and middle leg. (Fig. 3B, D, F). Short, bluntly pointed setae situated along inner margin of tibia.

Tarsi equipped with several rows of long hair-like setae along outer margin. Most regular row apparent on anterior surface, and accompanied by more irregular rows posteriorly. Length of rows of setae reaching ca 0.5 × length of tarsus in all legs. Occasional short spine-like setae present along inner margin of tarsus. Claws equipped with two rows of 3 or 4 flattened denticles, subapical striations, and minute subapical setae (Fig. 4E, F).

Hind wing pads vestigial (Fig. 5B).

Abdomen. Colour pale whitish with dark brown pattern (Fig. 1A). Tergite I pale, with dark stripe along posterior margin. Tergites II–VI mostly dark, with tiny paired pale dots submedially and several larger pale

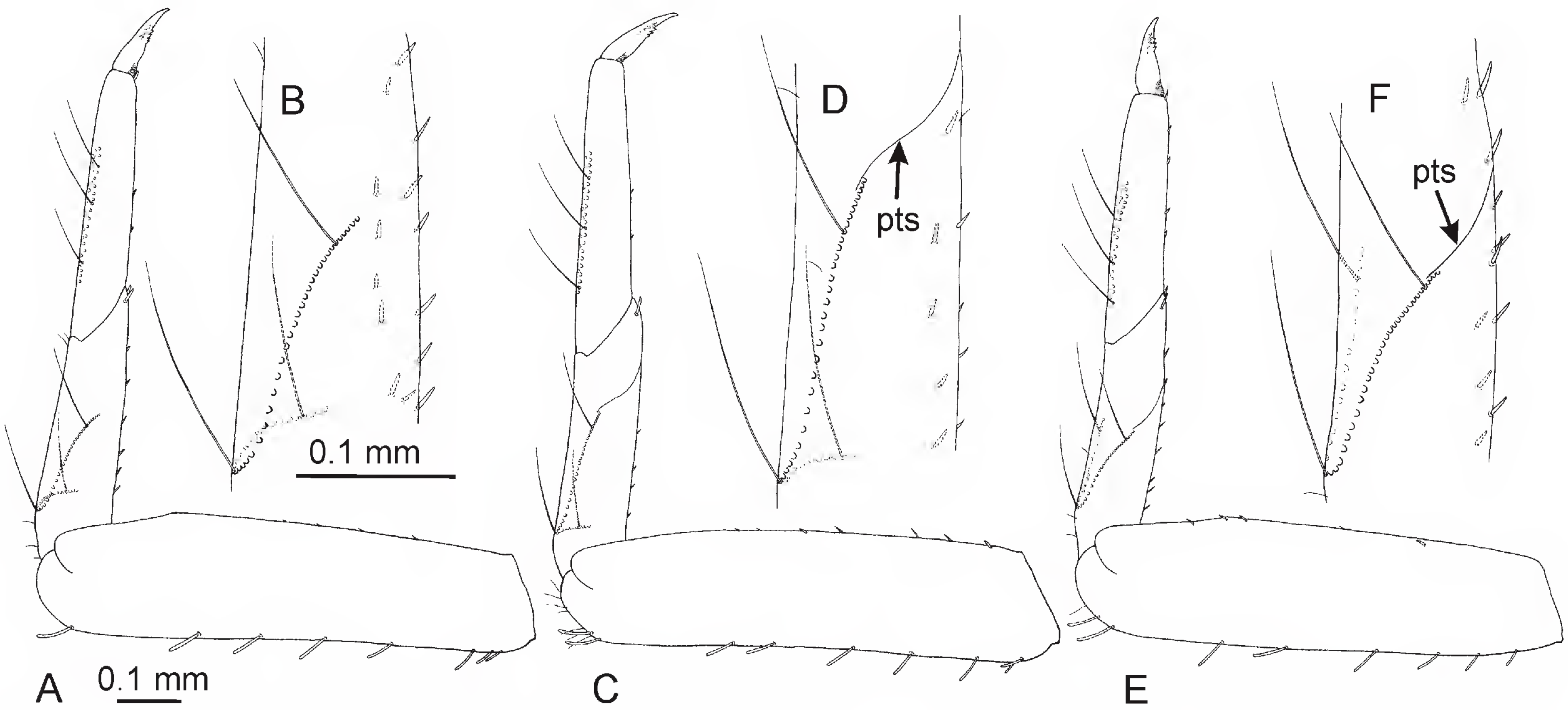

Figure 3. *Bungona* (*Chopralla*) *pontica* sp. n., legs. **A** Foreleg (dorsal, same scale bar for **A, C, E**). **B** Basal part of fore tibia (dorsal, same scale bar for **B, D, F**). **C** Middle leg (dorsal). **D** Basal part of middle tibia (dorsal). **E** Hind leg (dorsal). **F** Basal part of hind tibia (dorsal). Abbreviations: pts–patella-tibial suture.

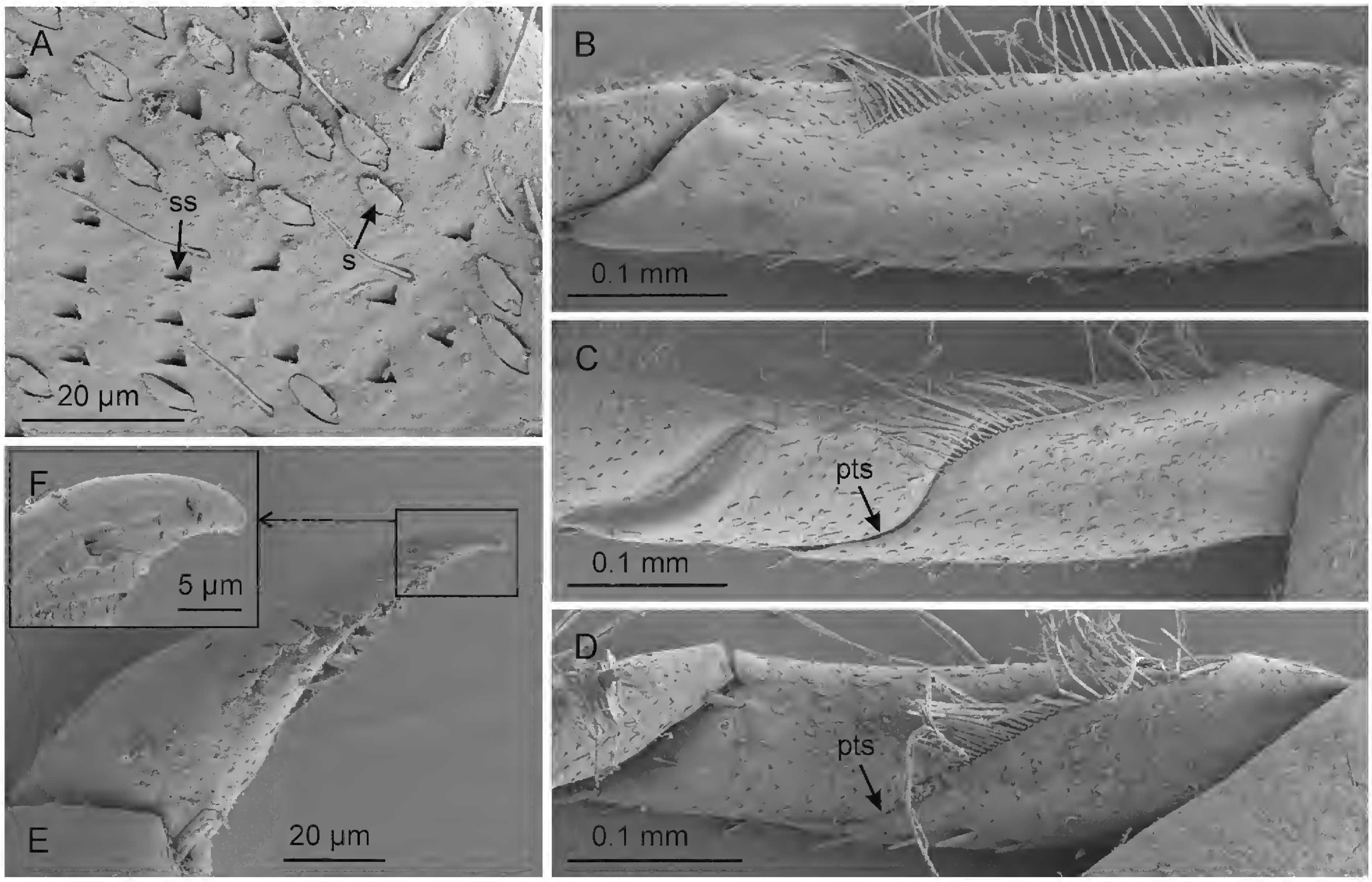

Figure 4. *Bungona* (*Chopralla*) *pontica* sp. n., legs. **A** Scales on surface of legs. **B** Foretibia (dorsal). **C** Middle tibia (dorsal). **D** Hind tibia (dorsal). **E** Claw. **F** Detail of claw apex. Abbreviations: s–scale, ss–scale socket, pts–patella-tibial suture.

areas medially, submedially, and laterally. Tergites VII–VIII mostly pale, darker stripes along posterior margins. Tergites IX–X darker, with pale area anteriorly on tergite IX. Sternites pale whitish, with darker longitudinal stripes sublaterally (Fig. 1B).

Tergites equipped with numerous elongate scales, scale bases and short hair-like setae on surface (Fig. 5C). Posterior margin of tergites bear triangular spines (Fig. 5C); limited to lateral side on tergite I, larger and more elongated spines on tergites II–VII generally with median spines

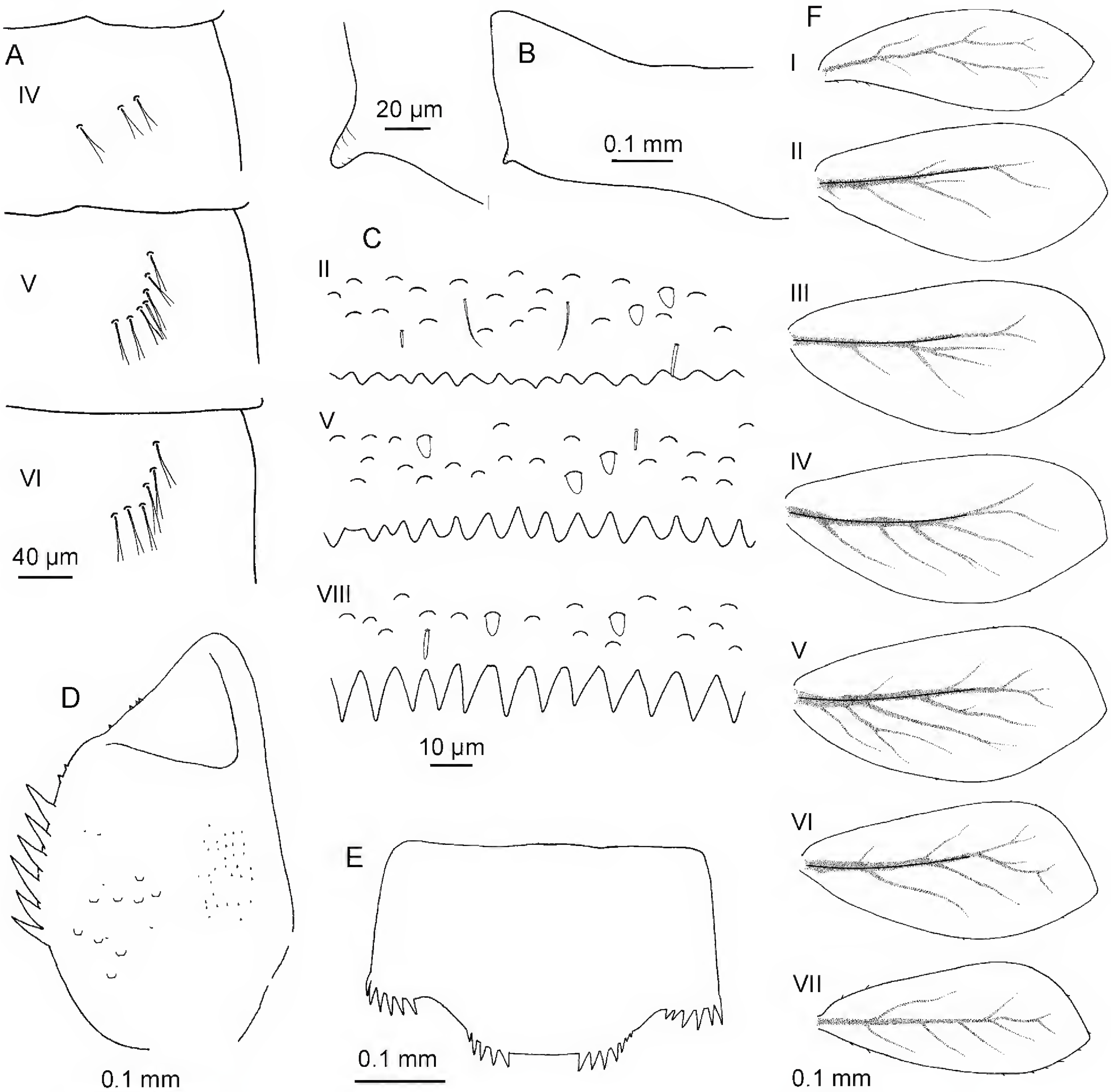

Figure 5. *Bungona* (*Chopralla*) *pontica* sp. n., thorax and abdomen. **A** Setae on abdominal sterna IV, V and VI. **B** Part of metathorax with vestigial hind wing pad. **C** Surface and posterior margin of abdominal terga II, V and VIII. **D** Paraproct. **E** Abdominal tergum X. **F** Gills.

shorter than lateral, tergites VIII and IX similar to previous ones except central spines more reduced or completely absent. Spines on posterior margin of tergite X in two groups laterally and further two groups submedially (Fig. 5E).

Sternites also equipped with scales and scale bases occasionally scattered over the surface. Posterior margins of sternites IV to IX with triangular spines, very reduced on sternite IV, more distinct on posterior segments; spines absent in segments I–III. Row of conspicuous long setae present on sternites IV–VI (row of shorter setae also present on sternite III; Fig. 5A).

Gills (Fig. 5F) present on segments I–VII, slightly asymmetrical, with indistinct tracheation, apically pointed, margins occasionally bearing short setae. Brownish line medially on dorsal surface, parallel with medial trachea, not distinguishable on gills I and VII.

Paraprocts (Fig. 5D) with six pronounced marginal spines sometimes accompanied with 1–2 smaller ones. Surface equipped with sparse scales and scale bases. Posterolateral extension with few small marginal spines, absent in some specimens.

Caudal filaments (Fig. 1A, B) whitish with dark rings on segment margins. Distal margin of each segment equipped with pointed spines and scales. Outer margin of cerci bears enlarged spines on every second segment. Secondary swimming setae present.

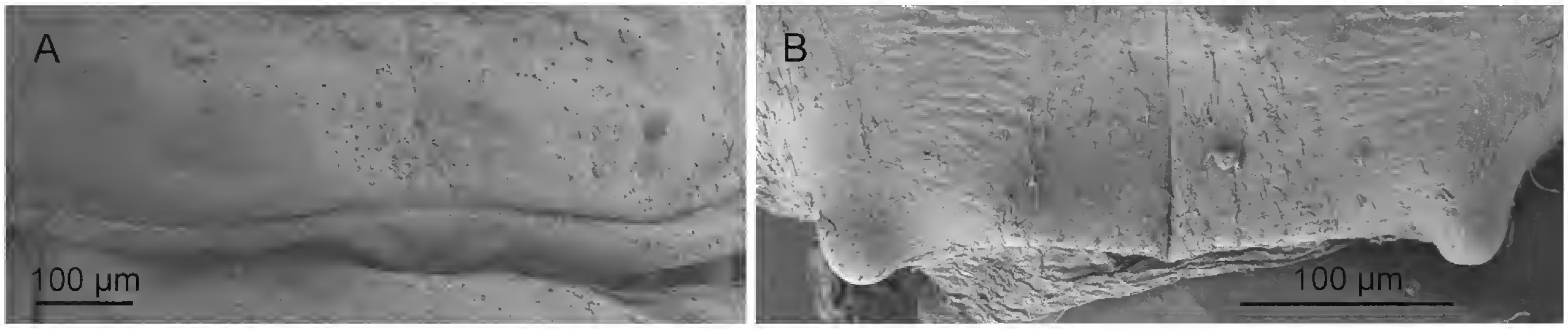

Figure 6. Difference in the arrangement of the posterior margin of pronotum between *Bungona* (*Chopralla*) *pontica* sp. n. (**A**) and *Bungona* (*Chopralla*) *liebenauae* (**B**).

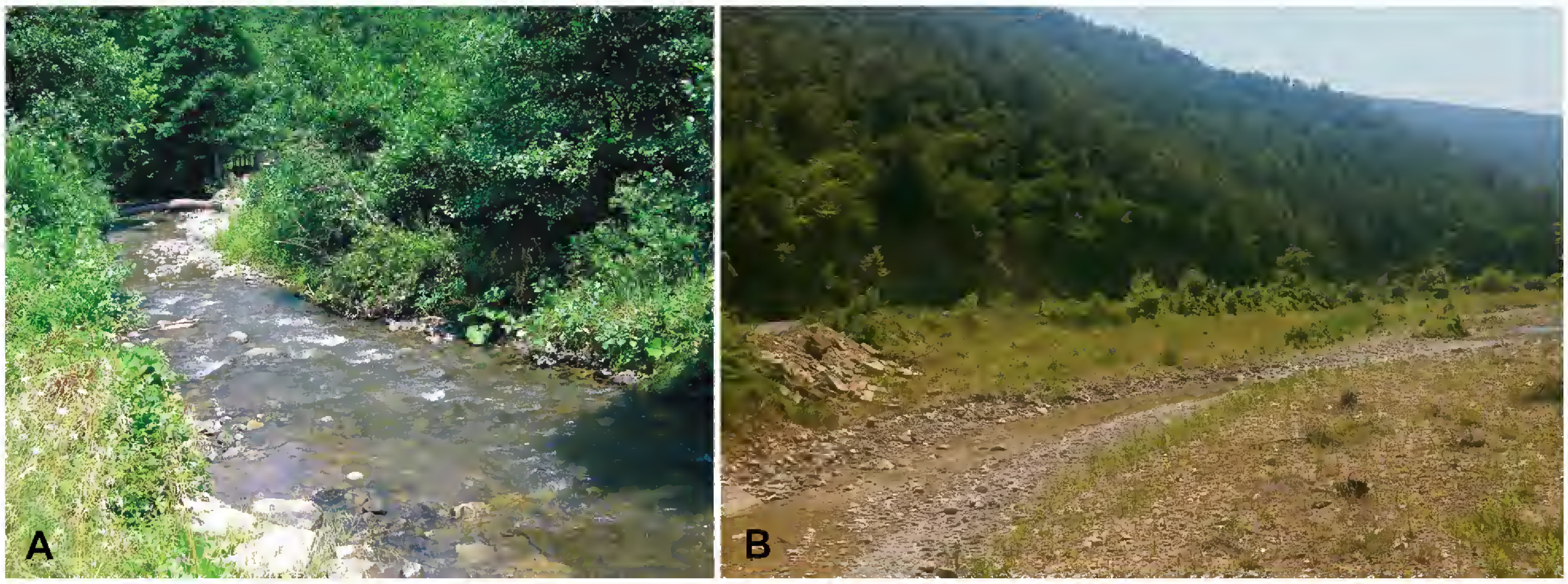

Figure 7. A Type locality of *Bungona* (*Chopralla*) *pontica* sp. n. (Dipsiz Önü stream near Gemiciler village). **B** Valley of Dipsiz Önü stream approximately 400 m downstream from the type locality.

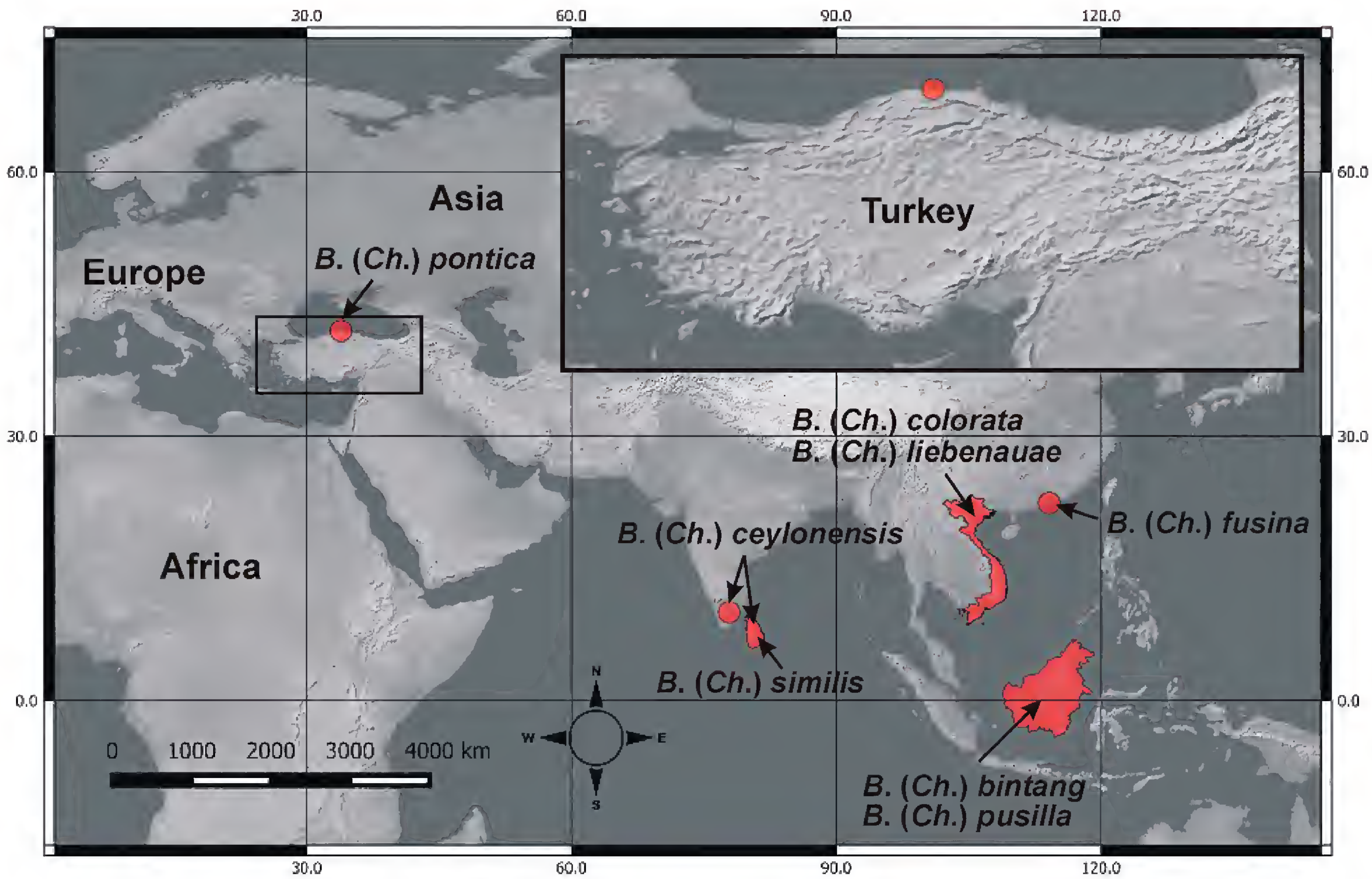

Figure 8. Distribution of *Bungona* (*Chopralla*) spp. Marked occurrence in Turkey encompass the position of both known localities of *Bungona* (*Chopralla*) *pontica* sp. n.

Etymology. "Pontus" in Latin means "Black Sea" in reference to the geographical region where the type material of the new species was collected.

Habitat and ecology. Larvae were found in two slightly eutrophic small streams of different size, the Dipsiz Önü and Ilişi streams. Both small streams flow in northern direction towards the Black Sea within shallow valleys in the westernmost part of the Pontic Mountains (Kuzey Anadolu Dağlari). The slopes surrounding both valleys are relatively steep, formed by hills reaching up to 450 m a.s.l. (Fig. 7B) and are densely overgrown by the typical Northern Anatolian conifer and deciduous forests (Euxine-Colchic deciduous forests ecoregion).

The Dipsiz Önü stream at the type locality at 50 m a.s.l. is small, only approximately 0.8–1.5 m wide, and partly shaded by vegetation (Fig. 7A). The bottom consists of relatively coarse stony substratum, partly covered by detritus in the littoral region. The current velocity was approximately 0.5 m/s and the water temperature reached 18 °C (measured ca 5 cm below the water surface).

The Ilişi stream, at the collecting site, was up to 4–4.5 m wide, had a relatively high velocity current (up to 0.7 m/s), well-expressed stream discharge, and a bottom structure consisting of relatively coarse stony substratum with a low concentration of detritus.

We can assume that the new species is probably very rare at the studied localities as well as in all Turkey. During extensive collecting trips in the Sinop Province in 2011 and 2017, only six larvae were found. *Bungona pontica* sp. n. larvae co-occurred with mayfly larvae of *Epeorus* sp., *Electrogena* sp., *Procloeon bifidum* (Bengtsson, 1912), *Baetis fuscatus* (Linnaeus, 1761), *B.* (*Rhodobaetis*) *rhodani* (Pictet, 1843), *B. vardarensis* Ikonomov, 1962, *Nigrobaetis digitatus* (Bengtsson, 1912), and *Serratella ignita* (Poda, 1761). Additional information on the species composition of the mayfly fauna within the Sinop and Kastamonu provinces was published by Tanatmış (2004), Ertorun and Tanatmış (2004) and further east, in the rivers of the Trabzon Province by Aydınli (2017). The presence of mature larvae at the beginning of July, indicates a flight period of *B.* (*Ch.*) *pontica* n. sp. during the first half of the summer.

Molecular reconstruction. In total, 61 haplotypes were reconstructed, including 19 previously unknown haplotypes. The new sequences were deposited at GenBank (Acc. nos in Table 1). The *cox1* tree detected *B.* (*Ch.*) *pontica* sp. n. as a discrete lineage which is not nested within other *Bungona* (*Chopralla*) species (Fig. 9). Two other *Bungona* (*Bungona*) species, namely *B.* (*B.*) *narilla* and *B.* (*B.*) *illiesi*, formed a paraphyletic group. The *Cloeodes* representatives from South America (i.e., *C. aymore*, *C. barituensis*, *C. ioachimi*, and *C. itajara*) together with *C. pseudogladius* from Madagascar formed a monophyletic clade. However, as the calculated branch support was very low, the phylogenetic relationships between species/genera remain mostly unsolved.

Discussion

Phylogenetic affinities

Recently, Salles et al. (2016) performed a comprehensive phylogenetic analysis of *Cloeodes* and related taxa. This reconstruction had considerable impacts on the systematics of the group: *Cloeodes* is restricted to Neotropical and Nearctic regions; all the African species were re-assigned to *Potamocloeon* or *Crassolus*; Oriental species were assigned to one of the three subgenerea of *Bungona*. Based on its morphology, the new species is attributable to the *Cloeodes*-complex sensu Salles et al. (2016), sharing all diagnostic characters (apex of maxillary palp slightly narrowing between one-half and apical one-third, presence of a row of long conspicuous setae at the base of tibiae and on tarsi, presence of a row of conspicuous long setae on the abdominal sterna, and apex of gill III or IV pointed).

Within the *Cloeodes*-complex, *B.* (*Ch.*) *pontica* sp. n. shows all the features delimiting the genus *Bungona* as defined by Salles et al. (2016): antenna short (Fig. 1B); spine-like setae between prostheca and mola of right mandible present (Fig. 2C); labial palp segment III distally expanded (Fig. 2E, G); setae on the margin of femur long (Fig. 3A, C, E); patella-tibial suture absent on fore tibia and located at middle length of the middle- and hind tibia (Fig. 3B, D, F); a row of conspicuous setae on the dorsal surface of the fore tibia exceeding half of the length of tibia (Fig. 3B); a row of conspicuous long setae present on abdominal sterna IV or V–VI (Fig. 5A); distance between the insertions of conspicuous long setae on the abdominal sterna greater than diameter of insertions (Fig. 5A); and secondary swimming setae on the outer margin of cerci present (Fig. 1A).

Bungona (*Ch.*) *pontica* also exhibits a characteristic shape of the claw with two rows of flattened denticles (Fig. 4E), a contrasting body colour pattern (Fig. 1A), and lanceolate scales on the surface of the body (Fig. 4A); all these characters are typical for the subgenus *Chopralla* (Salles et al. 2016). In fact, the only synapomorphy of *Chopralla* which is absent in the new species is the bifid shape of the right prostheca (Salles et al. 2016: fig. 4C–E). In *B.* (*Ch.*) *pontica* sp. n., as in *B.* (*Ch.*) *liebenauae* (Soldán, Braasch & Muu, 1987) from Vietnam, the slender medial process of the right prostheca is absent (Fig. 2C) and might represent a synapomorphy of this possibly closely related species or might be the result of independent reduction in both species. Despite their similarities, *B.* (*Ch.*) *pontica* can be separated from *B.* (*Ch.*) *liebenauae* by having shorter setae on the dorsal margin of the femur (their length reaching two-thirds of the femur width in *B.* (*Ch.*) *liebenauae* and one-quarter of the femur width in *B.* (*Ch.*) *pontica*) and by the absence of characteristic tubercles on the pronotum (present in *B.* (*Ch.*) *liebenauae*; Fig. 6).

According to the molecular reconstruction, it is clear that *B.* (*Ch.*) *pontica* sp. n. represents an isolated lineage, not forming a well-supported clade with any of the taxa

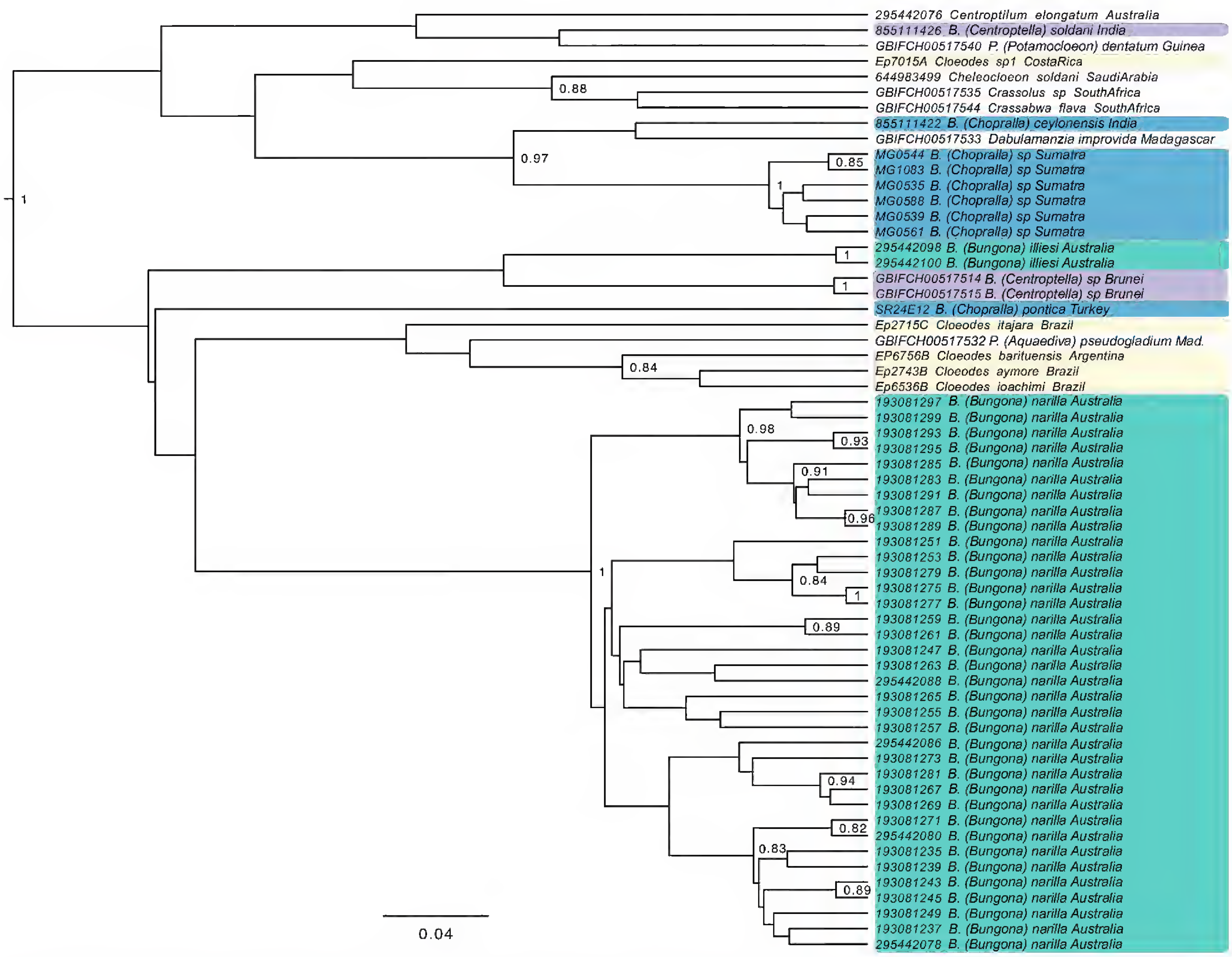

Figure 9. Molecular reconstruction including representative set of taxa of the *Cloeodes*-complex (comprising *Bungona* (*Chopralla*) *pontica* sp. n.) and additional taxa of other lineages. Bayesian inference was used to reconstruct the tree based on the mitochondrial DNA barcoding gene cytochrome *c* oxidase subunit 1. Bayesian posterior probabilities > 0.8 are indicated. Scale bar represents substitutions per site. Geographic origins of the specimens are indicated. Colours: green = *Bungona* (*Bungona*); blue = *Bungona* (*Chopralla*); purple = *Bungona* (*Centroptella*); yellow = *Cloeodes*; white = other genera.

included in the analysis (Fig. 9). Due to the general lack of support especially in the deeper nodes of the cladogram, the phylogenetic position of *B.* (*Ch.*) *pontica* sp. n. within the *Cloeodes*-complex remains unsolved. The presumed position based on the morphological data is near the clade containing *Bungona* (*Chopralla*) sp. from Sumatra and *B.* (*Ch.*) *ceylonensis* from India. These two species formed a well-supported monophyletic group together with *D. improvida* from Madagascar (Fig. 9). This study represents the first analysis of molecular data within the *Cloeodes*-complex. A fine-scaled geographic taxon sampling combined with the use of additional markers will be needed to resolve the phylogenetic position of *B.* (*C.*) *pontica* sp. n. and more in general to solve the phylogenetic relationships within the *Cloeodes*-complex.

Biogeography: presence of tropical elements in the Middle East mayfly fauna

Bungona (*Chopralla*) *pontica* sp. n. represents a tropical mayfly lineage in the Asia Minor fauna. Within the *Cloeodes*-complex, *B.* (*Ch.*) *pontica* sp. n. exhibits morphologically high similarity to the Oriental genus *Bungona*, which is distributed in Australia, New Guinea, and southern, eastern and southeastern Asia (Marle et al. 2016, Salles et al. 2016). The closest morphological relative is *B.* (*Ch.*) *liebenauae*, described from Vietnam (Soldán et al. 1987). Although not supported by our molecular approach, an Oriental origin of *B.* (*Ch.*) *pontica* sp. n. seems most likely, based on morphological data.

The discovery of this new species in Asia Minor is rather unexpected, as other Turkish mayfly taxa have Palaearctic or West Palaearctic distributions (Salur et al. 2016). Only a few taxa with tropical affinities have been reported from Turkey and the Middle East until now; however, most of them should be considered as misidentifications or at least as questionable observations (see below).

The heptageniid *Thalerosphyrus determinatus* (Walker, 1853) was recorded from Turkey based on findings of Demoulin (1965) and Berker (1981), although the genus *Thalerosphyrus* Eaton, 1881 is considered endemic to the Oriental realm (Webb and McCafferty 2008, Sartori 2014). Demoulin (1965) noted the resemblance of two immature larvae from near Ankara with *T. determinatus* as redescribed by Ulmer (1939) from Southeast Asia. Berker (1981) reported *T. determinatus* from the vicinity of the town of Elazığ but based this on the superficial similarity with Demoulin's (1965) figures. These figures (Demoulin 1965: fig. 4) do not show any of the diagnostic characters of *Thalerosphyrus* as defined in Webb and McCafferty (2008), and the specimens might represent some species of *Electrogena* or *Heptagenia*. *Thalerosphyrus determinatus* was included in recent Turkish checklists (Kazancı 2001, Kazancı and Türkmen 2012, Salur et al. 2016) but were highlighted as doubtfully occurring in Turkey. We conclude the occurrence of *T. determinatus* in Turkey is most probably based on misidentifications.

Another tropical mayfly lineage with a distribution pattern extended into the Middle East is the genus *Clypeocaenis* Soldán, 1978 (Caenidae), with most of its diversity occurring in the Oriental (Vietnam, Borneo, Sri Lanka, and India) and Afrotropical (Burkina Faso and South Africa) realms (Malzacher 2013). *Clypeocaenis bisetosa* Soldán, 1978 was partially collected in the Middle East (part of the type series comes from northern Iran, the other from India). Although the species was not recorded in Turkey, it undoubtedly represents an Oriental tropical element in the Middle East mayfly fauna (Soldán 1978).

In the family Baetidae, the fauna of the Arabian Peninsula shows clear affinities with the Afrotropical fauna. *Cloeon smaeleni* Lestage, 1924, is widely distributed in the Afrotropics; its distribution covers practically all of sub-Saharan Africa, including Madagascar and Reunion Island (Gattolliat and Rabeantoandro 2002), and it was recently reported as invasive in South America (Salles et al. 2014). In the Middle East, it was also reported from Yemen (Gillies 1985) and Saudi Arabia (Salles et al. 2014), but these populations probably represent a separate closely related species (Salles et al. 2014). Recent integrative studies have proven that the Afrotropical *Labiobaetis glaucus* (Agnew, 1961) also occurs along the south-western coast of Saudi Arabia (Gattolliat et al. 2018). However, these Afrotropical lineages reach their northern limit in the southern Arabian Peninsula and appear absent in Turkey and the Levant. *Baetis* (*Rhodobaetis*) *pseudogemellus* Soldán, 1977, was described from north-eastern Sudan (Soldán 1977) and was subsequently reported from south-eastern Turkey by Kazancı (2009) based on the observation of three larvae. Nevertheless, the identification of this material as *B.* (*R.*) *pseudogemellus* is highly questionable, taking into account that numerous similar species of *Rhodobaetis* occur in Turkey and surrounding areas (Godunko et al. 2015, Yanai et al. 2018).

Components of the Turkish fauna with tropical affinities were already described also in other freshwater invertebrates, including anostracans, caddisflies, sponges (Banarescu 1990, 1992), and most probably also gastropods (Heller 2007). Furthermore, many species of freshwater fish from the Middle East show an Oriental origin (Heller 2001), as well as several lineages of terrestrial invertebrates (Yom-Tov and Tcherov 1988). The tropical Oriental taxa were supposed to have invaded the Middle East westwards from the Euphrates–Tigris basin (Heller 2007).

Bungona (*Ch.*) *pontica* n. sp. is the first mayfly species showing this unusual biogeographic pattern. The species is probably very rare in Turkey; our results only include six individuals from two neighboring localities, despite our extensive collecting throughout the country. It was also not found by other Turkish researchers (Salur et al. 2016) and has not been recorded in neighboring Georgia (Gabelashvili et al. 2018), Iran (Bojková et al. 2018), or Syria (Koch 1988). It might represent a relict population left after previous connection to the Oriental region.

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References

Aydınli C (2017) Contribution to the knowledge of Ephemeroptera (Insecta) of the eastern Black Sea region. Journal of the Entomological Research Society 19(3): 95–107.

Banarescu P (1990) Zoogeography of fresh waters. Vol. 1: general distribution and dispersal of freshwater animals. Aula Verlag, Wiesbaden, 511 pp.

Banarescu P (1992) Zoogeography of fresh waters. Vol. 2: distribution and dispersal of freshwater animals in North America and Eurasia. Aula Verlag, Wiesbaden, 519–1091.

Bauernfeind E, Soldán T (2012) Mayflies of Europe. Apollo Books, Ollerup, 781 pp.

Berker F (1981) Keban barajı ve Keban'a dökülen nehirler ile Elazığ bölgesinin Ephemeroptera (Insecta) limnofaunasının (larvalarının) saptanması ve sistematik incelenmesi. Fırat Üniversitesi Veteriner Fakültesi Dergisi 6(1–2): 124–139.

Bojková J, Sroka P, Soldán T, Imanpour Namin J, Staniczek AH, Polášek M, Hrivniak Ľ, Abdoli A, Godunko RJ (2018) Initial commented checklist of Iranian mayflies, with new area records and description of *Procloeon caspicum* sp. n. (Insecta, Ephemeroptera, Baetidae). ZooKeys 749: 87–123. https://doi.org/10.3897/zookeys.749.24104

Bouckaert R, Heled J, Kuhnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. Plos Computational Biology 10: e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Chesters D (2013) collapsetypes.pl [computer software available at http://sourceforge.net/projects/collapsetypes/].

Demoulin G (1965) Résultats de l'Expédition Belge au Moyen-Orient (Avril–Août 1963) Ephemeroptera. Bulletin de l'Institut royal des Sciences naturelles de Belgique 41(28): 1–8.

Ertorun N, Tanatmış M (2004) Karasu çayı (Sinop)'nın Ephemeroptera (Insecta) limnofaunası. Anadolu Üniversitesi Bilim ve Teknoloji Dergisi 5 (1): 107–114.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3(5): 294–299.

Gabelashvili S, Mumladze L, Bikashvili A, Sroka P, Godunko RJ, Japoshvili B (2018) The first annotated checklist of mayflies (Ephemeroptera: Insecta) of Georgia with new distribution data and a new record for the country. Turkish Journal of Zoology 42: 252–262. https://doi.org/10.3906/zoo-1709-4

Gattolliat J-L, Kondratieff BC, Kaltenbach T, Al Dhafer HM (2018) *Labiobaetis* from the Kingdom of Saudi Arabia (Insecta, Ephemeroptera, Baetidae). Zookeys 774: 77–104. https://doi.org/10.3897/zookeys.774.25273

Gattolliat J-L, Rabeantoandro SZ (2002) The genus *Cloeon* (Ephemeroptera, Baetidae) in Madagascar. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 74: 195–209.

Gattolliat J-L, Rutschmann S, Monaghan MT, Sartori M (2018) From molecular hypotheses to valid species: description of three endemic species of *Baetis* (Ephemeroptera: Baetidae) from the Canary Islands. Arthropod Systematics & Phylogeny 76(3): 509–528.

Gillies MT (1985) A preliminary account of the East African species of *Cloeon* Leach and *Rhithrocloeon* gen. n. (Ephemeroptera). Aquatic Insects 7(1): 1–17.

Godunko RJ, Palatov DM, Martynov AV (2015) Mayflies of the Caucasus Mountains. III. A new representative of the subgenus *Rhodobaetis* Jacob, 2003 (Baetidae: *Baetis*) from the South-Western Caucasus. Zootaxa 3948: 182–202. https://doi.org/10.11646/zootaxa.3948.2.2

Heller J (2001) Near East ecosystems, animal diversity. In: Historic biogeography of the Levant. Levin SA (Ed.) Encyclopedia of biodiversity, Vol. 4. New York: Academic Press, 329–352.

Heller J (2007) A historic biogeography of the aquatic fauna of the Levant. Biological Journal of the Linnean Society 92: 625–639. https://doi.org/10.1111/j.1095-8312.2007.00850.x

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kazancı N (2001) Türkiye Ephemeroptera (Insecta) faunası. Ephemeroptera (Insecta) fauna of Turkey. Türkiye iç Suları Araştırmaları Dizisi 6. Ankara, Hacettepe Üniversitesi.

Kazancı N (2009) Ephemeroptera (Insecta) Fauna of Turkey: records from eastern Anatolia (Turkey). Review of Hydrobiology 2: 187–195.

Kazancı N, Türkmen G (2012) The checklist of Ephemeroptera (Insecta) species of Turkey. Review of Hydrobiology 5(2): 143–156.

Kazancı N, Türkmen G (2016) Comments on "An annotated catalogue of the mayfly fauna of Turkey (Insecta, Ephemeroptera)". Review of Hydrobiology 9(2): 85–121.

Koch S (1988) Mayflies of the Northern Levant (Insecta: Ephemeroptera). Zoology in the Middle East 2: 89–112

Kozlov A (2017) amkozlov/raxml-ng: RAxML-NG v0.5.0 BETA. https://doi.org/10.5281/zenodo.888146

Maddison W P, Maddison DR (2011) Mesquite: a modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org.

Malzacher P (2013) Caenidae from East Kalimantan, Borneo (Insecta: Ephemeroptera). With a discussion on phylogeny of the new tribe Clypeocaenini, subfamily Caeninae. Stuttgarter Beiträge zur Naturkunde A (N.S.) 6: 21–55.

Marle P, Salles FF, Gattolliat J-L (2016) Two new species of *Bungona* Harker, 1957 (Ephemeroptera: Baetidae) from Borneo, Indonesia. Zootaxa 4088(2): 221–235. https://doi.org/10.11646/zootaxa.4088.2.4

Monaghan MT, Wild R, Elliot M, Fujisawa T, Balke M, Inward DJ et al. (2009) Accelerated species inventory on Madagascar using coalescent-based models of species delineation. Systematic Biology 58(3): 298–311.https://doi.org/10.1093/sysbio/syp027

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67(5): 901–904. https://doi.org/10.1093/sysbio/syy032

Rutschmann S, Gattolliat J-L, Hughes SJ, Báez M, Sartori M, Monaghan MT (2014) Evolution and island-endemism of morphologically cryptic *Baetis* and *Cloeon* species (Ephemeroptera, Baetidae) on the Canary Islands and Madeira. Freshwater Biology 59: 2516–2527. https://doi.org/10.1111/fwb.12450

Rutschmann S, Detering H, Simon S, Funk DH, Gattolliat J-L, Hughes SJ, Raposeiro PM, DeSalle R, Sartori M, Monaghan MT (2017) Colonization and diversification of aquatic insects on three Macaronesian archipelagos using 59 nuclear loci derived from a draft genome. Molecular Phylogenetics & Evolution 107: 27–38. https://doi.org/10.1016/j.ympev.2016.10.007

Salles FF, Gattolliat J-L, Angeli KB, De-Souza MR, Gonçalves IC, Nessimian JL, Sartori M (2014) Discovery of an alien species of mayfly in South America (Ephemeroptera). ZooKeys 399: 1–16. https://doi.org/10.3897/zookeys.399.6680

Salles FF, Gattolliat J-L, Sartori M (2016) Phylogenetic analyses of *Cloeodes* Traver and related genera (Ephemeroptera: Baetidae). Systematic Entomology 41: 93–111. https://doi.org/10.1111/syen.12144

Salur A, Darilmaz M, Bauernfeind E (2016) An annotated catalogue of the mayfly fauna of Turkey (Insecta, Ephemeroptera). ZooKeys 620: 67–118. https://doi.org/10.3897/zookeys.620.9405

Sartori M (2014) The species of *Thalerosphyrus* Eaton, 1881 (Insecta, Ephemeroptera, Heptageniidae, Ecdyonurinae) in Java and Sumatra, with some comments on the diversity of the genus in the Oriental Realm. ZooKeys 420: 19–39. https://doi.org/10.3897/zookeys.420.7904

Selvakumar C, Sivaramakrishnan KG, Janarthanan S (2016) DNA barcoding of mayflies (Insecta: Ephemeroptera) from South India. Mitochondrial DNA Part B 1(1): 651–655. https://doi.org/10.1080/23802359.2016.1219623

Simon C, Frati F, Beckenback A, Crespi B, Liu H, Flook P (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Entomological Society of America 87: 651–701.

Soldán T (1977) Three new species of mayflies (Ephemeroptera) from the mist oasis of Erkwit, Sudan. Acta Entomologica Bohemoslovaca 74(5): 289–294.

Soldán T (1978) New genera and species of Caenidae (Ephemeroptera) from Iran, India and Australia. Acta Entomologica Bohemoslavaca 75(2): 119–129.

Soldán T, Braasch D, Muu LT (1987) Two new species of *Centroptella* (Ephemeroptera, Baetidae) from Vietnam, with a description of adult stages of the genus. Acta Entomologica Bohemoslovaca 84: 342–349.

Tanatmış M (2004) Gökırmak Nehir Havzası (Kastamonu) ile Cide (Kastamonu)-Ayancık (Sinop) arası sahil bölgesinin Ephemeroptera (Insecta) faunası. Türkiye Entomoloji Dergisi 28(1): 45–56.

Türkmen G, Kazancı N (2013) The key to the Ephemeroptera (Insecta) larvae in running waters of the Eastern Black Sea Basin (Turkey) with the new records. Review of Hydrobiology 6(1): 31–55.

Ulmer G (1939–1940) Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln. Archiv für Hydrobiologie Supplement 16: 443–692.

Waltz RD, McCafferty WP (1987) Revision of the genus *Cloeodes* Traver (Ephemeroptera: Baetidae). Annals of the Entomological Society of America 80: 191–207.

Webb JM, McCafferty WP (2008) Heptageniidae of the World. Part II: Key to the Genera. Canadian Journal of Arthropod Identification 7: 1–55. https://doi.org/10.3752/cjai.2008.07

Webb JM, Suter PJ (2010) Revalidation and redescription of *Bungona illiesi* (Lugo-Ortiz & McCafferty) (Ephemeroptera: Baetidae) from Australia, based on mitochondrial and morphological evidence. Zootaxa 2481: 37–51.

Yanai Z, Gattolliat J-L, Dorchin N (2018) Taxonomy of the mayfly genus *Baetis* Leach (Ephemeroptera: Baetidae) in Israel. ZooKeys: 45–84. https://doi.org/10.3897/zookeys.794.28214

Yom-Tov Y, Tchernov E (1988) The zoogeography of Israel. Dr Junk, Dordrecht, 600 pp.

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Herpetological surveys in two proposed protected areas in Liberia, West Africa

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Abstract

In March and April 2018 we surveyed amphibians and reptiles in two Proposed Protected Areas (PPAs) in Liberia. In the Krahn-Bassa Proposed Protected Area (KBPPA) in eastern Liberia 36 species of amphibians and 13 species of reptiles were recorded. In the Foya Proposed Protected Area (FPPA) in western Liberia 39 species of amphibians and 10 species of reptiles were recorded. The encountered herpetological communities in both sites were typical for West African rainforests. However, some species indicated disturbances, in particular at the edges of the study areas, the surrounding villages and plantations, and old artisanal gold mining sites within forests. Of particular conservation interest was the discovery of a high percentage of typical rainforest specialists with ranges restricted to the western part of the Upper Guinea rainforest biodiversity hotspot. Outstanding discoveries in KBPPA were two new species of puddle frogs, and the first country record for the arboreal, parachuting lizard *Holaspis guentheri*. Remarkable records in FPPA comprise a new species of stiletto snake, a new puddle frog and records of various frog species typically breeding in undisturbed rainforest streams, such as *Odontobatrachus natator* and *Conraua alleni*. Both study areas comprise an important proportion of the remaining rainforests in the Upper Guinea forest zone. The new discoveries indicate that within this biogeographic area, southeastern and western Liberian rainforest may still hold various undiscovered species and species of conservation concern. Further surveys in KBPPA and FPPA and nearby forests should clarify the distribution and conservation status of the new taxa.

This study also emphasizes that the western part of the Liberian forests comprise, at least partly, a herpetofauna which differs from that of the East of the country. The recorded threatened amphibian species are all specialized on relatively undisturbed rainforests and they all have only small geographic ranges. The remaining parts of undisturbed or little disturbed forests thus have high importance for the long-term survival of these species. In conclusion, the study areas have a high conservation potential and should be urgently protected from any further forest loss, degradation, and uncontrolled hunting.

Introduction

Amphibians and reptiles are amongst the world's most endangered organisms. Reasons are manifold, but the most important ones are unarguably habitat destruction, conversion, and fragmentation, presumably followed by pollution, disease and climate change (Stuart et al. 2004, 2008; Böhm et al. 2013). Amphibians in particular are very sensitive to environmental changes due to their semi-permeable skin and eggs and their usually complex life-cycle (Wells 2007). The Upper Guinea forests of West Africa ranges amongst the world's most important biodiversity hotspots, meaning areas with exceptional level of species richness and endemism, as well as various factors threatening this biodiversity (Myers et al. 2000). Penner et al. (2011) have shown that the composition of the West Africa amphibian

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fauna is unique, and amongst the very few regions in the World where the chytrid fungus (*Batrachochytrium dendrobatidis*) has not yet been detected (Penner et al. 2013). However, these authors have likewise shown that many areas of presumed exceptional amphibian diversity, i.e. in Liberia, are within regions of intense logging and mining activities and not safeguarded by any protected area (Penner et al. 2019). The Krahn-Bassa Proposed Protected Area (KBPPA) in eastern Liberia and the Foya Proposed Protected Area (FPPA) in western Liberia fall within these regions of little or no official protection and predicted high amphibian diversity. However, so far no herpetological survey has targeted KBPPA and FPPA in order to verify the predictions by Penner et al. (2019). We aimed to start closing this knowledge gap by surveying some regions within the KBPPA and FPPA for amphibians. We likewise aimed to record all reptiles which we encountered. However, in particular snakes are much more difficult to observe than amphibians and we did not expect an as complete figure of species richness for reptiles as it could be expected for amphibians.

Herpetological research in Liberia

Compared to neighboring Côte d'Ivoire, the herpetofauna of Liberia is only poorly known, although herpetological specimens from Liberia have been reported as early as the beginning of the last century (Johnston 1906). The most important herpetological surveys took place in the mid-1920s to early 1940s; most notable were the expeditions of the Museum of Comparative Zoology at Harvard and the Smithsonian Institution, which resulted in the description of various new frogs and one gecko (Barbour and Loveridge 1927, 1930; Loveridge 1941). The French ichthyologist and herpetologist Paul Chabanaud surveyed mostly what is now the Republic of Guinea, but also described species from present-day Liberia (Chabanaud 1921). Likewise, the French Jean Guibé and Maxime Lamotte dealt predominantly with the fauna of the Guinean part of Mount Nimba, but included Liberian material in their papers (Guibé and Lamotte 1958a, 1963). From the Liberian part of Mount Nimba a second species of viviparous toad, *Nimbaphynoides liberiensis*, was described (Xavier 1978), which was, however, later synonymized with the Guinean populations (Sandberger et al. 2010). Further Liberian records and new species were published by Parker (1936) and Taylor and Weyer (1958). Some amphibian species have been also made known through the work of parasitologists (e.g. Euzet et al. 1969). An important boost to the discovery of West African amphibians in general, and treefrogs in particular, was due to the work of the Belgian Raymond Laurent and the Dane Arne Schiøtz. The latter also worked and collected in Liberia (e.g. Laurent 1958; Schiøtz 1967, 1968).

These early discoveries were followed by a longer period without any herpetological data from Liberia. Liberia was always hard to access due to the lack of infrastructure such as roads in most parts of the country, but from 1989–2003 a particularly brutal civil war stopped all scientific exploration within the country. Only in 2005, on a Rapid Assessment organized by Conservation International, Annika Hillers surveyed amphibians and reptiles in three Liberian forests, reporting five frog species new for the country (Hillers and Rödel 2007). More recently Rödel et al. (2009a, 2010) described two new frog species from the Liberian part of Mount Nimba, one of which was later also recorded in the more southern Putu Range by Nopper et al. (2012). In recent years many surveys in various Liberian regions were undertaken by numerous researchers, usually working as consultants for logging and mining explorations. Unfortunately, none of these results have been so far made publicly available.

Material and methods

Study sites, study periods and sampling effort

Both study areas were surveyed during the beginning of the rainy season. The Krahn-Bassa Proposed Protected Area (KBPPA) is located in southeastern Liberia, across the Grand Gedeh, River Cess and Sinoe counties. The nearest larger town is Zwedru. KBPPA comprises 290,167 ha within the larger Krahn-Bassa National Forest (WCF & FDA 2017). We surveyed KBPPA on 23–26 March 2018 (Camp 1, in the north of the area; 06°02'39.9"N, 008°20'03.6"W) and 28–31 March 2018 (Camp 2, in the central-eastern part of the area; 05°39'02.1"N, 008°39'05.0"W). KBPPA is part of Liberia's two remaining forest blocks, the Taï-Grebo-Sapo forest complex (Taï being the largest remaining rainforest in neighboring Côte d'Ivoire). It consists of primary forest with high canopy cover, although the edges of the forest are partly heavily degraded by logging and agricultural encroachment. Most prominent signs of human activities in the core forest area were former artisanal gold mining pits and up to an average of one cartridge per 100 m, indicating a very high hunting pressure. Both camps were near a larger river. The surrounding forest was in good shape and comprised slightly undulating hilly areas with drier parts of high canopy forest, swampy areas in the valley and some smaller streams on sandy and rocky ground. In total we invested 142 person/hours (four persons working simultaneously) searching for amphibians and reptiles (Table 1).

The Foya Proposed Protected Area (FPPA) in western Liberia is the extension of the remaining block of the Gola Rainforest National Park in Sierra Leone and the Gola Forest National Park in Liberia. We surveyed areas in the north of FPPA on 4–6 April 2018 (Camp 1, ca 3 km south of Ducorbond; 08°00'46.0"N, 010°25'32.1"W) and 7–9 April 2018 (Ducorbond village; 08°02'37.9"N, 010°24'35.1"W). The forest is still partly primary (Fig. 1b) but was affected by logging since the 1980s. Huge areas around villages and along a road connecting to the Sierra Leonean border are cleared from forest and turned into agricultural land (Fig. 1d), i.e. swamps into rice paddies. The forest still maintains

Figure 1. Natural and disturbed habitats in the Krahn-Bassa (KBPPA) and Foya Proposed Protected Areas (FPPA). **a** Remaining puddles of a stream in Krahn-Bassa, habitat of *Aubria subsigillata*, *Amnirana* 'albolabris West', *Leptopelis macrotis*, *Hyperolius chlorosteus* and *Chiromantis rufescens*. **b** View on a near primary forest patch in FPPA. **c** Artisanal gold mining area near a small forest stream in FPPA, frogs breeding in these puddles were *Xenopus tropicalis, Sclerophrys maculata, Hyperolius picturatus, Phlyctimantis boulengeri, Ptychadena longirostris*, *P.* sp., and *Chiromantis rufescens*. **d** Recently slash and burn cleared forest patch in FPPA, prepared for establishing a cacao plantation.

high canopy cover and a high proportion of timber trees (SCNL 2017), however, traces of extraction of single, high value timber trees, as well as vast areas of artisanal gold mining were frequently found in various places (Fig. 1c). Most of the terrain is hilly, and in part, with steep slopes. Small to larger forest streams are present, some with torrent water and large boulders. Signs of hunting were present, but to a much lower degree than in FPPA. In total we invested 115 person/hours (four persons working simultaneously) searching for amphibians and reptiles in FPPA (Table 1).

Field work and vouchers

Amphibians and reptiles were recorded during visual and acoustic encounter surveys by four people. The surveys were undertaken during day and night. Searching techniques included visual scanning of the terrain and investigation of potential hiding places or very specific habitats (e.g. tree holes, small rivers, and waterfalls); for tadpoles we searched by dip-netting in all available potential breeding sites (Heyer et al. 1994; Rödel and Ernst 2004).

Our sampling design only provided qualitative and semi-quantitative data. We therefore calculated the estimated species richness and, hence, our sampling efficiency with the Jackknife 1 and Chao 2 estimators using EstimateS (Collwell 2005). These incidence based estimators were calculated based on the amphibian presence/absence data of discrete survey units. These units consisted of surveys of 1.5–4 h each, by four people, in different parts of the two areas, assuming that sampling effort of survey units were comparable. To visualize species accumulation as a relation of sampling effort, and to avoid order effects, we calculated sample-based rarefaction curves of amphibian species richness (999 permutations) using Past2.17 (Hammer et al. 2001).

The nomenclature for amphibians follows Frost (2018), and for reptiles we follow Uetz (2018). Vouchers were euthanized by either placing animals in a chlorobutanol solution (amphibians) or by putting some benzocaine paste (reptiles) in the mouth. After death, tissue samples (liver) were taken and preserved in 95% ethanol, the animals were injected with 75% ethanol. Voucher specimens and tissue samples are deposited in the zoological collection of the Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science, Berlin (ZMB).

Table 1. Details on study sites in the Krahn-Bassa (KBPPA) and Foya (FPPA) herpetological survey 2018. "Person/hours" calculated as time surveyed × four persons, geographic coordinates refer to initial points of survey transects.

Area	Date	Time of day	Person/ hours	Site details	latitude (N)	longitude (W)
KBPPA	24.03.18	morning	08:00	Closed forest parallel to small stream	06°02'39.9"	008°20'09.6"
KBPPA	24.03.18	afternoon	13:00	Closed forest parallel to small stream	06°02'39.9"	008°20'09.6"
KBPPA	24.03.18	night	08:00	Closed forest	06°02'39.9"	008°20'09.6"
KBPPA	25.03.18	morning	15:00	Closed forest	06°02'34.8"	008°20'10.3"
KBPPA	25.03.18	night	08:00	Closed forest	06°02'34.8"	008°20'10.3"
KBPPA	26.03.18	afternoon	08:40	Closed forest parallel to small stream	06°02'34.8"	008°20'10.3"
KBPPA	26.03.18	night	07:00	Closed forest	06°02'34.8"	008°20'10.3"
KBPPA	28.03.18	night	07:00	Closed forest parallel to large river	05°39'02.1"	008°39'05.0"
KBPPA	29.03.18	morning	16:00	Closed forest parallel to large river	05°39'02.1"	008°39'05.0"
KBPPA	29.03.18	night	11:40	Closed forest	05°39'02.1"	008°39'05.0"
KBPPA	30.03.18	afternoon	10:00	Closed forest	05°39'02.1"	008°39'05.0"
KBPPA	30.03.18	night	09:00	Closed forest and gold mining pits	05°39'02.1"	008°39'05.0"
KBPPA	31.03.18	morning	16:00	Closed forest parallel to large river	05°39'02.1"	008°39'05.0"
KBPPA	31.03.18	night	04:00	Closed forest and gold mining pits	05°39'02.1"	008°39'05.0"
FPPA	04.04.18	night	08:00	Closed forest along small stream	08°00'46.0"	010°25'32.1"
FPPA	05.04.18	morning	14:00	Closed forest	08°00'46.0"	010°25'32.1"
FPPA	05.04.18	night	14:00	Closed forest	08°00'21.3"	010°25'20.2"
FPPA	06.04.18	morning	19:00	Closed forest along small and large streams, including cascades	08°01'16.2"	010°25'31.4"
FPPA	06.04.18	night	12:00	Closed forest along small and large streams, including cascades	08°01'16.2"	010°25'31.4"
FPPA	07.04.18	night	07:00	Along road and cocoa plantations	08°02'37.9"	010°24'35.1"
FPPA	08.04.18	morning	18:00	Closed forest, along stream including cascades	08°03'18.6"	010°23'04.0"
FPPA	08.04.18	night	08:00	Closed forest, along stream including cascades	08°03'18.6"	010°23'04.0"
FPPA	09.04.18	morning	10:00	Closed forest and along streams	08°03'02.5"	010°23'15.9"
FPPA	09.04.18	night	05:20	Closed forest and along streams	08°03'02.5"	010°23'15.9"

Results

Commented species list

Numbers listed in brackets after study site abbreviations refer to voucher specimens (ZMB) and tissue (ZMB or RG numbers; RG = tissue only) accessioned in ZMB. In Table 2 we provide a summary of all species recorded in Krahn-Bassa Proposed Protected Area (KBPPA) and in Foya Proposed Protected Area (FPPA) with their preferred habitat, range, and IUCN Red List status.

Amphibia
Gymnophiona
Dermophiidae

***Geotrypetes* cf. *seraphini* (Duméril, 1859); KBPPA (ZMB 88492)**

Three *Geotrypetes* species are known from West Africa (Taylor 1968), which can be mainly distinguished by the number of primary and secondary annuli (body rings). The most common species is *Geotrypetes seraphini*, ranging from Sierra Leone to western Central Africa (Taylor 1968; Frost 2018). The fossorial amphibians are usually found in swampy areas of the rainforest zone. We detected one specimen (bluish purple) in KBPPA at night, near the second camp below a stone, in a swampy zone with small creeks which were heavily disturbed by previous artisanal gold mining. Unfortunately, it managed to escape into the ground. A second, greyer and larger individual was found dead in the leaf litter close to a river (Fig. 2a). As its hind part was apparently eaten by a predator, annuli counts were not possible in either specimens.

Anura
Pipidae

***Xenopus tropicalis* (Gray, 1864); KBPPA (ZMB 88454, 88466); FPPA (ZMB 88504)**

An aquatic species of forests, degraded forests, and gallery forests in the moist savanna zone, which can be found from Senegal to western Cameroon (Rödel 2000). Both adults and tadpoles were often found in natural waters but also in small water-filled pits resulting from gold mining.

Arthroleptidae

***Arthroleptis* sp. 1 & 2; KBPPA (ZMB 88476, 88477); FFPA (no voucher)**

Both direct developing species occur in forest (Ernst and Rödel 2005, 2006). While *Arthroleptis* sp. 1 tolerates degraded forest, *A.* sp. 2 usually only lives in primary forest. Call and calling sites between both taxa are distinctly different. Males of *Arthroleptis* sp. 1 have a typical insect-like longer trill call, are well concealed within low and dense vegetation, and are usually easy to detect but hard to catch. In contrast, males of *A.* sp. 2 have very

Table 2. Amphibian species recorded in Krahn-Bassa Proposed Protected Area (KBPPA) in eastern Liberia and Foya Proposed Protected Area (FPPA) in western Liberia (in alphabetic order) with preferred habitat, distribution and IUCN Red List category; # = number of records per site (number of individuals was usually much higher); pf = primary forest; df = degraded forest; oh = open habitat; wUG = western Upper Guinea; UG = Upper Guinea; wA = western Africa; A = Africa (any range beyond western Africa); ? = range not known; LC = Least Concern; NT = Near Threatened; VU = Vulnerable; NE = not evaluated.

Genus	Species	# KBPPA	# FPPA	pf	df	oh	wUG	UG	wA	A	IUCN
Afrixalus	*dorsalis*		5		1	1			1		LC
	fulvovittatus		2		1				1		LC
	nigeriensis	5	1	1				1			LC
Amnirana	'albolabris West'	7	6	1	1			1			NE
	occidentalis		1	1				1			EN
Arthroleptis	sp. 1	8	3	1	1		1				NE
	sp. 2	4	3	1			1				NE
Astylosternus	*occidentalis*	2	4	1			1				LC
Aubria	*subsigillata*	1		1	1				1		LC
Cardioglossa	*occidentalis*	5	5	1				1			NE
Chiromantis	*rufescens*	6	3	1					1		LC
Conraua	*alleni*	2	6	1			1				VU
Geotrypetes	*seraphini*	2		1	1				1		LC
Hoplobatrachus	*occipitalis*		2		1	1				1	LC
Hyperolius	*chlorosteus*	9	6	1			1				NT
	concolor	1	2		1	1			1		LC
	fusciventris	3			1				1		LC
	guttullatus	1	3		1	1			1		LC
	picturatus	7	2	1			1				LC
	soror		1	1			1				DD
	zonatus	1	1	1			1				NT
Leptopelis	*macrotis*	6	6	1				1			NT
	occidentalis	3	1	1				1			NT
	spiritusnoctis	7	6	1	1			1			LC
	viridis		3			1			1		LC
Odontobatrachus	*natator*		3	1			1				NT
Phlyctimantis	*boulengeri*		3		1				1		LC
Phrynobatrachus	*alleni*	7	4	1				1			NT
	'aff. alleni'	2		1			?				NE
	calcaratus	1			1	1			1		LC
	fraterculus		1		1		1				LC
	guineensis	2		1			1				NT
	gutturosus	3		1	1	1		1			LC
	,sp. gutturosus/tokba'	3		1			?				NE
	latifrons		1		1	1			1		LC
	liberiensis	7	5	1				1			NT
	phyllophilus	1	1	1			1				NT
	plicatus	8		1				1			LC
	'sp. Gola'		2	1			1				NE
	tokba	7	5	1	1		1				LC
	villiersi	2		1			1				VU
Ptychadena	aff. *aequiplicata*	6	1				1				NE
	cf. *bibroni*	1	3		1	1				1	LC
	longirostris	1	3	1	1			1			LC
	mascareniensis		1			1				1	LC
	sp.		6		1		?				NE
Sclerophrys	*maculata*	1	3		1	1				1	LC
	togoensis	2	2	1				1			NT
Xenopus	*tropicalis*	2	4	1	1				1		LC
49 species	**total**	**136**	**120**	**33**	**22**	**11**	**16**	**13**	**13**	**4**	

short and high-pitched, katydid-like calls. The calls usually sound as if they are coming from the canopy, and the frogs are extremely difficult to localize, although the males call fully exposed from the forest floor (M.-O. Rödel pers. obs.). Currently it is not possible to assign a valid scientific name to either of these species, as the taxonomy of this genus is not yet clarified (compare Rödel and Bangoura 2004; Blackburn 2010).

Figure 2. **a** *Geotrypetes* sp. (ZMB 88492) found dead in the leaf litter in KBPPA **b** *Leptopelis macrotis* male (ZMB 88439) from KBPPA **c**, **d** *Conraua alleni* tadpoles (ZMB 88526) from the same puddle in a small stream in FPPA, take note of the differing color, shape and place of insertion of tail fins.

***Cardioglossa occidentalis* Blackburn, Kosuch, Schmitz, Burger, Wagner, Gonwouo, Hillers & Rödel, 2008; KBPPA (ZMB 88462); FPPA (ZMB 88493, 88494)**

This species lives in the leaf litter along small rivers in primary and slightly degraded forest from Sierra Leone to Ghana (Rödel et al. 2001; Blackburn et al. 2008).

***Astylosternus occidentalis* Parker, 1931; KBPPA (ZMB 88457); FPPA (ZMB 88519, 88550)**

This species breeds in clear, in part fast flowing streams within the rainforest. However, adults may be also found at night in leaf litter far away from water. This species occurs in primary and slightly degraded forest of the western part of the Upper Guinea hotspot (Rödel et al. 2012). It was particularly abundant in FPPA.

***Leptopelis spiritusnoctis* Rödel, 2007; KBPPA (ZMB 88437); FPPA (no voucher)**

A very common small (males) to mid-sized (females) arboreal frog of degraded and primary forests. The quiet chucks and buzzes of adult males can be usually heard at night, a few meters up in dense vegetation near swampy areas (Schiøtz 1967; Rödel 2007; Rödel et al. 2014).

***Leptopelis macrotis* Schiøtz, 1967; KBPPA (ZMB 88439, 88440); FPPA (no voucher)**

This is a large arboreal frog with distinct black, parallel bands across the back (Fig. 2b). It lives high up in trees in primary forests of the Upper Guinea hotspot. Its meowing call can be heard along rivers (Schiøtz 1967; Rödel et al. 2014).

***Leptopelis occidentalis* Schiøtz, 1967; KBPPA (no voucher); FPPA (ZMB 88532)**

This is a mid-sized treefrog of primary forest in the western part of West Africa, usually calling from a few meters up in trees, near swampy parts of the forest or forest ponds (Schiøtz 1967; Rödel and Branch 2002).

***Leptopelis viridis* (Günther, 1869); FPPA (ZMB 88546)**

This is a savanna treefrog which enters the forest zone in areas where forest has been cleared (Schiøtz 1967; Rödel 2000). We heard the species frequently calling and found it around the village and in plantations around FPPA.

Bufonidae

***Sclerophrys maculata* (Hallowell, 1894); KBPPA and FPPA (ZMB 88499)**

This is a very common species in the savanna zone and heavily degraded areas in the forest zone, sometimes entering forest along logging roads (Rödel 2000; M.-O. Rödel pers. obs.). It ranges from West Africa into the western part of Central Africa (Poynton et al. 2016).

***Sclerophrys togoensis* (Ahl, 1924); KBPPA (ZMB 88456); FPPA (RG98, tissue only)**

This toad species lives in primary forests from Togo to Sierra Leone. It breeds in small forest streams, but adults may be found in the leaf litter in all parts of the forest (Rödel and Branch 2002; Rödel and Bangoura 2004; Rödel et al. 2004). Our specimens morphologically fit the syntypes of *S. togoensis*, as well as the description of *S. cristiglans* (Inger & Menzies, 1961), which was described from the Tingi Hills in Sierra Leone. The toads are morphologically very variable but genetically almost indistinguishable across their entire range from Togo to Sierra Leone and Guinea (A. Hillers, M.-O. Rödel et al. unpub. data). Therefore, we regard *S. cristiglans* as a junior synonym of *S. togoensis*.

Conrauidae

***Conraua alleni* (Barbour & Loveridge, 1927); KBPPA (ZMB 88459, 88490); FPPA (ZMB 88496; tadpoles: ZMB 88526, 88527)**

This aquatic frog occurs in slow and fast flowing rainforest streams in the western part of the Upper Guinea forests (Lamotte and Perret 1968; Rödel and Branch 2002; Rödel 2003; Rödel and Bangoura 2004). However, a complex of cryptic species seems to be hidden under that name (Hillers et al. 2008; M.-O. Rödel et al. unpubl. data). As the species was described from Liberia, the records in both study areas should be the real *C. alleni* (Barbour and Loveridge 1927, 1930). In a small, sandy to muddy stream in pristine forest of the FPPA, we collected unusually yellowish brown to reddish tadpoles, all belonging to this species, which had differing shapes and tail fins color (Fig. 2c, d). Frogs were found in stagnant parts of streams.

Dicroglossidae

***Hoplobatrachus occipitalis* (Günther, 1858); FPPA (no voucher)**

This is a large, fully aquatic species, which is widespread in savannas and degraded habitats throughout tropical Africa (Rödel 2000). It is often consumed as food (Mohneke et al. 2010), which was also confirmed by our guide for FPPA. We only heard it calling a few times in rice fields near the village next to FPPA.

Hyperoliidae

***Afrixalus dorsalis* (Peters, 1875); FPPA (ZMB 88525)**

This is a leaf-folding frog of the West and Central African forest zone. In gallery forest it usually ranges far into savanna areas (Rödel 2007; Amiet 2012). In the forest zone, it occurs in heavily degraded former forest, often in rice fields, and in swampy areas in secondary growth (Schiøtz 1967, 1999). We detected it only outside real forest near the village next to FPPA or in areas which have been heavily degraded by former artisanal gold mining.

***Afrixalus fulvovittatus* (Cope, 1861); FPPA (ZMB 88539)**

This is a leaf-folding frog of the West African forest zone, where it lives in heavily degraded former forest (Schiøtz 1967, 1999; Pickersgill 2007). We detected it in plantations around FPPA and around rice fields near the village (Fig. 3a).

***Afrixalus nigeriensis* Schiøtz, 1963; KBPPA (ZMB 88489); FPPA (ZMB 88524)**

This is a typical leaf-folding frog of primary closed canopy forest. The frogs are usually calling from high up in trees near forest ponds (Schiøtz 1967, 1999; Rödel and Branch 2002). Our records are only the third and fourth records of this species in Liberia. The previous records are from 2005 (Hillers and Rödel 2007) and 2010 (Hillers 2013).

***Hyperolius chlorosteus* (Boulenger, 1915); KBPPA (ZMB 88447); FPPA (ZMB 88511)**

The calls of this treefrog are the most common nocturnal sounds along rivers in primary forests of the western part of the Upper Guinea forest zone (Schiøtz 1967, 1999; Rödel and Branch 2002; Rödel 2003; Rödel et al. 2004a). We detected this species in both sites along all streams, from extremely small and slow flowing creeks to the edges of large or torrent rivers.

***Hyperolius concolor* (Hallowell, 1844); KBPPA (no voucher); FPPA (ZMB 88541-88543)**

This reedfrog lives in degraded parts of rainforest, as well as in humid savannas. It is absent from closed canopy forest (Schiøtz 1967, 1999; Rödel 2000). Adult females are green, and males are brown to yellow, often with a dark interorbital triangle, during the day. At night both sexes are more or less uniform yellow. Juveniles often exhibit a dorsal color pattern resembling other reedfrogs, such as *H. picturatus*, *H. sylavticus*, or *H. zonatus* (compare Fig. 4c with Figs 3c, 4a).

Figure 3. a Juvenile *Afrixalus fulvovitattus* (ZMB 88539) **b** Male *Hyperolius soror* (ZMB 88540), both from farmbush habitats in FPPA, note fine dark lines in the clear bands of *A. fulvovittatus*, the closely related *A. vittiger* is lacking these lines; **c–f)** dorsal and ventral views of *Hyperolius picturatus* **c** Female (ZMB 88487) from KBPPA with hourglass pattern, a pattern also often found in combination with dorsolateral line in males **d**, **e** Female (ZMB 88464) from KBPPA with common brown back and broad yellow dorsolateral bands and yellow venter **f** Translucent greenish venter of male (ZMB 88465) from KBPPA.

***Hyperolius fusciventris* Peters, 1876; KBPPA (ZMB 88491) and FPPA (no voucher)**

This small reedfrog occurs in the rainforest zones of western Africa (Schiøtz 1967, 1999; Rödel 1998; Amiet 2012). Several subspecies have been described that might deserve full species status (Schiøtz 1967; M.-O. Rödel unpubl. data). They are absent from closed canopy forest and most abundant in secondary growth and forest edges where they breed in swamps and ponds.

***Hyperolius guttulatus* Günther, 1858; KBPPA (no voucher); FPPA (ZMB 88531)**

This is a reedfrog of the western African rainforest and southern savanna zone, where it usually lives in and around open ponds with densely vegetated banks. It avoids closed forest (Schiøtz 1967, 1999; Rödel 2000; Amiet 2012; Kouamé et al. 2015). We detected this species in both areas but only in rice fields around the villages and in small ponds in parts of the forests which were heavily degraded due to prior artisanal mining activities.

Hyperolius picturatus **Peters, 1875; KBPPA (ZMB 88463-88488); FPPA (ZMB 88523)**

This reedfrog occurs in secondary growth and degraded forest habitats from Sierra Leone to central Ghana. It breeds in stagnant and slow flowing waters (Schiøtz 1967, 1999; Rödel and Branch 2002; Rödel and Bangoura 2004). It seems to comprise at least two different species (Schiøtz 1967). In KBPPA and FPPA, our female records were morphologically similar to animals from western Côte d'Ivoire in having a yellow belly, but males had green instead of yellow gular glands and almost transparent bellies (Fig. 3f). Most specimens had brown backs with irregular to distinct sharp-edged, yellow dorsolateral bands (Fig. 3d). Some showed brown backs with an hourglass pattern (Fig. 3c); thus, they are very similar to *H. sylvaticus* Schiøtz, 1967 and *H. zonatus* (Schiøtz 1967; Rödel and Branch 2002).

Hyperolius soror **(Chabanaud, 1921); FPPA (ZMB 88540)**

This reedfrog is only known from the western part of the Upper Guinea forest zone. It seems to be more closely associated with primary rainforest than the related *H. fusciventris* (Schiøtz 1967, 1999; Rödel 1998). However, we detected one male frog at the forest edge of FPPA (Fig. 3b).

Figure 4. a, b Dorsal and ventral view of male *Hyperolius zonatus* (ZMB 88446) from KBPPA, showing the white gular region with the roundish gland, lacking dilatable skin of a larger vocal sac **c** *H. concolor* (ZMB 88542) with juvenile pattern from FPPA **d** male *Phlyctimantis boulengeri* (ZMB 88514) from FPPA.

Hyperolius zonatus **Laurent, 1958; KBPPA (ZMB 88446); FPPA (ZMB 88522)**

This reedfrog occurs only in primary forest (Fig. 4a) from eastern Sierra Leone, southeastern Guinea, Liberia, to western and central Côte d'Ivoire (Schiøtz 1967, 1999; Rödel and Branch 2002; Rödel et al. 2004). It is best distinguished from the morphologically very similar *H. sylvaticus* by the small, white gular gland (in contrast to a larger yellow one) and the almost absence of an extendable vocal sac in males (Fig. 4b). This species breeds in stagnant forest waters.

Phlyctimantis boulengeri **Perret, 1986; FPPA (ZMB 88514)**

This is a large treefrog of the western Africa forest zone and occurs at forest edges and along dense vegetation of larger ponds (Schiøtz 1967, 1999; Rödel and Ernst 2001; Rödel et al. 2004a). We found the species in FPPA only in forest areas, which were heavily degraded due to former artisanal gold mining (Fig. 4d). We also heard them calling along open swampy areas near the village.

Odontobatrachidae

Odontobatrachus natator **(Boulenger, 1905); FPPA (ZMB 88530, 88534)**

The sable-toothed frog was, in part, very common along rocky creeks and rivers in primary and slightly degraded forests of FPPA. Morphologically similar species have been recently described within this genus (Barej et al. 2015), but based on the ranges published of these species, we assign our records to *O. natator*.

Phrynobatrachidae

Phrynobatrachus alleni **Parker, 1936; KBPPA (ZMB 88444)**

This is a typical frog of primary and slightly degraded forests of the Upper Guinea forest zone (Guibé and Lamotte 1963; Rödel and Branch 2002; Rödel 2003; Rödel and Ernst 2004). They have a very distinctive head shape and scapular ridges forming an X (the two 'arms' of the X are not connected in the center) which does not extend beyond half of the back. Males have distinctive bright-yellow throats and bellies, they reproduce in slow-flowing parts of small forest streams and puddles of swamps. Many different color morphs are known (M.-O. Rödel unpubl. data), and breeding males may turn completely yellow (Rödel 2003).

Phrynobatrachus **aff.** ***alleni;*** **KBPPA (ZMB 88460-88461, 88474-88475, 88479-88484); FPPA (ZMB 88498)**

These frogs are morphologically very similar to the previous species; however, adult males present distinctly different ventral coloration. These color differences are reflected by genetic differences (M.-O. Rödel and J. Glos unpubl. data). However, as *P. alleni* was described from Liberia and both taxa seem to be represented in the type series (M.-O. Rödel unpubl. data), it is so far unclear which of the two taxa represent the real *P. alleni*. The taxonomy of these frogs and the description of a new species will be the subject of a separate publication.

Phrynobatrachus calcaratus **(Peters, 1863); KBPPA (no voucher)**

These frogs comprise a complex of cryptic species (Rödel and Agyei 2003; Zimkus et al. 2010), which have been reported from forests and forested savanna from West to western Central Africa (Rödel 2000; Frost 2018). We only detected one individual in the leaf litter of a dry river bed in a closed canopy forest in KBPPA. Unfortunately this frog escaped.

Phrynobatrachus fraterculus **(Chabanaud, 1921); FPPA (ZMB 88506)**

This is a species of degraded forest and forest edges in the western part of the Upper Guinea forest region (Guibé and Lamotte 1963; Rödel and Bangoura 2004; Blackburn 2005; Rödel et al. 2009c). We found only one juvenile in FPPA.

Phrynobatrachus guineensis **Guibé & Lamotte, 1962; KBPPA (no voucher)**

This is a species specialized to breed in water-filled tree holes in rainforests (Rödel et al. 2004). It is currently known from western Côte d'Ivoire, south-western Guinea and eastern Liberia (Guibé and Lamotte 1963; Rödel et al. 2004b; Hillers and Rödel 2007). We found this species in low abundance and very patchily distributed in drier parts of the closed canopy forest in KBPPA.

Phrynobatrachus gutturosus **(Chabanaud, 1921); KBPPA and FPPA (no vouchers)**

This species was originally described from Sanikolé, Liberia (Chabanaud 1921). Currently, records are known from primary rainforest (Rödel and Ernst 2004), as well as from savanna from various parts of West African (Rödel 2000; Nago et al. 2006). It apparently is a complex of cryptic species (Zimkus et al. 2010; Ofori-Boateng et al. 2018), but our records are likely the real *P. gutturosus*, as the type locality is in Liberia (Chabanaud 1921). In both sites, usually near stagnant waters in primary forest, we heard this species' typical long buzzing call with single clicks at the end.

Phrynobatrachus **cf.** ***gutturosus/tokba;*** **KBPPA (ZMB 88435, 88436)**

In drier parts of primary forest, near camp 1 in KBPPA, we found numerous small *Phrynobatrachus* which mor-

Figure 5. a Undescribed *Phrynobatrachus* sp. from KBPPA exhibiting characters of *P. gutturosus* and *P. tokba* **b** *Ptychadena* sp. male (ZMB 88505) from river bank in FPPA **c, d** *Ptychadena mascareniensis*-complex females with green (c: ZMB 88535) and brown (d: ZMB 88537) vertebral bands from the same rice paddy in FPPA **e** *Chiromantis rufescens* female (not collected) from KBPPA.

phologically were most similar to *P. gutturosus* and *P. tokba* (Fig. 5a). Barcoding revealed that they were identical to *Phrynobatrachus* aff. *gutturosus* sensu Zimkus et al. (2010). A taxonomic clarification of these frogs requires the revision of the *P. gutturosus*-complex (Ofori-Boateng et al. 2018).

***Phrynobatrachus latifrons* Ahl, 1924; FPPA (ZMB 88544, 88545)**

This species occurs from heavily degraded rainforest habitats throughout all of West and western Central African savanna habitats into the southern Sahara (Rödel 2000; Trape 2015). We found it near FPPA around the village in burned swampy areas which were being prepared to be turned into rice paddies.

***Phrynobatrachus liberiensis* Barbour & Loveridge, 1927; KBPPA (ZMB 88449, 88478); FPPA (ZMB 88495)**

This is a species typical for swampy primary forests, where they occur near slow-flowing, often very shallow streams (Rödel and Branch 2002; Kouamé et al. 2018). This species was recorded from Sierra Leone to western Nigeria (Onadeko and Rödel 2009; Rödel et al. 2009b). Several genetic lineages are known across its range (Kpan et al. 2018), but the type locality is in Liberia (Barbour and Loveridge 1927).

***Phrynobatrachus phyllophilus* Rödel & Ernst, 2002; KBPPA (no voucher); FPPA (ZMB 88502)**

This is a characteristic species of swampy primary forest from eastern Côte d'Ivoire to Sierra Leone (Rödel and Ernst 2002b; Kouamé et al. 2008, 2018).

Phrynobatrachus plicatus **(Günther, 1858); KBPPA (ZMB 88445)**

This is a large species of *Phrynobatrachus* and is distributed from eastern Liberia to western Nigeria (Guibé and Lamotte 1963; Lamotte and Xavier 1966; Rödel et al. 2009b). It inhabits primary and slightly degraded rainforest and often breeds in puddles of forest roads (Rödel and Branch 2002; Kouamé et al. 2018).

Phrynobatrachus 'sp. Gola'; FPPA (ZMB 88497, 88520, 88521)

This species is morphologically almost identical to, but genetically different from, *P. plicatus* (A. Hillers and M.-O. Rödel unpub. data). It seems to be restricted to rainforests of the Sierra Leone–Liberia border region. A formal description of this species will be made in a separate publication.

Phrynobatrachus tokba **(Chabanaud, 1921); KBPPA (no voucher); FPPA (ZMB 88503)**

This small leaf-litter frog is known from western Guinea to Ghana (Guibé and Lamotte 1963; Rödel et al. 2004a, 2005b; Hillers et al. 2007). It deposits its clutches outside of water in moist leaves and has non-feeding, non-hatching tadpoles (Rödel and Ernst 2002a). This species occurs in primary forest but is most abundant in degraded forests and may even enter moist savanna adjacent to forest (Rödel 2003; Rödel and Bangoura 2004; Ernst and Rödel 2005). We heard it very frequently calling along forest edges and open forests at both sites.

Phrynobatrachus villiersi **Guibé, 1959; KBPPA (ZMB 88448, 88473)**

This is a very small leaf-litter frog, which is known to occur patchily from Ghana to Liberia in swampy parts of primary rainforest (Guibé 1959; Rödel and Branch 2002; Hillers and Rödel 2007; Ernst and Rödel 2008; Hillers et al. 2009). The record in KBPPA is only the second record of this species in Liberia (Hillers and Rödel 2007).

Ptychadenidae

Ptychadena **aff.** ***aequiplicata*****; KBPPA (ZMB 88441, 88442, 88455); FPPA (ZMB 88510)**

This is a typical rocket frog of leaf litter of lowland rainforests with terrestrial egg deposition (Rödel et al. 2002a). In contrast to previous assumptions (Guibé and Lamotte 1957, 1958b; Perret 1966), this species is not continuously distributed from West to Central Africa, but comprises various genetic lineages (M.F. Barej and M.-O. Rödel et al. unpubl. data). In KBPPA, we found frogs from two clades, ZMB 88441/88442 and ZMB 88455, respectively. ZMB 88510 from FPPA belonged to the same clade as ZMB 88455. The taxonomy of these frogs is currently being revised.

Ptychadena **cf.** ***bibroni*** **(Hallowell, 1845); KBPPA and FPPA (no voucher)**

This is a typical rocket frog living in savanna and degraded forest habitats, where it breeds in stagnant puddles and pools (Rödel 2000). We heard this species at the edges of forest and along the banks of a large river. As we could not collect a voucher, our identification is based on call characters only.

Ptychadena longirostris **(Peters, 1870); KBPPA (ZMB 88432, 88443); FPPA (ZMB 88513, 88515; tadpoles: 88508)**

This forest frog prefers open areas and puddles on forest roads where they may congregate to large choruses (Guibé and Lamotte 1954; Rödel 2000). We often found this species in former artisanal gold mining areas (Fig. 1c).

Ptychadena mascareniensis**-complex; FPPA (ZMB 88535-88538)**

This is a complex of rocket-frog species ranging across the whole of sub-Saharan Africa, Madagascar, the Seychelles, and the Mascarene Islands (Vences et al. 2004; Zimkus et al. 2017). The various lineages all live in open savanna-like habitats and often in rice paddies (Rödel 2000; Glaw and Vences 2007). We found it exclusively in the rice paddies surrounding the village near FPPA. Frogs of both sexes had either brown or green vertebral bands, even when coming from the same habitat (Fig. 5c, d).

Ptychadena **sp.; FPPA (ZMB 88505, 88548, 88517, 88518)**

We found these frogs (Fig. 5b) in very heavily degraded forest in areas of former artisanal gold mining, where they occurred along the banks of a medium-sized river. We heard their very distinctive croaking advertisement call in swampy areas around the village near FPPA. We have been unable to assign them to any of the described West African species of *Ptychadena* (Guibé and Lamotte 1957, 1958a; Lamotte and Ohler 1997, 2000; Perret 1997; Rödel 2000).

Pyxicephalidae

Aubria subsigillata **(Duméril, 1856); KBPPA (ZMB 88433, 88434)**

This is an aquatic frog, known to feed, amongst other prey, on small fish (Knoepffler 1976, Hughes 1979). The taxonomy is not entirely clear (Ohler and Kazadi 1990). West African populations have been described as *A. occidentalis* (Perret 1994), but were later synonymized with *A. subsigillata* by Ohler (1996). According to our experience specimens with red or beige colors occur across all habitats (Assemian et al. 2006, Rödel et al. 2005a,

Figure 6. a *Cophoscincopus simulans* male (ZMB 88507) from FPPA **b**, **c** *Holaspis guentheri* male (ZMB 88471) **d** *Holaspis guentheri* female (ZMB 88472) from KBPPA **e** Juvenile *Goniontophis klingi* (ZMB 88467) from KBPPA.

2007). We found various individuals of this species in an isolated part of a river in primary forest of KBPPA. The shallow to deep pond had no vegetation, neither on the banks nor submerged. The frogs were sitting along the sandy banks, instantly jumping into the water when disturbed (Fig. 1a).

Ranidae

Amnirana 'albolabris-West'; KBPPA (ZMB 88438, 88458); FPPA (ZMB 88512, 88549; tadpoles: 88528)

This is a median-sized to large leaf-litter frog which was believed to range from forested West Africa into western East Africa. Very recently Jongsma et al. (2018) showed that the Upper Guinea populations are a separate, undescribed species, which is the oldest lineage of the entire clade.

Amnirana occidentalis (Perret, 1960); FPPA (ZMB 88501)

A large leaf-litter frog patchily distributed along rainforest streams of the Upper Guinea forests (Perret 1960, 1983, Rödel and Branch 2002, Rödel and Bangoura 2004, Rödel et al. 2004a, Hillers and Rödel 2007).

Rhacophoridae

Chiromantis rufescens (Günther, 1869); KBPPA (no voucher); FPPA (ZMB 88516)

This is a complex of treefrogs which is widespread in West and Central African rainforests (Schiøtz 1999; Amiet 2012; A. Leaché et al. unpubl. data). In contrast to all other West African frogs, they deposit their eggs in foam nests above water to minimize predation. In West Africa, monkeys are known to feed regularly on these nests and may be the main predator of this species (Rödel et al. 2002). We found this species at both sites along stagnant rivers, near forest ponds, and in puddles, in primary as well as in highly degraded parts of the forest, including areas which have been heavily transformed by previous artisanal gold mining (Fig. 5e). These records are only the third and fourth records of this species in Liberia (Hillers and Rödel 2007; Hillers 2013).

Reptilia
Testudines
Trionychidae

***Trionyx triunguis* (Forskål, 1775); KBPPA (no voucher)**

According to our guide, these large soft-shelled turtles use a particular sandbank of one large river as their breeding site in KBPPA. We confirmed the presence of this species there by a carapace kept in the nearby village. This species is widely distributed in rivers and forests along Africa's western coast, but it is rarely encountered. It has been previously reported from Liberia (Gramentz 2005).

Crocodylia
Crocodylidae

***Osteolaemus tetraspis* Cope, 1861; KBPPA (no voucher)**

We encountered an adult specimen (103 cm length) of this threatened dwarf crocodile at night, near a swampy part of primary rainforest in KBPPA. This species was believed to be widely distributed in forests of West and western Central Africa (Villiers 1958; Trape et al. 2012), where it lives in rainforest, but it may be encountered further north, following gallery forests deep into the savanna zone (Rödel and Garbow 1995). Recent analyses suggest that West Africa is inhabited by two species of dwarf crocodiles, which are both distinct from the Central African *O. osborni* Schmidt, 1919 (Brochu 2007; Shirley et al. 2014).

Sauria
Agamidae

***Agama agama* (Linnaeus, 1758); KBPPA and FPPA (no voucher)**

These common rock- and tree-dwelling lizards (Trape et al. 2012) were often observed in all villages and all disturbed non-forested areas in both sites. We observed no other rainbow agama during our survey. We identified the species as *A. agama*, following Trape et al. (2012). However, more recent work by Leaché et al. (2014, 2017) on the systematics of these lizards suggest that *Agama picticauda* Peters, 1877 is likely the valid name for our populations.

Gekkonidae

***Hemidactylus fasciatus* Gray, 1842; KBPPA (no voucher)**

This widespread West African forest gecko (Trape et al. 2012; Wagner et al. 2014) was only observed once at night on the base of a tree trunk. This was in an area impacted by former artisanal gold mining.

***Hemidactylus muriceus* Peters, 1870; KBPPA (ZMB 88450); FPPA (no voucher)**

This is a widespread species in western African forests (Trape et al. 2012), which we occasionally encountered in both sites at night on smaller trees and shrubs or even in the leaf litter (Henle and Böhme 2003).

Lacertidae

***Holaspis guentheri* Gray, 1863; KBPPA (ZMB 88471, 88472)**

This is an arboreal lizard of West and Central African rainforests and occurs east to Uganda (Spawls et al. 2004; Trape et al. 2012). We collected two specimens during the day in a clearing in the KNPPA while they were chasing each other to the ground. This represents the first record of this elusive lizard for Liberia (Fig. 6b–d).

Scincidae

***Cophoscincopus simulans* (Vaillant, 1884); FPPA (ZMB 88500, 88507, 88509)**

Water skinks were occasionally encountered in the leaf litter along small streams in primary forest of FPPA (Fig. 6a). They are widespread in West African rainforests (Böhme et al. 2000; Trape et al. 2012).

***Trachylepis affinis* (Gray, 1838); KBPPA and FPPA (no voucher)**

This skink is frequently seen in clearings or degraded parts of the forest. This species-complex is widely distributed in forests (rainforest and the humid savanna zone) of West and Central Africa (Freedman et al. 2010; Trape et al. 2012; Allen et al. 2017; Uetz 2018).

***Trachylepis maculilabris* (Gray, 1845); KBPPA and FPPA (no voucher)**

This skink is broadly distributed throughout Africa (Trape et al. 2012; Uetz 2018). We found it at both sites, usually in forest clearings. For a key to West and western Central African *Trachylepis*, see Allen et al. (2017).

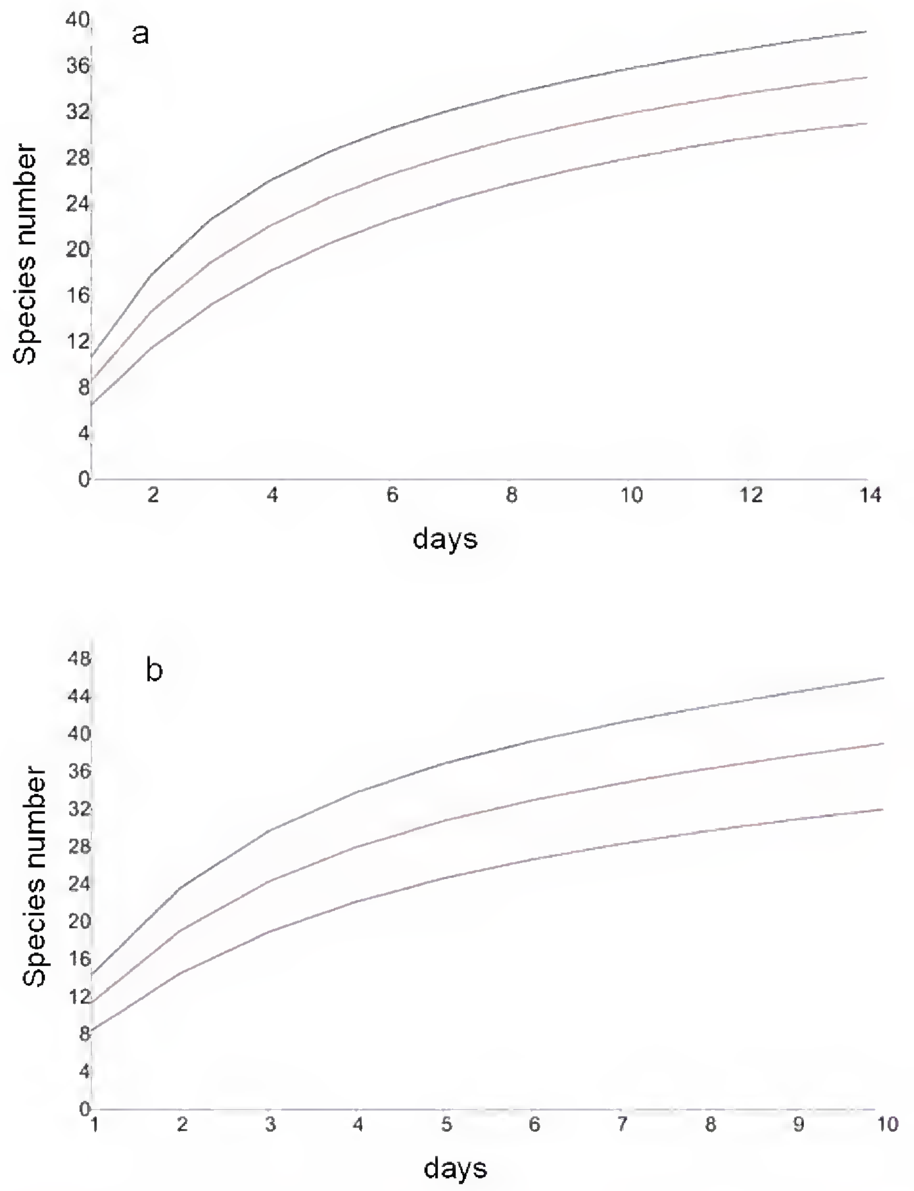

Figure 7. Permutated species accumulation curves (=sample-based rarefaction curve; red line: mean, blue lines: 95% confidence intervalls) of amphibian species richness in **a** the Krahn-Bassa Proposed Protected Area in eastern Liberia and **b** the Foya Proposed Protected Area in western Liberia during the March/April 2018 survey. Y-axis: estimated amphibian species richness, x-axis: sample units (each comprising six to 16 man/hour surveys in different localities within the respective areas).

Varanidae

***Varanus ornatus* Gray, 1845; KBPPA and FPPA (no voucher)**

We observed adult specimens foraging during the day in the leaf litter of drier parts of the rainforest. The validity of this taxon was recently doubted, and it was consequently synonymized by Dowell et al. (2015) with *V. niloticus* (Linnaeus, 1766), although distinct genetic lineages were found within their samples (Uetz 2018). As we (here and elsewhere in West Africa) can easily assign monitor lizards to either *V. niloticus* or *V. ornatus*, following Böhme and Ziegler (1997) in considering the number of transverse rows of spots across body, the color of the tongue, and different ecological requirements (and in order to make later assignments of records to different taxa possible), we do not follow the arguments from Dowell et al. (2015) and treat our observations as being distinct from *V. niloticus* sensu stricto.

Serpentes
Colubridae

***Afronatrix anoscopus* (Cope, 1861); KBPPA (ZMB 88469)**

We collected at night in KBPPA one specimen of these common aquatic snakes. This species ranges from Senegal to Cameroon (Chippaux 2001). Individuals of this species were foraging in ponds and puddles near a small forest creek originating from a former artisanal gold mining area.

***Toxicodryas blandingii* (Hallowell, 1844); FPPA (no voucher)**

In FPPA, we observed at night a large adult snake high in the trees over a rocky torrential stream, apparently searching for food. The species has a wide distribution from Guinea in the west to Kenya in the east and mostly is living in forest habitats (Chippaux 2001).

Lamprophiidae

***Atractaspis* sp. n.; FPPA (ZMB 88529)**

We collected a stiletto snake at night in FPPA on the steep banks of a rocky stream in primary rainforest. A detailed comparison of characters among all described species of *Atractaspis* revealed that our specimens is an undescribed species. This taxon will be formally described elsewhere.

***Boaedon lineatus* Duméril, Bibron & Duméril, 1854; FPPA (ZMB 88547)**

We found a juvenile snake in a degraded area near a small stream in a cleared area surrounded by forest. This species is widespread in forest and savanna habitats in West Africa (Chippaux 2001).

***Gonionotophis klingi* Matschie, 1893; KBPPA (ZMB 88467)**

This West African species lives in leaf litter in rainforests (Rödel and Mahsberg 2000). Chippaux (2001) did not include it in his list of species in Liberia, but Uetz (2018) did include the country within its range. We caught our juvenile specimen at night in leaf litter in a drier part of the forest in KBPPA (Fig. 6e).

***Lycophidion nigromaculatum* (Peters, 1863); KBPPA (ZMB 88468); FPPA (no voucher)**

In KBPPA, this terrestrial, lizard-eating snake was found at night near a small pond in an area of former artisanal gold mining. In FPPA it was found at night climbing on a tree trunk which was bridging a small forest stream. This species lives in West African rainforests and is known from Ghana to eastern Liberia (Chippaux 2001). According to Chippaux's (2001) map, our FPPA record would seem to be the westernmost record for the species. However, the species has been also found in the Gola National Park in Sierra Leone (M.-O. Rödel unpubl. data).

Viperidae

Atheris chlorechis **(Pel, 1852); KBPPA (no voucher)**

This is a species of small arboreal viper, which is widely distributed in the Upper Guinea rainforests (Rödel and Masberg 2000; Chippaux 2001). We observed several specimens of various ages in primary parts of KBPPA.

Additional species

In KBPPA we also found the skin of a large snake, most likely a forest cobra, *Naja guineensis* Broadley, Trape, Chirio, Ineich & Wüster, 2018 (Wüster et al. 2018). An adult forest cobra was observed in the morning on the main road, when driving back to Monrovia. We received reliable descriptions from our guides for the following species: slender-snouted crocodile *Mecistops cataphractus* (Cuvier, 1825); tortoises, most likely *Kinixys homeana* Bell, 1827 and *Kinixys erosa* (Schweigger, 1812); freshwater turtles, *Pelusios* spp.; and two large forest vipers, *Bitis nasicornis* (Shaw, 1802) and *Bitis rhinoceros* (Schlegel, 1855). We also believe, based on published records in other Liberian forests and nearby Taï National Park in Côte d'Ivoire (Rödel and Ernst 2004; Hillers and Rödel 2007), that the following frogs and toads should also occur in KBPPA: *Sclerophrys chevalieri* (Mocquard, 1908)[treated as subspecies of *S. superciliaris* (Boulenger, 1888) in Barej et al. 2011], *Sclerophrys taiensis* (Rödel & Ernst, 2000), *Phrynobatrachus annulatus* Perret, 1966, *Acanthixalus sonjae* Rödel, Kosuch, Veith & Ernst, 2003, *Afrixalus vibekensis* Schiøtz, 1967, *Kassina lamottei* Schiøtz, 1967, *Kassina cochranae* (Loveridge, 1941), and *Ptychadena superciliaris* (Günther, 1858).

In FPPA, our guide and various villagers gave reliable descriptions of the following additional species: rainbow toad, *Sclerophrys chevalieri*; rock python, *Python sebae* (Gmelin, 1789); crocodiles, *Osteolaemus tetraspis* and *Mecistops cataphractus*; tortoises, *Kinixys* spp.; turtles, *Pelusios* spp.; forest vipers, *Bitis nasicornis* and *Bitis rhinoceros*; and cobra, *Naja guineensis.* A previous preliminary survey in FPPA (SNCL 2017) revealed the presence of the frogs: *Phrynobatrachus annulatus*, *P. villiersi*, *Ptychadena oxyrhynchus* (Smith, 1849), and *Afrixalus vibekensis*, and the reptiles *Lepidothyris fernandi* (Burton, 1836) and *Dipsadoboa brevirostris* Sternfeld, 1908 (identified from photos by A. Hillers). Based on their presence at other Liberian (Hillers and Rödel 2007; A. Hillers unpub. data) and nearby Sierra Leonean sites, the presence in FPPA of *Sclerophrys taiensis* and *Ptychadena superciliaris* is likely.

Amphibian diversity

Because our data for amphibians are much more complete than those for reptiles, we only analyse the former. We found at both sites combined a minimum of 49 amphibian species (1 caecilian, 48 anurans) but did not count cryptic species within, e.g., the *P. aequiplicata*-complex.

In KBPPA, we recorded 36 amphibian species (1 caecilian, 35 anurans), which were mostly forest specialists and included only a very few open-habitat species (Table 2). Twenty-four species are only known from the Upper Guinea forests and half of them even only from the western part of this biodiversity hotspot. Less than a third of the species occur across West and western Central Africa (8 species) or have even larger ranges (2 species; Table 2). Of the species recorded, the majority is dependent on rainforest and has restricted ranges within West Africa. Only two species are listed by the IUCN as threatened (both Vulnerable; *Conraua alleni* and *Phrynobatrachus villiersi*). Most species are either not assessed or are lower risk, assessed as Near Threatened or Least Concern. Species richness estimators estimated species richness in KBPPA as 38.7 ± 3.5 (mean ± SD; Chao 2) and 43.4 ± 3.2 (Jackknife 1). This and the species accumulation curve (Fig. 7a) indicate that the species list is not complete but shows a good representation of the amphibian species community active in KBPPA at the time of the survey.

In FPPA, we recorded 39 amphibian species (all anurans), with most being forest specialists and less than a quarter typically from open habitats (Table 2). Twenty-five species are only known from the Upper Guinea forests, and half of these are known only from the western part of this biodiversity hotspot. Less than a quarter of the species occur across West and western Central Africa (8 species) or have even larger ranges (4 species; Table 2). Most species recorded in FPPA are dependent on rainforest and have restricted ranges within West Africa. Only two species are listed by the IUCN as being threatened (Vulnerable, *Conraua alleni* and Endangered, *Amnirana occidentalis*). Most species have not yet been assessed or they are lower risk, assessed as Near Threatened or Least Concern. Species richness estimators estimated species richness in FPPA as 53.0 ± 10.6 (mean ± SD; Chao 2) and 50.7 ± 4.7 (Jackknife 1). This and the species accumulation curve (Fig. 7b) indicate that the species list is not complete and that considerably more (> 10) species should be expected in the amphibian community in FPPA.

Discussion

Whereas we obtained a very good overview of the amphibian fauna, the reptile data are too incomplete to allow for meaningful discussions. We recorded a few interesting reptile species, but for snakes more than 50 species might be expected in both sites (e.g. Roux-Esteve 1969;

Böhme 2000; Rödel and Mahsberg 2000). Of special importance was our first country record of *Holaspis guentheri* and the discovery of a new species of *Atractaspis*. In the following we will focus on the amphibian data of our survey.

We recorded between 36 and 39 amphibian species at both sites, and we estimated the presence of another 15–20 species that we could not find. Compared to data available from other forest sites within the western part of the Upper Guinea forest region (Rödel and Branch 2002; Rödel and Bangoura 2004; Rödel and Ernst 2004; Rödel et al. 2004a; Hillers and Rödel 2007), this estimate seems realistic. Given that we only surveyed for a short time in small areas, the estimates are likely to be at the lower range of what might be expected in these forests. Our data also support former findings, that the western part of the Upper Guinea forest hotspot has a higher amphibian species richness than the equally unique forests further east (Rödel and Agyei 2003; Rödel et al. 2005a, 2007; Leaché et al. 2006; Hillers et al. 2009; Kpan et al. 2014).

We found the amphibian and reptile fauna in KBPPA to be very similar, but not identical to that of Taï National Park in Côte d'Ivoire (Rödel and Ernst 2004; Ernst and Rödel 2006). The two potentially new *Phrynobatrachus* species underline the uniqueness of KBPPA. In FPPA, the presence of an undescribed species of *Phrynobatrachus*, *Odontobatrachus natator*, and a potentially new species of *Ptychadena*, indicate a fauna similar to KBPPA, but still clearly distinct and including unknown species.

We conclude that both KBPPA and FPPA have very high conservation values, based on the amphibian species richness, which is due to the high proportion of forest specialists, species with restricted ranges, undescribed taxa, and our estimate that more species should be detectable. However, these areas were seriously affected by artisanal logging and mining, agricultural encroachment, and hunting. These principal threats lend urgency to the immediate protection of the remaining forests. As our data and the published faunal list of Hillers and Rödel (2007) show, the formerly vast rainforests of Liberia may harbor local species assemblages, including species new to science. This conclusion also applies to the whole country as well (compare predictions by Penner et al. 2019), and therefore, the remaining areas of forest should be desperately surveyed, not only for amphibians and reptiles, but for as many animal and plant taxa as possible. Whenever possible, such efforts should include the training of Liberian biologists, who are needed to establish the necessary long-term expertise in the country for maintaining its unique biodiversity.

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References

Allen KE, Tapondjou NWP, Welton LJ, Bauer AM (2017) A new species of *Trachylepis* (Squamata: Scincidae) from Central Africa and a key to the *Trachylepis* of West and Central Africa. Zootaxa 4268: 255–269. https://doi.org/10.11646/zootaxa.4268.2.5

Amiet JL (2012) Les rainettes du Cameroun. Édition J.-L. Amiet & La Nef des Livres, Nyons/Saint Nazaire, 591 pp.

Assemian NE, Kouamé NG, Tohé B, Gourène G, Rödel MO (2006) The anurans of the Banco National Park, Côte d'Ivoire, a threatened West African rainforest. Salamandra 42: 41–51.

Barbour T, Loveridge A (1927) Some undescribed frogs and a new gecko from Liberia. Proceedings of the New England Zoölogical Club 10: 13–18.

Barbour T, Loveridge A (1930) Reptiles and amphibians from Liberia. In: Strong RP (Ed.) The African Republic of Liberia and the Belgian Congo, Based on the Observations Made and Material Collected During the Harvard African Expedition 1926–1927, Vol. 2. Greenwood Press, New York, 769–786.

Barej MF, Schmitz A, Menegon M, Hillers A, Hinkel H, Böhme W, Rödel MO (2011) Dusted off – the African *Amietophrynus superciliaris*-species complex of giant toads. Zootaxa 2772: 1–32.

Barej MF, Schmitz A, Penner J, Doumbia J, Sandberger-Loua L, Hirschfeld M, Brede C, Emmrich M, Kouamé NG, Hillers A, Gonwouo NL, Nopper J, Adeba PJ, Bangoura MA, Gage C, Anderson G, Rödel MO (2015) Life in the spray zone – overlooked diversity in West African torrent-frogs (Anura, Odontobatrachidae, *Odontobatrachus*). Zoosystematics and Evolution 91: 115–149. https://doi.org/10.3897/zse.91.5127

Blackburn DC (2005) *Cardioglossa liberiensis* Barbour & Loveridge 1927 is a junior synonym of *Phrynobatrachus fraterculus* (Chabanaud 1921). African Journal of Herpetology 54: 171–179. https://doi.org/10.1080/21564574.2005.9635530

Blackburn DC (2010) A new squeaker frog (Arthroleptidae: *Arthroleptis*) from Bioko Island, Equatorial Guinea. Herpetologica 66: 320–334. https://doi.org/10.1655/09-039.1

Blackburn DC, Kosuch J, Schmitz A, Burger M, Wagner P, Gonwouo LN, Hillers A, Rödel MO (2008) A new species of *Cardioglossa* (Anura: Arthroleptidae) from the Upper Guinean forests of West Africa. Copeia 2008: 603–612. https://doi.org/10.1643/CH-06-233

Böhm M, Collen B, Baillie JEM, Chanson J, Cox N, Hammerson G, Hoffmann M, Livingstone SR, Ram M, Rhodin AGJ, Stuart SN, van Dijk PP, Young B, Afuang LE, Aghasyan A, Aguayo AG, Aguilar C, Ajtic R, Akarsu F, Alencar LRV, Allison A, Ananjeva N, Anderson S, Andrén C, Ariano-Sánchez D, Arredondo JC, Auliya M, Austin CC, Avci A, Baker PJ, Barreto-Lima AF, Barrio-Amorós CL, Basu D, Bates MF, Batistella A, Bauer A, Bennett D, Böhme

W, Broadley D, Brown R, Burgess J, Captain A, Carreira S, Castaneda MR, Castro F, Catenazzi A, Cedeño-Vázquez JR, Chapple D, Cheylan M, Cisneros-Heredia DF, Cogalniceanu D, Cogger H, Corti C, Costa GC, Couper PJ, Courtney T, Crnobrnja-Isailovic J, Crochet PA, Crother B, Cruz F, Daltry J, Daniels RJR, Das I, de Silva A, Diesmos AC, Dirksen L, Doan TM, Dodd K, Doody JS, Dorcas ME, Duarte de Barros Filho J, Egan VT, El Mouden EH, Embert D, Espinoza RE, Fallabrino A, Feng X, Feng ZJ, Fitzgerald L, Flores-Villela O, França FGR, Frost D, Gadsden H, Gamble T, Ganesh SR, Garcia MA, García-Pérez JE, Gatus J, Gaulke M, Geniez P, Georges A, Gerlach J, Goldberg S, Gonzalez JCT, Gower DJ, Grant T, Greenbaum E, Grieco C, Guo P, Hamilton AM, Hammerson G, Hare K, Hedges B, Heideman N, Hilton-Taylor C, Hitchmough R, Hoffmann M, Hollingsworth B, Hutchinson M, Ineich I, Iverson J, Jaksic FM, Jenkins R, Joger U, Jose R, Kaska Y, Kaya U, Keogh JS, Köhler G, Kuchling G, Kumlutaş Y, Kwet A, La Marca E, Lamar W, Lane A, Lardner B, Latta C, Latta G, Lau M, Lavin P, Lawson D, LeBreton M, Lehr E, Limpus D, Lipczynski N, Livingstone S, Lobo AS, López-Luna MA, Luiselli L, Lukoschek V, Lundberg M, Lymberakis P, Macey R, Magnusson WE, Mahler DL, Malhotra A, Mariaux J, Maritz B, Marques OAV, Márquez R, Martins M, Masterson G, Mateo JA, Mathew R, Mathews N, Mayer G, McCranie JR, Measey GJ, Mendoza-Quijano F, Menegon M, Métrailler S, Milton DA, Montgomery C, Morato SAA, Mott T, Muñoz-Alonso A, Murphy J, Nguyen TQ, Nilson G, Nogueira C, Nunez H, Orlov N, Ota H, Ottenwalder J, Papenfuss T, Pasachnik S, Passos P, Pauwels OSG, Pérez-Buitrago N, Pérez-Mellado V, Pianka ER, Pleguezuelos J, Pollock C, Ponce-Campos P, Powell R, Pupin F, Quintero Díaz GE, Radder R, Ramer J, Rasmussen AR, Raxworthy C, Reynolds R, Richman N, Rico EL, Riservato E, Rivas G, Rocha PLB, Rödel MO, Rodríguez Schettino L, Roosenburg WM, Sadek R, Sanders K, Santos-Barrera G, Schleich HH, Schmidt BR, Schmitz A, Sharifi M, Shea G, Shi H, Shine R, Sindaco R, Slimani T, Somaweera R, Stafford P, Stuebing R, Sweet S, Sy E, Temple H, Tognielli MF, Tolley K, Tolson PJ, Tuniyev B, Tuniyev S, Üzüm N, van Buurt G, Van Sluys M, Velasco A, Vences M, Veselý M, Vinke S, Vinke T, Vogel G, Vogrin M, Vogt RC, Wearn OR, Werner YL, Whiting MJ, Wiewandt T, Wilkinson J, Wilson B, Wren S, Zamin T, Zhou K, Zug G (2013) The conservation status of the world's reptiles. Biological Conservation 157: 372–385. https://doi.org/10.1016/j.biocon.2012.07.015

Böhme W (2000) Diversity of a snake community in a Guinean rainforest (Reptilia, Serpentes). In: Rheinwald G (Ed.) Isolated vertebrate communities in the tropics: Proceedings of the 4th International Symposium in Bonn. Bonner Zoologische Monographien 46: 69–78.

Böhme W, Schmitz A, Ziegler T (2000) A review of the West African skink genus *Cophoscincopus* Mertens (Reptilia: Scincidae: Lygosominae): resurrection of *C. simulans* (Vaillant, 1884) and description of a new species. Revue Suisse de Zoologie 107: 777–791. https://doi.org/10.5962/bhl.part.80148

Böhme W, Ziegler T (1997) A taxonomic review of the *Varanus* (*Polydaedalus*) *niloticus* (Linnaeus, 1766) species complex. The Herpetological Journal 7: 155–162.

Brochu CA (2007) Morphology, relationships, and biogeographical significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. Zoological Journal of the Linnean Society 150: 835–863. https://doi.org/10.1111/j.1096-3642.2007.00315.x

Chabanaud P (1921) Contribution à l'étude de la faune herpétologique de l'Afrique Occidentale. Bulletin du Comité d'Études Historiques et Scientifiques de l'Afrique Occidentale Française 1921: 445–472.

Chippaux JP (2001) Les serpents d'Afrique Occidentale et Centrale. Collection Faune et Flore tropicales 35. IRD éditions, Paris, 292 pp.

Collwell RK (2005) EstimateS Version 6.0b1. Statistical estimation of species richness and shared species from samples. http://viceroy.eeb.uconn.edu/estimates [Accessed on: 2019-1-16]

Dowell SA, Portik DM, de Buffrénil V, Ineich I, Greenbaum E, Kolokotronis SO, Hekkala ER (2015) Molecular data from contemporary and historical collections reveal a complex story of cryptic diversification in the *Varanus* (*Polydaedalus*) *niloticus* species group. Molecular Phylogenetics and Evolution 94: 591–604. https://doi.org/10.1016/j.ympev.2015.10.004

Ernst R, Rödel MO (2005) Anthropogenically induced changes of predictability in tropical anuran assemblages. Ecology 86: 3111–3118. https://doi.org/10.1890/04-0800

Ernst R, Rödel MO (2006) Community assembly and structure of tropical leaf-litter anurans. Ecotropica 12: 113–129.

Ernst R, Rödel MO (2008) Patterns of community composition in two tropical tree frog assemblages: separating spatial structure and environmental effects in disturbed and undisturbed forests. Journal of Tropical Ecology 24: 111–120. https://doi.org/10.1017/S0266467407004737

Euzet L, Combaz C, Knoepffler LP (1969) Parasites d'amphibiens de Côte d'Ivoire et du Liberia: Polystomatidae (Monogenea). Biologia Gabonica 3: 217–221.

Freedman AH, Thomassen HA, Buermann W, Smith TB (2010) Genomic signals of diversification along ecological gradients in a tropical lizard. Molecular Ecology 19: 3773–3788. https://doi.org/10.1111/j.1365-294X.2010.04684.x

Frost DR (2018) Amphibian species of the World: an online reference. Version 6.0. http://research.amnh.org/herpetology/amphibia/index.html [Accessed on: 2018-8-14]

Glaw F, Vences M (2007) A Field Guide to the Amphibians and Reptiles of Madagascar. Vences & Glaw Verlag, Köln, 496 pp.

Gramentz D (2005) Die Nilweichschildkröte *Trionyx triunguis*. Edition Chimaira, Frankfurt/M., 166 pp.

Guibé J (1959) Description d'un batracien nouveau de Côte d'Ivoire: *Phrynobatrachus villiersi* n. sp. Bulletin du Musée National d'Histoire Naturelle 31: 134–136.

Guibé J, Lamotte M (1954) Étude comparée de *Rana (Ptychadena) longirostris* Peters et *R. (Pt.) aequiplicata* Werner. Bulletin du Musée National d'Histoire Naturelle (2e Série) 26: 318–321.

Guibé J, Lamotte M (1957) Révision systématique des *Ptychadena* (Batraciens Anoures Ranidés) d'Afrique Occidentale. Bulletin de l'Institute Fondamental d'Afrique Noire (Série A) 19: 937–1003.

Guibé J, Lamotte M (1958a) La réserve naturelle intégrale du Mont Nimba. XII. Batraciens (sauf *Arthroleptis, Phrynobatrachus* et *Hyperolius*). Mémoires de l'Institute Fondamental d'Afrique Noire 53: 241–273.

Guibé J, Lamotte M (1958b) Les *Ptychadena* (Batraciens, Ranidés) du Cameroun. Bulletin de l'Institute Fondamental d'Afrique Noire (Série A) 20(4): 1448–1463.

Guibé J, Lamotte M (1963) La réserve naturelle intégrale du Mont Nimba. XXVIII. Batraciens du genre *Phrynobatrachus*. Mémoires de l'Institute Fondamental d'Afrique Noire 66: 601–627.

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics software package for education and data analysis. Paleontologica Electronica 4(1): 9 pp.

Henle K, Böhme W (2003) A new species of *Hemidactylus* (Squamata: Gekkonidae) from West Africa, and comments on species hitherto confused with *H. muriceus*. African Journal of Herpetology 52: 23–38. https://doi.org/10.1080/21564574.2003.9635474

Heyer WR, Donnelly MA, McDiarmid RW, Hayek LAC, Foster MS (1994) Measuring and Monitoring Biological Diversity, Standard Methods for Amphibians. Smithsonian Institution Press, Washington DC, 364 pp.

Hillers A (2013) Final report on the activities of the research unit, Across the River: A Transboundary Peace Park for Sierra Leone and Liberia, 2010–2013. Unpublished report, BirdLife and other contributors.

Hillers A, Boateng CO, Segniagbeto GH, Agyei AC, Rödel M-O (2009) Assessment of the amphibians in the forests of southern Ghana and western Togo. Zoosystematics and Evolution 85: 127–141. https://doi.org/10.1002/zoos.200800019

Hillers A, Loua NS, Rödel MO (2008a) A preliminary assessment of the amphibians of the Fouta Djallon, Guinea, West Africa. Salamandra 44: 113–122.

Hillers A, Rödel MO (2007) The amphibians of three national forests in Liberia, West Africa. Salamandra 43: 1–10.

Hillers A, Veith M, Rödel MO (2008b) Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. Conservation Biology 22: 762–772. https://doi.org/10.1111/j.1523-1739.2008.00920.x

Hughes B (1979) Feeding habits of the frog *Aubria subsigillata* in Ghana. Bulletin de l'Institute Fondamental d'Afrique Noire (Série A) 41: 654– 663.

Inger RF, Menzies JI (1961) A new species of toad (*Bufo*) from Sierra Leone. Fieldiana Zoology 39: 589–594.

Johnston H (1906) Fauna: reptiles, amphibians, and fish. In: Liberia Vol. II. Hutchinson & Co., London, 807–838.

Jongsma GFM, Barej MF, Barratt CD, Burger M, Conradie W, Ernst R, Greenbaum E, Hirschfeld M, Leaché AD, Penner J, Portik DM, Zassi-Boulou AG, Rödel MO, Blackburn DC (2018) Diversity and biogeography of frogs in the genus *Amnirana* (Anura: Ranidae) across sub-Saharan Africa. Molecular Phylogenetics and Evolution 120: 274–285. https://doi.org/10.1016/j.ympev.2017.12.006

Knoepffler LP (1976) Food habitats of *Aubria subsigillata* in Gabon. Zoologica Africana 11: 369–371. https://doi.org/10.1080/00445096.1976.11447542

Kouamé AM, Kouamé NG, Konan JCBYN, Adepo-Gourène AB, Rödel MO (2015) Contributions to the reproductive biology and behaviour of the dotted reed frog, *Hyperolius guttulatus*, in southern-central Ivory Coast, West Africa. Herpetology Notes 8: 633–641.

Kouamé NG, Tohé B, Assemian NE, Gourène G, Rödel MO (2008) Prey composition of two syntopic *Phrynobatrachus* species in the swamp forest of Banco National Park, Ivory Coast. Salamandra 44: 177–186.

Kouamé NG, Tohé B, Assemian NE, Gourène G, Rödel MO (2018) Spatio-temporal distribution of five species of West African leaf-litter frogs. Salamandra 54: 21–29.

Kpan TF, Adeba PJ, Kouamé NG, Koné I, Kouassi KP, Rödel MO (2014) The anuran fauna of a Volunteer Nature Reserve: the Tanoé-Ehy Swamp Forests, south-eastern Ivory Coast, West Africa. Zoosystematics and Evolution 90: 261–270. https://doi.org/10.3897/zse.90.8796

Kpan TF, Kouamé NG, Barej MF, Adeba PJ, Emmrich M, Ofori-Boateng C, Rödel MO (2018) A new Puddle Frog, genus *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae), from the eastern part of the Upper Guinea biodiversity hotspot, West Africa. Zootaxa 4388: 221–237. https://doi.org/10.11646/zootaxa.4388.2.5

Lamotte M, Ohler A (1997) Redécouverte de syntypes de *Rana bibroni* Hallowell, 1845, désignation d'un lectotype et description d'une espèce nouvelle de *Ptychadena* (Amphibia, Anura). Zoosystema 19: 531–543.

Lamotte M, Ohler A (2000) Révision des espèces du groupe de *Ptychadena stenocephala* (Amphibia, Anura). Zoosystema 22: 569–583.

Lamotte M, Perret JL (1968) Révision du genre *Conraua* Nieden. Bulletin de l'Institute Fondamental d'Afrique Noire (Série A) 30: 1603–1644.

Lamotte M, Xavier F (1966) Étude comparée de deux espèces de *Phrynobatrachus* souvent confondues: *Phr. plicatus* Günther et *Phr. auritus* Boulenger. Bulletin de l'Institute Fondamental d'Afrique Noire (Série A) 28: 1605–1619.

Laurent RF (1958) Les rainettes du genre *Hyperolius*. Mémoires de l'Institute Fondamental d'Afrique Noire 53: 275–299. [3 pls]

Leaché AD, Grummer JA, Miller M, Krishnan S, Fujita MK, Böhme W, Schmitz A, LeBreton M, Ineich I, Chirio L, Ofori-Boateng C, Eniang EA, Greenbaum E, Rödel MO, Wagner P (2017) Bayesian inference of species diffusion in the West African *Agama agama* species group (Reptilia, Agamidae). Systematics and Biodiversity 15: 192–203. https://doi.org/10.1080/14772000.2016.1238018

Leaché AD, Wagner P, Linkem CW, Böhme W, Papenfuss TJ, Chong RA, Lavin BR, Bauer AM, Nielsen SV, Greenbaum E, Rödel MO, Schmitz A, LeBreton M, Ineich I, Chirio L, Ofori-Boateng C, Eniang EA, Baha El Din S, Lemmon AR, Burbrink FT (2014) A hybrid phylogenetic-phylogenomic approach for species tree estimation in African *Agama* lizards with applications to biogeography, character evolution, and diversification. Molecular Phylogenetics and Evolution 79: 215–230. https://doi.org/10.1016/j.ympev.2014.06.013

Loveridge A (1941) Report on the Smithsonian-Firestone expedition collection of reptiles and amphibians from Liberia. Proceedings of the United States National Museum 91(3128): 113–140. https://doi.org/10.5479/si.00963801.91-3128.113

Mohneke M, Onadeko AB, Hirschfeld M, Rödel MO (2010) Dried or fried: amphibians in local and regional food markets in West Africa. TRAFFIC Bulletin 22: 117–128.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi:10.1038/35002501

Nago SGA, Grell O, Sinsin B, Rödel MO (2006) The amphibian fauna of the Pendjari National Park and surroundings, northern Benin. Salamandra 42: 93–108.

Nopper J, Gonwouo LN, Hillers A, Sandberger L, Ohler A, Rödel MO (2012) New data on the distribution and morphology of the West African squeaker frog *Arthroleptis langeri* Rödel, Doumbia, Johnson & Hillers, 2009 (Amphibia: Anura: Arthroleptidae). Zootaxa 3170: 64–68.

Ofori-Boateng C, Leaché AD, Obeng-Kankam B, Kouamé NG, Hillers A, Rödel MO (2018) A new species of Puddle Frog, genus *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from Ghana. Zootaxa 4374: 565–578. https://doi.org/10.11646/zootaxa.4388.2.5

Ohler A (1996) Systematics, morphometrics and biogeography of the genus *Aubria* (Ranidae, Pyxicephalinae). Alytes 13: 141–166.

Ohler A, Kazadi M (1990) Description d'une nouvelle espèce du genre *Aubria* Boulenger, 1917 (Amphibiens, Anoures) et redescription du type d'*Aubria subsigillata* (A. Duméril, 1856). Alytes 8: 25–40.

Onadeko AB, Rödel MO (2009) Anuran surveys in south-western Nigeria. Salamandra 45: 1–14.

Parker HW (1936) Amphibians from Liberia and the Gold Coast. Zoologische Mededelingen 19: 87–102.

Penner J, Adum GB, McElroy MT, Doherty-Bone T, Hirschfeld M, Sandberger L, Weldon C, Cunningham AA, Ohst T, Wombwell E, Portik DM, Reid D, Hillers A, Ofori-Boateng C, Oduro W, Plötner J, Ohler A, Leaché AD, Rödel MO (2013) West Africa – a safe haven for frogs? A sub-continental assessment of the chytrid fungus (*Batrachochytrium dendrobatidis*). PLoS ONE 8(2): e56236. https://doi.org/10.1371/journal.pone.0056236

Penner J, Augustin M, Rödel MO (2019) Modelling the spatial baseline for amphibian conservation in West Africa. Acta Oecologica 94: 31–40. https://doi.org/10.1016/j.actao.2017.11.018

Penner J, Wegmann M, Hillers A, Schmidt M, Rödel MO (2011) A hotspot revisited – a biogeographical analysis of West African amphibians. Diversity and Distributions 17: 1077–1088. https://doi:10.1111/j.1472-4642.2011.00801.x

Perret JL (1960) Etudes herpétologiques africaines II. Bulletin de la Société Neuchâteloise des Sciences Naturelles 83: 93–100 + 2 pls.

Perret JL (1966) Les amphibiens du Cameroun. Zoologische Jahrbücher (Systematik) 8: 289–464.

Perret JL (1983) Nouvelles données sur *Hylarana occidentalis* Perret (Amphibia, Ranidae). Bulletin de la Société Neuchâteloise des Sciences Naturelles 106: 109–113.

Perret JL (1994) Revision of the genus *Aubria* Boulenger 1917 (Amphibia Ranidae) with the description of a new species. Tropical Zoology 7: 255–269. https://doi.org/10.1080/03946975.1994.10539257

Perret JL (1997) Description de *Ptychadena arnei* n. sp. (Amphibia, Ranidae) une espèce méconnue d'Afrique Occidentale. Bulletin de la Société Neuchâteloise des Sciences Naturelles 120: 77–86.

Pickersgill M (2007) A redefinition of *Afrixalus fulvovittatus* (Cope, 1860) and *Afrixalus vittiger* (Peters, 1876) (Amphibia, Anura, Hyeroliidae). African Journal of Herpetology 56: 23–37. https://doi:10.1080/21564574.2007.9635551

Poynton JC, Loader SP, Conradie W, Rödel MO, Liedtke HC (2016) Designation and description of a neotype of *Sclerophrys maculata* (Hallowell, 1854), and reinstatement of *Sclerophrys pusilla* (Mertens, 1937) (Amphibia: Anura: Bufonidae). Zootaxa 4098: 73–94. https://doi.org/10.11646/zootaxa.4098.1.3

Rödel MO (1998) A new *Hyperolius* species from Tai National Park, Ivory Coast (Anura: Hyperoliidae: Hyperoliinae). Revue française d'aquariologie herpétologie 25: 123–130.

Rödel MO (2000) Herpetofauna of West Africa, Vol. I: Amphibians of the West African savanna. Edition Chimaira, Frankfurt/M., 332 pp.

Rödel MO (2003) The amphibians of Mont Sangbé National Park, Ivory Coast. Salamandra 39: 91–110.

Rödel MO (2007) The identity of *Hylambates hyloides* Boulenger, 1906 and description of a new small species of *Leptopelis* from West Africa. Mitteilungen aus dem Museum für Naturkunde Berlin, Zoologische Reihe 83: 90–100. https://doi.org/10.1002/mmnz.200600031

Rödel MO, Agyei AC (2003) Amphibians of the Togo–Volta highlands, eastern Ghana. Salamandra 39: 207–234.

Rödel MO, Bangoura MA (2004) A conservation assessment of amphibians in the forêt Classée du Pic de Fon, Simandou Range, southeastern Republic of Guinea, with the description of a new *Amnirana* species (Amphibia Anura Ranidae). Tropical Zoology 17: 201–232. https://doi.org/10.1080/03946975.2004.10531206

Rödel MO, Bangoura MA, Böhme W (2004a) The amphibians of south-eastern Republic of Guinea (Amphibia: Gymnophiona, Anura). Herpetozoa 17: 99–118.

Rödel MO, Barej MF, Hillers A, Leaché AD, Kouamé NG, Ofori-Boateng C, Assemian NE, Tohé B, Penner J, Hirschfeld M, Doumbia J, Gonwouo LN, Nopper J, Brede C, Diaz R, Fujita MK, Gil M, Segniagbeto GH, Ernst R, Sandberger L (2012) The genus *Astylosternus* in the Upper Guinea rainforests, West Africa, with the description of a new species (Amphibia: Anura: Arthroleptidae). Zootaxa 3245: 1–29.

Rödel MO, Boateng CO, Penner J, Hillers A (2009b) A new cryptic *Phrynobatrachus* species (Amphibia: Anura: Phrynobatrachidae) from Ghana, West Africa. Zootaxa 1970: 52–63.

Rödel MO, Branch WR (2002) Herpetological survey of the Haute Dodo and Cavally forests, western Ivory Coast, Part I: Amphibians. Salamandra 38: 245–268.

Rödel MO, Brede C, Schiefenhövel P, Penner J, Sinsin B, Nago SGA (2007) The amphibians of the Lokoli Forest, a permanently inundated rainforest in the Dahomey Gap, Benin. Salamandra 43: 231–238.

Rödel MO, Doumbia J, Johnson AT, Hillers A (2009a) A new small *Arthroleptis* (Amphibia: Anura: Arthroleptidae) from the Liberian part of Mount Nimba, West Africa. Zootaxa 2302: 19–30.

Rödel MO, Emmrich M, Penner J, Schmitz A, Barej MF (2014) The taxonomic status of two West African *Leptopelis* species: *L. macrotis* Schiøtz, 1967 and *L. spiritusnoctis* Rödel, 2007 (Amphibia: Anura: Arthroleptidae). Zoosystematics and Evolution 90: 21–31. https://doi:10.3897/zse.90.7120

Rödel MO, Ernst R (2001) Redescription of the tadpole of *Phlyctimantis boulengeri* Perret, 1986, with preliminary comments on the biology of the species. Alytes 18: 178–186.

Rödel MO, Ernst R (2002a) A new reproductive mode for the genus *Phrynobatrachus*: *Phrynobatrachus alticola* has nonfeeding, nonhatching tadpoles. Journal of Herpetology 36: 121–125. https://doi.org/10.1670/0022-1511(2002)036[0121:ANRMFT]2.0.CO;2

Rödel MO, Ernst R (2002b) A new *Phrynobatrachus* from the Upper Guinean rain forest, West Africa, including a description of a new reproductive mode for the genus. Journal of Herpetology 36: 561–571. https://doi.org/10.1670/0022-1511(2002)036[0561:ANPFTU]2.0.CO;2

Rödel MO, Ernst R (2004) Measuring and monitoring amphibian diversity in tropical forests. I. An evaluation of methods with recommendations for standardization. Ecotropica 10: 1–14.

Rödel MO, Gil M, Agyei AC, Leaché AD, Diaz RE, Fujita MK, Ernst R (2005a) The amphibians of the forested parts of south-western Ghana. Salamandra 41: 107–127.

Rödel MO, Grabow K (1995) Die Schildkröten und Krokodile des Comoé-Nationalparks, Elfenbeinküste (Reptilia: Testudines et Crocodylia). Faunistische Abhandlungen des Museums für Tierkunde Dresden 20: 133–144.

Rödel MO, Kosuch J, Kouamé NG, Ernst R, Veith M (2005b) *Phrynobatrachus alticola* Guibé & Lamotte, 1961 is a junior synonym of *Phrynobatrachus tokba* (Chabanaud, 1921). African Journal of Herpetology 54: 93–98. https://doi.org/10.1080/21564574.2005.9635522

Rödel MO, Krätz D, Ernst R (2002a) The tadpole of *Ptychadena aequiplicata* (Werner, 1898) with the description of a new reproductive mode for the genus (Amphibia, Anura, Ranidae). Alytes 20: 1–12.

Rödel MO, Mahsberg D (2000) Vorläufige Liste der Schlangen des Taï-Nationalparks / Elfenbeinküste und angrenzender Gebiete. Salamandra 36: 25–38.

Rödel MO, Ohler A, Hillers A (2010) A new extraordinary *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from West Africa. Zoosystematics and Evolution 86: 257–261. https://doi.org/10.1002/zoos.201000008

Rödel MO, Range F, Seppänen JT, Noë R (2002b) Caviar in the rain forest: monkeys as frog spawn predators in Taï National Park, Ivory Coast. Journal of Tropical Ecology 18: 289–294. https://doi:10.1017/S0266467402002195

Rödel MO, Rudolf VHW, Frohschammer S, Linsenmair KE (2004b) Life history of a West African tree-hole breeding frog, *Phrynobatrachus guineensis* Guibé & Lamotte, 1961 (Amphibia: Anura: Petropedetidae). In: Lehtinen RM (Ed.) Ecology and evolution of phytotelm-breeding anurans. Miscellaneous Publications of the Museum of Zoology, University of Michigan 193: 31–44.

Rödel MO, Sandberger L, Doumbia J, Hillers A (2009c) Revalidation of *Phrynobatrachus maculiventris* Guibé & Lamotte, 1958 and description of its aposematic coloured tadpole. African Journal of Herpetology 58: 15–27. https://doi.org/10.1080/21564574.2009.9635576

Rödel MO, Schorr G, Ernst R. (2001) Zur Biologie von *Cardioglossa leucomystax* (Boulenger, 1903), im Taï-Nationalpark, Elfenbeinküste. Salamandra 37: 239–260.

Roux-Esteve R (1969) Les serpents de la région de Lamto (Côte d'Ivoire). Annales de l'Université d'Abidjan (Serie E) 2: 81–140.

Sandberger L, Hillers A, Doumbia J, Loua NS, Brede C, Rödel MO (2010) Rediscovery of the Liberian Nimba toad, *Nimbaphrynoides liberiensis* (Xavier, 1978) (Amphibia: Anura: Bufonidae), and reassessment of its taxonomic status. Zootaxa 2355: 56–68. https://doi.org/10.11646/zootaxa.2355.1.3

Schiøtz A (1967) The treefrogs (Rhacophoridae) of West Africa. Spolia zoologica Musei hauniensis 25: 1–346.

Schiøtz A (1968) On a collection of amphibia from Liberia and Guinea. Videnskabelige Meddelelser fra dansk Naturhistorik Forening 131: 105–108.

Schiøtz A (1999) Treefrogs of Africa. Edition Chimaira, Frankfurt/M., 350 pp.

Shirley MH, Vliet KA, Carr AN, Austin JD (2014) Rigorous approaches to species delimitation have significant implications for African crocodilian systematics and conservation. Proceedings of the Royal Society B 281: 20132483. https://doi.org/10.1098/rspb.2013.2483

SNCL (Society for the Conservation of Nature of Liberia) (2017) Report of Foya Forest rapid feasibility study for the establishment of Foya Nature Reserve in response to the expansion of protected area in Liberia. Unpublished report, Monrovia, Liberia.

Spawls S, Howell K, Drewes R, Ashe J (2004) A Field Guide to the Reptiles of East Africa. A. & C. Black, London, 543 pp.

Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783–1786. https://doi.org/10.1126/science.1103538

Stuart SN, Hoffmann M, Chanson JS, Cox NA, Berridge RJ, Ramani P, Young BE (2008) Threatened Amphibians of the World. Lynx Edicions, Barcelona, Spain, 758 pp.

Taylor EH (1968) The Caecilians of the World, a Taxonomic Review. University of Kansas Press, Lawrence, 848 pp.

Taylor EH, Weyer D (1958) Report on a collection of amphibians and reptiles from Harbel, Republic of Liberia. The University of Kansas Science Bulletin 38: 1191–1229. https://doi.org/10.5962/bhl.part.10973

Trape JF (2015) Amphibiens et reptiles du Borkou – Ennedi – Tibesti et quelques observations d'autres vertébrés dans le nord du Tchad. Bulletin de la Société Herpétologique de France 154: 1–34.

Trape JF, Trape S, Chirio L (2012) Lézards crocodiles et tortues d'Afrique occidentale et du Sahara. IRD éditions, Marseille, 503 pp.

Uetz P (2018) The Reptile Database. http://www.reptile-database.org [Accessed on: 2018-9-14]

Vences M, Kosuch J, Rödel MO, Lötters S, Channing A, Glaw F, Böhme W (2004) Phylogeography of *Ptychadena mascareniensis* suggests transoceanic dispersal in a widespread African-Malagasy frog lineage. Journal of Biogeography 31: 593–601. https://doi.org/10.1046/j.1365-2699.2003.01031.x

Villiers A (1958) Tortues et crocodiles de l'Afrique noire Française. Initiations Africaines XV, Institut Français d'Afrieque Noire, Dakar, 354 pp.

Wagner P, Leaché AD, Fujita MK (2015) Description of four new West African forest geckos of the *Hemidactylus fasciatus* Gray, 1842 complex, revealed by coalescent species delimitation. Bonn Zoological Bulletin 63: 1–14.

Wells KD (2007) The Ecology and Behaviour of Amphibians. University of Chicago Press, Chicago, 1148 pp. https://doi.org/10.7208/chicago/9780226893334.001.0001

WCF (Wild Chimpanzee Foundation) & FDA (Forestry Development Authority (2017) Baseline wildlife and anthropogenic survey in the proposed Krahn-Bassa Conservation Area. Unpublished report, Monrovia, Liberia.

Wüster W, Chirio L, Trape JF, Ineich I, Jackson K, Greenbaum E, Barron C, Kusamba C, Nagy ZT, Storey R, Hall C, Wuster CE, Barlow A, Broadley DG (2018) Integration of nuclear and mitochondrial gene sequences and morphology reveals unexpected diversity in the forest cobra (*Naja melanoleuca*) species complex in Central and West Africa (Serpentes: Elapidae). Zootaxa 4455: 68–98. https://doi.org/10.11646/zootaxa.4455.1.3

Xavier F (1978) Une espèce nouvelle de *Nectophrynoides* (Anura, Bufonidae) des Monts Nimba, *N. liberiensis* n. sp. I – description de l'espèce. Bulletin de la Société Zoologique de France 103: 431–441.

Zimkus BM, Lawson LP, Barej MF, Barratt CD, Channing A, Dash KM, Dehling M, Du Preez L, Gehring PS, Greenbaum E, Gvoždík V, Harvey J, Kielgast J, Kusamba C, Nagy ZT, Pabijan M, Penner J, Rödel MO, Vences M, Lötters S (2017) Leapfrogging into new territory: How Mascarene ridged frogs diversified across Africa and Madagascar to maintain their ecological niche. Molecular Phylogenetics and Evolution 106: 254–269. https://doi.org/10.1016/j.ympev.2016.09.018

Zimkus BM, Rödel MO, Hillers A (2010) Complex patterns of continental speciation: Molecular phylogenetics and biogeography of sub-Saharan puddle frogs (*Phrynobatrachus*). Molecular Phylogenetics and Evolution 55: 883–900. https://doi.org/10.1016/j.ympev.2009.12.012

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Three new species of the *Macrophya maculitibia* group (Hymenoptera, Tenthredinidae) with a key to known species from China

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Abstract

The *Macrophya maculitibia* group is proposed and defined. Five species are reported from China, among them three new species, *Macrophya longifossa* **sp. n.**, *M. motuoa* **sp. n.,** and *M. yunnana* **sp. n.**, and two known species, *M. maculitibia* Takeuchi, 1933, and *M. jiuzhaina* Chen & Wei, 2005. A key to the Chinese species of the *M. maculitibia* group is provided.

Key Words

Hymenoptera
Macrophya maculitibia group
sawfly
taxonomy
Tenthredinidae

Introduction

Macrophya Dahlbom, 1835, the third largest genus in the subfamily Tenthredininae (Hymenoptera: Tenthredinidae) contains 301 species worldwide (Li et al. 2018a, b, c, d, 2019; Liu et al. 2018, 2019; Xie et al. 2018). In China, 162 *Macrophya* species have been recorded (Li et al. 2018a, b, c, d, 2019; Liu et al. 2018, 2019; Xie et al. 2018).

In the *Macrophya maculitibia* group, two species, *M. maculitibia* Takeuchi, 1933 from Heilongjiang and Jilin provinces, and *M. jiuzhaina* Chen & Wei, 2005 from Sichuan Province, have been reported in China. In the present paper, three new species of the *Macrophya maculitibia* group are described and illustrated from China: *M. longifossa* sp. n., *M. yunnana* sp. n., and *M. motuoa* sp. n. All Chinese species are with similar general morphology and external genitalia characteristics, forming a peculiar species group of *Macrophya*. Previously, we have found the characteristics of this group, but it has not been proposed. From its geographical distribution in China, we think that additional new species remain to be discovered, though we do not expect the number of species to increase significantly, as the *M. maculitibia* group is relatively small. According to the available data, species in this group are mainly distributed in the southwest, northwest, and northeast of China, while *M. maculitibia* Takeuchi, 1933 is also found in Siberia, Korea, and Japan. Therefore, the *Macrophya maculitibia* species group is here proposed and defined, and three new species from China are described. Its description is a necessary part of a broader effort to review all *Macrophya* species in China. A key to the five species in this group found in China is provided.

Materials and methods

The specimens were examined with a Motic-SMZ-171 stereomicroscope. Adult images were taken with a Nikon

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D700 digital camera and focus-stacked using Helicon Focus (HeliconSoft, Kharkiv, Ukraine). All images were further processed with Adobe Photoshop CS 11.0.

Morphological descriptions of these new species are based on the holotype. The terminology of genitalia follows Ross (1945) and the general morphology follows Viitasaari (2002), although for a few terms (e.g., middle fovea and lateral fovea) we follow Takeuchi (1952).

The specimens examined in this study, including the holotype and paratypes of three new species, are deposited in the Insect Collection of Central South University of Forestry and Technology, Changsha, Hunan, China (**CSCS**).

Abbreviations:

OCL The distance between the lateral ocellus and the occipital carina, or the hind margin of the head where this carina would be if it were developed (Benson 1954).

OOL The distance between the eye and the lateral ocellus.

POL The distance between the mesal margins of the 2 lateral ocelli.

Results

Macrophya maculitibia group

Remarks. Body black without metallic luster; posterior margin of metepimeron with a distinct appendage, appendage strongly elongated and polished, without long hairs; antennae and all trochanters black entirely; lancet narrow and long, with 20–21 serrulae, serrulae somewhat oblique, almost linear, middle serrulae each with 2 proximal and 12 or so distal teeth, subbasal teeth somewhat small and clear. This species group is a small lineage of *Macrphya* and is very close to the *Macrophya imitator* group but can be distinguished from the latter by having the posterior margin of metepimeron straight or slightly concave and the metepimeral appendage differentiated, but not elongated, at least partly punctured and evenly pilose, and without basin.

Description. Body slender; black, always with a few white maculae on mandibles and subbasal part on dorsal side of hind tibia; sometimes with a few white maculae on anterior of fore femur and anterior largely of fore tibia; stigma and veins black; usually apical 1/3 of below stigma with smoky macula; clypeus slightly broader than the shortest distance between lower inner orbits; lateral margins convergent forwards, anterior margin shallowly incised to approximately 1/5–1/4 length of clypeus, apex of lateral lobe obtuse; malar space narrower than diameter of an ocellus; postocellar area broader than long; antenna slender, antennomere III clearly longer than antennomere IV, as long as antennomeres IV–V together; mesoscutellum rounded and elevated; mesoscutellar appendage with a high and acute middle carina; posttergite with a low and short middle carina; dorsal margin of mesepimeron with a distinct platform, as broad as diameter of an ocellus; posterior margin of metepimeron with a distinct appendage, appendage strongly elongated and polished, without long hairs and basin; anal cell of fore wing shortly constricted at approximately basal 1/4, with a long spot-like vein; anal cell of hind wing petiolate; inner spur of hind leg slightly longer than 1/2 length of metabasitarsus, metabasitarsus always slender, slightly longer than following four tarsomeres together; claw with inner tooth slightly shorter than outer tooth; dorsal side of head densely punctured; mesoscutellum densely or somewhat densely punctured; abdominal terga without reticulate microsculpture; penis valve longer than broad, harp narrow towards apex, ergot short.

So far, the *M. imitator* group is the second largest group in *Macrophya*, with 17 species, which are all present in China: *M. bui* Wei & Li, 2012, *M. changbaina* Li, Liu & Heng, 2015, *M. circulotibialis* Li, Liu & Heng, 2015, *M. curvatisaeta* Wei & Li, 2010, *M. curvatitheca* Li, Liu & Heng, 2015, *M. flactoserrula* Chen & Wei, 2002, *M. funiushana* Wei, 1998, *M. imitatoides* Wei, 2007, *M. imitator* Takeuchi, 1937, *M. jiaozhaoae* Wei & Zhao, 2010, *M. kangdingensis* Wei & Li, 2012, *M. nigromaculata* Wei & Li, 2010, *M. omeialpina* Li, Jiang & Wei, 2018, *M. parimitator* Wei, 1998, *M. postscutellaris* Malaise, 1945, *M. semipunctata* Li, Liu & Wei, 2018, and *M. weni* Wei, 1998 (Li et al. 2018d). Among them, *M. imitator* Takeuchi is also distributed in Japan, Korea, and East Siberia (Takeuchi 1937), and *M. postscutellaris* Malaise is also distributed in Myanmar (Malaise 1945). This two species groups are easily to be distinguished by the key to species groups worldwide by Li et al. (Li et al. 2018d).

The *M. maculitibia* species group includes two known species and three new species described here. They can be separated by the following key.

Key to the Chinese species of the *Macrophya maculitibia* group

1 Basal 2/3 of fore wing hyaline, apical 1/3 of below stigma with smoky macula (Figs 1, 2, 21, 37) 2

– Fore wing hyaline, without smoky macula (Figs 13, 29) 4

2 Metepimeronal appendage somewhat narrow and long, very shiny and smooth, without punctures or long hairs (Fig. 25); mesoscutellum higher than top of mesonotum. China (Jilin, Liaoning), Siberia, Japan, North Korea .... *M. maculitibia* Takeuchi, 1933

– Metepimeronal appendage usually broad and shallow, less shiny, with somewhat dense fine punctures and long hairs; mesoscutellum as high as top of mesonotum 3

3 Postocellar area 1.9× broader than long (Fig. 38); metepimeronal appendage 3× as long and twice as broad as the diameter of median ocellus (Fig. 41); apical margin of ovipositor sheath slightly roundish and acute in lateral view; middle serrulae of lancet in female each with two proximal and 6–11 distal teeth (Fig. 44). China (Yunnan)....*M. yunnana* sp. n.

– Postocellar area 2.3 × broader than long (Fig. 3); metepimeronal appendage larger, 4× as long and 3× as broad as the diameter of median ocellus (Fig. 6); apical margin of ovipositor sheath rounded and somewhat obtuse in lateral view; middle serrulae of lancet in female each with two proximal and 10–13 distal teeth (Fig. 9). China (Gansu, Shaanxi, Ningxia, Hubei, Sichuan) ....*M. jiuzhaina* Chen & Wei, 2005

4 Metepimeronal appendage broad and large, apical margin rounded, longer than broad (Fig. 16); malar space 0.5× diameter of median ocellus (Fig. 15); subapical antennomeres dilated, somewhat broader than pedicel (Fig. 17); anterior 2/5 of katepimeron smooth and shiny (Fig. 16); mesoscutellum without peak and carina, as high as top of mesonotum. China (Ningxia, Shaanxi) ....*M. longifossa* sp. n.

– Metepimeronal appendage somewhat narrow and small, nearly triangular, apical margin somewhat rounded, as long as broad (Fig. 33); malar space 0.8× diameter of median ocellus (Fig. 31); subapical antennomeres slightly dilated, slender than pedicel (Fig. 32); anterior margin of katepimeron narrow and smooth (Fig. 33); posterior of mesoscutellum with a peak, middle carina and lateral carina just visible, higher than top of mesonotum. China (Tibet)...........*M. motuoa* sp. n.

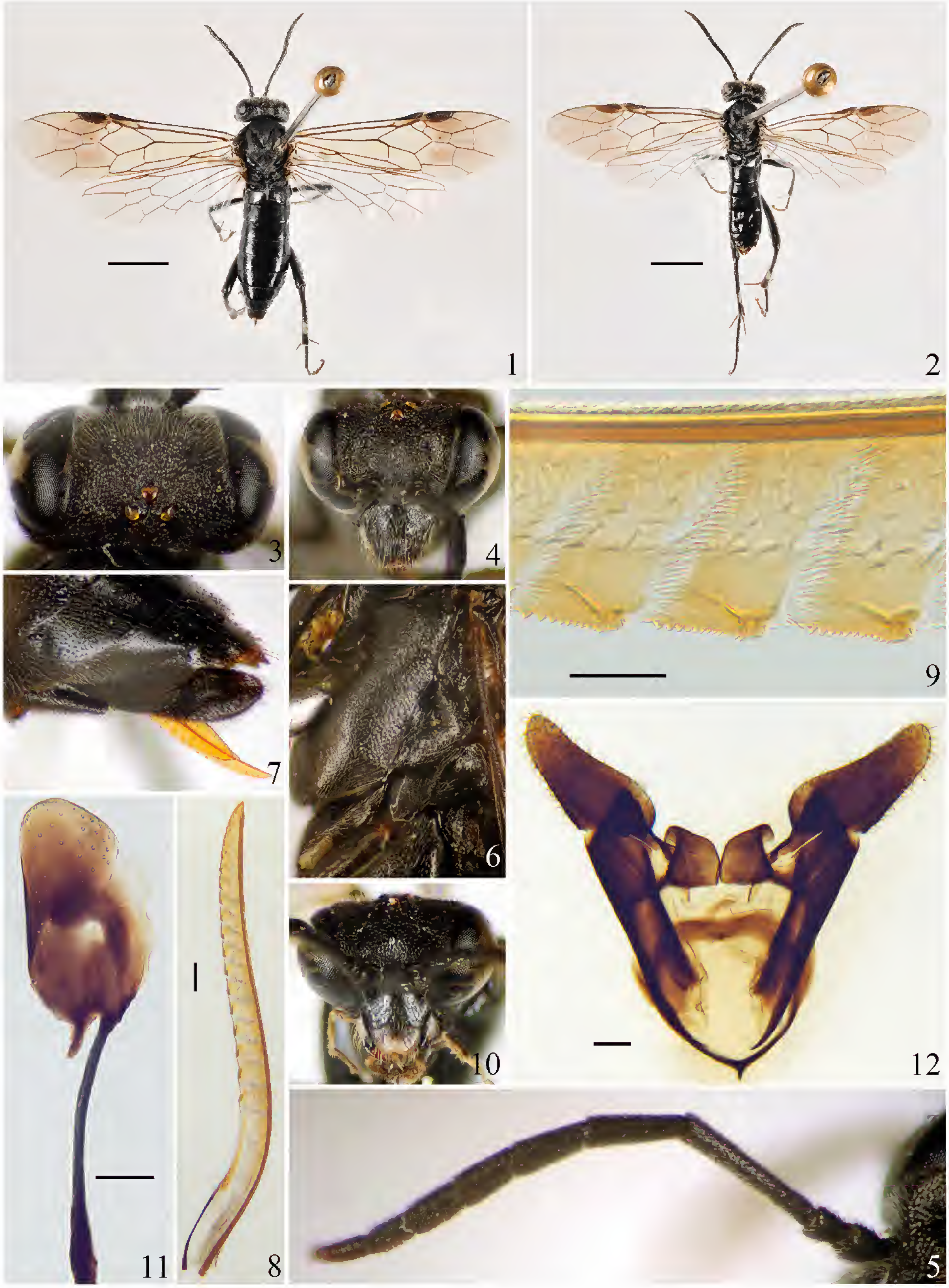
Macrophya jiuzhaina Chen & Wei, 2005

Figures 1–12

Macrophya jiuzhaina Chen and Wei 2005: 86.

Material examined. China: Gansu Province: 7♀, Mt Taizishan, Diaoqi Forest Farm, Linxia City, 35°14.202'N, 103°25.314'E, 2500 m, 10.vii.2010, leg. Zejian Li & Xiaohua Wang; Shaanxi Province: 3♀, CSCS14075, Mt taibaishan, Kaitianguan, Mei County, 34°00.572'N, 107°51.477'E, 1852 m, 05.vi.2014, leg. Mengmeng Liu & Ting Liu, Ethylacetate; Shaanxi Province: 1♀, CSCS14134, Foping County, Sanguanmiao, 33°39.000'N, 107°48.000'E, 1529 m, 20.vi.2014, leg. Liwei Qi & Weinan Kang, Ethylacetate; Shaanxi Province: 2♀, CSCS14080, Mei County, Mt Taibaishan, Kaitianguan, 34°00.572'N, 107°51.477'E, 1852 m, 20.vi.2014, leg. Mengmeng Liu & Ting Liu, Ethylacetate; Shaanxi Province: 1♀, CSCS14104, Taibai County, Mt Qingfengxia, diertingchechang, 34°0.713'N, 107°26.167'E, 1792 m, 11.vi.2014, leg. Meicai Wei, KCN; Shaanxi Province: 1♀, CSCS14127, Foping County, Liangfengyading, 33°41.117'N, 107°51.250'E, 2128 m, 18.vi.2014, leg. Liwei Qi & Weinan Kang, Ethylacetate; Shaanxi Province: 1♀, CSCS17099, Mt Taibaishan, Kaitianguan, 34°0'33.79"N, 107°51'33.72"E, 1815 m, 19.vi.2017, leg. Meicai Wei & Hannan Wang, Ethylacetate; Shaanxi Province: 2♀, CSCS18055, Mt Taibaishan, Kaitianguan, Mei County, 34°0.572'N, 107°51.477'E, 1852 m, 10.vi.2018, leg. Kaiwen Gao, Ethylacetate; Ningxia Province: 1♀, Mt Liupanshan, Elonghe, 35°23.380'N, 106°20.701'E, 1945 m, 06.vii.2008, leg. Fei Liu; Ningxia Province: 2♀, Mt Liupanshan, Xixia, 35°29.604'N, 106°18.777'E, 1974 m, 1~2.vii.2008, leg. Fei Liu; Hubei Province: 1♀, CSCS11022, Mt Shennongjia, Guitouwan, Yichang City, 31°28.439'N, 110°08.872'E, 2150 m, 25~28.v.2011, leg. Zejian Li; Hubei Province: 1♀, CSCS15140, Mt Shennongjia, Banbiyan, 31°26.053'N, 110°14.021'E, 2650 m, 02.viii.2015, leg. Wei Xiao, Ethylacetate; Sichuan Province: 1♀, Jinding, Mt Emeishan, 3000 m, 18.vii.2001, leg. Meicai Wei; Sichuan Province: 1♀, Longlongba, Daocheng County, Yading, 3760 m, 22.vii.2005, leg. Hu Zhou; Sichuan Province: 2♀, Mt Hailuogou, Luding County, 2600–2700 m, 17.vii.2003, leg. Wei Xiao; Sichuan Province: 1♀, Mt Emeishan, Leidongping, 29°32.540'N, 103°19.638'E, 2458 m, 29.vii.2008, leg. Deming Wang; Sichuan Province: 7♀, Mt Hailuogou, Luding County, 3000~3100 m, 18.vii.2003, leg. Weixing Liu; Sichuan Province: 2♀, Mt Emeishan, Leidongping, 29°32.476'N, 103°19.890'E, 2400 m, 25~26.vii.2006, leg. Meicai Wei & Yihai Zhong; Sichuan Province: 6♀, 8♂, Mt Emeishan, Leidongping, 29°546'N, 103°327'E, 2350 m, 07.vii.2009, leg. Meicai Wei & Gengyun Niu; Sichuan Province: 2♀, Mt Hailuogou, Luding County, 29°603'N, 102°076'E, 2200 m, 03.vii.2009, leg. Gengyun Niu; Sichuan Province: 1♀, Mt Hailuogou, Luding County, 29°600'N, 102°000'E, 2900 m, 30.vi.2009, leg. Yihai Zhong; Sichuan Province: 3♀, CSCS142304, Wenchuan County, Wolong Town, Dengshenggou, 31°58.677'N, 103°6.533'E, 2200 m, 16.viii.2014, leg. Wei Xiao & Yilin Xiao, Ethylacetate; 3♀, CSCS142302, Wenchuan County, Wolong Town, Dengshenggou, 31°58.677'N, 103°6.533'E, 2200 m, 16.viii.2014, leg. Liwei Qi, Ethylacetate; Sichuan Province: 1♀, CSCS142305, Wenchuan County, Wolong Town, Yinchanggou, 31°58.333'N, 103°6.967'E, 2188 m, 16.viii.2014, leg. Liwei Qi, Ethylacetate; Sichuan Province: 5♀, CSCS16201, Menghuocheng, Shimian County, 28°53'23"N, 102°21'17"E, 2591 m, 25.vii.2016, leg. Hannan Wang, Ethylacetate; Sichuan Province: 1♀, CSCS16199, Menghuocheng, Shimian County, 28°53'23"N, 102°21'17"E, 2591 m, 23.vii.2016, leg. Hannan Wang, Ethylacetate.

Diagnosis. The species is similar to *M. maculitibia* Takeuchi, 1933 in general morphological characteristics: body and legs mainly black; lancet narrow and long, serrulae somewhat oblique, almost linear, middle serrulae each with 2 proximal and 9–13 distal teeth, subbasal teeth somewhat small and clear in both, but can be distinguished from the latter in having metepimeronal appendage less shiny than the latter, broad and large, with dense and fine punctures and some long hairs; postocellar area



Figures 1–12. *Macrophya jiuzhaina* Chen & Wei, 2005 **1** Adult female, dorsal view **2** Adult male, dorsal view **3** Head of female, dorsal view **4** Head of female, anterior view **5** Antenna of female, lateral view **6** Mesopleuron and metapleuron of female; **7** Ovipositor sheath, lateral view **8** Lancet **9** The 8th–10th middle serrulae **10** Head of male, anterior view **11** Penis valve **12** Gonoforceps. Scale bars: 2 mm (**1, 2**); 100 μm (**8, 11, 12**); 50 μm (**9**).

2.3× broader than long; antenna as long as head and thorax together; mesoscutellum elevated, rounded, as high as top of mesonotum. *M. maculitibia*: metepimeronal appendage very shiny than the former, somewhat narrow and smooth, without punctures or long hairs; postocellar area 2.5× broader than long; antennae somewhat longer than head and thorax together; mesoscutellum elevated, somewhat higher than top of mesonotum.

Variability. Some female specimens with hind tibia entirely black, dorsal side without a small white macula subapically. This macula is described as present in the original description (Chen et al. 2015).

Host plants. Unknown.

Distribution. China (Gansu, Shaanxi, Ningxia, Hubei, Sichuan).

Macrophya longifossa sp. n.

http://zoobank.org/DC548309-0BAB-4574-848F-4D1BFEBEFBEA

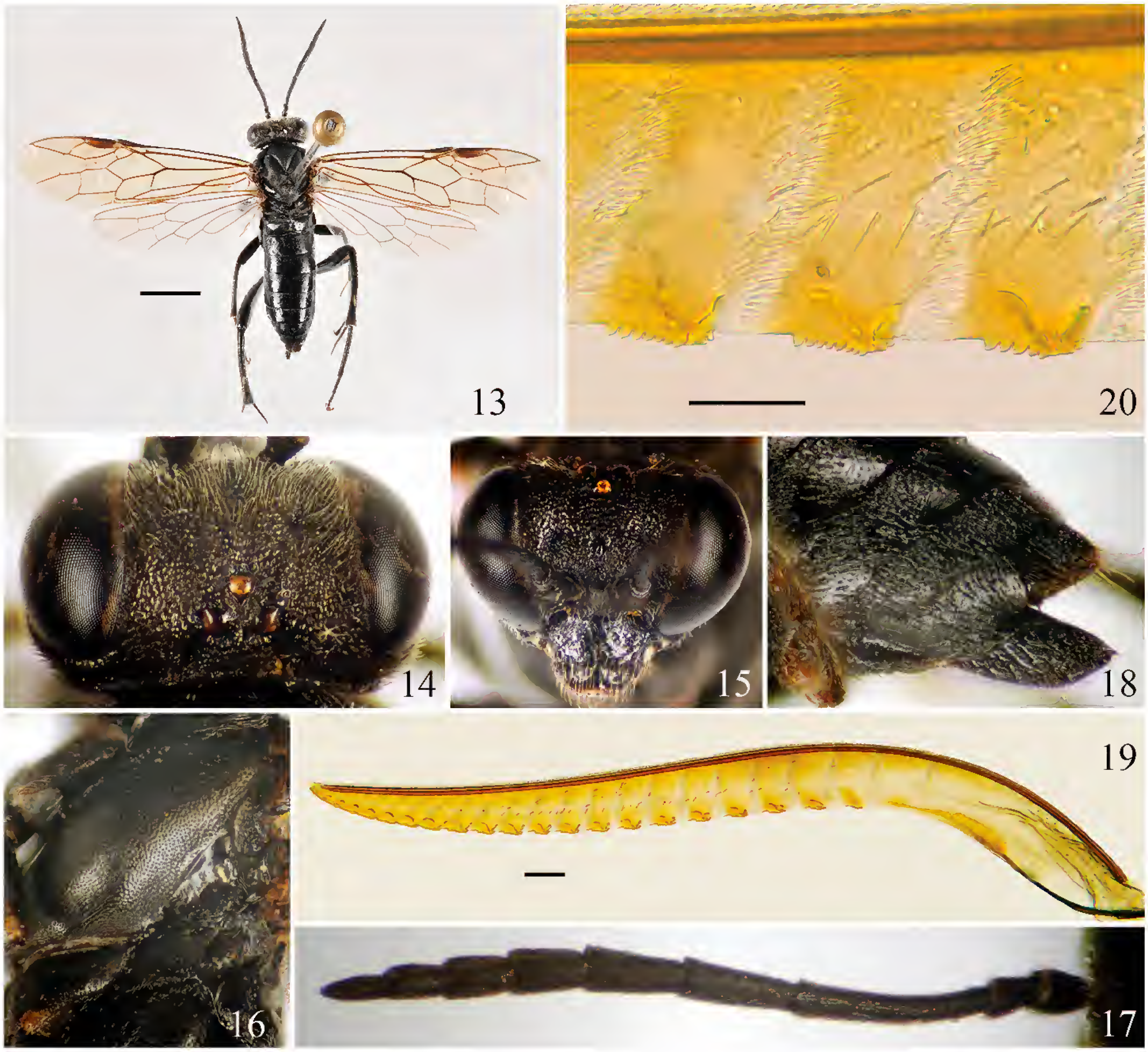
Figures 13–20

Diagnosis. This new species is similar to *M. jiuzhaina* Chen & Wei, 2005 in general morphological characteristics: body and legs mainly black; lancet narrow and long, serrulae somewhat oblique, almost linear, middle serrulae each with 2 proximal and 5–13 distal teeth, subbasal teeth somewhat small and clear in both, but can be distinguished from the latter by the following: malar space 0.5× diameter of median ocellus; subapical antennomeres dilated, slightly broader than pedicel; apical part of fore wing without smoky macula; anterior 2/5 of katepimeron smooth and shiny; metepimeronal appendage broad and shallow, 4.5× as long and 3× as broad as diameter of median ocellus; fore wing hyaline, below stigma without smoky macula. *M. jiuzhaina*: malar space 0.7× diameter of middle ocellus; subapical antennomeres not dilated, slightly slender than pedicel; apical 1/3 of fore wing with smoky macula, basal 2/3 hyaline; anterior margin of katepimeron narrow and smooth; metepimeronal appendage slightly smaller than the former, 4× as long and 3× as broad as diameter of median ocellus; basal 2/3 of fore wing hyaline, apical 1/3 below stigma with smoky macula.

Description. Holotype: female. Body length 9.5 mm. Body and legs black, following parts white: basal half of mandibles, apex in anterior surface of fore femur, anterior surface of fore tibia, subbasal part on dorsal side of hind tibia. Body hairs pale brown, setae on sheath black brown. Wings hyaline, without smoky macula, stigma and veins black brown (Fig. 13).

Dorsum of head somewhat shiny; frons with somewhat dense and rugose punctures, without smooth interspaces between punctures (Fig. 14); labrum and clypeus somewhat polished, with sparse and shallow punctures, microsculpture fine. Mesonotum somewhat shiny, punctures on mesonotum smaller and finer than punctures on head, without smooth interspaces between punctures, with fine but distinct microsculpture; punctures on mesoscutellum somewhat large and rugose, microsculpture just visible; metascutellum with some indistinct punctures and microsculpture; mesepisternum densely punctured, interspaces with fine microsculpture, upper 1/3 with somewhat large punctures, lower 2/3 with minute punctures; anepimeron dull, punctures and wrinkles rugose; anterior 2/5 of katepimeron smooth and shiny, without punctures or microsculpture, posterior 3/5 of katepimeron coarsely punctured and rugose; lateral region of metepisternum dull, minutely and densely punctured, microsculpture fine; metepimeron somewhat shiny, depressed area of metepimeron weakly punctured, elevated part of metepimeron coarsely punctured; metepimeronal appendage with fine punctures and microsculpture; anterior with a distinct smooth and obtuse carina (Fig. 16). All abdominal terga shiny, center of abdominal tergum I with fine microsculpture, lateral sides with distinct punctures; other abdominal terga with fine microsculpture and very sparse but distinct punctures. Hind coxa and outer side of hind femur somewhat shiny, with slightly dense minute punctures, interspaces between punctures with fine microsculpture. Surface of sheath with fine punctures and faint microsculpture.

Anterior margin of labrum truncate; clypeus somewhat elevated in lateral view, broader than distance between the shortest distance between lower inner orbits; lateral sides convergent forwards, anterior margin shallowly incised to nearly 1/5× length of clypeus, lateral corner subquadrate, apical margin short and obtuse (Fig. 15); malar space 0.5× diameter of median ocellus; frons flat, as high as top of eyes in lateral view; middle fovea shallow and fine; lateral foveae slightly deep, furrow-like; interocellar furrow distinct, postocellar furrow indistinct; POL: OOL: OCL = 6: 15: 8; postocellar area slightly elevated, not higher than top of eyes, approximately 2.3× broader than long (9 : 4), lateral furrows deep and divergent backwards; head narrowed behind eyes in dorsal view, occipital carina complete. Antenna slender, as long as head and thorax together, 0.8× length of abdomen; antennomere II 1.4× as long as broad (24: 17), antennomere III 1.7× as long as antennomere IV (19: 11), slightly shorter than antennomeres IV and V together (95 : 103), subapical antennomeres dilated and slightly broader than pedicel, weakly compressed, the ratio of antennomeres IV–IX = 55 : 48 : 35 : 32 : 30 : 33 (Fig. 17). Mesoscutellum elevated roundish, posterior with fine peak, lateral sides with fine carina, without middle carina, as high as top of mesonotum; mesoscutellar appendage with a high and acute middle carina, metascutellum with a low and short middle carina; dorsal-posterior platform of mesepimeron as broad as diameter of median ocellus; metepimeronal appendage broad and large, approximately 4.5× as long and 3× as broad as diameter of median ocellus; mesopleuron and metapleuron as in Figure 16; distance between cenchri twice as broad as a cenchrus. Inner spur of hind tibia 0.7



Figures 13–20. *Macrophya longifossa* **sp. n.**, ♀, holotype **13** Female adult, dorsal view **14** Head of female, dorsal view **15** Head of female, anterior view **16** Mesopleuron and metapleuron of female **17** Antenna of female, lateral view **18** Ovipositor sheath, dorsal view **19** Lancet **20** The 8th–10th middle serrulae. Scale bars: 2 mm (**13**); 100 µm (**19**); 50 µm (**20**).

times length of metabasitarsus (43 : 60); metabasitarsus slender, approximately 1.1× length of following four tarsomeres together (12 : 11); claw with inner tooth slightly shorter than outer tooth. Ovipositor sheath slightly shorter than metabasitarsus (14 : 15), apical sheath longer than basal sheath (29 : 25), apical margin slightly acute and somewhat rounded in lateral view (Fig. 18). Fore wing with vein cu-a joining cell 1M in basal 1/3, vein 2r joining cell 2Rs in apical 1/5, cell 2Rs slightly shorter than cell 1Rs, vein 2r-m slightly oblique, anal cell with a long spot-like vein; petiole of anal cell in hind wing as long as vein cu-a. Lancet with 21 serrulae (Fig. 19), serrulae oblique and weakly protruding, middle serrulae each with two proximal and 5–8 distal teeth, subbasal teeth slightly large and few, annular spine bands narrow, the 8th –10th middle serrulae as in Figure 20.

Male. Unknown.

Type material. Holotype, ♀, China: Shaanxi Province: Chang'an Region, Jiwozi, 33°51.319'N, 108°49.193'E, 1765 m, 27.vi.2008, leg. Xun Zhu. **Paratypes**, Ningxia Province: 3♀, CSCS17109, Guyuan City, Jingyuan County, Erlonghe, 35°18'59"N, 106°21'3"E, 2176m, 30.vi.2017, leg. Meicai Wei & Hannan Wang, Ethylacetate; Ningxia Province: 1♀, CSCS17110, Guyuan City, Jingyuan County, Yehegu, Waigou, 35°29'53"N, 106°13'22"E, 2281 m, 01.vii.2017, leg. Meicai Wei & Hannan Wang, Ethylacetate; Ningxia Province: 1♀, CSCS17107, Guyuan City, Jingyuan County, Sutai Forest Farm, 35°27'23"N, 106°12'2"E, 2281m, 28.vii.2017, leg. Meicai Wei & Hannan Wang, Ethylacetate.

Host plants. Unknown.

Distribution. China (Ningxia, Shaanxi).

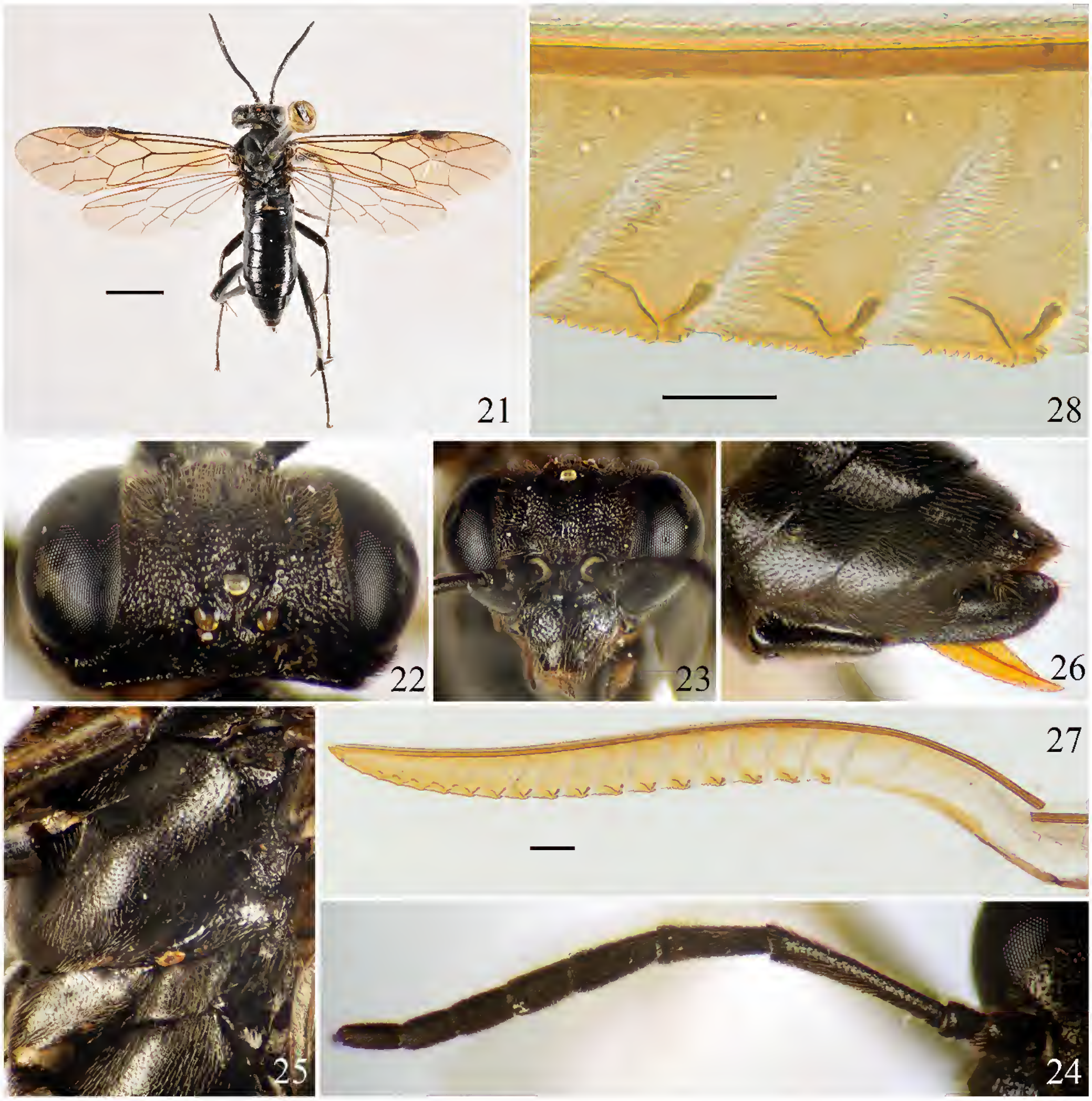
Etymology. The specific name is derived from two Latin words "*longus*" and "*fossa*" referring to the long and large fossa of the metepimeronal appendage.

Macrophya maculitibia Takeuchi, 1933

Figures 21–28

Macrophya maculitibia Takeuchi 1933: 27–28.

Material examined. China: Jilin Province: 2♀, Mt Changbaishan, 1300 m, 02.vii.1999, leg. Meicai Wei & Haiyan Nie; Jilin Province: 3♀, Mt Changbaishan, Huangsongpu Forest Farm, 42°10.979'N, 128°10.278'E, 1145 m, 24.vii.2008, leg. Gengyun Niu & Yuan Zhang; Jilin Province: 3♀, Mt Changbaishan, Wenquanpubu, 42°02.673'N, 128°03.540'E, 1866 m, 23.vii.2008, leg. Meicai Wei & Gengyun Niu; Jilin Province: 5♀, Mt Changbaishan, Dixiasenlin, 42°05.264'N, 128°04.489'E, 1600 m, 26.vii.2008, leg. Meicai Wei & Yuan Zhang; Jilin Province: 1♀, Mt Changbaishan, 05.viii.2008, leg. Maoling Sheng; Jilin Province: 6♀, CSCS12140, Mt Changbaishan, Changbaipubu, Baihe Town, 42°02.962'N, 128°03.372'E, 1850 m, 25.vii.2012, leg. Zejian Li & Jigang Jiang; Jilin Province: 3♀, CSCS12142, Mt Changbaishan, Huangsongpu Forest Farm, Baihe Town,



Figures 21–28. *Macrophya maculitibia* Takeuchi, 1933 **21** Female adult, dorsal view **22** Head of female, dorsal view **23** Head of female, anterior view **24** Antenna of female, lateral view **25** Mesopleuron and metapleuron of female **26** Ovipositor sheath, dorsal view **27** Lancet **28** The 8th–10th middle serrulae. Scale bars: 2 mm (**21**); 100 um (**27**); 50 um (**28**).

42°14.107'N, 128°10.704'E, 1030 m, 27.vii.2012, leg. Zejian Li & Mengmeng Liu; Jilin Province: 2♀, CSCS12126, Mt Changbaishan, Huangsongpu Forest Farm, Baihe Town, 42°14.107'N, 128°10.704'E, 1030 m, 20.vii.2012, leg. Zejian Li & Mengmeng Liu; Jilin Province: 2♀, CSCS12129, Mt Changbaishan, Huangsongpu Forest Farm, Baihe Town, 42°14.107'N, 128°10.704'E, 1030 m, 21.vii.2012, leg. Jigang Jiang & Lanlan Deng; Jilin Province: 2♀, CSCS12134, Mt Changbaishan, Huangsongpu Forest Farm, Baihe Town, 42°14.107'N, 128°10.704'E, 1030 m, 23.vii.2012, leg. Zejian Li & Mengmeng Liu; Jilin Province: 1♀, CSCS12139, Mt Changbaishan, Daxitaihe, Baihe Town, 42°13.796'N, 128°11.808'E, 1035 m, 24.vii.2012, leg. Jigang Jiang & Lanlan Deng; Jilin Province: 1♀, CSCS14194, Mt Changbaishan, Fanghuoliaowangta, 42°04'58"N, 128°13'43"E, 1400 m, 09.vii.2014, leg. Biao Chu, Ethylacetate; Jilin Province: 1♀, CSCS14191, Mt Changbaishan, Dixiasenlin, 42°05'10"N, 128°04'26"E, 1600 m, 05.vii.2014, leg. Biao Chu, Ethylacetate; Jilin Province: 1♀, CSCS14190, Mt Changbaishan, Changbaipubu, 42°02'30"N, 128°03'30"E, 1900 m, 05.vii.2017, leg. Biao Chu, Ethylacetate; Jilin Province: 1♀, CSCS14192, Erdaobaihe Town, Daxitaihe, 42°13'04"N, 128°10'50"E, 1060 m, 08.vii 2014., leg. Biao Chu, Ethylacetate; Liaoning Province, 1♀, Gaolingzi, 02~05.viii.1955, Chinese Academy Sciences; Liaoning Province: 1♀, Gaolingzi, 20.vii.1954, Chinese Academy Sciences.

Diagnosis. The species is similar to *M. jiuzhaina* Chen & Wei, 2005 in general morphology characteristics which are body and legs mainly black; lancet narrow and long, serrulae somewhat oblique, almost linear, middle serrulae each with 2 proximal and 9–13 distal teeth, subbasal teeth somewhat small and clear in both, but can be distinguished from the latter in having metepimeronal appendage very shiny, somewhat narrow and smooth, without punctures or long hairs; postocellar area 2.5 × broader than long; antennae somewhat longer than head and thorax together; mesoscutellum elevated, somewhat higher than top of mesonotum. *M. maculitibia*: metepimeronal appendage less shiny, broad and large, with dense and fine punctures and some long hairs; postocellar area 2.3 × broader than long; antenna as long as head and thorax together; mesoscutellum elevated, rounded, as high as top of mesonotum.

Host plants. Unknown.

Distribution. China (Jilin, Liaoning), Siberia, North Korea, Japan.

Macrophya motuoa sp. n.

http://zoobank.org/9643BB46-2FEB-4B06-93D6-80F30BF6EC7E

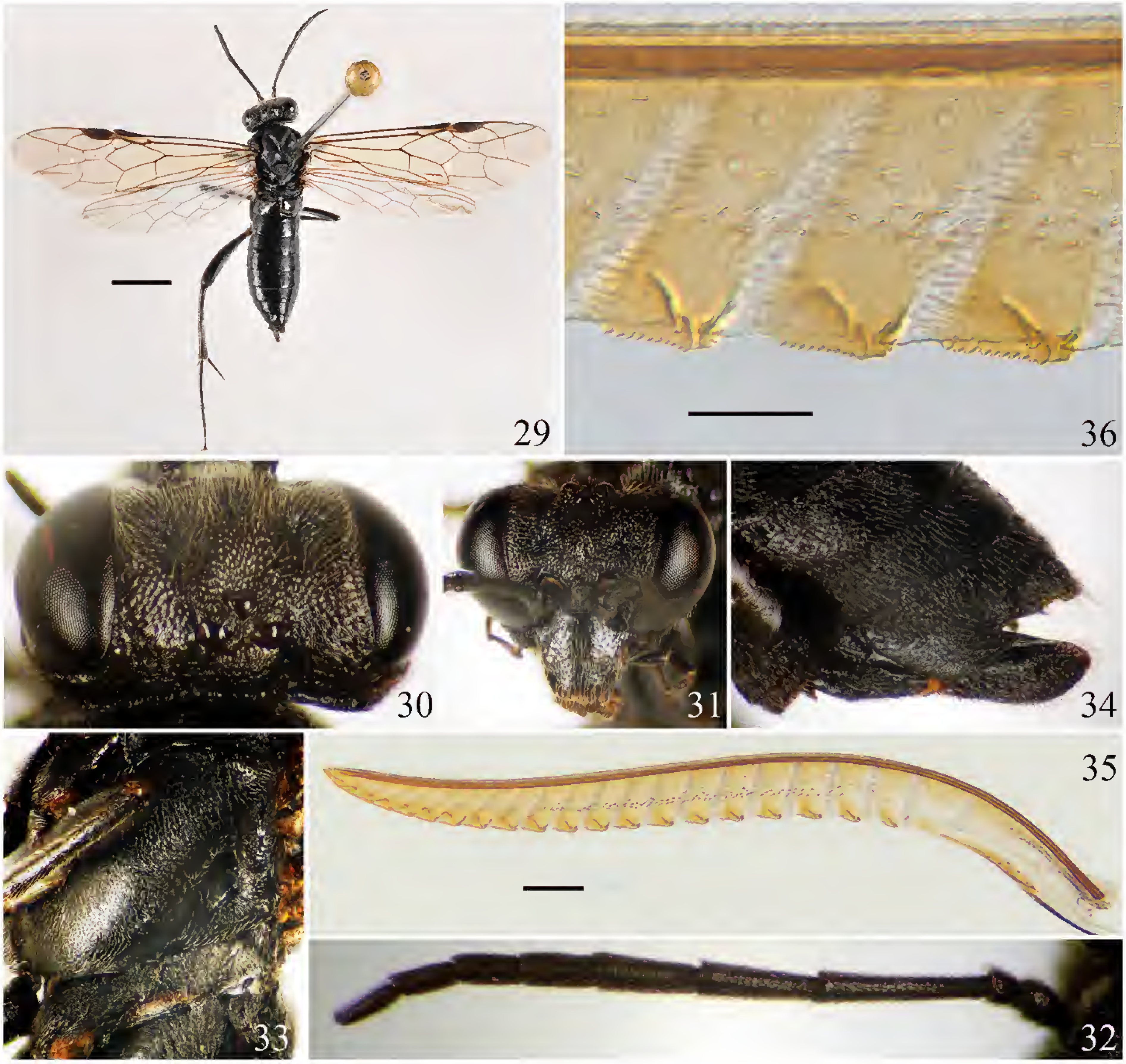
Figures 29–36

Diagnosis. This new species is similar to *M. jiuzhaina* Chen & Wei, 2005 in general morphological characteristics: body and legs mainly black; lancet narrow and long, serrulae somewhat oblique, almost linear, middle serrulae each with 2 proximal and 10–13 distal teeth, subbasal teeth somewhat small and clear in both, but can be distinguished from the latter by the following: postocellar area 2× broader than long; metepimeronal appendage somewhat narrow and small, nearly triangular, apical margin slightly roundish, 2.5× as long and broad as diameter of median ocellus; mesoscutellum distinctly elevated, posterior with a peak, lateral sides and center with slightly distinct carina, slightly higher than top of mesonotum; fore wing hyaline, below stigma without smoky macula. *M. jiuzhaina*: postocellar area 2.3× broader than long; metepimeronal appendage broad and shallow, not triangular, 4× as long and 3× as broad asdiameter of median ocellus; posterior of mesoscutellum without a peak, center without a middle carina, with fine lateral carinae, as high as top of mesonotum; basal 2/3 of fore wing hyaline, apical 1/3 below stigma with smoky macula.

Description. Holotype: female. Body length 9.5 mm. Body and legs black; following parts white: basal half of mandibles, anterior surface of fore femur partly and subbasal part in dorsal side of hind tibia. Body hairs pale brown, setae on sheath hairs pale black-brown. Wings hyaline, without smoky macula, stigma and veins black brown. (Fig. 29)

Dorsum of head shiny, frons with somewhat dense and rugose punctures, interspaces between punctures narrow, with fine microsculpture (Fig. 30); labrum and clypeus somewhat shiny, punctures on labrum sparse, punctures on clypeus somewhat dense, punctures largely shallow and flat. Dorsum of mesonotum somewhat shiny, punctures on mesonotum minutely and densely punctured, without smooth interspaces between punctures, with fine microsculpture; punctures on mesoscutellum somewhat large and rugose; mesoscutellar appendage dull, with indistinct punctures and microsculpture faint; mesepisternum somewhat shiny, minutely and densely punctured, interspaces with fine microsculpture; anepimeron dull, wrinkles rugose; anterior 1/5 of katepimeron smooth and shiny, without punctures or microsculpture; posterior 4/5 of katepimeron with distinct punctures and microsculpture; lateral region of metepisternum dull, with fine punctures and microsculpture; metepimeron somewhat shiny, depressed area of metepimeron with sparse and fine punctures, microsculpture faint; metepimeronal appendage somewhat shiny, with fine punctures and indistinct microsculpture, anterior with a smooth and obtuse carina (Fig. 33). All abdominal terga shiny, center of abdominal tergum 1 with fine microsculpture, lateral sides with distinct punctures; other abdominal terga with fine microsculpture and very sparse but distinct punctures. Hind coxa and outer side of hind femur somewhat shiny, with somewhat dense minute punctures, interspaces between punctures with fine microsculpture. Surface of sheath with fine punctures and faint microsculpture.

Anterior margin of labrum more or less truncate; clypeus slightly elevated in lateral view, broader than dis-



Figures 29–36. *Macrophya motuoa* **sp. n.**, ♀, holotype **29** Female adult, dorsal view **30** Head of female, dorsal view **31** Head of female, anterior view **32** Antenna of female, lateral view **33** Mesopleuron and metapleuron of female **34** Ovipositor sheath, dorsal view **35** Lancet **36** The 8th–10th middle serrulae. Scale bars: 2 mm (**29**); 100 um (**35**); 50 um (**36**).

tance between the shortest distance between lower inner orbits; lateral sides convergent forwards, anterior margin shallowly incised to approximately 1/5× length of clypeus; lateral corner subquadrate, apical margin short and obtuse (Fig. 31); malar space 0.8× diameter of median ocellus; frons flat, as high as top of eyes in lateral view; middle fovea shallow and fine; lateral foveae slightly deep, furrow-like; interocellar furrow distinct, postocellar furrow indistinct; POL : OOL : OCL = 3 : 7 : 4; postocellar area slightly elevated, not higher than top of eyes, approximately 2× broader than long (17 : 8), lateral furrows deep and divergent backwards; head narrowed behind eyes in dorsal view, occipital carina complete. Antenna slender, 1.1× longer than head and thorax together, 0.8 × longer than abdomen; antennomere II 1.2 × longer than broad (6 : 5), antennomere III 1.4× as long as antennomere IV (17 : 12), 0.8× as long as antennomeres IV and V together (17 : 22), subapical antennomeres not dilated and slightly narrower than pedicel, weakly compressed, the ratio of antennomeres IV–IX = 60 : 50 : 40 : 33 : 30 : 32 (Fig. 32). Mesoscutellum distinctly elevated, posterior with a peak, lateral sides and center with weak carina, slightly higher than top of mesonotum; mesoscutellar appendage with a high and acute middle carina, metascutellum with a low and short middle carina; dorsal-posterior platform of mesepimeron as broad as diameter of median ocellus; metepimeronal appendage narrow and small, nearly triangular, apical margin roundish, approximately 2.5× as long and broad as diameter of median ocellus; mesopleuron and metapleuron as in Figure 33; distance between cenchri 2× as broad as a cenchrus. Inner spur of hind tibia 0.7× length of metabasitarsus (7 : 10); metabasitarsus slender, 1.1× length of following four tarsomeres together (15 : 14); claw with inner tooth slightly shorter than outer tooth. Ovipositor sheath slightly shorter than metabasitarsus (11 : 12), apical sheath slightly longer than basal sheath (9 : 7), apical margin somewhat narrow and rounded in lateral view (Fig. 34). Fore wing with vein cu-a joining cell 1M in basal 1/4, vein 2r joining cell 2Rs in apical 1/5, cell 2Rs as long as cell 1Rs, vein 2r-m slightly oblique, anal cell with a short vein and slightly shorter than vein 1r-m; petiole of anal cell in hind wing as long as vein cu-a. Lancet with 20 serrulae (Fig. 35), serrulae oblique and flat, middle serrulae each with two proximal and 10–11 distal teeth, subbasal teeth slightly small, annular spine bands narrow, the 8th –10th middle serrulae as in Figure 36.

Male. Unknown.

Type examined. Holotype, ♀, China: Tibet: Motuo County, Hanmi, 29°22'N, 95°07'E, 2180 m, 16.vi.2009, leg. Zejian Li. **Paratypes**, Tibet: 3♀, CSCS142261, Linzhi District, Motuo County, 44K, 29°42.1'N, 95°33.967'E, 2730 m, 20.vii.2014, leg. Liwei Qi, Ethylacetate; Tibet: 1♀, CSCS142263, Linzhi District, Motuo County, 44K, 29°42.1'N, 95°33.967'E, 2730 m, 20.vii.2014, leg. Wei Xiao & Yilin Xiao, Ethylacetate.

Host plants. Unknown.

Distribution. China (Tibet).

Etymology. The specific name is derived from the locality of the new species which is Motuo County, Tibet in China.

Macrophya yunnana sp. n.

http://zoobank.org/38454BEC-CC06-426B-80B8-CC7A18077800

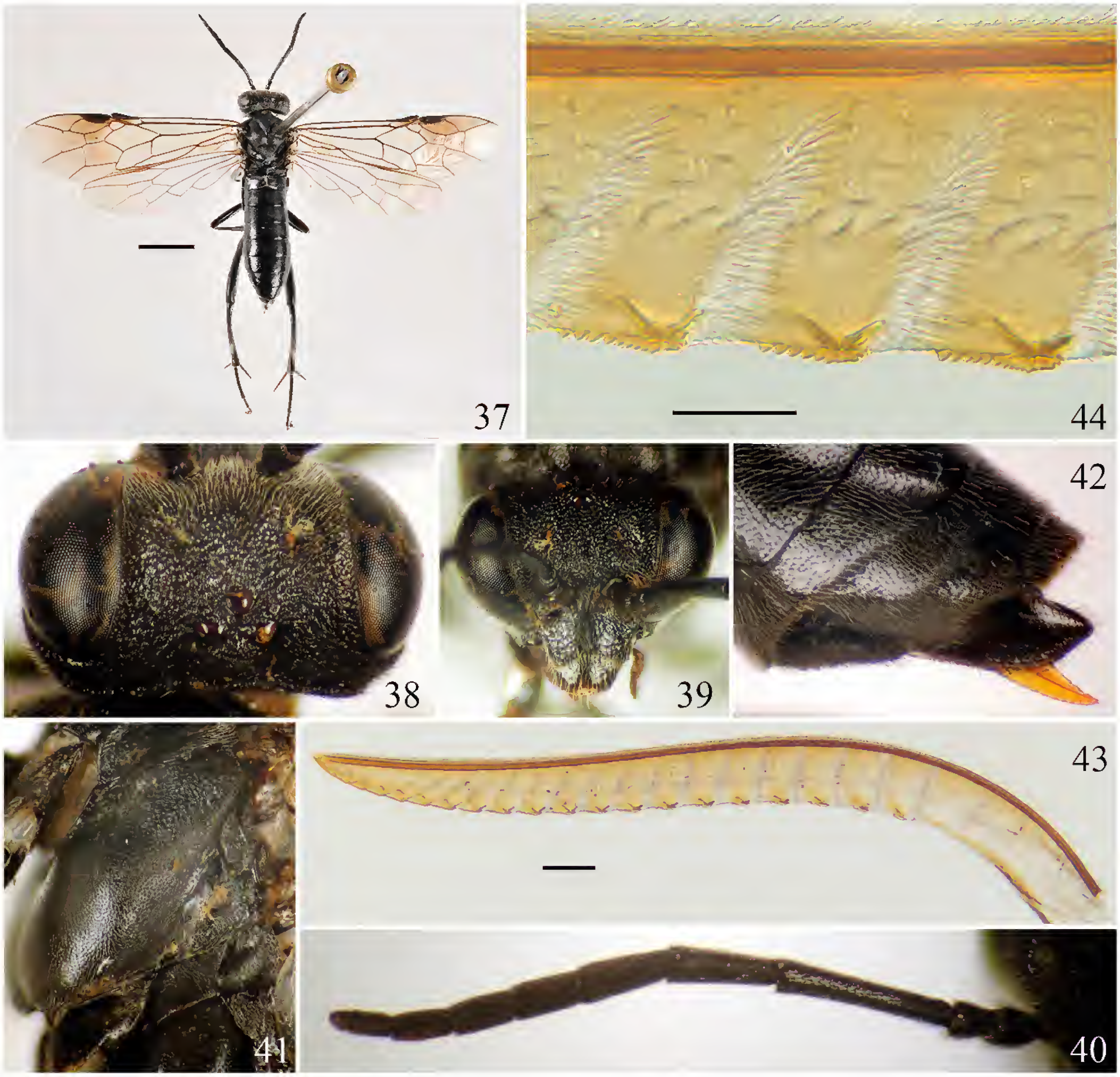
Figures 37–44

Diagnosis. This new species is very similar to *M. jiuzhaina* Chen & Wei, 2005 in general morphological characteristics: body and legs mainly black; basal 2/3 of fore wing hyaline, apical 1/3 of below stigma with smoky macula; metepimeronal appendage usually broad and shallow, less shiny, with somewhat dense fine punctures and long hairs; mesoscutellum as high as top of mesonotum; lancet narrow and long, serrulae somewhat oblique, almost linear, middle serrulae each with 2 proximal and 6–13 distal teeth, subbasal teeth somewhat small and clear in both, but can be distinguished from the latter by the following: postocellar area 1.9× broader than long; metepimeronal appendage 3× as long and twice as broad as diameter of median ocellus; apical margin of ovipositor sheath somewhat rounded and acute in lateral view; middle serrulae of lancet in female each with two proximal and 6–11 distal teeth. *M. jiuzhaina*: postocellar area 2.3× broader than long; metepimeronal appendage 4× as long and 3× as broad as diameter of median ocellus; apical margin of ovipositor sheath rounded and slightly obtusein lateral view; middle serrulae of lancet in female each with two proximal and 10–13 distal teeth.

Description. Holotype: female. Body length 9.5 mm. Body and legs black; following parts white: basal half of mandibles, apical half on anterior surface of fore femur, anterior surface largely of fore tibia, subbasal part of dorsal side of hind tibia. Body hairs pale brown; setae on sheath black-brown. Wings largely hyaline, apical 1/3 of fore wing with smoky macula, stigma, and veins black-brown. (Fig. 37)

Dorsum of head somewhat shiny, frons rugose with dense punctures, interspaces with fine microsculpture (Fig. 38); labrum and clypeus somewhat shiny, punctures on labrum sparse, punctures on clypeus more dense, punctures largely shallow and flat, microsculpture fine. Dorsum of mesonotum somewhat shiny, punctures on mesonotum minute and dense, interspaces with fine microsculpture; mesoscutellum rugose with somewhat large punctures; mesoscutellar appendage somewhat shiny, with indistinct punctures and weak microsculpture; metascutellum dull, with distinct microsculpture; mesepisternum somewhat shiny, with minute and shallow punctures, interspaces with fine microsculpture; anepimeron dull, wrinkles rugose; anterior 1/5 of katepimeron smooth and shiny, without punctures or microsculpture; posterior 4/5 of katepimeron with distinct punctures and microsculpture; lateral region of metepisternum somewhat shiny, with fine punctures and microsculpture; metepimeron someahat shiny, depressed area of metepimeron with sparse and fine punctures, microsculpture faint; metepimeronal appendage somewhat shiny, with fine punctures and indistinct microsculpture, anterior with a smooth and obtuse carina (Fig. 41). All abdominal terga shiny, center of abdominal tergum 1 with fine microsculpture, lateral sides with distinct punctures; other abdominal terga with very sparse and distinct punctures, microsculpture fine but distinct. Hind coxa and outer side of hind femur somewhat shiny, with slightly dense and minute punctures, interspaces between punctures with fine microsculpture. Surface of sheath with fine punctures and indistinct microsculpture.

Anterior margin of labrum more or less truncate; clypeus slightly elevated in lateral view, broader than distance between the shortest distance between lower inner orbits; lateral sides convergent forwards, anterior margin shallowly incised to approximately 1/5× length of clypeus; lateral corner of clypeus subquadrate, apical margin of lateral lobes short and obtuse (Fig. 39); malar space 0.6× diameter of median ocellus; frons flat, as high as top of eyes in lateral view; median fovea shallow and fine; lateral foveae slightly deep, furrow-like; interocellar furrow distinct, postocellar furrow indistinct; POL : OOL : OCL = 3 : 7 : 4; postocellar area slightly elevated, not higher than top of eyes, approximately 1.9× broader than long (15 : 8), lateral furrows deep and divergent backwards; head narrowed behind eyes in dorsal view,



Figures 37–44. *Macrophya yunnana* **sp. n.**, ♀, holotype **37** Female adult, dorsal view **38** Head of female, dorsal view **39** Head of female, anterior view **40** Antenna of female, lateral view **41** Mesopleuron and metapleuron of female **42** Ovipositor sheath, dorsal view **43** Lancet **44** The 8th–10th middle serrulae. Scale bars: 2 mm (**37**); 100 um (**43**); 50 um (**44**)

occipital carina complete. Antenna slender, 1.3× longer than head and thorax together, 0.9× longer than abdomen; antennomere II 1.3× longer than broad (23: 18), antennomere III 1.7× as long as antennomere IV (92 : 55), as long as antennomeres IV and V together (92 : 105), subapical antennomeres slightly dilated and broader than pedicel, weakly compressed, the ratio of antennomeres IV–IX = 55 : 50 : 36 : 32 : 30 : 33 (Fig. 40). Mesoscutellum elevated, rounded, posterior with a faint peak, lateral sides and center with indistinct carina, as high as top of mesonotum; mesoscutellar appendage with a high and acute median carina, metascutellum with a low and short middle carina; dorsal-posterior platform of mesepimeron as broad as diameter of median ocellus; metepimeronal appendage somewhat broad and shallow, apical margin round, approximately 3× as long and 2× as broad as diameter of median ocellus;mesopleuron and metapleuron as in Fig. 41; distance between cenchri 2× as broad as a cenchrus. Inner spur of hind tibia 0.7× length of metabasitarsus (20 : 29); metabasitarsus slender, 1.1× length of following four tarsomeres together (29 : 26); claw with inner tooth slightly shorter than outer tooth. Ovipositor sheath slightly shorter than metabasitarsus (55 : 58), apical sheath slightly longer than basal sheath (31: 21), apical margin somewhat narrow and rounded in lateral view (Fig. 42). Fore wing with vein cu-a joining cell 1M in basal 1/4, vein 2r joining cell 2Rs in apical 1/3, cell 2Rs slightly longer than cell 1Rs, vein 2r-m slightly oblique, anal cell with a short long spot-like vein; petiole of anal cell in hind wing as long as vein cu-a. Lancet with 21 serrulae (Fig. 43), serrulae oblique and flat, middle serrulae each with two proximal and 6–11 distal teeth, subbasal teeth slightly small, annular spine bands narrow, the 8th–10th middle serrulae as in Figure 44.

Male. Unknown.

Type material. Holotype, ♀, China: Yunnan Province: Mt Yulongxueshan, Lijiang City, 2700~3100 m, 25.vii.2004, leg. Wei Xiao. **Paratypes,** Yunnan Province: 1♀, Xiaozhongdian, Xianggelila City, 3000 m, 19.vii.2004, leg. Wei Xiao; Yunnan Province: 1♀, Mt Baimaxueshan, Deqin County, 28°443'N, 98°950'E, 3471 m, 19.vi.2009, leg. Yihai Zhong; Yunnan Province: 1♀, Mt Daorenshan, Yunlong County, 25°32.893'N, 99°11.267'E, 2265 m, 03.vi.2009, leg. Zejian Li.

Host plants. Unknown.

Distribution. China (Yunnan).

Etymology. The specific name is derived from the locality of the new species which is Yunnan Province in Southwest China.

Discussion

The *Macrophya maculitibia* group is a medium-sized species group in the genus *Macrophya* Dahlbom, 1835. At present, there are five species including three new species from China in this group: *M. jiuzhaina* Chen & Wei, 2005, *M. longifossa* sp. n., *M. maculitibia* Takeuchi, 1933, *M. yunnana* sp. n., and *M. motuoa* sp. n. (Chen et al. 2005; Takeuchi 1933). The species hosts of this group are unknown. The *M. maculitibia* group was proposed in a book by Li et al. (2018d) but not reviewed due to a limits on the number of words. With the new material now available, three new species are described and reported, as well as a key is presented to all known Chinese species.

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References

Benson RB (1954) Some sawflies of the European Alps and the Mediterranean region (Hymenoptera: Symphyta). Bulletin of the British Museum (Natural History), Entomology 3(7): 267–295. https://doi.org/10.5962/bhl.part.1054

Chen ML, Huang NT, Zhong YH (2005) Three new species of *Macrophya* Dahlbom (Hymenoptera: Tenthredinidae). Journey of Central South Forestry University 25(2): 85–87.

Li ZJ, Jiang B, Liu MM, Wei MC (2018a) Two new species of the *imitator* group in *Macrophya* Dahlbom (Hymenoptera, Tehthredinidae) from Sichuan, China. Entomotaxonomia 40(2): 95–103.

Li ZJ, Liu MM, Yu JC, Wei MC (2018b) A new species of the *Macrophya flavomaculata* group (Hymenoptera: Tenthredinidae) from China. Entomotaxonomia 40(1): 7–13.

Li ZJ, Liu MM, Wei MC, Zhu CD (2018c) Review of the *Macrophya regia* group (Hymenoptera: Tenthredinidae) from China with the descriptions of two new species. Entomological Research 48(5): 405–415.

Li ZJ, Liu MM, Wei MC (2019) A new species of *Macrophya* Dahlbom (Hymenoptera: Tenthredinidae) with a key to species of the *Macrophya coxalis* group from China. Entomological Research 49(1). https://doi.org/10.1111/1748-5967.12335

Li ZJ, Wei MC, Liu MM, Chen ML (2018d) *Macrophya* Dahlbom in China. China Agricultural Science and Technology Press, Beijing, 456 pp.

Liu MM, Li ZJ, Wei MC (2018a) Two new species of the *ligustri* group in *Macrophya* Dahlbom (Hymenoptera, Tenthredinidae) from Anhui and Jiangxi, China. Entomotaxonomia 40(2): 85–94.

Liu MM, Zhong YH, Li ZJ, Wei MC (2019) Two new species of *Macrophya flavomaculata* group (Hymenoptera, Tenthredinidae) from China. Entomotaxonomia 41(1). [In press]

Malaise R (1945) Tenthredinoidea of South-Eastern Asia with a general zoogeographical review. Opuscula Entomologica 4(Supplement): 1–288.

Ross HH (1945) Sawfly genitalia: terminology and study techniques. Entomological News 61(10): 261–268.

Takeuchi K (1933) Undescribed sawflies from Japan. The Transations of the Kansai Entomological Society, Osaka 4: 17–34.

Takeuchi K (1937) A study on the Japanese species of the genus *Macrophya* Dahlbom (Hymenoptera, Tenthredinidae). *Tenthredo*. Acta Entomologica 1(4): 376–454.

Takeuchi K (1952) A Generic Classification of the Japanese Tenthredinidae (Hymenoptera: Symphyta). Kyoto, 90 pp.

Viitasaari M (2002) The suborder Symphyta of the Hymenoptera. In: Viitasaari M (Ed.) Sawflies (Hymenoptera, Symphyta) I – A Review of the Suborder, the Western Palaearctic Taxa of Xyeloidea and Pamphilioidea. Tremex, Helsinki, 11–174.

Xie JQ, Song YD, Liu MM, Li ZJ, Wei MC (2018) Two new species of the *Macrophya annulitibia* group (Hymenoptera, Tenthredinidae) from China. Entomotaxonomia 40(3): 189–198.

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Phylogeny and species delimitation based on molecular approaches on the species of the *Australoheros autrani* group (Teleostei, Cichlidae), with biogeographic comments

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Abstract

Three distinct and independent molecular-based species delimitation analyses were performed among the species and populations included within the *Australoheros autrani* group, based on sequences of the mitochondrial gene Cytochrome b: a tree-based method proposed by Wiens and Penkrot (WP), a Character-based DNA Barcoding (CBB) and coalescent species delimitation method termed the Bayesian Implementation of the Poisson tree processes (bPTP). The congruence of WP and CBB delimited 11 independent lineages (species), while the bPTP delimited just nine lineages. We did not favour any of the methods, and we considered the possibility of two slightly variant scenarios. A time-calibrated phylogenetic analysis is proposed based on the predominant congruence of the results of these three species delimitation methods herein applied. The monophyly of the *A. autrani* species group was highly supported with maximum node support value and diagnosed by 11 nucleotide substitutions. The sister clade of the *A. autrani* species group is the clade comprising *A.* sp. Timbé do Sul and *A. minuano*. The phylogenetic analysis supports three main clades within the *A. autrani* species group, supported by maximum node support value, with the Southern Mata Atlântica clade as the most basal clade. Divergence time estimates indicate that the diversification of the *Australoheros* originated during the early Neogene, but only in the late Neogene did the processes of diversification in the southeast and north regions occur. Diversification within the *Australoheros autrani* species group occurred synchronically for the three main clades during the beginning of the Quaternary. It is demonstrated that molecular characters are valuable tools for species recognition, particularly in speciose groups with inconspicuous or difficult to record morphological characters. The resulting phylogeny of the *Australoheros autrani* group is highly compatible with the geological and biogeographic scenarios proposed for the Neogene and Quarternary shaping of the extant river basins of eastern Brazil. Despite the origin of the *A. autrani* group being dated to the late Miocene, species level diversification occurred in the Pleistocene and was probably driven by headwater capture events and sea-level fluctuations.

Introduction

Over the past two decades, research on cryptic species have exponentially increased, mainly due to the improvement of molecular methods and availability of DNA sequences (Bickford et al. 2006). Cryptic or hidden species are those species which are: morphologically indistinguishable, since speciation is not always accompanied by morphological change or are at least superficially morphologically difficult to be differentiated; species which

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are, or have been, erroneously classified as a single nominal species on formal grounds; or any taxa comprising taxonomically confused "species", that in fact consist of a number of valid but undiagnosed species (Bickford et al. 2006; Adams et al. 2014). Among cryptic species complexes, the number of species is likely to be greater than that estimated by traditional alpha-taxonomy, because speciation is not always accompanied by morphological differentiation (Bickford et al. 2006; Adams et al. 2014). Many species are expected cryptic, similar morphologically, usually difficult to be identified based only on preserved specimens. In particular this applies to species properly diagnosed by, for example, colouration in life, behaviour, and acoustic or electric discharge characters. In these cases, the use of additional tools and methods such as molecular and DNA data and methods are important to evaluate the diversity within taxonomically unresolved groups (Wiens and Penkrot 2002; Bickford et al. 2006; De Queiroz 2007; Goldstein and Desalle 2010; Costa et al. 2012, 2014). However, diagnosing species using only molecular characters is possible, but is not yet a widespread practice (Cook et al. 2010; Pante et al. 2015), especially in animals, although recent papers have increasingly included molecular data in species descriptions (Goldstein and Desalle 2010; Pante et al. 2015).

The ongoing destruction and disturbance of natural ecosystems and the resultant increase in extinction rates, makes it urgent to catalogue and describe biodiversity, as well as to develop approaches directed to the study of species complexes (Brook et al. 2006; Costa et al. 2012). Molecular data proved to be very useful in revealing cryptic species (Bickford et al. 2006; Adams et al. 2014), which have been subsequently supported by morphological, ethological, and/or ecological data, or in evidencing a hypothesis of species identity when these are morphologically quite similar or undistinguishable. Thus, molecular methods should be incorporated into alpha taxonomy, thereby improving the accuracy of biodiversity estimates. Underestimation of species diversity and misidentification of cryptic species could have severe consequences, mainly in the field of conservation biology. Among the main consequences related to species misidentification is the possibility of endangered species being hidden in cryptic species complexes, and consequently not being taken into account by conservation policies and protective efforts. Other consequences were widely discussed by Bickford et al. (2006).

The Neotropical region, known for its rich species diversity, has inspired classical studies on evolutionary biology. In this region the most diverse fauna of freshwater fishes in the world is found, exhibiting intriguing and unique specializations (e.g. Reis et al. 2003, 2016). Cichlids are among the main components of the Neotropical ichthyofauna; they are a teleost family occurring in tropical and subtropical regions of the Americas, Africa, and Asia (Kullander 1998, 2003; Nelson et al. 2016). Cichlidae is one of the most species-rich vertebrate families (Mcmahan et al. 2013; Near et al. 2013; Nelson et al. 2016), comprising more than 1700 valid species (Fricke et al. 2018). Despite the predominantly marine habits of closely related families in the Ovalentaria clade (Betancur et al. 2013; Near et al. 2013, Nelson et al. 2016), cichlids inhabit freshwater environments, with species occasionally tolerating brackish water (Kullander 1998; Nelson et al. 2016).

Australoheros Říčan & Kullander, 2006 is a South American cichlid genus of the tribe Heroini, which was described to include species previously placed in *Cichlasoma* Swainson, 1839. Before 1995, all the 29 nominal species presently contained in *Australoheros* were considered to belong to a single species, *Cichlasoma facetum*, which was thought to be geographically widespread between southeastern Brazil and northeastern Argentina (Casciotta et al. 1995; Říčan and Kullander 2003; Ottoni and Costa 2008). In recent years, taxonomic studies have revealed high species diversity, mostly concentrated in the lower La Plata river basin and adjacent coastal river basins (Casciotta et al. 1995, 2006; Říčan and Kullander 2003, 2006, 2008; Ottoni and Cheffe 2009; Říčan et al. 2011) as well as in coastal basins of eastern Brazil and adjacent headwaters of the upper Paraná and upper São Francisco river basins (Ottoni and Costa 2008; Ottoni 2010, 2012, 2013a, b; Ottoni et al. 2011).

Říčan and Kullander (2008) delimited four *Australoheros* species groups for taxa endemic to the La Plata river basin which occur in the rivers system of the Paraná–Paraguay–Uruguay based on both morphological and molecular data [cytochrome b (CYTB)]: the *A. scitulus* species group, *A. forquilha* species group, *A. facetus* species group, and *A. kaaygua* species group. A fifth species group was later proposed by Ottoni (2010, 2012), and named the *A. autrani* group based on morphological characters, to include species from eastern Brazilian basins.

Presently, the *A. autrani* group includes 16 nominal species (Ottoni and Costa 2008; Ottoni 2010, 2012; Ottoni et al. 2011), including *A. sanguineus*, not previously placed in any species group (Ottoni 2013). However, Říčan et al. (2011) suggested that the number of valid species in this group was overestimated, with all nominal species belonging to a single species (probably *A. facetus*), in spite of the several morphological characters previously used to diagnose and distinguish them (see Ottoni et al. 2008, 2011; Ottoni and Costa 2008; Ottoni 2010, 2011). The assumption that all species of the *A. autrani* group belong to a single lineage (*A. facetus*) relied on morphology-based phylogenetic analyses, including only 38 characters. Of these, only 10 characters were applicable for species of the *A. autrani* group (Ottoni 2012), resulting in a low resolution and a poorly supported tree. In addition, no nominal species of the *A. autrani* species group have been examined for the analyses (the information was obtained only from original descriptions), therefore weakening the original basis of the statement. Subsequently, Ottoni (2012, 2013a) contested this hypothesis and presented a set of morphological character states useful to distinguish species of the *A. autrani* group from *A. facetus*, and some papers providing evidence of the morphological discontinuity between species and populations within the *A. autrani* group were published (e.g. Ottoni 2012, 2013a, b; Ottoni et al. 2014; Ottoni and Schindler 2014). The present study is the first to approach the diversity of the *A. autrani* group through molecular data and different species delimitation methods, providing a clearer panorama on the *A. autrani* group species and lineage diversification. In view of the two confronting perspectives on diversity in the *A. autrani* group, testing species limits within this group is the main goal of the present study. It is especially warranted when considering future conservation policies and efforts. In addition, this study provides the first phylogenetic analysis of the *A. autrani* group, testing its monophyly and establishing its intrarelationships. Another aim of the present research is to approach the *A. autrani* group diversification in a temporal perspective, through a time calibrated analysis, looking for major paleogeographic and paleoclimatic events that may have contributed to species diversification and distribution.

Material and methods

Material

Specimens of the *A. autrani* group were fixed in absolute ethanol immediately after collection and later preserved in the same solution (see Suppl.material 1: Table S1 for list of specimens, taxonomic names, author and year of publication of analysed taxa, respective geographic location, and GenBank accession numbers; for localities see also Fig. 1). The voucher specimens are deposited in the ichthyological collection of the Institute of Biology, Federal University of Rio de Janeiro (UFRJ). For each focal species, specimens were collected at type localities or nearby, but some additional populations were also sampled. Sequences of congeners belonging to other species groups were obtained from GenBank, following identifications proposed by Říčan et al. (2011), as well as sequences from other Heroini genera (Suppl. material 1: Table S1).

The collected specimens were euthanized in a buffered solution of tricaine methane sulphonate (MS-222) at a concentration of 250 mg/L, for a period of 10 min, following the guidelines of the Journal of the American Veterinary Medical Association (AVMA Guidelines) (Leary et al. 2013) and European Commission DGXI consensus for fish euthanasia (Close et al. 1996, 1997).

DNA extraction, amplification, sequencing and alignment

The genomic material was extracted from muscle tissue of the caudal peduncle region through the commercial DNeasy Blood and Tissue Kit (Qiagen). We used the primers CytB-F (Palumbi et al. 1991) and TrucCytB-R (Martin and Bermingham 1998) to amplify a fragment of 1039 bp of the mitochondrial encoded gene Cytochrome b (CYTB). Polymerase chain reaction (PCR) was performed in 50 µl reaction mixtures containing 5× Green GoTaq (Promega), 3.2 mM MgCl2, 1 µM of each primer, 75 ng of total genomic DNA, 0.2 mM of each dNTP and 1U of Taq polymerase. The thermocycling profile was: (1) 1 cycle of 1 minutes at 94 °C, (2) 40 cycles of 1 min at 92 °C, 1 min at 45–60 °C and 1 min at 72 °C, and (3) 1 cycle of 4 min at 72 °C. Negative controls were used to check DNA contamination in all PCR reactions. Amplified PCR products were purified using the Wizard SV Gel and PCR Clean-Up System (Promega). The sequencing reactions were purified, and the samples were run on an ABI 3130 Genetic Analyzer. Sequences were edited using MEGA 7.0 (Kumar et al. 2016), aligned using ClustalW (Chenna et al. 2003), and subsequently the aligned fragments were translated into amino acid residues to verify the presence of premature stop codons or indels.

Species delimitation

Three distinct operational criteria (species delimitation methods), based on molecular data, were performed: a tree-based method as proposed by Wiens and Penkrot (2002) [hereafter WP, following Sites and Marshall (2003)], a coalescent species delimitation method termed the Bayesian implementation of the Poisson tree processes [hereafter bPTP, following Zhang et al. (2013)], and a character-based DNA barcoding as proposed by Desalle et al. (2005) (hereafter CBB). All species delimitation methods here adopted were performed including only Cytochrome b (Cytb) sequences, as it is a mitochondrial gene with fast evolution rate, indicated for species delimitation approaches (Avise 2000).

The WP is based on the direct inspection of haplotype trees generated from the phylogenetic analyses having as terminals at least two individuals (haplotypes) of each focal species. In this method, the term "exclusive" is used instead of monophyletic, since the term monophyly is considered inapplicable below the species level (Wiens and Penkrot 2002). Clustered haplotypes with concordant geographic distribution forming mutual and well supported clades (exclusive lineages) are considered strong evidence for species discrimination (absence of gene flow with other lineages). The failure of haplotypes from the same population to cluster together instead, is considered potential evidence for gene flow within populations, therefore suggesting the lack of divergence between lineages (species) (Wiens and Penkrot 2002). Statistical support for clades is assessed by the posterior probability value, considered as significant at values about 0.95 or higher (Alfaro and Holder 2006). When only one haplotype (specimen) from one putative population was available, the species delimitation was based on the exclusivity of the sister clade of this single haplotype, supported by significant values, allowing us to perform the test in populations with only one haplotype (Wiens and Penkrot 2002). In addition, the method allows recognition of nonexclusive lineages as species since their sister clades are exclusive and supported by significant values (Wiens

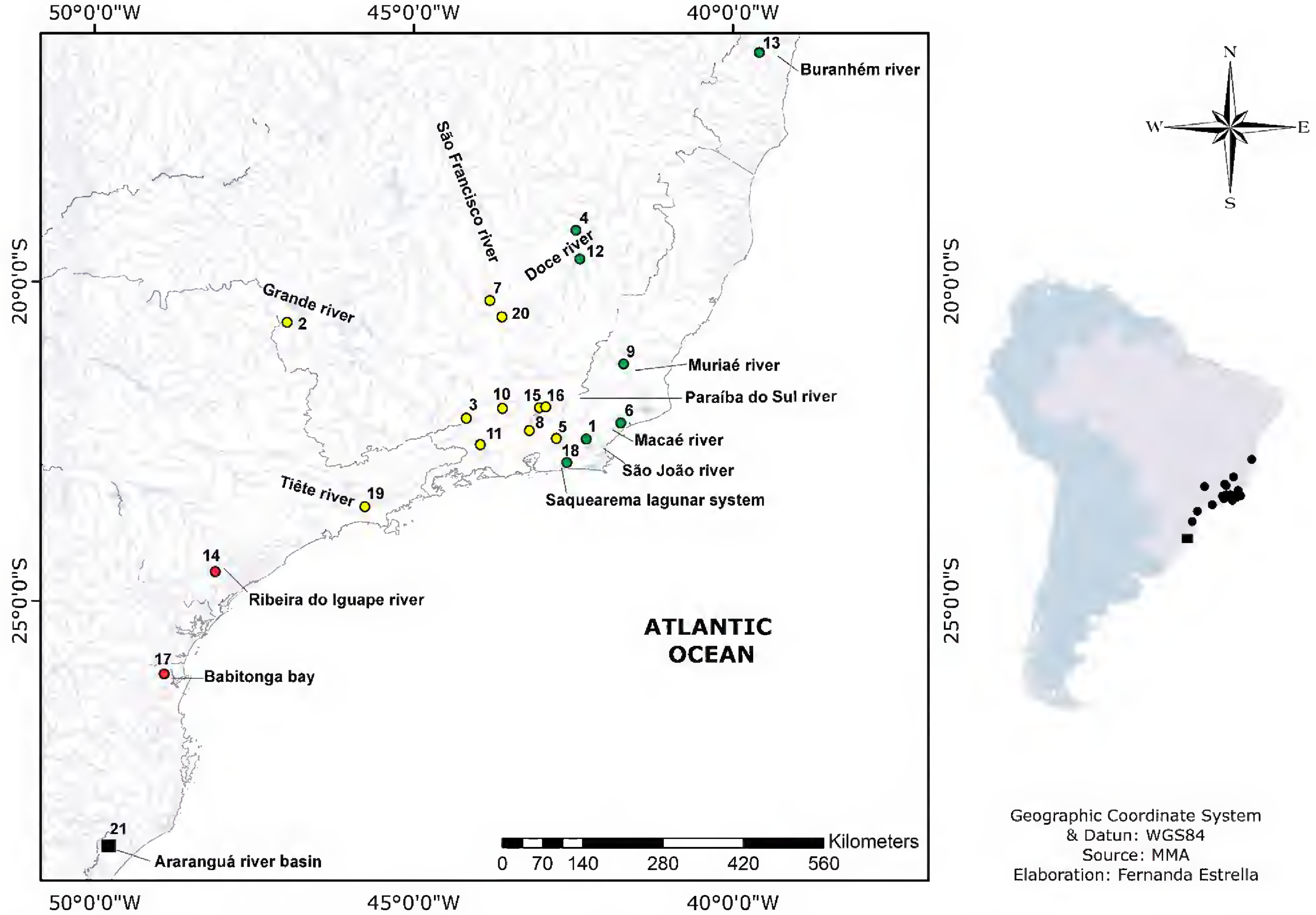

Figure 1. Map of the samples obtained for the present work. Circles = *Australoheros autrani* species group; Red circles = Southern Mata Atlântica clade; Yellow circles = Upper/middle Paraíba do Sul river basin and adjacent drainages clade; Green circles – Northern Mata Atlântica clade; and Square = *A.* sp. Timbé do Sul. Localities: *A. autrani* = 1 and 18, *A. barbosae* = 2, 3, 10, 11 and 19, *A. ipatinguensis* = 4, *A. macacuensis* = 5, *A. macaensis* = 6, *A. muriae* = 9, *A. perdi* = 12, *A. ribeirae* = 14, *A. robustus* = 7, 8, 15, 16 and 20, *A. sanguineus* = 17, *A.* cf. *capixaba* = 13, and *A.* sp. Timbé do Sul = 21.

and Penkrot 2002). Terminal in-group taxa were the a priori morphologically defined species and populations of the *A. autrani* group. Terminal out-group taxa included several lineages representing all the other *Australoheros* species groups proposed by Říčan and Kullander (2008), an additional population from the south of Santa Catarina state, and more distantly *Trichromis salvini* (Suppl. material 1: Table S1). When performing the WP species delimitation method, the protein-coding CYTB sequences were partitioned by codon position. Jmodeltest 2.1.7 program (Darriba et al. 2012) was used to define the most appropriate evolutionary model for each partition, and the choice for the best model was based on the Akaike information criterion. First codon position HKY+I, 2nd codon position F81 and 3rd codon position GTR+I.

The topology for the WP approach was generated by Bayesian inference analysis performed in the MrBayes 3.2.5 program (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) with the following settings: two Markov chain Monte Carlo (MCMC) runs of four chains each for 10 million generations, and sampling frequency of 100. All parameters between partitions except topology and branch lengths were unlinked. The convergence of the MCMC chains were graphically assessed by evaluating the stationary phase of the chains using Tracer v. 1.6 (Rambaut et al. 2014). Consensus topology and posterior probabilities were obtained after applying a burn-in of the first 25% of the generated trees. The resulting haplotype tree topology is presented in Figure 2.

The CBB is similar to the population aggregation analysis proposed by Davis and Nixon (1992), but directed to nucleotides as an alternative method for diagnosing taxa through DNA barcodes. This is because the original method is based on subjective cut-off distance measures to make inferences about species designation (e.g. Hebert et al. 2003a, b, 2004a, b), which have been questioned by several authors both as theoretical and practical aspects (e.g. Desalle et al. 2005; Brower 2006; Meier et al. 2006). This method delimits species based on a unique combination of nucleotides within a site shared by individuals of the same population or group of populations. In addition, species were molecularly diagnosed by nucleotide substitutions as proposed by Costa et al. (2014). Optimization of nucleotide substitutions among

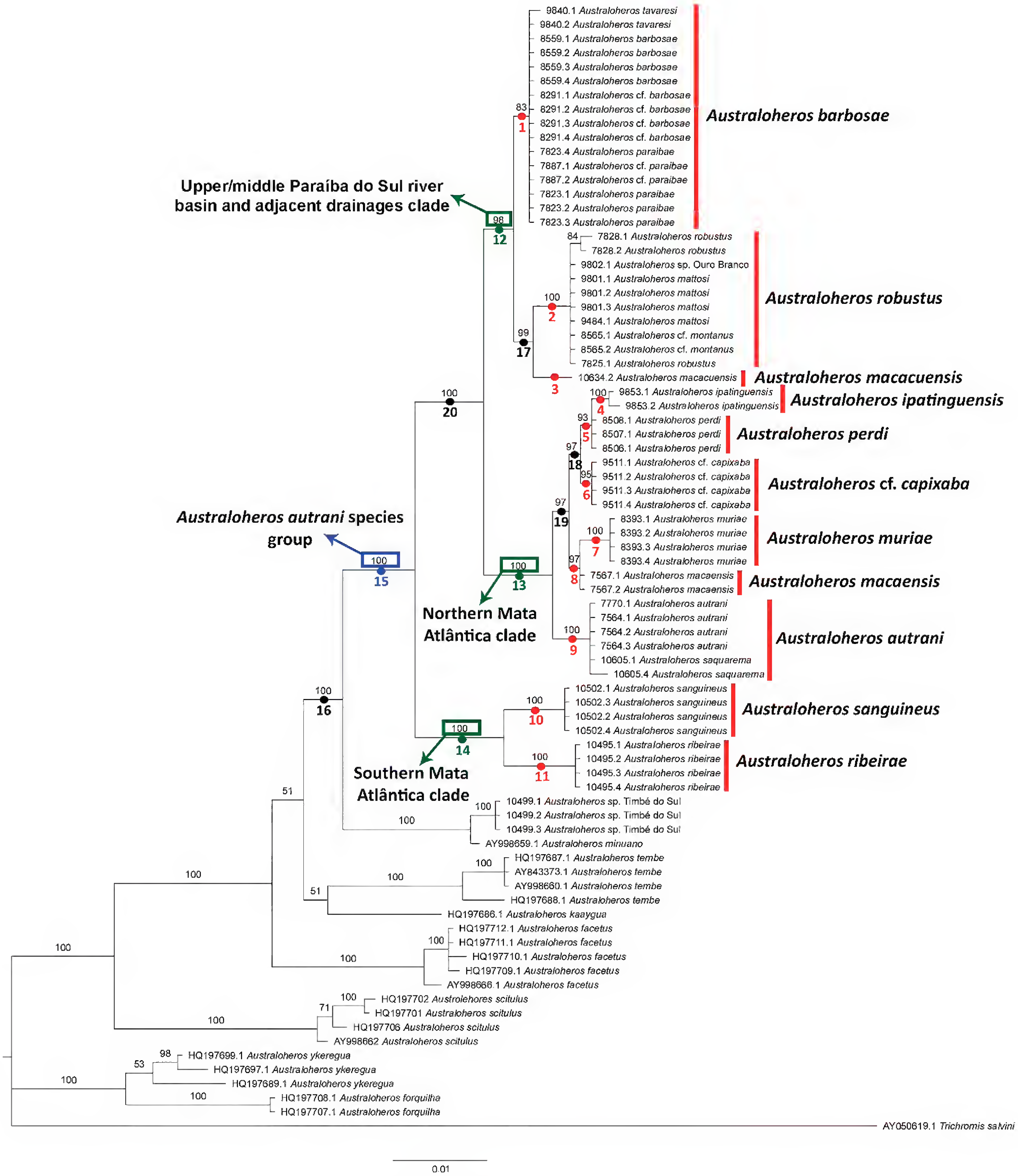

Figure 2. Phylogenetic haplotype tree based on Bayesian Inference (BI). Numbers above branches are posterior probability values, and below branches are numbered nodes which represent the combination of nucleotide substitution which define the species (in CBB) or clades. The nucleotide substitutions (CBB) can be checked in box1. Posterior probability value supporting the *Australoheros autrani* group is indicated in blue, as well as, the three clades herein proposed within this species group are indicated in green. Species of the in-group delimited though the tree based method (WP) are indicated with red bars, as well as, the species of the in-group delimited by nucleotide substitution method (CBB) have their nodes marked in red.

lineages of *Australoheros* were obtained from the Bayesian topology, using PAUP4 (Ronquist et al. 2002). Each nucleotide substitution is represented by its relative numeric position determined through sequence alignment with the complete mitochondrial genome of *Astronotus ocellatus* (Mabuchi et al. 2007), followed by the specific nucleotide substitution in parentheses. The results are presented in Figure 2 and Box 1.

Box 1. List of nucleotide substitutions from each lineage (species) and some crucial points of the cladogram of the Fig. 2. **1–11** the delimited species of the *Australoheros autrani* species group according to the CBB, **12–14** the three clades herein proposed within *A. autrani* group, **15** the *A. autrani* group, **16–20** other points of the cladogram. When a nucleotide substitution is exclusive from that lineage or clade, not occurring in any other point of the cladogram it is marked with "*", when a nucleotide substitution is exclusive within the *A. autrani* group it is marked with "**".

CBB:

1 (exclusive combination of nucleotide substitution of *A. barbosae*) - Cytb258 (C→T*), Cytb474 (T→C), **2 (exclusive combination of nucleotide substitution of *A. robustus*) -** Cytb348 (G→A**), Cytb612 (G→A), Cytb 684 (C→T**),Cytb 978 (G→A),Cytb 1.032 (A→G*), **3 (exclusive combination of nucleotide substitution of *A. macacuensis*) -** Cytb120 (T→C), Cytb 127 (G→A**), Cytb 561 (T→C), Cytb 822 (T→C**), Cytb 939 (A→G*), **4 (exclusive combination of nucleotide substitution of *A. ipatinguensis*) -** Cytb 78 (T→C), Cytb 1.070 (T→C*), **5 (exclusive combination of nucleotide substitution of *A. ipatinguensis* + *A. perdi*. *Australoheros perdi* differs from *A. ipatinguensis* by the absence of the nucleotide substitutions listed in number 4) -** Cytb 700 (A→G*), **6 (exclusive combination of nucleotide substitution of *A.* cf. *capixaba*) -** Cytb 837 (C→T**), **7 (exclusive combination of nucleotide substitution of *A. muriae*) -** Cytb 435 (C→T**), Cytb 519 (T→C), Cytb 653 (A→G*), Cytb 960 (A→G**), **8 (exclusive combination of nucleotide substitution of *A. macaensis* + *A. muriae*. *Australoheros macaensis* differs from *A. muriae* by the absence of the nucleotide substitutions listed in number 7) -** Cytb 1.041 (T→ C**), **9 (exclusive combination of nucleotide substitution of *A. autrani*) -** Cytb 270 (C→T*), Cytb 357 (T→C**), Cytb 519 (T→C), Cytb 564 (C→T**), Cytb 864 (A→G*), **10 (exclusive combination of nucleotide substitution of *A. sanguineus*) -** Cytb 63 (C→A*), Cytb 120 (T→C), Cytb 204 (C→T*), Cytb 219 (A→G*), Cytb 405 (A→G**), Cytb 474 (T→C), Cytb 967 (T→C*), Cytb 1.044 (T→C**), **11 (exclusive combination of nucleotide substitution of *A. ribeirae*) -** Cytb 114 (A→C*), Cytb 364 (C→T), Cytb 390 (C→T*), Cytb 408 (A→G), Cytb 528 (A→C*), Cytb 741 (T→C**), Cytb 786 (G→A**), Cytb 813 (A→G*), Cytb 870 (G→A**), Cytb 897 (T→C**), Cytb 1.003 (T→C*).

Other relevant nucleotide substitutions:

12- Cytb 465 (C→T**), Cytb 846 (A→G*), Cytb 917 (T→C**), **13 –** Cytb 364 (C→T), Cytb 408 (A→G), Cytb 540 (C→T*), Cytb 552 (C→T*), Cytb 784 (T→C**), Cytb 825 (A→G*), Cytb 867 (A→G**), Cytb 954 (G→A**), Cytb 978 (G→A), Cytb 993 (T→C**), **14-** Cytb 352 (G→A**), Cytb 354 (T→C*), Cytb 438 (T→C*), Cytb 630 (T→C*), Cytb 688 (T→C**), Cytb 690 (A→G*), Cytb 726 (T→C*), Cytb 906 (A→G*), Cytb 916 (G→A**), Cytb 945 (T→C**), Cytb 1.020 (A→G**), Cytb 1.047 (T→C**), Cytb 1.074 (T→C), **15 -** Cytb 345 (T→C), Cytb 474 (C→T),Cytb 589 (C→T*), Cytb 723 (C→T), Cytb 741 (C→T),Cytb 795 (G→A), Cytb 807 (A→G*), Cytb 852 (T→C), Cytb 897 (C→T), Cytb 978 (A→G), Cytb 1.038 (A→C), **16 –** Cytb 303 (G→A), Cytb 768 (C→T*), Cytb 954 (A→G), Cytb 960 (G→A*), Cytb 1.026 (C→A*), **17 –** Cytb 585 (T→C**), Cytb 721 (G→A**), **18-** Cytb 561 (T→C), **19 –** Cytb 114 (A→G**), Cytb 612 (G→A), **20 –** Cytb 78 (C→T**), Cytb 141 (A→G*), Cytb 174 (T→C*), Cytb 351 (T→C*), Cytb 600 (T→C**), Cytb 750 (G→A**), Cytb 891 (C→T*), Cytb 924 (C→T**).

The bPTP is a coalescent phylogeny-based species delimitation method intended to delimit species based on single locus molecular data (Zhang et al. 2013). An advantage of bPTP is that it does not need an ultrametric calibration like other coalescent approaches, avoiding errors and computer intensive processes (Zhang et al. 2013). The method relies on the number of substitutions between haplotypes and assumes that more molecular variability is expected between species than within a species (Zhang et al. 2013). In the present bPTP analysis, the dataset was reduced to include only unique haplotypes from species of the *A. autrani* group. Outgroups were restricted to *A. facetus* (AY998666.1), *A. kaaygua*, *A. minuano* and *Australoheros* sp. Timbé do Sul. The evolution model HKY+G for the reduced dataset was calculated in Jmodeltest 2.1.7 program (Darriba et al. 2012). The input phylogenetic tree was performed in Beast v.1.8 (Drummond et al. 2012) with a lognormal uncorrelated relaxed clock model and coalescent constant size tree priors. Bayesian inference was performed with the following settings: 50 million MCMC generations, and a sampling frequency of 100. The value of parameters of the analyses, sample size and the stationary phase of the chains were evaluated using Tracer v. 1.6 (Rambaut et al. 2014). A birth-death speciation process was applied as the tree prior (Gernhard 2008).

The bPTP analysis was performed in the Exelixis Lab's web server http://species.h-its.org/ptp/, following the default parameters except for a 20% burn-in and the tree was rooted on *A. facetus*. The results are presented in Figure 3.

Phylogenetic analysis

After performing the different species delimitation methods, only one haplotype from each species recovered by the congruence of all species delimitation methods was included (Suppl. material 1: Table S1) to avoid confusion, and a phylogenetic analysis was conducted. The terminal out-group taxa comprised several lineages representing all *Australoheros* species groups proposed by Říčan and Kullander (2008), an additional population from southern Santa Catarina state, and more distantly *Trichromis salvini*, *Heros appendiculatus*, and more distantly *Hoplarchus psittacus* (Suppl. material 1: Table S1).

The protein-coding sequences were partitioned by codon position. The Jmodeltest 2.1.7 program (Darriba et al. 2012) was used to define the most appropriate evolutionary model for each partition, and the choice for the best model was based on the Akaike information criterion. The first codon position was SYM+I+G, the 2nd codon position HKY+I and the 3rd codon position GTR+G. The topology was generated by Bayesian inference (BI)

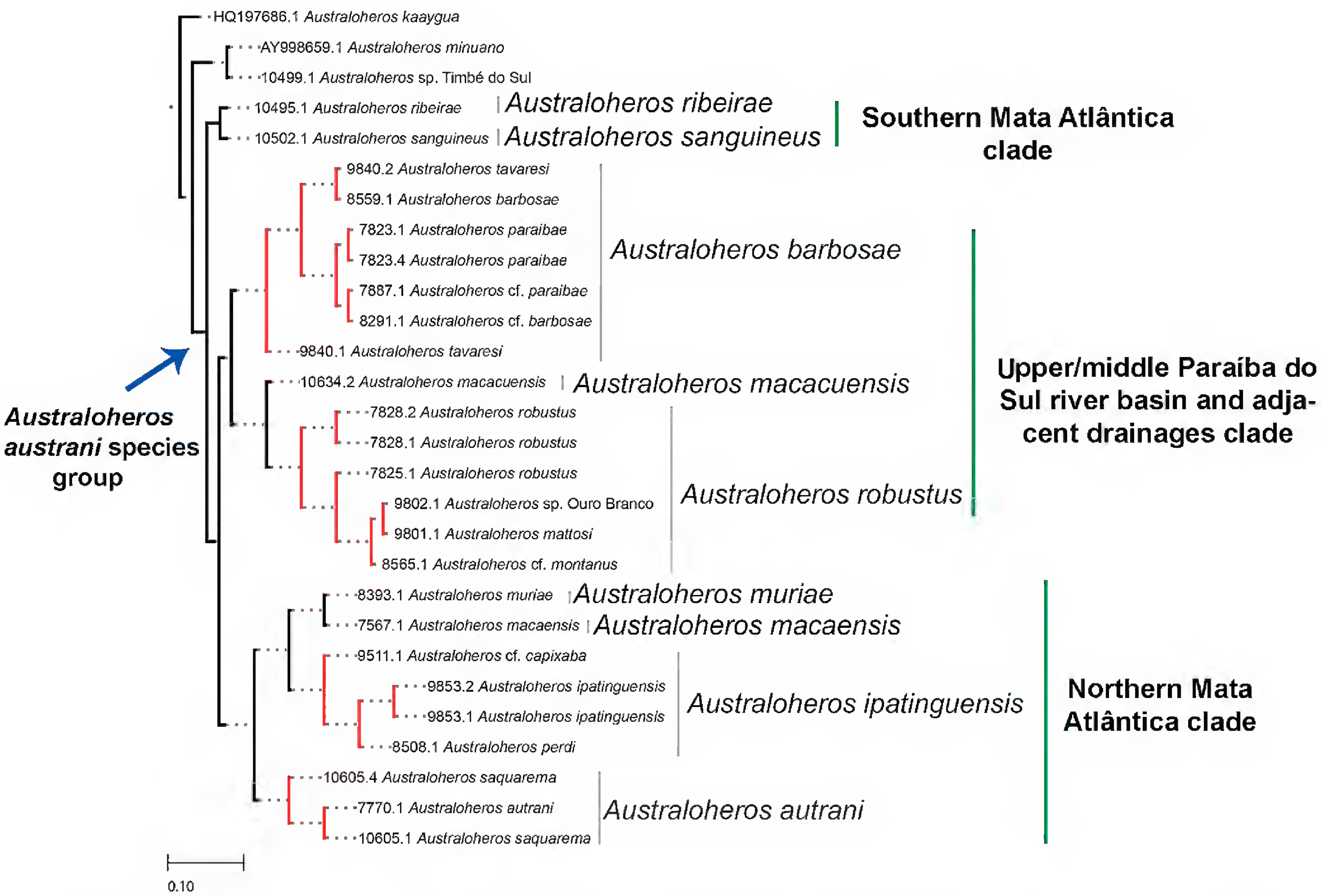

Figure 3. Species delimitation tree generated by the Bayesian Poisson Tree Processes (bPTP) model, using a fragment of the mitochondrial gene CYTB. Black lines indicate branching processes among species, red lines indicate branching processes within species. Species of the *A. autrani* species group delimited through bPTP are indicated with grey bars.

using MrBayes 3.2.5 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). It was performed with the following settings: two Markov chain Monte Carlo (MCMC) runs of four chains each for 20 million generations, sampling frequency of 1000. All parameters between partitions except topology and branch lengths were unlinked. The convergence of the MCMC chains were graphically assessed by evaluating the stationary phase of the chains using Tracer v. 1.6 (Rambaut et al. 2014). Consensus topology and posterior probabilities were obtained after applying a burn-in of the first 25% of the generated trees.

The divergence time analysis was performed in Beast v.1.8 (Drummond et al. 2012), using the same dataset, partitions and evolution models as described above, and a lognormal uncorrelated relaxed clock model. Bayesian inference was performed with 50 million generations of MCMC runs and a sampling frequency of 1000. A Yule speciation process was applied as the tree prior (Gernhard 2008). Due to the absence of closely related fossils, we used indirect calibration points, comprising two node date estimates by Matschiner et al. (2017). The oldest node was the divergence between the clade *Hoplarchus* Kaup, 1860 plus *Hypselecara* Kullander, 1986 and the clade containing the *Heros* Heckel, 1840 clade plus the *Australoheros* clade (prior setting: normal distribution, mean = 53 and standard deviation = 2.0). The second node was the divergence between the clade comprising the genera *Heros*, *Symphysodon* Heckel, 1840, *Mesonauta* Günther, 1862, *Uaru* Heckel, 1840, and the *Australoheros* clade (prior setting: normal distribution, mean = 47 and standard deviation = 2.0).

Results

Species delimitation

WP and CBB

These species delimitation analyses produced identical results, delimiting 11 lineages (species) within the *A. autrani* group (Fig. 2, Box 1). Among them, seven species (*A. ipatinguensis, A. macaensis*, *A. macacuensis*, *A. muriae*, *A. perdi*, *A. sanguineus*, and *A. ribeirae*) previously delimited on the basis of morphological characters are corroborated. One species tentatively identified as *A. capixaba* is herein corroborated. Seven nominal species (*A. autrani*, *A. barbosae*, *A. mattosi*, *A. paraibae*, *A. robustus*, *A. saquarema*, and *A. tavaresi*) and one species tentatively identified as *A. montanus* were clustered into

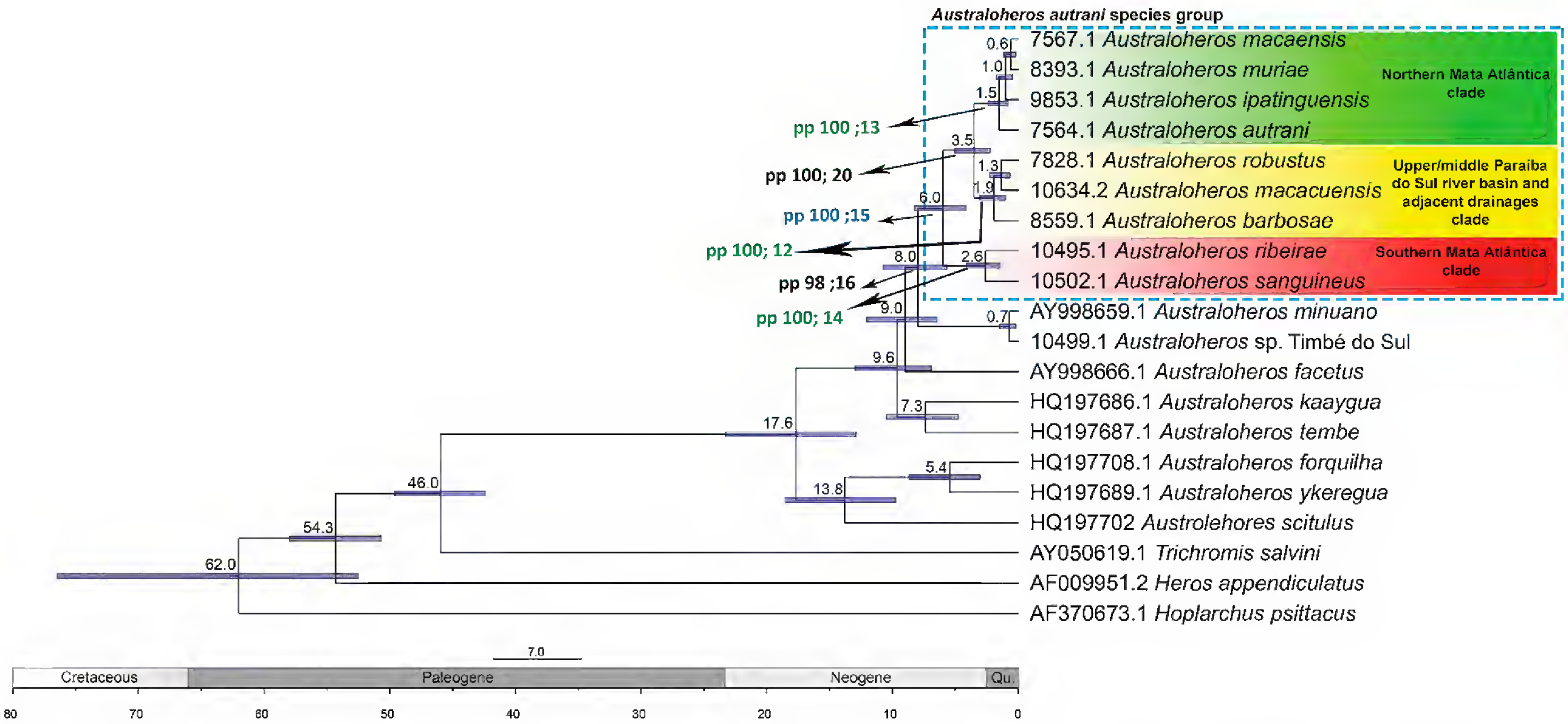

Figure 4. Time-scaled phylogeny obtained from the Bayesian analysis in BEAST. Values above nodes are mean average ages of the nodes, followed below blue bars representing the 95% highest posterior densities intervals for estimated ages; numbers indicated by arrows are the posterior probability obtained from the Bayesian analysis in MrBayes followed by the node number, corresponding to the node numbers of the Figure 2 and Box 1. PP means posterior probability.

three species, which following chronological priority for zoological species names are hereafter called *A. autrani*, *A. barbosae*, and *A. robustus* (Fig. 2, Box 1).

bPTP

This species delimitation analysis indicates nine lineages (species) within the *A. autrani* group (Fig. 3). Among them, five species (*A. macacuensis*, *A macaensis*, *A. muriae*, *A. ribeirae*, and *A. sanguineus*) previously delimited on the basis of morphological characters are corroborated. Nine nominal species (*A. autrani*, *A. barbosae*, *A. ipatinguensis*, *A. mattosi*, *A. paraibae*, *A. perdi*, *A. robustus*, *A. saquarema*, and *A. tavaresi*) and two species tentatively identified as *A. capixaba* and *A. montanus* were clustered into four species, which following chronological priority for zoological species names are hereafter called *A. autrani*, *A. barbosae*, *A. ipatinguensis*, and *A. robustus* (Fig. 3).

Phylogeny

The monophyly of the *A. autrani* species group was highly supported with maximum node support value and diagnosed by 11 nucleotide substitutions (Fig. 4, Box 1). The sister clade of the *A. autrani* species group was the clade comprising *Australoheros* sp. Timbé do Sul and *A. minuano*, and this sister group relationship was supported by 98% of posterior probability and by five synapomorphic nucleotide substitutions (Fig. 4, Box 1).

The phylogenetic analyses support three main clades within the *A. autrani* species group. First an Upper/middle Paraíba do Sul river basin and adjacent drainages clade: including *A. barbosae*, *A. macacuensis*, and *A. robustus*, sister group of the Northern Mata Atlântica clade, supported by maximum value, and three synapomorphic nucleotide substitutions (Fig. 4, Box 1). This clade occurs along the upper/middle Rio Paraíba do Sul basin, Rio Macacu basin, upper Rio Tietê, and Rio Grande drainages, tributaries of the upper Rio Paraná river basin, and upper Rio Paraopebas, and Rio das Velhas drainages, tributaries of the upper Rio São Francisco basin, as well as, in a headwaters border area between the Rio Doce and São Francisco river basins, eastern Brazil (Fig. 1).

Second, a Northern Mata Atlântica clade: including *A. autrani*, *A. ipatinguensis*, *A. macaensis*, and *A. muriae*; sister group to the aforementioned clade, corroborated by maximum node support value and by 10 synapomorphic nucleotide substitutions (Fig. 4, Box 1). This clade occurs along the coastal river basins from the Saquarema lagoon system, in south-eastern Brazil, to the Buranhém river basin, in northeastern Brazil, including tributaries of the lower Rio Paraíba do Sul and from the Rio Doce basin (Fig. 1).

Third, a Southern Mata Atlântica clade: including *A. ribeirae* and *A. sanguineus*, the most basal clade within the *A. autrani* species group, corroborated by maximum node support value and by 13 synapomorphic nucleotide substitutions (Fig. 4, Box 1). This clade occurs in the Rio Ribeira do Iguape basin, and in the Rio Cubatão basin of Baía de Babitonga system, eastern Brazil (Fig. 1).

Divergence-time estimation

Divergence time estimates (Fig. 4) indicate that the origin of the *Australoheros* and its diversification occurred around 46 million years ago (hereafter MYA), during the middle Eocene, and around 17.6 MYA (ranging from 12.2 to 22.7 MYA following 95% highest posterior density interval [HPD]), during the middle Miocene, respectively. The origin of the *A. autrani* group occurred during the late Miocene (8 MYA; 95% HPD: 5.5–10.4 MYA), and its diversification started at about 6 MYA. The diversification within the three main clades of the *Australoheros autrani* species group occurred almost synchronically, between 2.6 and 1.5 MYA during the Pleistocene (Fig. 4).

Discussion

Species delimitation and species diversity

Many species of *Australoheros* can be definitely considered cryptic species for three reasons. This is especially true of the species which are distributed in eastern Brazil. (1) In previous studies, these were identified and classified as *Australoheros facetus*, a species whose type locality is in the north of Uruguay. Even now, in some cases, species and populations of the *A. autrani* group have been erroneously classified and considered as populations of *A. facetus*. (2) According to Říčan et al. (2011), many of the species from the *A. autrani* group are very similar morphologically and difficult to diagnose. Some of those are distinguished only based on characters of colouration in life, that cannot be observed in preserved specimens deposited in collections and museums, or based on characters of internal anatomy (e.g. Ottoni et al. 2008; Ottoni 2010, 2011, 2012, 2013a, b; Ottoni and Schindler 2014; Ottoni et al. 2014). And, for practical reasons, are not used in the vast majority of ichthyological inventories. (3) The genus *Australoheros* has a taxonomically "confused" and controversial history, including different lists of nominal species.

The coastal river basins of eastern Brazil are characterized by a low diversity of fish groups when compared to other areas, such as the Amazon basin. However, in spite of this relatively low diversity, the groups that occur in this region present a high degree of endemism along the river drainages, and speciation events along eastern Brazil are probably related to a complex palaeogeographical history (Ribeiro 2006; Buckup 2011; Thomaz and Knowles 2018). The high degree of endemism of freshwater fish in this region has been already suggested by Bizerril (1994) and Ribeiro (2006). This has provided the basis for the delimitation of this region as constituting a particular biogeographical area named the "south-eastern Brazil province" and different versions of the "eastern Brazil province" (Eigenmann 1909; Géry 1969; Ringuelet 1975; Lévêque et al. 2008). More recently, these provinces were subdivided into a series of ecoregions or subprovinces, based on specific ecological and faunistic characteristics (e.g. Carvalho 2007; Abell et al. 2008). It is interesting to note that there is general correspondence between Pleistocene paleodrainages and these proposed biogeographic regions (Thomaz and Knowles 2018). In addition, the present geomorphologically isolated eastern coastal river basins were probably isolated in the past as suggested by the limits of proposed Pleistocene paleodrainages (Thomaz and Knowles 2018). Thus, it is clear that the river drainages of eastern Brazil do not correspond to a single uniform biogeographic area of endemism (Menezes 1988; Bizerril 1994; Carvalho 2007; Abell et al. 2008; Buckup 2011; Thomaz and Knowles 2018). The existence of mountainous areas and elevated regions, often more than 1000 m in altitude in south-eastern Brazil, also contributed to the isolation of river drainages and populations, and probably promoted speciation events (Buckup 2011).

The speciation events within the *A. autrani* species group occurred about 2.6–0.6 MYA during the Pleistocene (Fig. 4). The species delimitation methods conducted herein demonstrate a high degree of endemism within this group, as expected according to the biogeographic history of the region. The WP and CBB were more sensitive than the other method (bPTP), delimiting 11 lineages within the *Australoheros autrani* species group: *A. autrani*, *A. barbosae*, *A. ipatinguensis*, *A. macaensis*, *A. macacuensis*, *A. muriae*, *A. perdi*, *A. ribeirae*, *A. robustus*, *A. sanguineus*, and *A.* cf. *capixaba* (Fig. 2, Box 1). The bPTP method was more conservative, delimiting just nine lineages: *A. autrani*, *A. barbosae*, *A. ipatinguensis*, *A. macaensis*, *A. macacuensis*, *A. muriae*, *A. ribeirae*, *A. robustus*, and *A. sanguineus* (Fig. 3). Despite the distinct number of delimited lineages among these methods, the results are fully congruent if considering two of the three clades of the *A. autrani* species group, except for the Northern Mata Atlântica clade. In this specific clade, the WP and CBB delimit the same lineages and more species than the bPTP (six against four) (Figs 2, 3, Box 1). According to De Queiroz (2007) and Goldstein and Desalle (2010), species delimited by multiple pieces of evidence and different species delimitation methods produce stronger hypotheses. However, as argued by De Queiroz (2005, 2007), any criteria (species delimitation methods) may separately provide evidence about the species limits independently from other criteria, and any property that provides evidence of lineage separation is relevant to infer boundaries and number of species. In addition, the same author also argued that distinct operational criteria could delimit different lineages, as they could have different degrees of sensitivity in relation to the lineages divergence (speciation) and different cut-offs for considering a separately evolving lineage (De Queiroz 2007: fig. 1). It is important to emphasize that every species is a hypothesis, which potentially is refuted or corroborated by subsequent studies (De Queiroz 2005, 2007). Therefore, we do not favour any of the methods, and we consider the possibility of two slightly variant scenarios: one based on the congruent results between WP and CBB, considering 11 lineages (species) along the river drainages of eastern Brazil (Fig. 2, Box 1) and the other based on the result of bPTP, considering only nine lineages (species) (Fig. 3). However, for the phylogenetic analysis we decided to follow the congruence of these species delimitation methods herein applied to avoid confusion. Thus, we considered just nine species for the time calibrated phylogenetic analysis.

Similar to the *A. autrani* group, in that several species occur along the latitudinal zonation of eastern Brazil, a congruent distribution pattern and endemism is also shared by other freshwater fish groups in this region, such as: Delturinae (family Loricariidae) (Reis et al. 2006; Buckup 2011), Neoplecostominae (family Loricariidae) (Abell et al. 2008; Buckup 2011; Roxo et al. 2014), the genera *Mimagoniates* Regan, 1907 and *Oligosarcus* Günther, 1864 (family Characidae) (Menezes et al. 2007, 2008; Buckup 2011; Ribeiro and Menezes 2015), the genus *Brycon* Müller & Troschel, 1844 (Bryconidae) (Menezes et al. 2007; Abe et al. 2014; Travenzoli et al. 2015), the genus *Characidium* Reinhardt, 1867 (Crenuchidae) (Menezes et al. 2007; Poveda-Martínez et al. 2016), the genera *Listrura* de Pinna, 1988, *Microcambeva* Costa & Bockmann, 1994, and *Trichomycterus* Valenciennes, 1832 (family Trichomycteridae) (Barbosa and Costa 2010; Abell et al. 2008; Buckup 2011; Mattos and Lima 2012; Villa-Verde et al. 2013; Katz and Barbosa 2014), the genus *Microglanis* Eigenmann, 1912 (family Pseudopimelodidae) (Sarmento-Soares et al. 2006; Ruiz and Shibatta 2010; Mattos et al. 2013), several killifish genera (family Aplocheiliidae) (Abell et al. 2008; Buckup 2011; Costa 2014, Costa and Amorim 2014; Costa et al. 2014), the genus *Phalloceros* Eigenmann, 1907 (family Poeciliidae) (Lucinda 2008), and the "*Geophagus brasiliensis*" species group and the genus *Crenicichla* Heckel, 1840 (family Cichlidae) (Kullander and Lucena 2006; Mattos 2014; Mattos et al. 2015; Mattos and Costa 2018).

In addition to the complex paleogeographical history of eastern Brazil, which probably promoted speciation in *Australoheros*, we also cannot ignore the behavioural characteristics of cichlids. Species from this family are usually territorial, not carrying out extensive migratory movements, forming pairs during the reproductive periods, and with different strategies of parental care, from protection of eggs to juveniles in their early stages of life (Kullander 2003). Such ethological characteristics, together with the history of the drainages, probably reflect species dispersal. It usually favours restricted geographic distribution to a single river, or even in one or a few streams and tributaries (Kullander 2003). This is taken as supporting evidence, reinforcing the present result recognizing several species of *Australoheros* along eastern Brazil and making the idea of the existence of just one species of *Australoheros* along the river systems of eastern Brazil more unlikely.

Monophyly, phylogeny and age of the *Australoheros autrani* species group, and internal clades

The origin of the genus *Australoheros* lineage is dated herein from about 46 MYA, during the middle Eocene (Fig. 4), and its diversification from about 17.6 MYA age, during middle Miocene. The sister group of the *A. autrani* species group is a clade comprising *Australoheros* sp. Timbé do Sul, known from a coastal river drainage in southern Brazil and *A. minuano*, a species distributed in tributaries of the middle and lower Uruguay river in Brazil (Rio Grande do Sul state) and Uruguay (Říčan and Kullander 2008). This relationship is herein suggested for the first time and is highly supported by 98% of the posterior probability value and by five synapomorphic nucleotide substitutions (Fig. 4, Box 1). The *A. autrani* species group is corroborated as a monophyletic clade by maximum node support value and by 11 nucleotide substitutions (Fig. 4, Box 1). The origin of the *A. autrani* species group is dated from about 8 MYA, during the late Miocene, when this lineage diverged from its sister group (including *Australoheros* sp. Timbé do Sul and *A. minuano*). However, its diversification occurred only about 6 MYA. The *A. autrani* species group is divided into three clades. The Southern Mata Atlântica clade is the most basal clade within the *A. autrani* species group, and its origin is dated from about 6 MYA, during the late Miocene, when this clade diverged from the lineage comprising the two other clades within the *A. autrani* species group (Fig. 4). The Southern Mata Atlântica clade includes the species that occur in the Ribeira do Iguape river basin, and in the Cubatão river basin of the Babitonga bay system, eastern Brazil (Fig. 1). The Northern Mata Atlântica clade includes the species that occur along the coastal river basins from the Saquarema lagoon system, in south-eastern Brazil, to the Buranhém river basin, in north-eastern Brazil, including the Doce river tributaries and the lower Paraíba do Sul river basin (Fig. 1). This clade has its origin about 3.5 MYA, during the middle Pliocene, when it diverged from the upper/middle Paraíba do Sul river basin and adjacent drainages clade with the same age of origin (Fig. 4). This latter clade includes the species which occur along the upper/middle Paraíba do Sul river basin, Macacu river basin, upper Tietê and Grande river drainages, of the upper Paraná river basin, and upper Paraopebas and das Velhas river drainages, of upper São Francisco river basin, eastern Brazil (Fig. 1).

Biogeographic history of the river systems of eastern Brazil and its impact on *Australoheros* diversification pattern

Geological evidence suggests that the continental margin of south-eastern Brazil passed through instability events during three main phases (90–75 MYA; 50–40 MYA; and 25–0 MYA), separated by quieter intervals, coinciding with phases of Andean orogeny (Ribeiro 2006). In the more recent geological instability phase of the eastern region of the Brazilian shield, several cases of changing boundaries, headwater captures and connections of drainage systems between coastal and inland rivers occurred (Ribeiro 2006; Buckup 2011). These headwater captures promoted faunistic exchange between river basins, but likewise changing headwater catchments and boundaries of drainage systems certainly would have contributed towards isolation of populations too, which in some cases resulted in speciation events. This is considered responsible for shaping the extant freshwater fauna to large extent.

This geological instability of the region resulting in headwater stream capture events and connections of drainage systems was first observed by Ihering (1898), who proposed an ancient connection between the Paraíba do Sul river basin and the upper Tietê river drainage (tributary of the Paraná river basin). Several other authors have also suggested this ancient connection between these two river basins based on ichthyofaunistic, geological, or paleontological similarities (e.g. Ab'saber 1957; Menezes 1970; Langeani 1989; Riccomini 1990; Lundberg et al. 1998; Malabarba 1998; Ribeiro 2006). Thereby part of the Paraíba do Sul river basin (its upper portion) was subject to a faunistic exchange with the upper Tietê river basin (Menezes 1970; Langeani 1989; Buckup 2011).

The results of the present study corroborate the idea of this complex biogeographic history. The Paraíba do Sul is the river basin of south-eastern Brazil revealing the highest diversity for the genus *Australoheros*. The present paper demonstrates three lineages (species) of *Australoheros* occurring along that river basin: *A. barbosae*, occurring in its upper/middle portion, *A. robustus*, occurring in the middle portion, and *A. muriae*, occurring in the lower portion. This fact is not common along the river basins of south-eastern Brazil, most of which only include one *Australoheros* species (Fig. 1).

Australoheros barbosae, besides occurring in the upper/middle Paraíba do Sul river basin, also occurs in the upper Tietê river drainage, corroborating the suggested hypothesis of the existence of an ancient connection between these river basins. The species also occurs in the upper Grande river drainage (another river drainage of the Paraná river basin), which also suggests a possible ancient connection between these river drainages. *Australoheros robustus*, besides occurring in the middle portions of the Paraíba do Sul river basin, also occurs in the river drainages of the Paraopeba and Rio das Velhas (tributaries of the upper São Francisco river basin) (Fig. 1). This indicates that faunistic exchange also occurred between the Paraíba do Sul river basin and other hydrographic basins of south-eastern Brazil, caused by headwater captures during phases of instability in the Brazilian Shield (Buckup 2011). In addition, a similar case occurs with *A. macacuensis* which occurs in the Macacu river basin, a coastal river discharging at the Guanabara Bay, despite being member of the Upper/middle Paraiba do Sul river basin and adjacent drainages clade. This suggests a former close relationship between these river systems, and possibly another stream capture event (Figs 1–3).

However, the geologically documented separation of the Tietê river basin from the Upper Paraíba do Sul river basin, which in ancient times were connected discharging directly into the Atlantic ocean, occurred between 20–11.8 MYR (Lundberg et al. 1998). This dating is well before the molecular dating of the origin and diversification of the *A. autrani* species group (about 8.0 and 6.0 MYA, respectively) and even more so before the origin and diversification of the Upper/middle Paraíba do Sul river basin and adjacent drainages clade (about 3.5 and 1.9 MYA, respectively) (Fig. 4). Therefore, the occurrence of *A. barbosae* both in the Paraíba do Sul and in the Upper Tietê river basins must be the result of more recent headwater captures and river drainages connections between these river systems, allowing species dispersal, although not followed by a speciation event. Another kind of event that may contribute to the distribution pattern and diversity of the freshwater fish species of the region were sea-level fluctuations (Weitzman et al. 1988; Lundberg et al. 1998). These continuously isolated and reconnected river and basins estuaries, allowing both dispersals of species (when rivers or basins were connected) or isolation of populations, which in some cases was reflected in speciation events. Sea-level fluctuation occurred all through the history of the South American continent (Lundberg et al. 1998), convincingly demonstrated from the Late Miocene to today (8 MYA to the present). Mainly during the Pleistocene, this phenomenon was cyclical and may have resulted directly in the connection and isolation of river systems. However, as pointed out by Thomaz and Knowles (2018), the Brazilian Pleistocene coastal paleodrainages were characterized by pronounced isolation and past connections and disconnections forced by sea-level changes have not been broadly considered as a factor greatly interfering with speciation processes within freshwater fish groups.

However, in the *A. autrani* group some species could have been affected by the sea-level fluctuation. One example is *A. autrani*, which nowadays forms isolated populations in small isolated coastal river systems (São João river basin and Saquarema lagoon system). These isolated populations had some degree of contact during the Pleistocene regression of the sea level. Similarly, we cannot discard the role of sea-level fluctuations in the Pleistocene diversification patterns among the Northern Mata Atlântica clade, opposing to the idea presented by Thomaz and Knowles (2018). In contrast, the biogeographical pattern corroborates the isolation of *A. ribeirae* and *A. sanguineus*, from the Southern Mata Atlântica clade, as suggested by Thomaz and Knowles, arguing that Pleistocene paleodrainages are much more isolated than previously suggested, promoting a high degree of endemism.

Conclusions and future perspectives

This study confirms the importance of integrating different methods for species delimitation, as suggested by several proponents of "Integrative Taxonomy" (e.g. Wiens and Penkrot 2002; De Queiroz 2007; Goldstein and Desalle 2010; Padial et al. 2010, Costa et al. 2012, 2014). The application of different approaches and reconciliation of different lines of evidence makes the delimitation of species more reliable and accurate (Goldstein and Desalle 2010). The recognition and confirmation of morphologically hidden or intricate lineages (species) is especially promising by using molecular methods (Bickford et al. 2006; Adams et al. 2014). This type of approach is highly recommended for groups including cryptic species or/and with a confusing and controversial taxonomy.

Accurate estimates of biodiversity are of utmost importance due to the rapid loss, degradation, intense destruction and modification of natural environments by anthropic actions, especially in tropical areas (Wilson 1985; Brook et al. 2006). Thus, cataloguing and recognizing the biological diversity of different taxonomic groups with high accuracy is crucial for the field of species conservation and should be treated as a priority (Wilson 1985; Brooks et al. 2002; Brook et al. 2006; Wheeler 2008; Costa et al. 2012).

The present study recognizes nine lineages (species) or 11 within the *A. autrani* species group, depending on the species delimitation method, grouped into three distinct and highly supported clades: the Southern Mata Atlântica clade, the Upper/middle Paraíba do Sul river basin and adjacent drainages clade, and the Northern Mata Atlântica clade. Four to five formerly described species are not resolved with the genetic species delimitation methods used in this study, but the majority of the species of the *A. autrani* group are well supported. However, it does not mean that knowledge of the number of lineages (species) occurring along the coastal river basins of eastern Brazil is complete. If more haplotypes of other populations are included in these species delimitation tests more lineages (species) may be recovered, whereas some lineages could be coalesced. Therefore, analyses including more populations and more genes are encouraged, in particular for the Northern Mata Atlântica clade, which is the clade within the *A. autrani* species group that presents incongruences related to the number of delimited species between methods here employed.

According to the present study, is clear that the *A. autrani* species group represents a valid and monophyletic group. It also contrasts the hypothesis that all species represent a widely distributed *A. facetus*. In fact, *A. facetus* was not even recovered as sister to the *A. autrani* group. This study thus represents a major contribution towards the knowledge and conservation of *Australoheros*. Finally, the time calibrated analysis provides dates of origin and diversification of *Australoheros* for the first time. Despite the origin of the *A. autrani* group in the late Miocene, species level diversification occurred in the Pleistocene and was probably driven by headwater capture events and sea-level fluctuations.

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References

Ab'saber AN (1957) O problema das conexões antigas e da separação da drenagem do Paraíba e Tietê. Boletim Paulista de Geografia 26: 38–49.

Abe KT, Mariguela T, Avelino G, Foresti F, Oliveira C (2014) Systematic and historical biogeography of the Bryconidae (Ostariophysi: Characiformes) suggesting a new rearrangement of its genera and an old origin of Mesoamerican ichthyofauna. BMC Evolutionary Biology 14: 152. https://doi.org/10.1186/1471-2148-14-152

Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrak N, Balderas SC, Bussing W, Stiassny MLJ, Skelton P, Allen GR, Unmack P, Naseka A, Ng R, Sindorf N, Robertson J, Armijo E, Higgins JV, Heibel TJ, Wikramanayake E, Olson D, López HL, Reis RE, Lundberg JG, Sabaj Pérez MH, Petry P (2008) Freshwater ecoregions of the world: a new map of biogeographic units for freshwaters biodiversity conservation. Biosciense 58: 403–414. https://doi.org/10.1641/B580507

Adams M, Raadik TA, Burridge CP, Georges A (2014) Global biodiversity assessment and hyper-cryptic species complexes: more than one species of elephant in the room? Systematic Biology 63: 518–533. https://doi.org/10.1093/sysbio/syu017

Alfaro ME, Holder MT (2006) The posterior and the prior in Bayesian phylogenetics. Annual Review of Ecology, Evolution and Systematics 37: 19–42. https://doi.org/10.1146/annurev.ecolsys.37.091305.110021

Avise JC (2000) Phylogeography: the history and formation of species. Oxford University Press, Cambridge, 464 pp.

Barbosa MA, Costa WJEM (2010) Seven news species of the catfish genus *Trichomycterus* (Teleostei: Siluriformes: Trichomycteridae) from southeastern brazil and redescription of *T. brasiliensis*. Ichthyological Exploration of Freshwaters 21: 97– 122.

Betancur RR, Broughton RE, Wiley EO, Carpenter K, López JA, Li C, Holcroft NI, Arcila D, Sanciangco M, Cureton II JC, Zhang F, Buser T, Campbell MA, Ballesteros JA, Roa-Varon A, Willis S, Borden WC, Rowley T, Reneau PC, Hough DJ, Lu G, Grande T, Arratia G, Ortí G (2013) Tree of life and new classification of bony fishes. Edition 1. Plos Currents Tree of Life, 2013. The Tree of Life and a New Classification of Bony Fishes. PLOS Currents Tree of Life. https://doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288

Bickford D, Lohman DJ, Sodhi NS, NG PKL, Meier R, Winker K, Ingram KK, Das I (2006) Cryptic species as a window on diversity and conservation. Trends in Ecology and Evolution 22: 148–155. https://doi.org/10.1016/j.tree.2006.11.004

Bizerril CRSF (1994) Análise taxonômica e biogeográfica da ictiofauna e água doce do leste brasileiro. Acta Biologica Leopoldensia 16: 51–80.

Brook BW, Bradshaw CJA, Koh LP, Sodhi NS (2006) Momentum drives the crash: mass extinction in the tropics. Biotropica 38: 302–305. https://doi.org/10.1111/j.1744-7429.2006.00141.x

Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C (2002) Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16: 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x

Brower AVZ (2006) Problems with DNA barcodes for species delimitation: ‘ten species’ of *Astraptes fulgerator* reassessed (Lepidoptera: Hesperiidae). Systematics and Biodiversity 4: 127–132. https://doi.org/10.1017/S147720000500191X

Buckup PA (2011) The eastern Brazilian Shield. In: Albert JS, Reis RE (Eds) Historical Biogeography of Neotropical Freswater Fishes. University of California Press, Berkley/Los Angeles, 203–210. https://doi.org/10.1525/california/9780520268685.003.0012

Carvalho TP (2007) Distributional patterns of freshwater fishes in coastal Atlantic draineges of eastern Brazil: a preliminary study applying parsimony analysis of endemism. Darwiniana 45: 65–67.

Casciotta JR, Gómez SE, Toresani NL (1995) “*Cichlasoma*” *tembe*, a new cichlid species from the rio Paraná basin, Argentina (Osteichthyes: Labroidei). Ichthyological Exploration of Freshwaters 6: 193–200.

Casciotta JR, Almirón AE, Gómez SE (2006) A new species of *Australoheros* (Teleostei: Perciformes: Cichlidae) from the río Iguazú basin, Argentina. Zoologische Abhandlungen 55: 77–83.

Chenna R, Sugawara H, Koike T, Lopez R, Gibson TJ, Higgins DG, Thompson JD (2003) Multiple sequence alignment with the Clustal series of programs. Nucleic Acids Research 31: 3497–500. https://doi.org/10.1093/nar/gkg500

Close B, Banister K, Baumans V, Bernoth EM, Bromage N, Bunyan J, Erhardt W, Flecknell P, Gregory N, Hackbarth H, Morton D, Warwick C (1996) Recommendations for euthanasia of experimental animals: part 1. Laboratory Animals 30: 293–316. https://doi.org/10.1258/002367796780739871

Close B, Banister K, Baumans V, Bernoth EM, Bromage N, Bunyan J, Erhardt W, Flecknell P, Gregory N, Hackbarth H, Morton D, Warwick C (1997) Recommendations for euthanasia of experimental animals: part 2. Laboratory Animals 3: 1–32. https://doi.org/10.1258/002367797780600297

Cook LG, Edwards RD, Crisp MD, Hardy NB (2010) Need morphology always be required for new species descriptions? Invertebrate Systematics 24: 322–326. https://doi.org/10.1071/IS10011

Costa WJEM (2014) Four new species of the genus *Atlantirivulus* (Cyprinodontiformes: Rivulidae) from the Brazilian Atlantic Forest. Vertebrate Zoology 64: 9–21.

Costa WJEM, Amorim PF (2014) Integrative taxonomy and conservation of seasonal killifishes, *Xenurolebias* (Teleostei: Rivulidae), and the Brazilian Atlantic Forest. Systematics and Biodiversity 12: 350–365. https://doi.org/10.1080/14772000.2014.918062

Costa WJEM, Amorim PF, Mattos JL (2012) Species delimitation in annual killifishes from the Brazilian Caatinga, the *Hypsolebias flavicaudatus* complex (Cyprinodontiformes: Rivulidae): implications for taxonomy and conservation. Systematics and Biodiversity 10: 71–91. https://doi.org/10.1080/14772000.2012.664177

Costa WJEM, Amorim PF, Aranha GN (2014) Species limits and DNA barcodes in *Nematolebias*, a genus of seasonal killifishes threatened with extinction from the Atlantic Forest of south-eastern Brazil, with description of a new species (Teleostei: Rivulidae). Ichthyological Exploration of Freshwaters 24: 225–236.

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

Davis JI, Nixon KC (1992) Populations, genetic variation, and the delimitation of phylogenetics species. Systematic Biology 41: 421–435. https://doi.org/10.1093/sysbio/41.4.421

De Queiroz K (2005) Different species problems and their resolution. BioEssays 27: 1263–1269. https://doi.org/10.1002/bies.20325

De Queiroz K (2007) Species concepts and species delimitation. Systematic Biology 56: 879–886. https://doi.org/10.1080/10635150701701083

Desalle R, Egan MG, Siddall M (2005) The unholy trinity: taxonomy, species delimitation and DNA barcoding. Philosophical Transactions of the Royal Society B 360: 1905–1916. https://doi.org/10.1098/rstb.2005.1722

Drummond AJ, Suchard Ma, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology Evolution 29: 1969–1973. https://doi.org/10.1093/molbev/mss075

Eigenmann CH (1909) The fresh-water fishes of Patagonia and examination of the Archiplata-Archhelenis theory. Reports of the Princeton University Expeditions to Patagonia (1896–1899). Zoology 3: 227–374.

Fricke R, Eschmeyer WN, Fong JD (2018) Catalog of fishes: Species by Family/Subfamily. http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp [Accessed on: 2018–11–7]

Gernhard T (2008) The conditioned reconstruction process. Journal of Theoretical Biology 253: 769–778. https://doi.org/10.1016/j.jtbi.2008.04.005

Géry J (1969) The fresh-water fishes of South America. In: Fittkau EJ, Illies J, Kingle H, Schwabe GH, Sioli H (Eds) Biogeography and Ecology in South America. Dr. W. Junk Publishers, Dordrecht, 828–848.

Goldstein PZ, Desalle R (2010) Integrating DNA barcode data and taxonomic practice: determination, discovery, and description. Bioessays 33: 135–147. https://doi.org/10.1002/bies.201000036

Hebert PDN, Cywinska A, Ball SL, deWaard JR (2003a) Biological identifications through DNA barcodes. Proceedings of the Royal Society B 270: 313–321. https://doi.org/10.1098/rspb.2002.2218

Hebert PDN, Ratnasingham S, deWaard JR (2003b) Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. Proceedings of the Royal Society B 270: S96–S99. https://doi.org/10.1098/rsbl.2003.0025

Hebert PDN, Penton EH, Burns JM, Janzen DH, Hallwachs W (2004a) Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astraptes fulgerator*. Proceedings of the National Academy of Sciences 101: 14812–14817. https://doi.org/10.1073/pnas.0406166101

Hebert PDN, Stoeckle MY, Zemlak TS, Francis CM (2004b) Identification of birds through DNA barcodes. PLoS Biology 2:1657–1663. https://doi.org/10.1371/journal.pbio.0020312

Huelsenbeck J, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17: 754–755.

Ihering H (1898) Observações sobre os peixes fósseis de Taubaté. Revista do Museu Paulista 3: 71–75.

Katz AM, Barbosa MA (2014) Re-description of the *Trichomycterus cubataonis* Bizerril, 1999 (Siluriformes: Trichomycteridae) from the Cubatão river basin, southern Brazil. Vertebrate Zoology 64: 3–8.

Kullander SO (1998) A phylogeny and classification of the South American Cichlidae (Teleostei: Perciformes). In: Malabarba LR, Reis RE, Vari RP, Lucena, ZM, Lucena CAS (Eds) Phylogeny and classification of Neotropical fishes. EDIPUCRS, Porto Alegre, 461–498.

Kullander SO (2003) Family Cichlidae. In: Reis RE, Kullander SO, Ferraris CJ JR (Eds) Check List of the Freshwater Fishes of South and Central America. EDIPUCRS, Porto Alegre, 605–654.

Kullander SO, Lucena CASD (2006) A review of the species of *Crenicichla* (Teleostei: Cichlidae) from the Atlantic coastal rivers of southeastern Brazil from Bahia to Rio Grande do Sul states, with descriptions of three new species. Neotropical Ichthyology 4: 127–146. https://doi.org/10.1590/S1679-62252006000200001

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874. https://doi.org/10.1093/molbev/msw054

Langeani F (1989) Ictiofauna do alto curso do Rio Tietê (SP): taxonomia. Dissertação (mestrado). Dissertação de mestrado, Universidade Estadual Paulista, São José do Rio Preto, 231 pp.

Leary S, Underwood W, Anthony R, Cartner S, Corey D, Grandin T (2013) AVMA Guidelines for the Euthanasia of Animals. http://works.bepress.com/cheryl_greenacre/14 [Accessed on: 2018–5–15]

Lévêque C, Oberdorff T, Paugy D, Stiassny MLJ, Tedesco PA (2008) Global diversity of fishes (Pisces) in freswater. Hydrobiologia 595: 545–567. https://doi.org/10.1007/s10750-007-9034-0

Lucinda PHF (2008) Systematics and biogeography of the genus *Phalloceros* Eigenmann, 1907 (Cyprinodontiformes: Poeciliidae: Poeciliinae), with the description of twenty-one new species. Neotropical Ichthyology 6: 113–158. https://doi.org/10.1590/S1679-62252008000200001

Lundberg JG, Marshall LG, Gerrero J, Horton B, Malabarba MCSL, Wesselingh F (1998) The stage for Neotropical fish diversification: a history of tropical South American rivers. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS (Eds) Phylogeny and Classification of Neotropical Fishes. EDIPUCRS, Porto Alegre, 13–48.

Mabuchi K, Miya M, Azuma Y, Nishida M (2007) Independent evolution of the specialized pharyngeal jaw apparatus in cichlid and labrid fishes. BMC Evolutionary 7: 10. https://doi.org/10.1186/1471-2148-7-10

Malabarba MCSL (1998) Phylogeny of fossil Characiformes and paleobiogeography of the Tremembe formation, São Paulo, Brazil. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS (Eds) Phylogeny and Classification of Neotropical Fishes. EDIPUCRS, Porto Alegre, 13–48.

Martin AP, Bermingham E (1998) Systematics and evolution of lower Central America Cichlidsinferred from analysis of cytochrome b gene sequences. Molecular Phylogenetics and Evolution 9: 192–203. https://doi.org/10.1006/mpev.1997.0461

Matschiner M, Musilová Z, Barth LM, Starostová Z, Salzburger W, Mike Steel M, Bouckaert R (2017) Bayesian phylogenetic estimation of clade ages supports trans-Atlantic dispersal of cichlid fishes. Systematic Biology 66: 3–22. https://doi.org/10.1093/sysbio/syw076

Mattos JLO, Lima S (2012) *Microcambeva draco*, a new species from northeastern Brazil (Siluriformes: Trichomycteridae). Ichthyological Exploration of Freshwaters 21: 233–238.

Mattos JLO, Ottoni F, Barbosa MA (2013) *Microglanis pleriqueater*, a new species of catfish from the Sao Joao river basin, eastern Brazil (Teleostei: Pseudopimelodidae). Ichthyological Exploration of Freshwaters 24: 147–154.

Mattos JLO (2014) Filogenia e Taxonomia do grupo de espécies *Geophagus brasiliensis* (Quoy & Gaimard, 1824) (Cichlidae: Geophagini). Tese (Doutorado), Programa de Pós-Graduação em Zoologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro,130 pp.

Mattos JLO, Costa WJEM (2018) Three new species of the '*Geophagus*' *brasiliensis* species group from the northeast Brazil (Cichlidae, Geophagini). Zoosystematics and Evolution 94: 325–337. https://doi.org/10.3897/zse.94.22685

Mattos JLO, Costa WJEM, Santos ACA (2015) *Geophagus diamantinensis*, a new species of the *G. brasiliensis* species group form Chapada Diamantina, north-eastern Brazil (Cichlidae: Geophagini). Ichthyological Exploration of Freshwaters 26: 209–220.

Mcmahan CD, Chakrabarty P, Sparks JS, Smith WL, Davis MP (2013) Temporal patterns of diversification across global cichlid biodiversity (Acanthomorpha: Cichlidae). PLoS ONE 8: e71162. https://doi.org/10.1371/journal.pone.0071162

Meier R, Shyang K, Vaidya G, Ng PKL (2006) DNA barcoding and taxonomy in Diptera: a tale of high intraspecific variability and low identification success. Systematic Biology 55: 715–728. https://doi.org/10.1080/10635150600969864

Menezes NA (1970) Distribuição e origem da fauna de peixes de água doce das grandes bacias fluviais do brasil. In Poluição e Piscicultura –notas sobre Poluição, Ictiologia e Piscicultura. Faculdade de Saúde Pública da USP, Secretaria da agricultura, Instituto de Pesca, São Paulo, 216 pp.

Menezes NA (1988) Implications of the distribution patterns of the species of *Oligosarcus* (Teleostei, Characidae) from Central and Southern South America. In: Vanzolini PE, Heyer WR (Eds) Proceedings of a Workshop on Neotropical Distribution Patterns. Academia Brasileira de Ciências, Rio de Janeiro, 295–304.

Menezes NA, Ribeiro AC, Weitzman SH, Torres RA (2008) Biogeography of Glandulocaudinae (Teleostei: Characiformes: Characidae) revisited: phylogenetic patterns, historical geology and genetic connectivity. Zootaxa 1726: 33–48.

Menezes NA, Weitzman SH, Oyakawa OT, Lima FCT, Castro RMC, Weitzman MJ (2007) Peixes de água doce da Mata Atlântica: lista preliminar das espécies e comentários sobre conservação de peixes de água doce neotropicais. Museu de Zoologia, Universidade de São Paulo, São Paulo, 408 pp.

Near TJ, Dornburg A, Eytan RI, Keck B, Smith WL (2013) Proceedings of the National Academy of Sciences 110: 12738–12743. https://doi.org/10.1073/pnas.1304661110

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the World. John Wiley and Sons, Hoboken, New Jersey, 651 pp. https://doi.org/10.1002/9781119174844

Ottoni FP (2010) *Australoheros capixaba*, a new species of *Australoheros* from south-eastern Brazil (Labroidei: Cichlidae: Cichlasomatinae). Vertebrate Zoology 60: 19–25.

Ottoni FP (2011) Revisão taxonômica do grupo de espécies *Australoheros autrani* (Teleostei: Cichlidae: Heroini). Dissertação (Mestrado), Programa de Pós-graduação em Zoologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 168 pp.

Ottoni FP (2012) Three new species of *Australoheros* from southeastern Brazil, with taxonomic notes on *Chromys oblonga*, *Heros autochton* and *H. jenynsii* (Teleostei: Labroidei: Cichlidae). Vertebrate Zoology 62: 83–96.

Ottoni FP (2013a) *Australoheros sanguineus* sp.n. – a new cichlid species from the Rio Cubatão basin, southern Brazil (Cichlidae: Heroini). Vertebrate Zoology 63: 161–169.

Ottoni FP (2013b) Life colouration of three *Australoheros* species from the Rio Paraíba do sul basin, southeastern Brazil (Teleostei: Labroidei: Cichlidae). Vertebrate Zoology 63: 9–13.

Ottoni FP, Bragança PHN, Schindler I (2014) Lebendfärbung und Habitat von *Australoheros tavaresi* (Teleostei: Cichlidae). DCG-informationen 45: 196–199.

Ottoni FP, Cheffe MM (2009) A new species of *Australoheros* from the upper Rio das Antas, laguna dos Patos System, southern Brazil (Labroidei, Cichlidae, Cichlasomatinae). Spixiana 32: 153–159.

Ottoni FP, Costa WJEM (2008) Taxonomic revision of the genus *Australoheros* Říčan & Kullander, 2006 (Teleostei: Cichlidae) with descriptions of nine new species from south-eastern Brazil. Vertebrate Zoology 58: 207–232.

Ottoni FP, Oyakawa OT, Costa WJEM (2018) A new species of the genus *Australoheros* from the rio Ribeira do Iguape basin, São Paulo, Brazil (Labroidei: Cichlidae: Cichlasomatinae). Vertebrate Zoology 58: 75–81.

Ottoni FP, Lezama AQ, Triques ML, Fragoso-Moura EN, Lucas CCT, Barbosa FAR (2011) *Australoheros perdi*, new species (Teleostei: Labroidei: Cichlidae) from the lacustrine region of the Doce river valley, southeastern Brazil, with biological informations. Vertebrate Zoology 61: 137–145.

Ottoni FP, Schindler I (2014) Zur Lebendfärbung zweier *Australoheros*-Arten aus Südost-Brasilien (Teleostei: Cichlidae). DCG-informationen 45: 111–114.

Padial JM, Miralles MA, De La Riva I, Vences M (2010) The integrative future of taxonomy. Frontiers in Zoology 7: 16. https://doi.org/10.1186/1742-9994-7-16

Pante E, Schoelinck C, Puillandre N (2015) From intregative taxonomy to species descriptions: one step beyond. Systematic Biology 64: 152–160. https://doi.org/10.1093/sysbio/syu083

Palumbi S, Martin AP, Romano S, Mcmillan WO, Stice L, Grabowski G (1991) The Simple Fool's Guide to PCR: Version 2.0. University of Hawaii Press, Honolulu, 94 pp.

Poveda-Martínez D, Sosa, CC, Chacón-Vargas K, García-Merchán VH (2016) Historical biogeography of five *Characidium* fish species: dispersal from the Amazon paleobasin to southeastern South America. PLoS ONE 11: e0164902. https://doi.org/10.1371/journal.pone.0164902

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. http://tree.bio.ed.ac.uk/software/tracer/

Reis RE, Kullander SO, Ferraris CJJR (2003) Check List of the Freshwater Fishes of South and Central America. EDIPUCRS, Porto Alegre, 729 pp.

Reis RE, Pereira EHL, Armbruster JW (2006) Delturinae, a new loricariid catfish subfamily (Teleostei, Siluriformes), with revisions of *Delturus* and *Hemipsilichthys*. Zoological Journal of the Linnean Society 147: 277–299. https://doi.org/10.1111/j.1096-3642.2006.00229.x

Reis RE, Albert JS, Di Dario F, Mincarone MM, Petry P, Rocha LA (2016) Fish biodiversity and conservation in South America. Journal of Fish Biology 89: 12–47. https://doi.org/10.1111/jfb.13016

Ribeiro AC (2006) Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: An example of faunal evolution associated with a divergent continental margin. Neotropical Icthyology 4: 225–246. https://doi.org/10.1590/S1679-62252006000200009

Ribeiro A, Menezes N, (2015) Phylogenetic relationships of the species and biogeography of the characid genus *Oligosarcus* Günther, 1864 (Ostariophysi, Characiformes, Characidae). Zootaxa 3494: 41–81. https://doi.org/10.11646/zootaxa.3949.1.2

Říčan O, Kullander SO (2003) "*Cichlasoma*" *scitulum*: a new species of cichlid fish from the río de La Plata region in Argentina, Brazil, and Uruguay. Copeia 2003: 794–802. https://doi.org/10.1643/IA03-019.1

Říčan O, Kullander SO (2006) Character and tree-based delimitation of species in the "*Cichlasoma*" *facetum* group (Teleostei, Cichlidae) with the description of a new genus. Journal of Zoological Systematics and Evolutionary Research 44: 136–152. https://doi.org/10.1111/j.1439-0469.2005.00347.x

Říčan O, Kullander SO (2008) The *Australoheros* (Teleostei: Cichlidae) species of the Uruguay and Paraná river drainages. Zootaxa 1724: 1–51. https://doi.org/10.5281/zenodo.181173

Říčan O, Piálek L, Almirón A, Casciotta J (2011) Two new species of *Australoheros* (Teleostei: Cichlidae), with notes on diversity of the genus and biogeography of the río de la Plata basin. Zootaxa 2982: 1–26.

Riccomini C (1990) O Rift Continental do Sudeste do Brasil. 1990. Tese (Doutorado em Geologia Sedimentar), Instituto de Geociências, Universidade de São Paulo, São Paulo, 319 pp. https://doi.org/10.11606/T.44.1990.tde-18032013-105507

Ringuelet RA (1975) Zoogeografia y ecologia de los peces de águas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de américa de Sur. Ecosur 2: 1–151.

Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Ronquist F, Teslenko M, Vandermark P, Ayres D, Sowfford D (2002) PAUP* Phylogenetic Analysis Using Parsimony (* and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Roxo FF, Albert JS, Silva GSC, Zawadzki CH, Foresti F, Oliveira C (2014) Molecular phylogeny and biogeographic history of the armored Neotropical catfish subfamilies Hypoptopomatinae, Neoplecostominae and Otothyrinae (Siluriformes: Loricariidae). PLoS ONE 9 (8): e105564. https://doi.org/10.1371/journal.pone.0105564

Ruiz WBG, Shibatta OA (2010) A new species of *Microglanis* (Siluriformes, Pseudopimelodidae) from lower Rio Tocantins basin, Pará, Brazil, with description of superficial neuromasts and pores of lateral line system. Zootaxa 2632: 53–66. https://doi.org/10.11646/zootaxa.2632.1.3

Sarmento-Soares LM, Martins-Pinheiro RF, Chamon CC, Aranda AT (2006) *Microglanis pataxo*, a new catfish from southern Bahia coastal rivers, northeastern Brazil (Siluriformes: Pseudopimelodidae). Neotropical Ichthyology 4:157–166. https://doi.org/10.1590/S1679-62252006000200003

Sites JW, Marshall JC (2003) Delimiting species: a renaissance issue in systematic biology. Trends in Ecology and Evolution 18: 462–470. https://doi.org/10.1016/S0169-5347(03)00184-8

Thomaz AT, Knowles LL (2018) Flowing into the unknown: inferred paleodrainages for studying the ichthyofauna of Brazilian coastal rivers. Neotropical Ichthyology 16: e180019. https://doi.org/10.1590/1982-0224-20180019

Travenzoli NM, Silva PC, Santos U, Zanuncio JC, Oliveira C, Dergam JA (2015) Cytogenetic and molecular data demonstrate that the Bryconinae (Ostariophysi, Bryconidae) species from Southeastern Brazil form a phylogenetic and Phylogeographic unit. PLoS ONE 10: e0137843. https://doi.org/10.1371/journal.pone.0137843

Villa-Verde L, Ferrer J, Malabarba LR (2013) A new species of *Listrura* from Laguna dos Patos System, Brazil: the southernmost record of the Glanapteryginae (Siluriformes: Trichomycteridae). Copeia 2013: 641–646. https://doi.org/10.1643/CI-13-027

Weitzman SH, Menezes NA, Weitzman MJ (1988) Phylogenetic biogeography of the Glandulocaudini (Teleostei: Characiformes, Characidae) with comments on the distributions of other freshwater fishes in eastern and southeastern Brazil. In: Proceedings of a workshop on neotropical distribution patterns. Academia Brasileira de Ciências, Rio de Janeiro, 79–427.

Wheeler DQ (2008) The New Taxonomy. The Systematics Association Special Volume Series 76. CRC Press, New York, 237 pp.

Wiens JJ, Penkrot TA (2002) Delimiting species using DNA and morphological variation and discordant limits in spiny lizards (Sceloporus). Systematic Biology 51: 69–91. https://doi.org/10.1080/106351502753475880

Wilson EO (1985) The biological diversity crisis: a challenge to science. Issues in Science and Technology 2: 20–29.

Zhang J, Kapli P, Pavlidis P, Stamatakis A (2013) A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29: 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

Supplementary material 1

Taxon sampling, voucher catalogue number, GenBank accession number, gene sequenced country, drainage and new sequence in the present study

Authors: Felipe Polivanov Ottoni, José L. O. Mattos, Axel M. Katz, Pedro H.N. Bragança

Data type: Adobe PDF file

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Illustrated catalogue of type specimens of Volutidae (Gastropoda) in the Malacological Collection of the Museo de La Plata, Argentina

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Abstract

The Malacology Collection of the Museo de La Plata contains more than 13,000 lots from various regions of Argentina and other South American countries. The Collection also includes 511 type lots. Among the oldest type specimens are a large series of marine gastropods from Patagonia which were studied by Fernando Lahille in 1895. He was one of the first's naturalists of the Museo de La Plata, and there between 1893 and 1899, he made several studies in zoology. During that time, he described three species and forty varieties of Volutidae. Herein, we compare Lahille's type specimens, label data, number, and specimen information to the original descriptions and illustrations of these taxa. Each taxon has been photographed in multiple views. This historic type material is entirely composed of shells. This work is the first of a series of photographic catalogues of type material from the Malacology Collection of the Invertebrate Division of Museo de La Plata.

Introduction

The Malacology Collection of the Museo de La Plata contains specimens from five mollusc groups, including from terrestrial, marine, and freshwater ecosystems. Of the over 13,000 lots that form the collection, almost 70% of these have been identified to species level. The collection includes 511 type lots. The specimens come from various regions of Argentina, and from other countries such as Brazil, Chile, Paraguay, Peru, Uruguay; a few are from other parts of the world. The lots are preserved in the traditional way, i.e. dry, wet, SEM stubs, and microscope slides, as well as frozen tissue for molecular studies.

The collection is continuously growing through projects from the museum's researchers, as well as by donations and legacies from outside researchers and collectors. It has also been expanded by various expeditions over the years, such as Hassler in 1870–1871, Hauthal in 1898, Bentart in 1898, Beaufils in 1898, Lahille in 1898, Moreno in 1899, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires in 1920, Merkle in 1921, Harvard/Bahamas in 1935, Museo de La Plata in 1928, 1948, 1958, 1962, 1970, and 1980, Monte Hermoso in 1948, Butantán in 1949, Walter Herwig in 1966 and 1971, San Antonio Oeste (SAO), Río Negro Province in 1971, and Shinkai Maru XI in 1979.

The mollusc collection of the Museo de La Plata is also the result of the contributions of researchers that are historically important figures in the natural sciences in South America. Among them are F. Lahille, F.P. Moreno, and C.L. Spegazzini at the end of the 19th century, M. Doello Jurado and J. Durione at the start of the 20th century, and W.K Weyrauch, J.J. Parodiz, M.I. Hylton Scott, J. Frengüelli, Z.A. de Castellanos, J.P.M. Birabén, and A.A. Bonetto in the mid-20th century. In the collection, 65% of the material is gastropods and 2.85% (248 lots) are volutids, which include 39 type lots.

Fernando Lahille, who was born in and studied in France, arrived in Argentina in 1893. He had been invit-

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ed by Francisco Pascasio Moreno, who was, at that time, the director of the Museo de La Plata. F. Lahille carried out his scientific activities and directed and organised the Zoology Section until 1899. During that period, he described three volutid species and 40 varieties, depositing the type specimens in this institution.

Volutids are marine snails with large, thick, shiny coiled shells. They inhabit diverse habitats in tropical to cold waters, from intertidal to subtidal depths to at least 500 m, and on sand, mud or sand-mud substrates. The family is globally distributed and comprises about 200 species, of which nearly 30 occur in the Southwestern Atlantic from Venezuela to Argentina. Sixteen species of this family inhabit Argentine waters (Scarabino 1977; Castellanos and Landoni 1992; Lasta et al. 2000).

Most volutids present ornate shells, with an elongated aperture and columellar folds. Most species have no operculum. The smallest species is about 9 mm long, but some reach over 500 mm. They possess a highly developed foot that allows them to bury themselves in the substrate and come out to feed and copulate (Poppe and Goto 1992). They are mostly predators or scavengers and feed on molluscs and other invertebrates (Morton 1986). Their fertilised eggs are deposited in masses that are generally fixed to hard substrates; crawling juveniles emerge directly from the eggs, and there is no free-swimming larval stage. *Pachycymbiola brasiliana* (Lamarck, 1811) is a particular case where ovicapsules are not fixed to a substrate and are freely transported by the currents (Penchaszadeh and de Mahieu 1976). Volutids often have small geographic ranges and isolated populations that develop their own characters of shell shape and colour pattern. These populations are frequently very close geographically but are separated by some sort of barrier, such as a deepwater channel. These variations have led to the description of varieties of most species.

Besides preserving the type material, one of the responsibilities of the Museo de La Plata is to grant accessibility to its collections. Part of this role is achieved through catalogues, and the Invertebrate Division of the Museo de La Plata currently has published nine catalogues (Arrozpide 1986; Pereira et al. 1999, 2004; Sutton and Damborenea 2000; Martín and César 2004; César and Damborenea 2010, 2016; Lunaschi et al. 2012; Díaz et al. 2017).

The present work, starting with the Volutidae, is the beginning of a series of photographic catalogues of type material from the Malacology Collection of the Invertebrate Division of the Museo de La Plata. The type materials of this family is entirely composed of the shells of the species and varieties described by Lahille in 1895.

Material and methods

During this project, the type materials of the Lahille Collection were separated, label data, number of specimens, and specimen information were compared to the original description (Lahille 1895). Specimens photographed in Lahille (1895) have the corresponding plate and figure numbers on them. We included collection catalogue numbers of the Malacological Collection of the Museo de La Plata (MLP-Ma), type status, and specimen number. We also compared all the specimens with the original figures, and we present some remarks.

For each taxon, we selected and photographed a morphologically representative specimen in apertural, lateral, dorsal, apical, and umbilical view. The rest of the specimens, which were earlier figured by Lahille, were only photographed in apertural view. Photographs were taken with a Nikon d80 camera, a Nikon DX af-s nikkor 18–135mm 1:3.5–5.6G ED lens, and using a Tiffen colour control chart.

The resulting catalogue is presented in alphabetical order according to species name in its original combination, followed by authority and year of publication, current name, and a summary of the description provided by Lahille. For each species, the varieties are detailed starting with *typica* and followed by the rest in alphabetical order. Name, combination, authority, and varieties are kept as mentioned by Lahille (1985).

Results

Voluta ambigua Lahille, 1895

Current name: *Odontocymbiola magellanica* (Gmelin, 1791); after Rosenberg (2009).

Lahille (1895) described this species and remarked that its adult stage is very similar to *V. magellanica* Chemnitz, 1788, but differs from that species by the presence of numerous eroded tubercles. Juveniles, which have smooth shells, differ from *V. magellanica* in having the last whorl strongly vaulted and less elongated. Lahille also noted that this species is also similar to *V. ancilla* Solander, 1786 [currently *Adelomelon ancilla* (Lightfoot, 1786)].

This material was revised in 2004 (Wiggers and Veitenheimer-Mendes 2008).

Voluta ambigua typica Lahille, 1895

Syntypes: MLP-Ma 10858, 4 specimens figured by Lahille (1895) (Table 1; Figs 1, 2).

This variety has, according to Lahille (1895), a shell that is 150 mm long by 75 mm wide, with the first whorls not carinate and the tubercles only on the last whorl of the spire. There are generally four columellar folds.

Voluta ambigua constricta Lahille, 1895

Syntypes: MLP-Ma 10856, 2 specimens figured by Lahille (1895: pl. VIII, figs 163, 164); label reads "*constricta*" (Fig. 3).

The shells are less elongated and last whorl less expanded than the variety *subnodosa*, so the grey to purple apertures are regularly arched and much narrower. The superficial ornamentation of the first whorls is more accentuated, as are the carina and tubercles, which reach the last whorl.

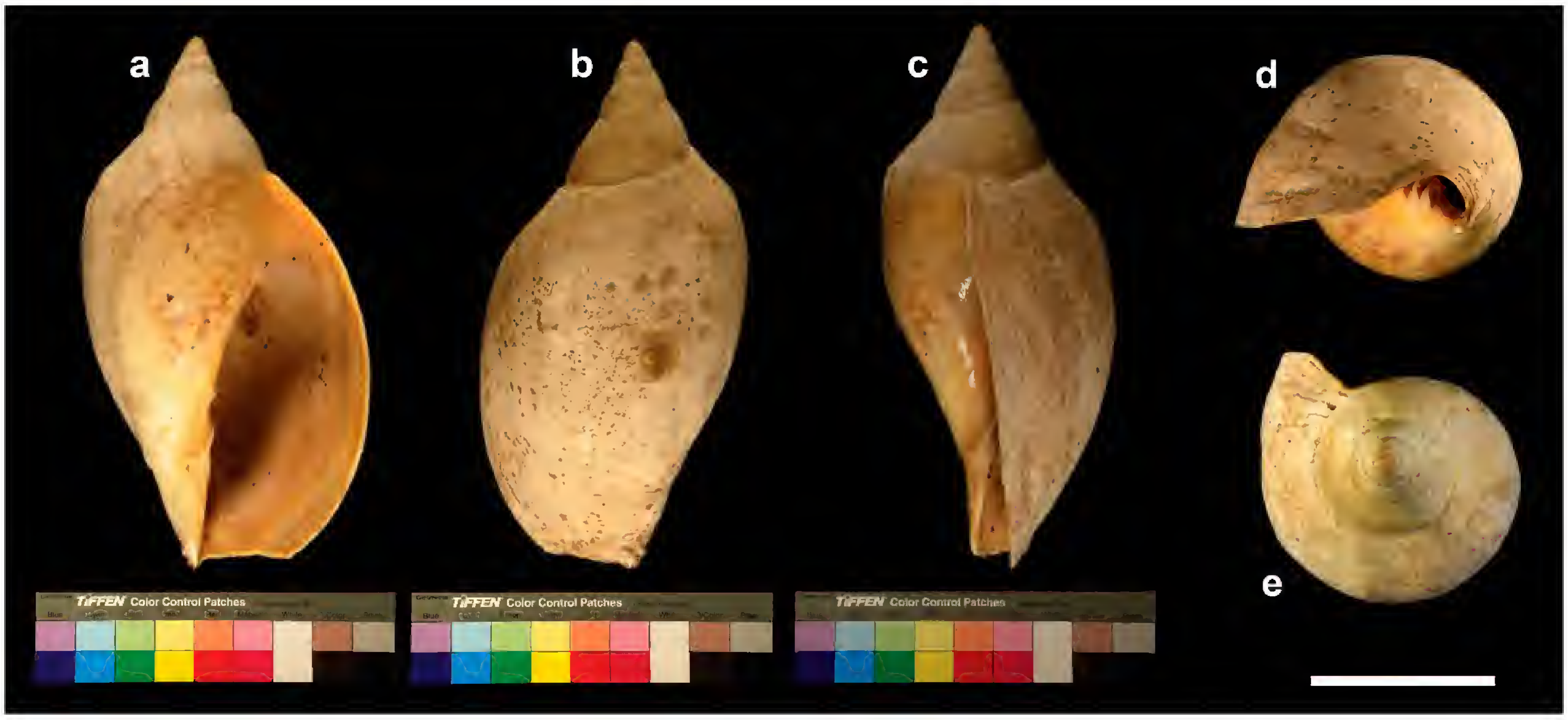

Figure 1. *Voluta ambigua typica*, specimen figured by Lahille (1895: pl. XII, fig. 16). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

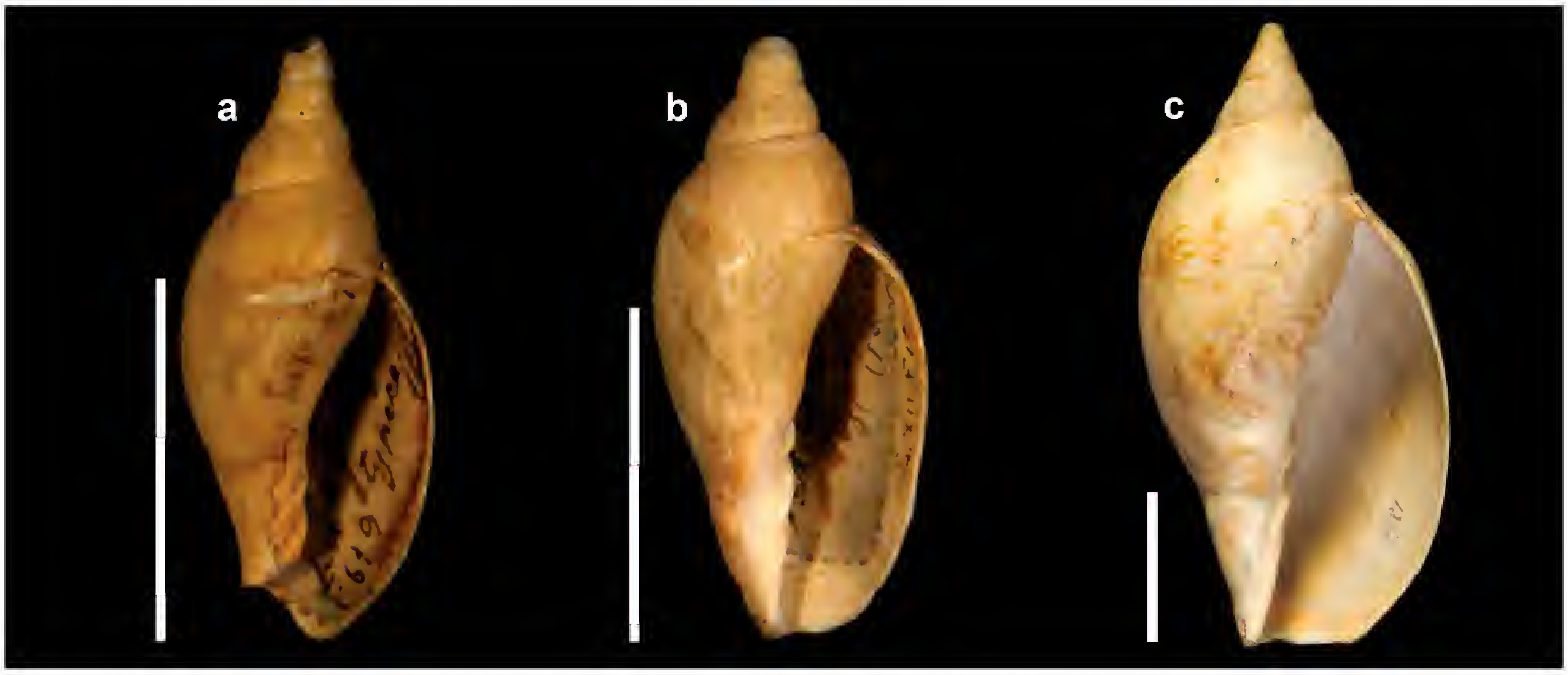

Figure 2. *Voluta ambigua typica*, specimens figured by Lahille (1895). See references on Table 1. Scale bars: 3 cm.

Table 1. *Voluta ambigua typica*, specimens figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. XII, fig. 16	478	1
Pl. II, fig. 61; pl. XII, fig. 11	"1.*Magellanica typica* 1°S"	2a
Pl. XII, fig. 12	"2.*Magellanica typica* 1°S"	2b
Pl. XII, fig. 15	481	2c

Voluta ambigua pseudotuberculata Lahille, 1895

Holotype: MLP-Ma 10855, ca 106 mm long × 62 mm wide, figured by Lahille (1895: pl. XI, fig. 6). Label reads: "1.*Pseudo-tuberculata*" (Fig. 4).

The shell has accentuated coloured lines. It has a carina and tubercles on every whorl, slightly attenuated on the last whorl of the spire. The suture of the last whorl of the spire is almost at the same level as the row of tubercles of the penultimate one. The aperture is regularly arched and with three columellar folds.

Voluta ambigua subnodosa Lahille, 1895

Holotype: MLP-Ma 10857, ca 120 mm long × 65 mm wide, figured by Lahille (1895: pl. XI, fig. 9). Label reads: "1.*subnodosa*" (Fig. 5).

Lahille (1895) mentioned that *V. subnodosa* Leach, 1814, is similar to this variety of *V. ambigua*. The shell has the last whorl expanded and smooth, and there are almost always

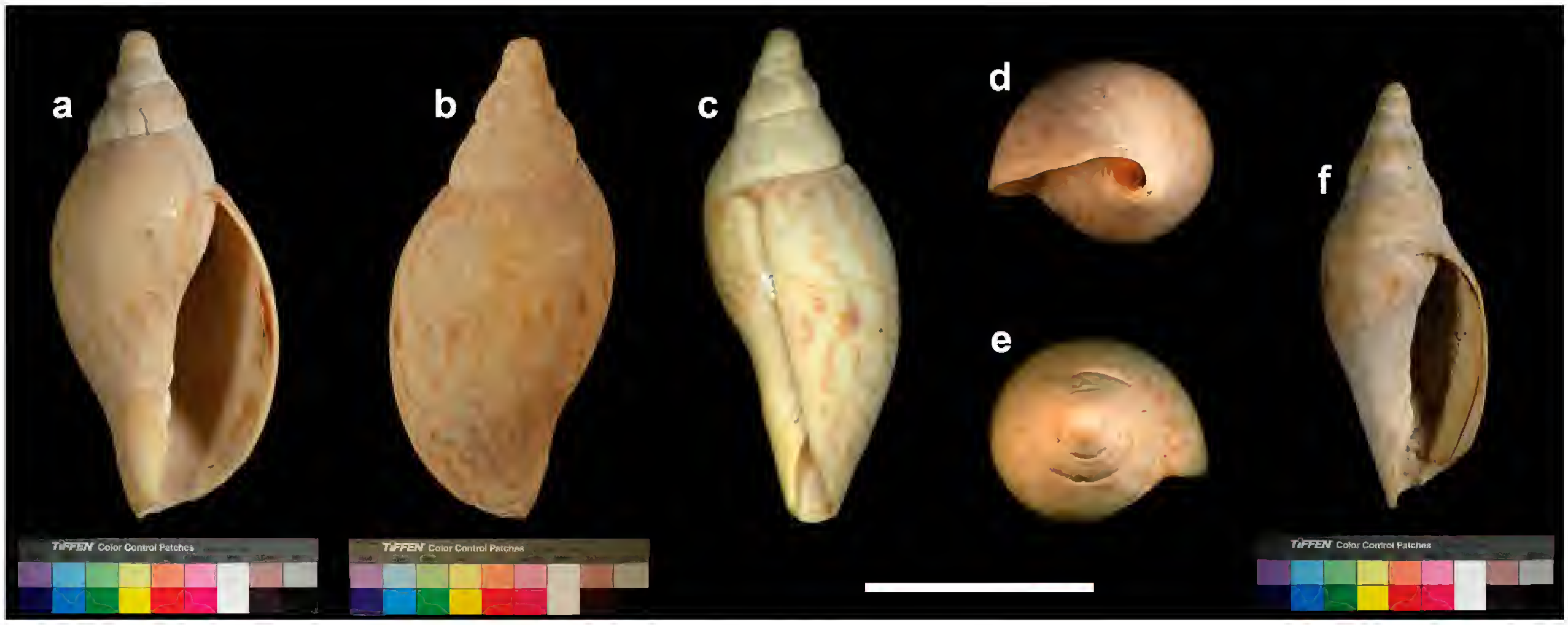

Figure 3. *Voluta ambigua constricta.* **a–e** Specimen figured by Lahille (1895: pl. VIII, fig. 164) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895, pl. VIII, fig. 163) in apertural view. Scale bar: 3 cm.

Figure 4. *Voluta ambigua pseudotuberculata*, holotype figured by Lahille (1895: pl. XI, fig. 6) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

three very dark, narrow, angular transverse lines. The spire is short and consists of six whorls, of which the third and fourth whorl are subcarinate at the middle with small tubercles. The aperture is wide, pale orange-brown, and there are three columellar folds. The inferior fold is smaller than the others.

Voluta ancilla Solander, 1786

Current name: *Adelomelon ancilla* (Lightfoot, 1786).

Lahille (1895) postulated that this species might be very common on the Patagonian shore, and described six varieties.

Voluta ancilla typica Lahille, 1895

Syntypes: MLP-Ma 10862, 7 specimens figured by Lahille (1895) (Table 2), 12 other specimens not figured by Lahille. Some specimens more than 150 mm long. Lahille (1895) separated these specimens in two series (Figs 6, 7).

Table 2. *Voluta ancilla typica*, specimens figured by Lahille (1895) with the details of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. VIII, fig. 191	"15. *typica* (2°serie). 192"	6
Pl. I, fig. 9; pl. VIII, fig. 159	"12. *typica* (1°S)"	7a
Pl. II, fig. 63a; pl. VIII, fig. 189	"7. *typica* (2°s). 350"	7b
Pl. XI, fig. 8	"6. *typica* (1°s)"	7c
Pl. II, fig. 63; pl. VIII, fig. 187	"5. *typica* (2°s)"	7d
Pl. VIII, fig. 186	"1. *typica*"	7e
Pl. VIII, fig. 184; pl. XII, fig. 35		7f

Lahille (1895) described this variety as having a pale, fusiform shell, with a smooth surface and only fine growth lines. The shell is yellowish with dark longitudinal lines, some of which are almost straight and others are deeply sinuous. The long spire is formed by seven whorls that are separated by deep sutures. In

Figure 5. *Voluta ambigua subnodosa*, holotype figured by Lahille (1895: pl. XI, fig. 9) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

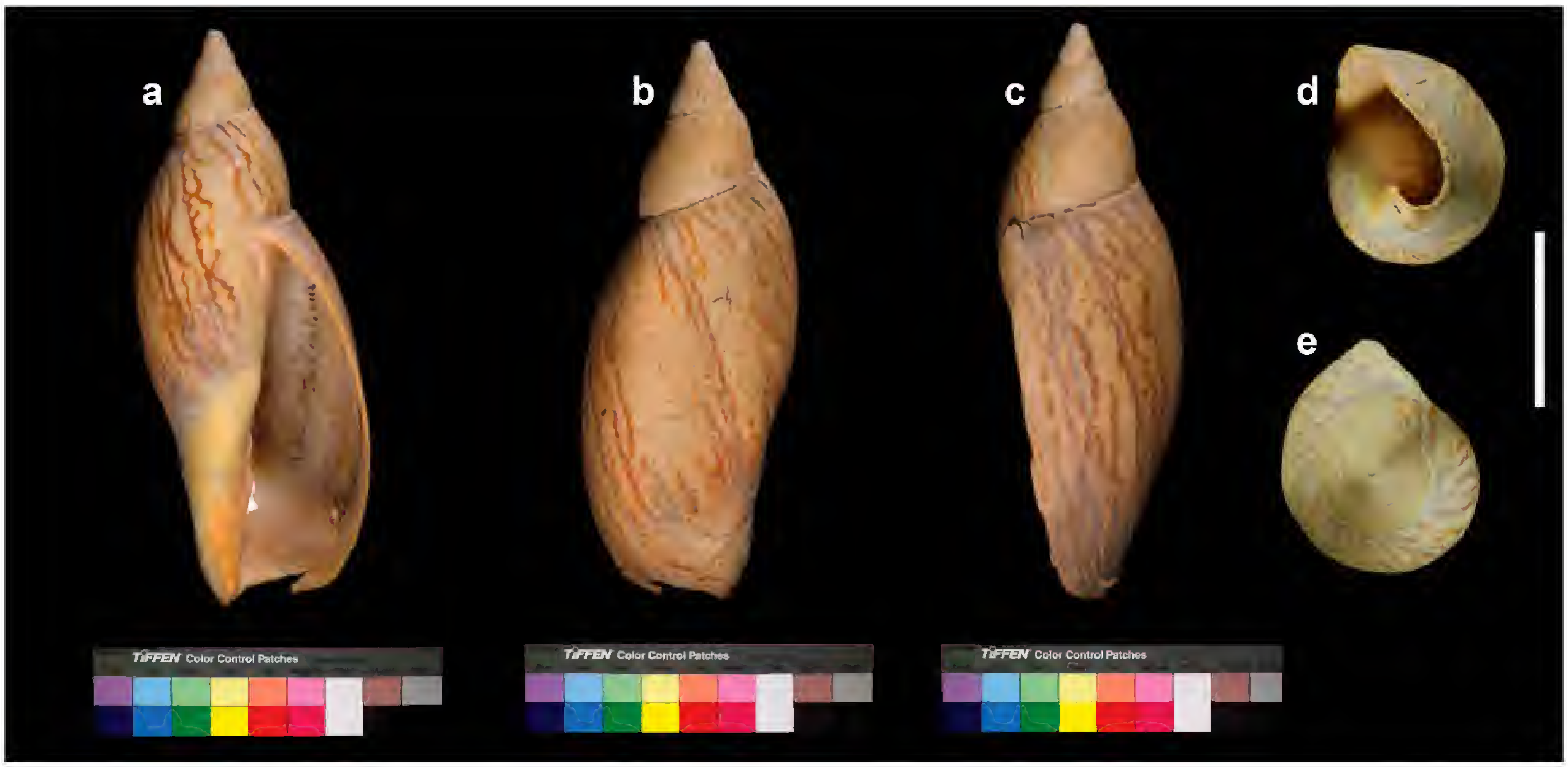

Figure 6. *Voluta ancilla typica*, specimen figured by Lahille (1895: pl. VIII, fig. 192) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

most specimens, the length of the last whorl is two-thirds of the total length. The free and columellar edges are thin. The colour of the aperture varies from yellowish-white to orange. Generally, there are four columellar folds and the inferior one is strong. They live almost completely buried, so the upper part of the shell is frequently eroded.

Voluta ancilla abbreviata Lahille, 1895

Syntypes: MLP-Ma 10863, 2 specimens figured by Lahille (1895: pl. II, fig. 66; pl. VIII, fig. 158; pl. XI, fig. 3) (Fig. 8). The label of one specimens reads: "*ponderosa*".

According to Lahille (1895), this variety has a "horn-shaped" spire.

Voluta ancilla elongata Lahille, 1895

Holotype: MLP-Ma 10860, 195 mm long, figured by Lahille (1895: pl. XI, fig. 2). Label reads: "2.*elongata* 455" (Fig. 9).

This variety has shells with a high spire. In a shell of 100 mm long aperture, the spire is 80 mm long from its tip to the upper angle of the aperture.

Voluta ancilla expansa Lahille, 1895

Syntypes: MLP-Ma 10859, 1 specimen figured by Lahille (1895: pl. XI, fig. 1), label reads: "4.*expansa*"; 3 other specimens not figured by Lahille (Fig. 10).

The diameter of the last whorl is higher than the double the diameter of the penultimate whorl.

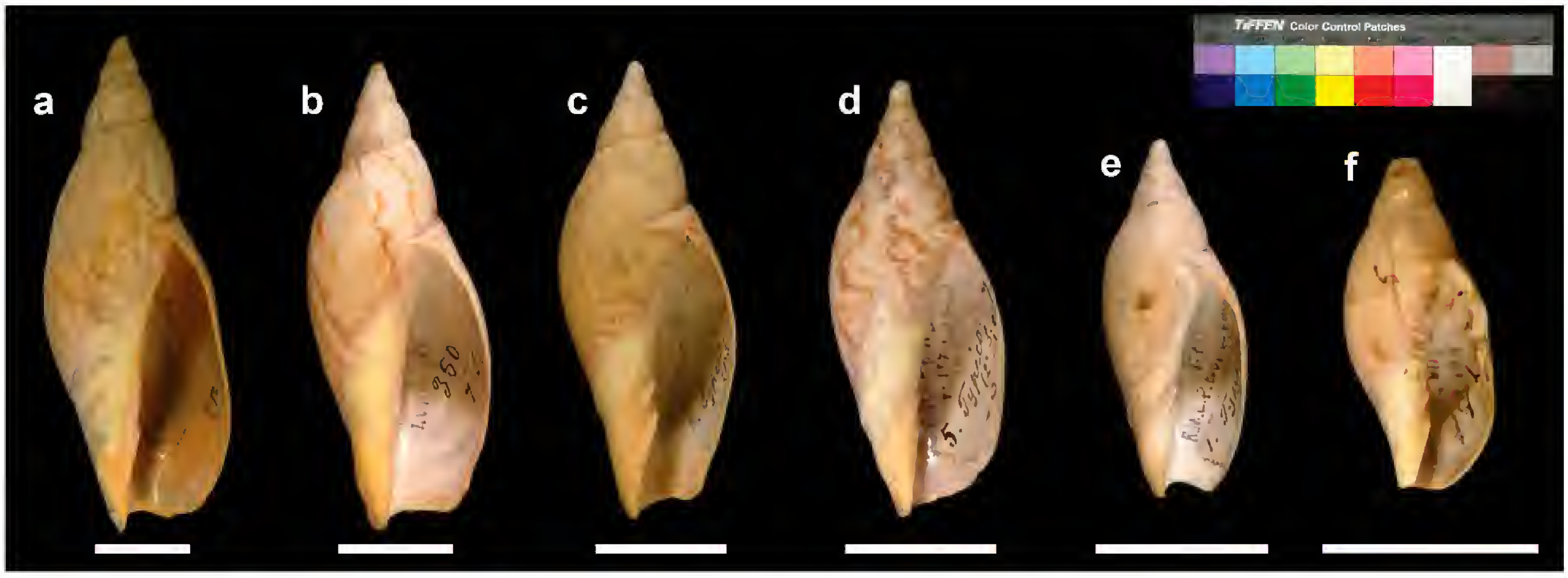

Figure 7. *Voluta ancilla typica*, specimens figured by Lahille (1895: pls I, II, VIII, XI, XII. See references on Table 2. Scale bars: 3 cm.

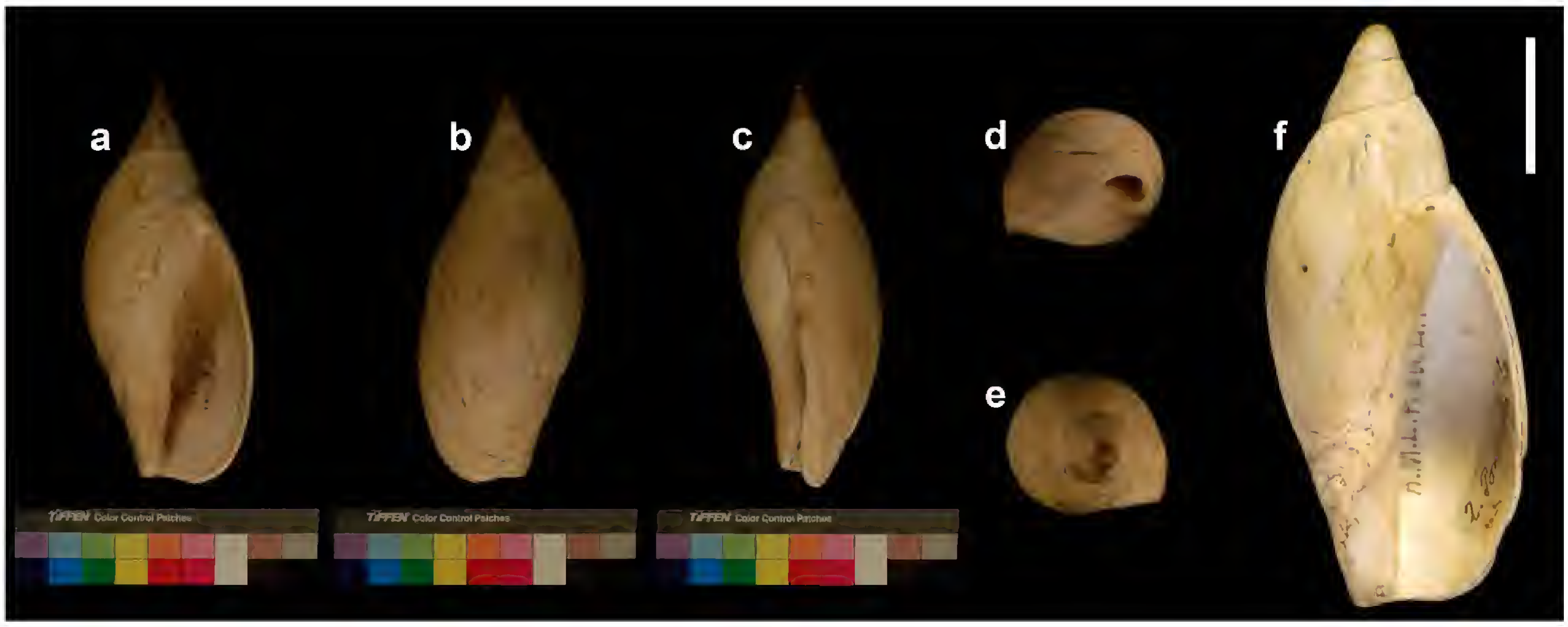

Figure 8. *Voluta ancilla abbreviata*, figured by Lahille (1895). **a–e** Correspond to pl. XI, fig. 3 and pl. VIII, fig.158 **f** Corresponds to pl. II, fig. 66 **a, f** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

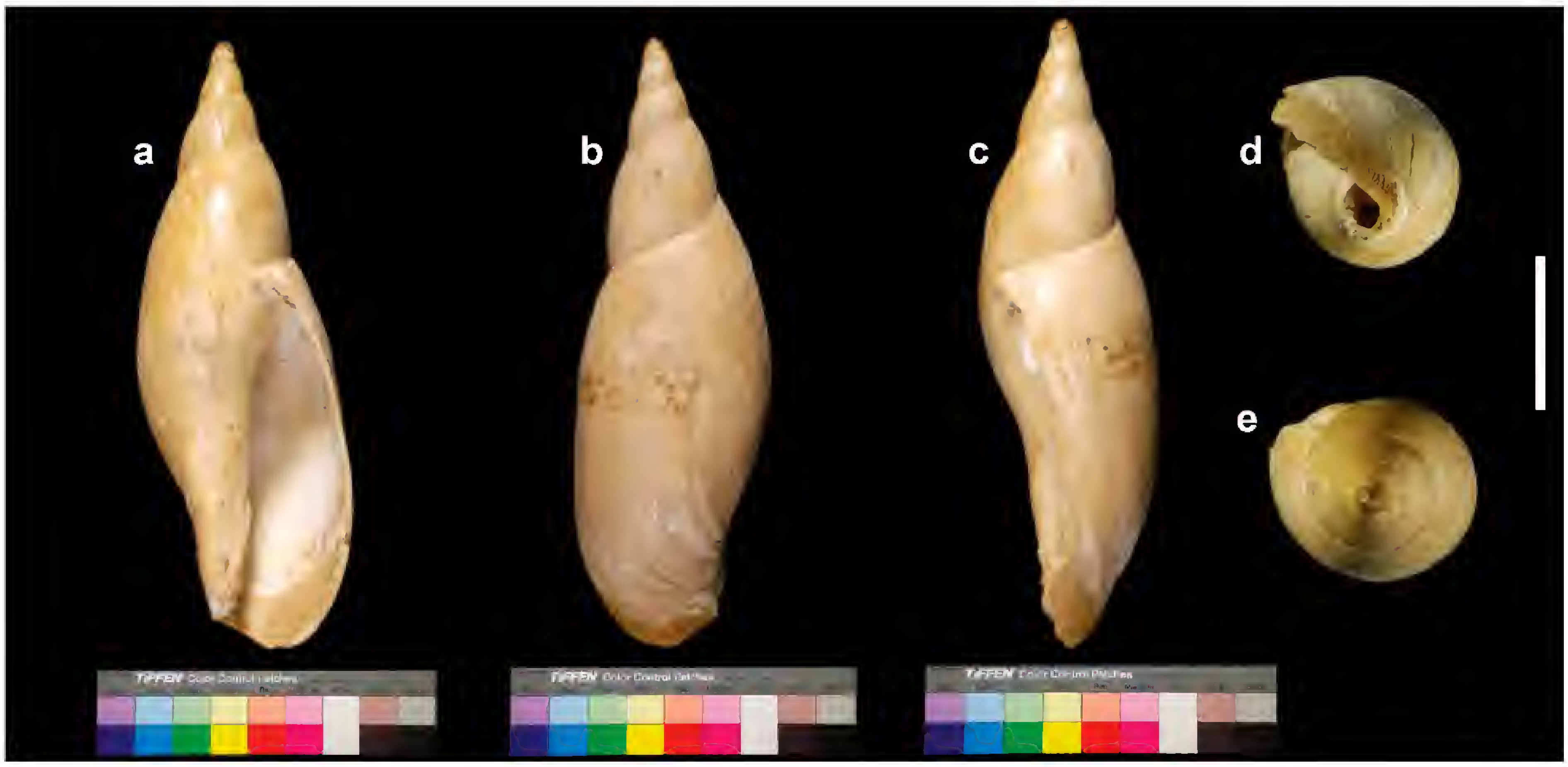

Figure 9. *Voluta ancilla elongata*, holotype figured by Lahille. **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

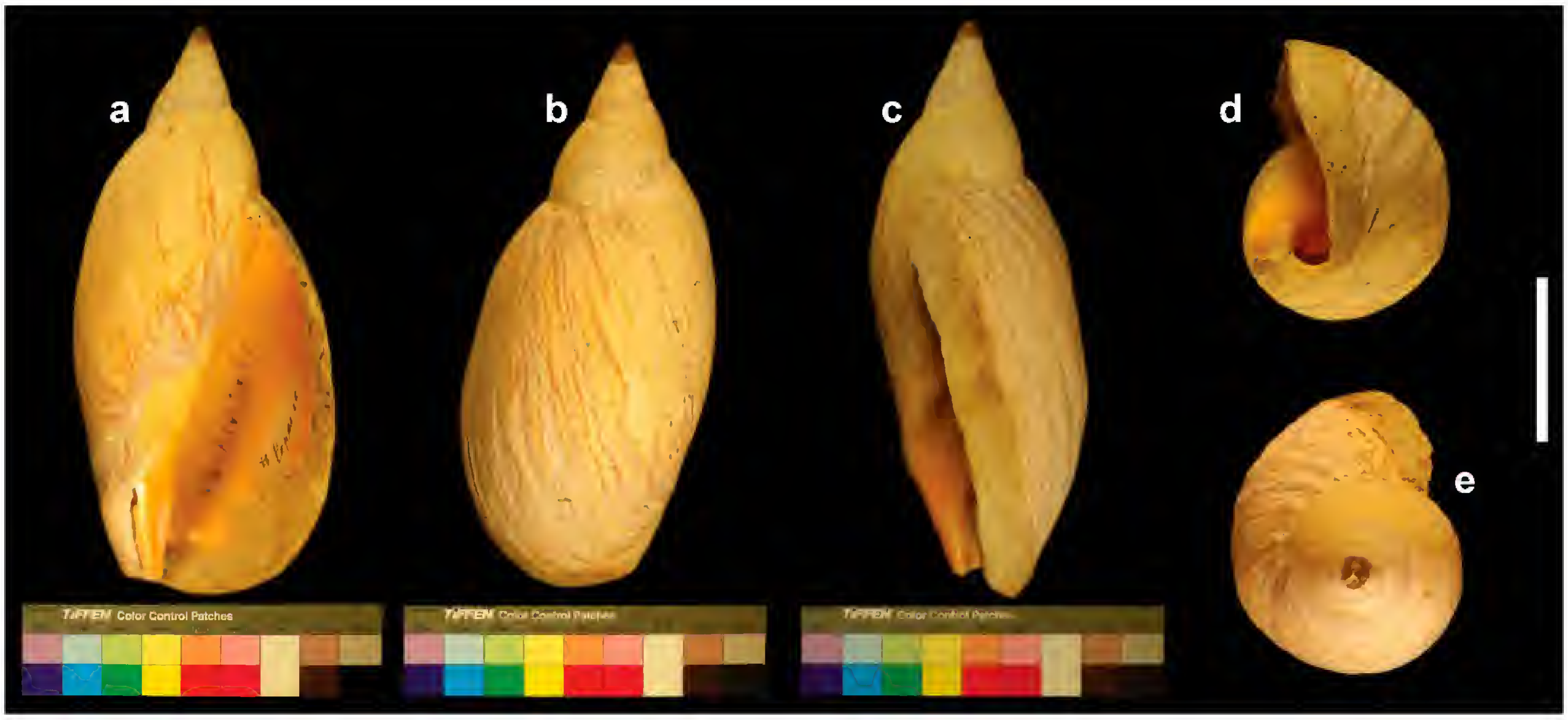

Figure 10. *Voluta ancilla expansa*, specimen figured by Lahille. **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

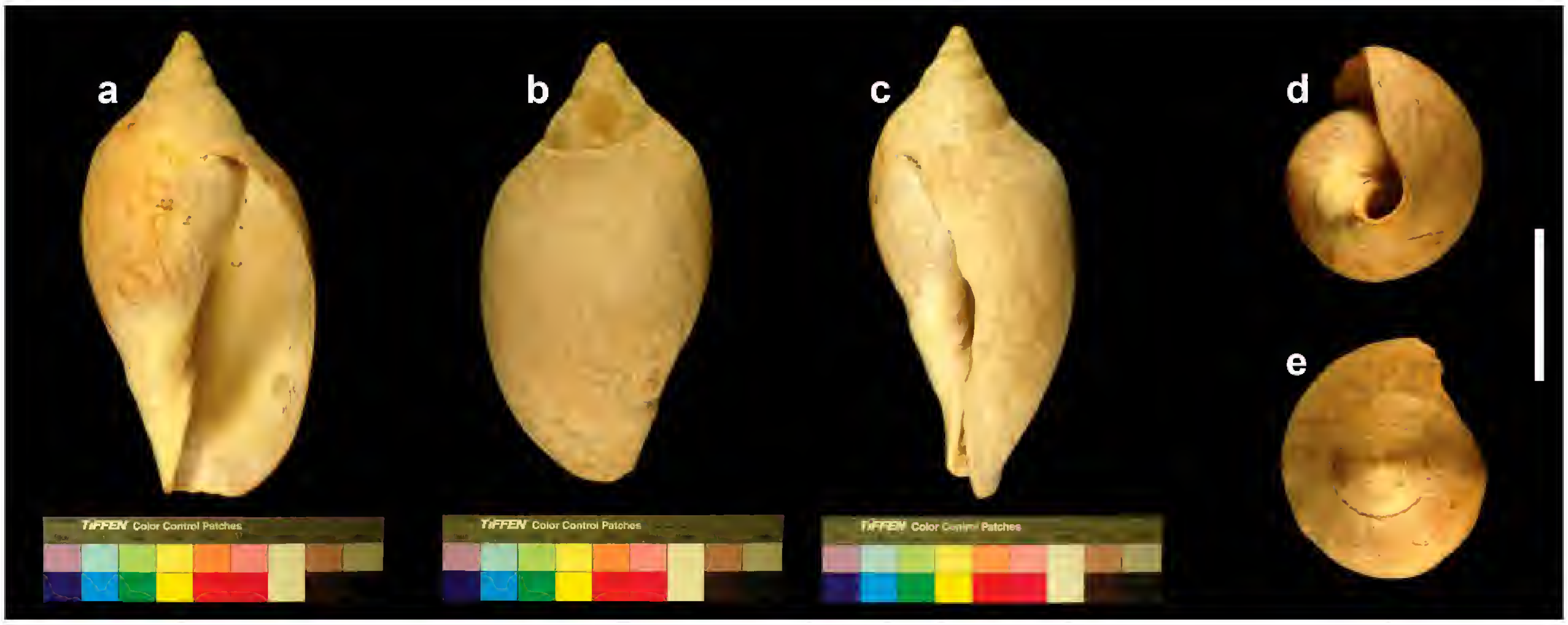

Figure 11. *Voluta ancilla inflata*, holotype. **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

Voluta ancilla inflata Lahille, 1895

Holotype: MLP-Ma 14243, 142.5 mm long, not figured by Lahille (1895) (Fig. 11).

The last whorl of the spire has a dilation that is much more accentuated upwards, and forms a false carina. The shells are thin and generally with three columellar folds.

Voluta ancilla ponderosa Lahille, 1895

Syntypes: MLP-Ma 10861, 4 specimens figured by Lahille (1895) (Table 3); 2 other specimens not figured by Lahille (Figs 12, 13).

This variety differs from the variety *typica* by having heavier shells and in being larger, with specimens over 190 mm long. The specimens that Lahille (1895) figured in plate VIII, figures 170 and 173 have not been found.

Table 3. *Voluta ancilla ponderosa*, specimens from the MLP Collection figured by Lahille (1895) with the details of the inscriptions on their shells and figures here.

Figure of Lahille (1895)	Detail	Figure
Pl. VIII, fig. 171	“1.*Curvata*. 171”	12
Pl. VIII, fig. 183	“9.*Ponderosa*. 258. 183”	13a
Pl. VIII, fig. 180	“3.*Ponderosa*”	13b
Pl. VIII, fig. 178	“460”	13c

***Voluta angulata* (Swainson, 1821)**

Current name: *Zidona dufresnei* (Donovan, 1823).

This species has a shell with longitudinal orange-brown lines, and without nodes. Lahille (1895) described seven varieties.

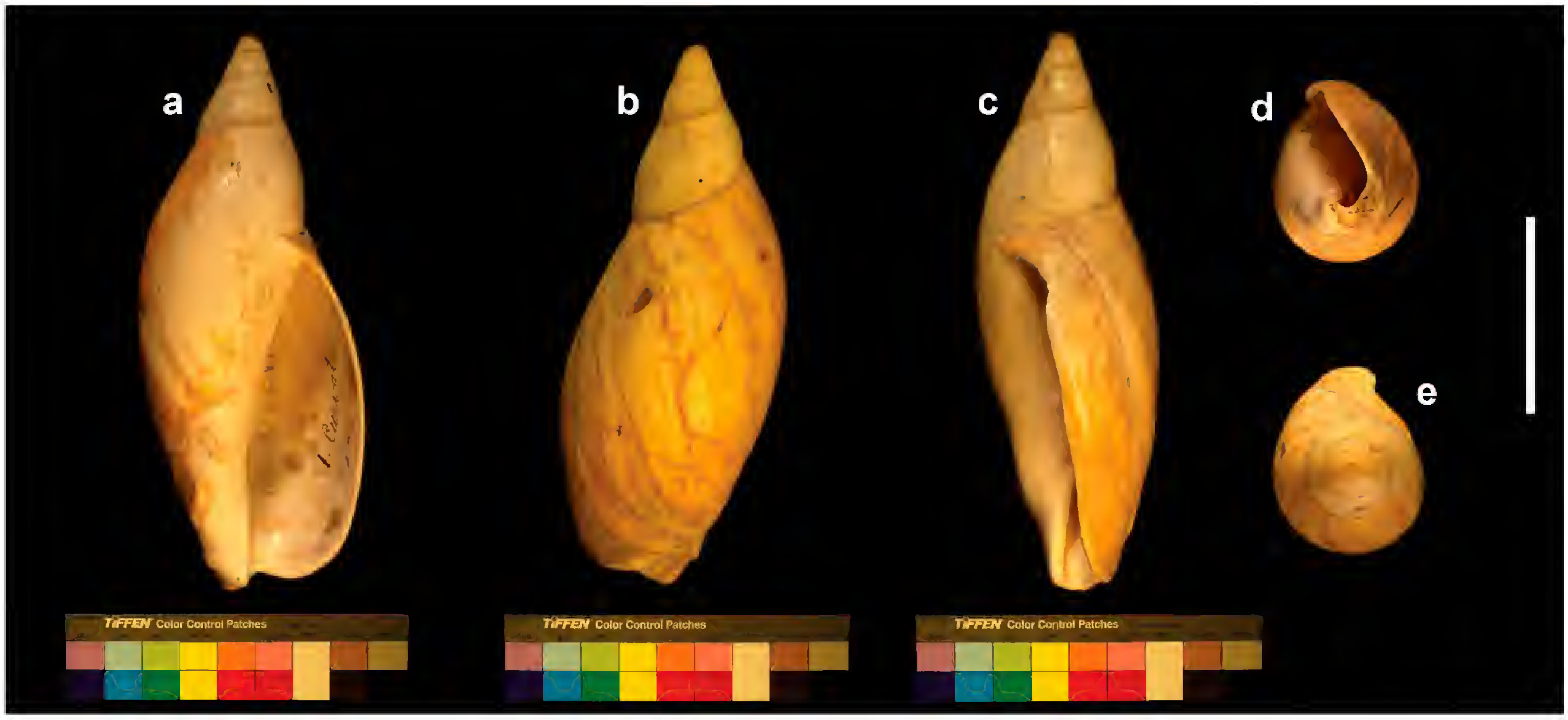

Figure 12. *Voluta ancilla ponderosa*, specimen figured by Lahille (1895: pl. VIII, fig. 171), shell reads "*curvata*". **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

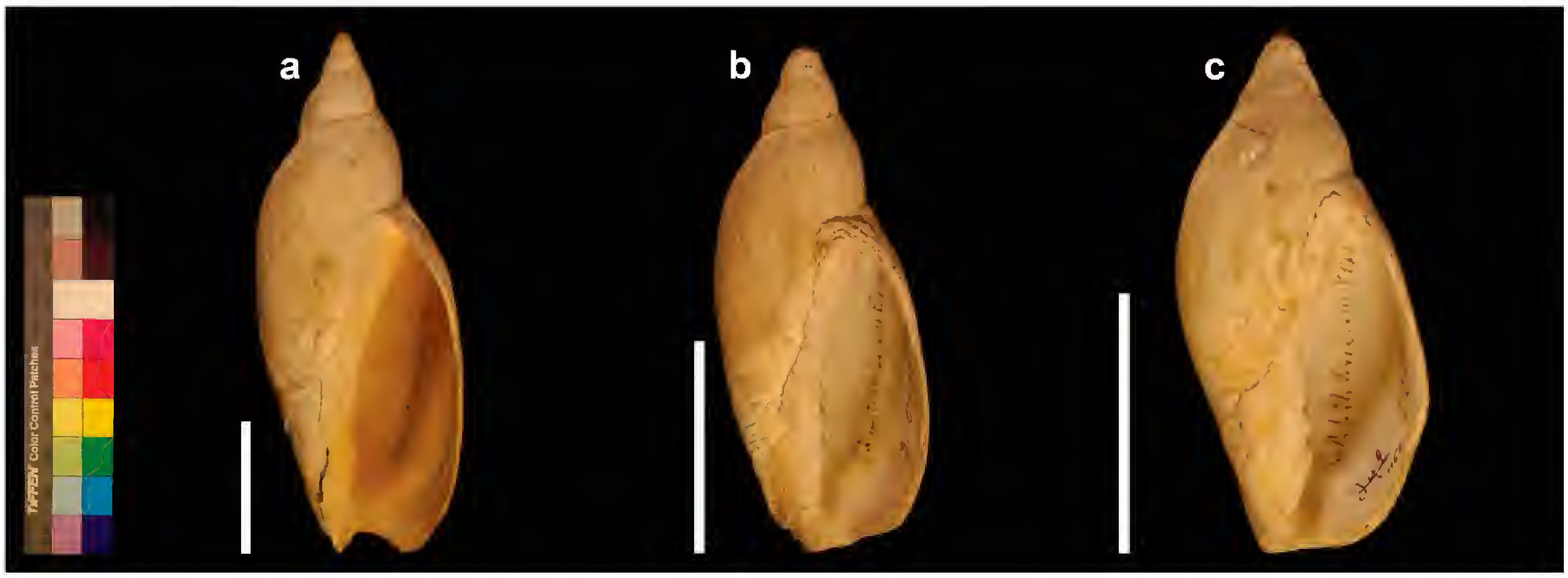

Figure 13. *Voluta ancilla ponderosa*, specimens figured by Lahille (1895: pl. VIII). **a** Correspond to fig. 183 **b** Corresponds to fig. 180 **c** Corresponds to fig. 178. Scale bars: 5 cm.

Voluta angulata typica Lahille, 1895

Syntypes: MLP-Ma 10869, 11 specimens figured by Lahille (1895) (Table 4); 4 other specimens not figured by Lahille. Specimens from 36 to 142 mm long (Figs 14, 15).

Lahille described this variety with fusiform or subturbinated shells, with a smooth surface (almost completely covered by the mantle). The colour is pale yellow with dark longitudinal zigzag lines. The last whorl is strongly carinate, almost perpendicular to shell axis. The aperture is broadly ear-shaped, with a triangular slit on the upper side, and three equal columellar folds. The total length of the shell is shorter than twice the width.

Voluta angulata affinis Lahille, 1895

Syntypes: MLP-Ma 10870, 8 specimens figured by Lahille (1895) (Table 5), from 39 to 94 mm long (Figs 16, 17).

Table 4. *Voluta angulata typica*, specimens figured by Lahille (1895) with the details of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. VI, fig. 104; pl. IX, fig. 4	"9.*Angul. typica* (1°s). 104"	14
Pl. VI, fig. 99	"4. *Angul. typica* (1°s)"	15a
Pl. II, fig. 74a; pl. VI, fig. 110	"5.*Angul. typica* (1°s)" (according to legend of plate VI, fig. 110, it corresponds to the *distincta* variety)	15b
Pl. VI; fig. 101	"7.*Angul. typica* (1°s)"	15c
Pl. VI; fig. 102	"2.*Ang. nebulosa*. 102"	15d
Pl. II, fig. 74b; pl. VI, fig. 103; pl. IX, fig. 7	"8.*Angul. typica* (1°s)"	15e
Pl. I, fig. 5; pl. VI, fig. 106	"11.*Angul. typica* (1°s)" (according to legend of fig. 5, it corresponds to the *luteola* variety)	15f
Pl. VI, fig. 98	"2.*Angul. typica* (1°s)"	15g
Pl. XII, fig. 33	"8. *Typica jov*."	15h
Pl. II, fig. 72	"*Typ.*"	15i
Pl. II, fig. 69; pl. XII, fig. 30	"5."	15j

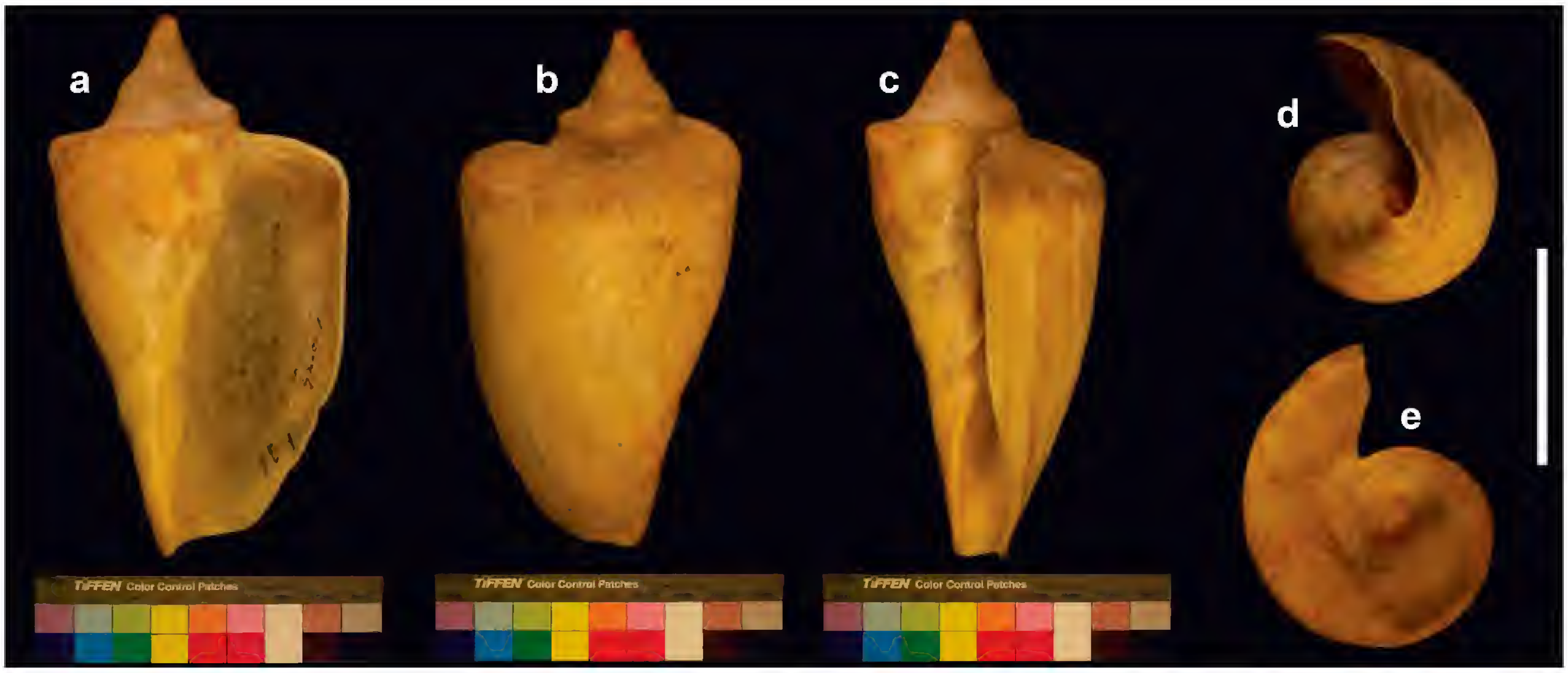

Figure 14. *Voluta angulata typica*, specimen figured by Lahille (1895: pl. VI, fig. 104; pl. IX, fig. 4) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

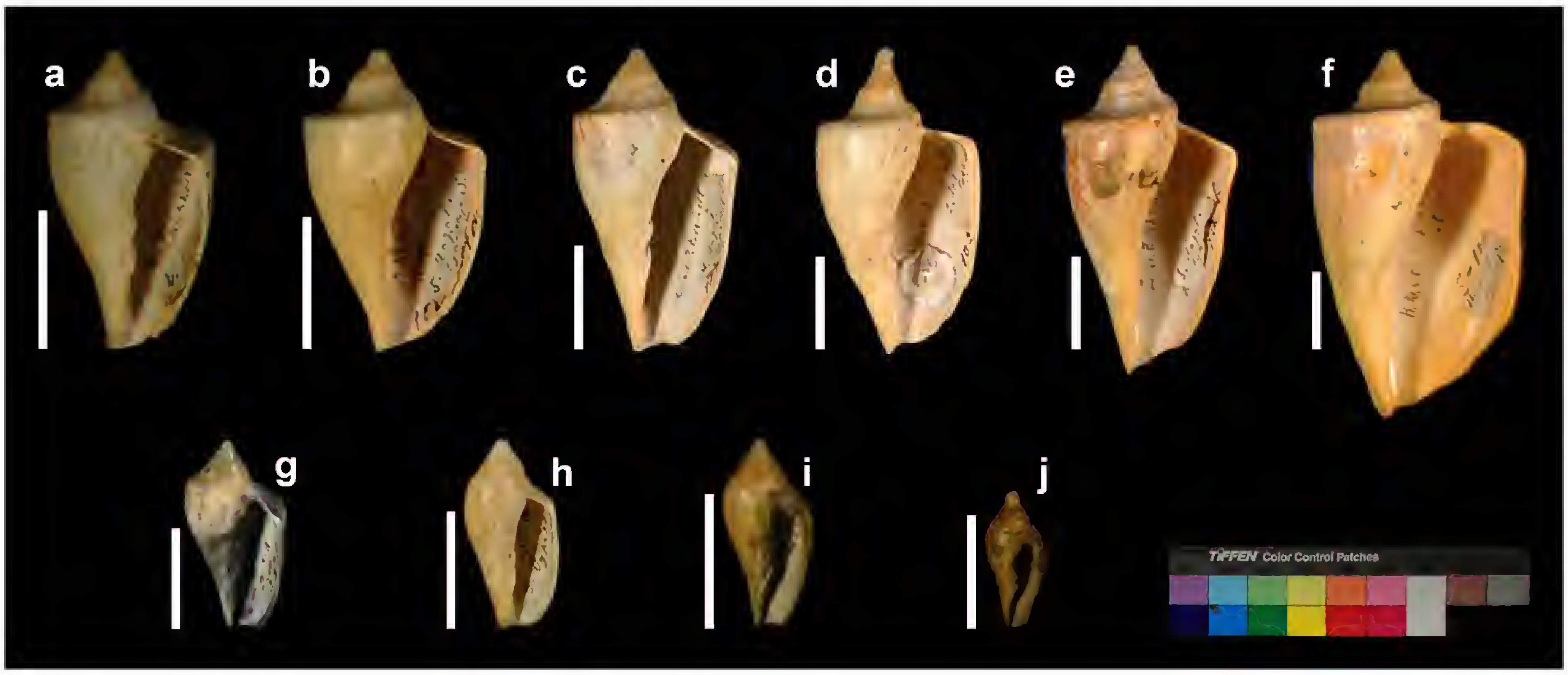

Figure 15. *Voluta angulata typica*, specimens figured by Lahille (1895). See references on Table 4. Scale bars: 3 cm.

According to Lahille's description, the shells are thick-walled, dark, and can be up to 100 mm long by 45 mm wide. The upper part of the last whorl is regularly concave.

Voluta angulata distincta Lahille, 1895

Syntypes: MLP-Ma 10871, 4 specimens figured by Lahille (1895) (Table 6), from 72 to 146 mm long (Figs 18, 19).

The specimens are elongated, with shells thinner than those of the *typica* variety. The aperture is narrow, almost regular oval. The carina of the last whorl is not evident and forms a roundish angle. The last whorl of the spire is convex.

Carcelles (1944) treated this taxon as valid in his study of marine molluscs of the southern coast of Buenos Aires.

Table 5. *Voluta angulata affinis* specimens figured by Lahille (1895) with the details of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. II, fig. 75b; pl. VI, fig. 91; pl. VIII, fig. 160; pl. IX, fig. 9	"7.*affinis*"	16
Pl. II, fig. 76	"2.*affinis*"	17a
Pl. II, fig. 75; pl. VI, fig. 87	"3.*affinis*"	17b
Pl. VI, fig. 88	"4.*affinis*"	17c
Pl. II, fig. 78; pl. VI, fig. 89	"5. *affinis*" (fig. 78 reads *Voluta angulata ventricosa*)	17d
Pl. II, fig. 75a; pl. VI, fig. 90	"6.*affinis*"	17e
Pl. II, fig. 71; pl. XII, fig. 31	"6"	17f
Pl. VI, fig. 85	"1.*affinis*"	17g

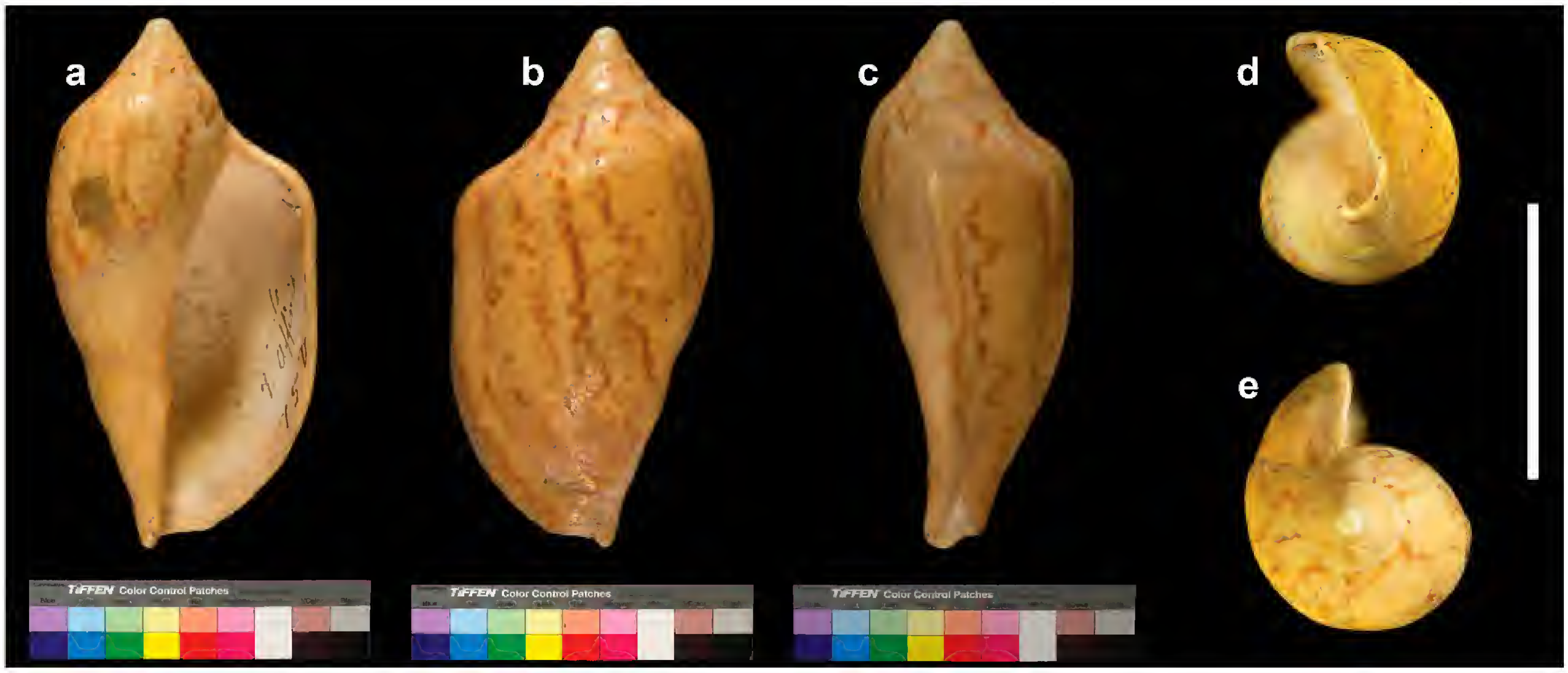

Figure 16. *Voluta angulata affinis*, specimen figured by Lahille (1895: pl. II, fig. 75b; pl. VI, fig. 91; pl. IX, fig. 9; pl. VIII, fig. 160). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm

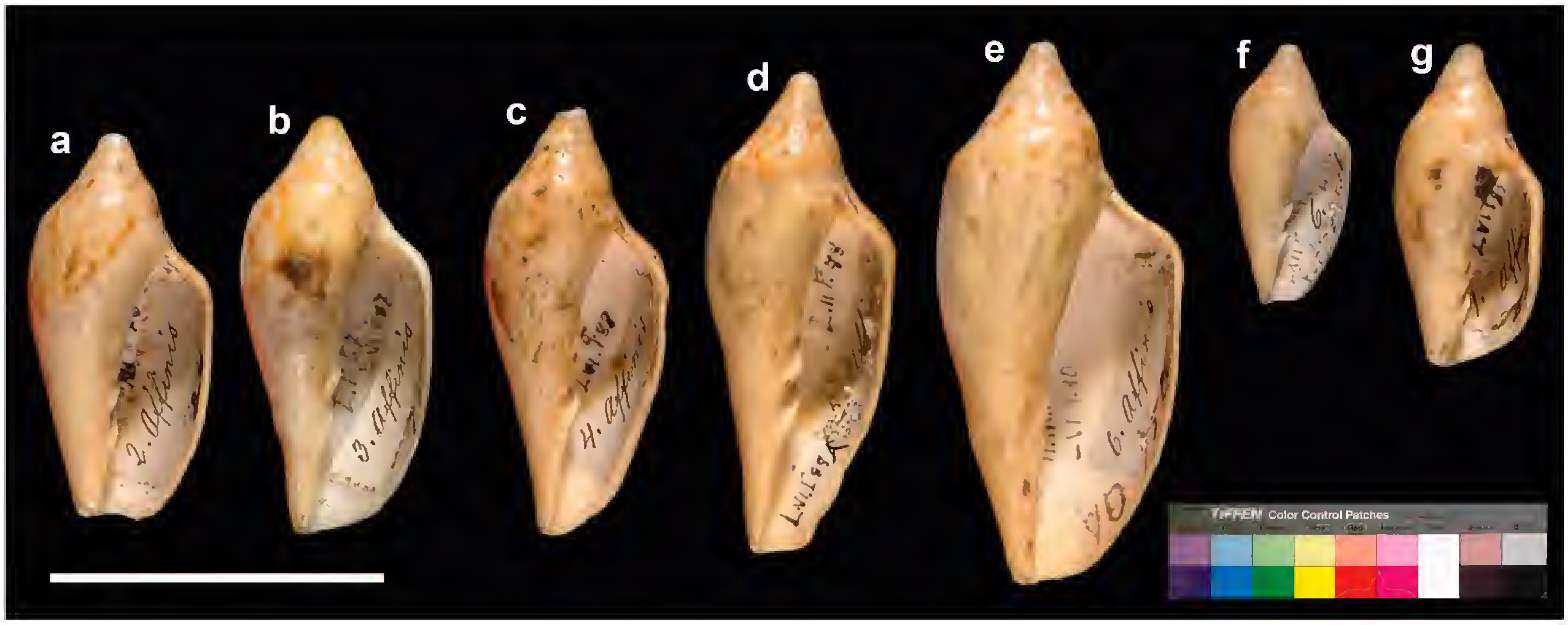

Figure 17. *Voluta angulata affinis*, specimens figured by Lahille (1895). See references on Table 5. Scale bar: 5 cm.

Table 6. *Voluta angulata distincta*, specimens figured by Lahille (1895) with the detail of the inscriptions in their shells and figures here.

Figure of Lahille (1895)	Detail	Figure
Pl. I, fig.8; pl. VI, fig.117; pl. IX, fig. 6	"4.*distincta typica*"	18
Pl. VI, fig. 118	"1.*distincta typica*" (Figure legend reads *Voluta angulata ventricosa*)	19a
Pl. VI, fig.116	"3.*distincta typica*"	19b
Pl. II, fig. 77a; pl. VIII, fig.169	"*distincta*"	19c

Table 7. *Voluta angulata luteola*, specimens figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure of Lahille (1895)	Detail	Figure
Pl. VI, fig. 114	"1. *Ang. luteola*"	20
Pl. VI, fig. 79	"10. *calcarea*" (variety not described)	21a
Pl. VI, fig. 81	"7. *calcarea*" (variety not described)	21b
Pl. II, fig. 73b	"5. *Ang. luteola*" (it also reads Pl. VII, fig. 115, however, fig. 115 is in pl. VI and corresponds to the *similis* variety)	21c
Pl. VI, fig. 81	"5. *calcarea*" (variety not described)	21d

Voluta angulata luteola Lahille, 1895

Syntypes: MLP-Ma 10868, 5 specimens figured by Lahille (1895) (Table 7), 4 other specimens not figured by Lahille. Specimens from 99 to 151 mm long (Figs 20, 21).

According to Lahille (1895), the shells are longer than twice their width, and the last whorls are carinate. The upper columellar folds are not evident.

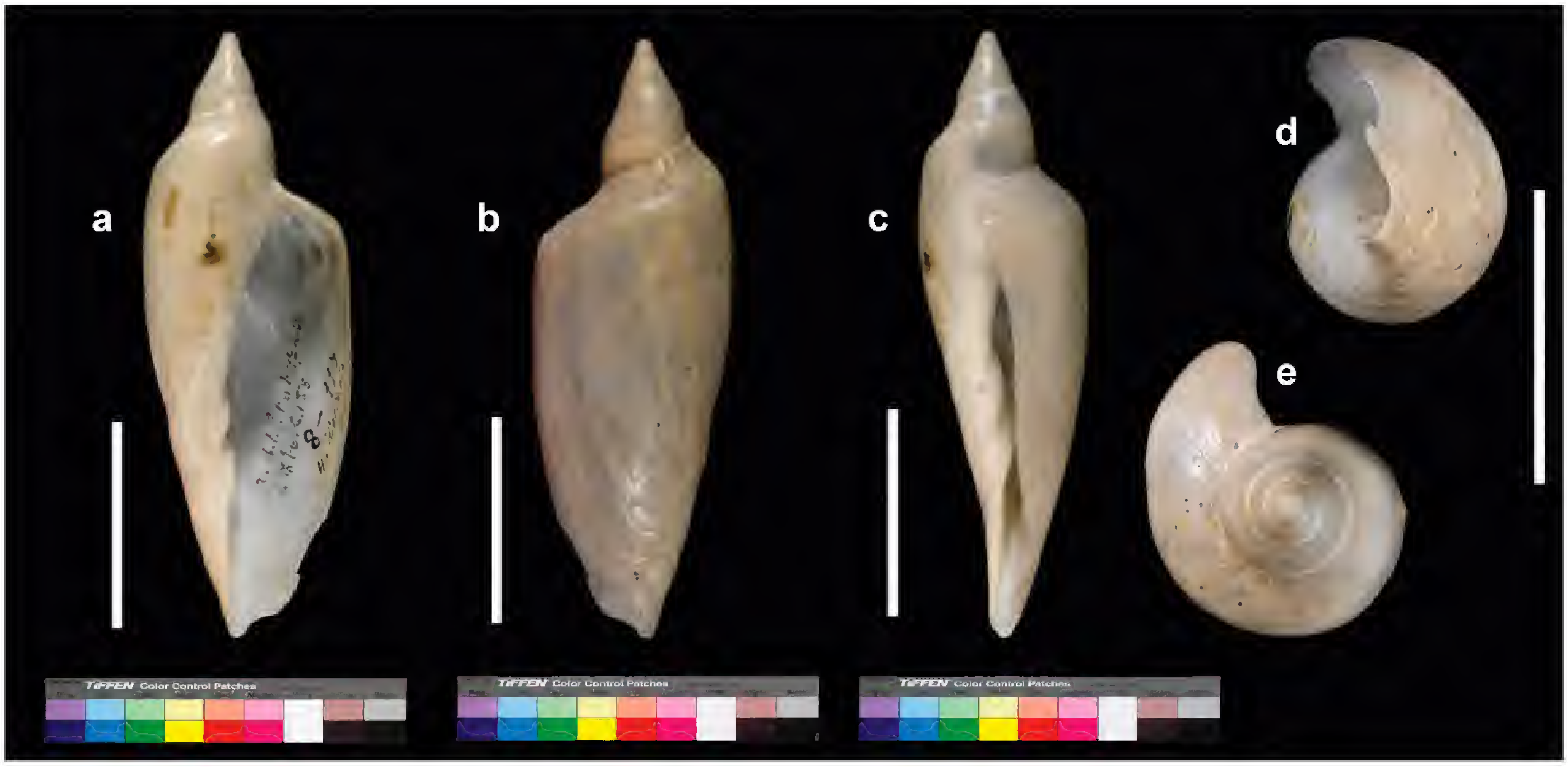

Figure 18. *Voluta angulata distincta*, specimen figured by Lahille (1895: pl. I, fig. 8; pl. VI, fig. 117; pl. IX, fig. 6). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bars: 5 cm.

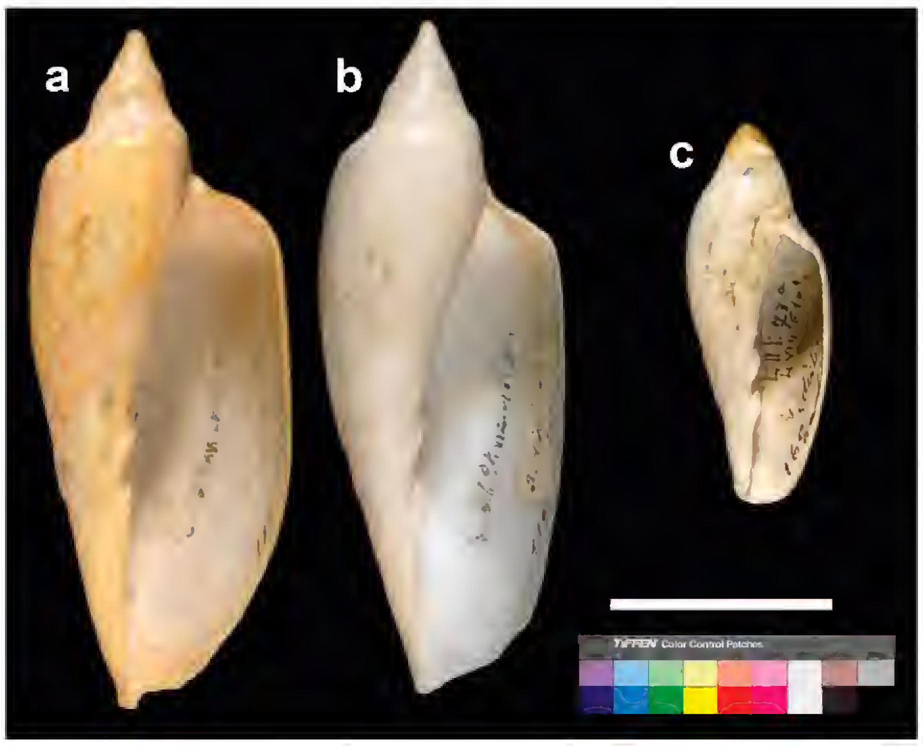

Figure 19. *Voluta angulata distincta*, specimens figured by Lahille (1895). See references on Table 6. Scale bar: 5 cm.

Voluta angulata mixta Lahille, 1895

Holotype: MLP-Ma 10864, ca 70 mm long, figured by Lahille (1895: pl. IX, fig. 8, pl. VI, fig. 82) (Fig. 22).

The total shell length of this variety is almost as long as twice its width. The first few whorls are convex, and the aperture white.

Voluta angulata similis Lahille, 1895

Syntypes: MLP-Ma 10865, 5 specimens figured by Lahille (1895) (Table 8), from 70 to 135 mm long (Figs 23, 24).

The proportions of the shell of this variety are similar to *luteola*, but the carina is strongly oblique to the columellar axis.

Table 8. *Voluta angulata similis*, specimens figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. IX, fig.5	–	23
Pl. VI, fig. 84	"2. *Ang. luteola*" (however fig. 84 corresponds to the *similis* variety)	24a
Pl. VI, fig. 83	"5. *typica joven*" (however fig. 83 corresponds to the *similis* variety)	24b
Pl. VI, fig. 113	"14. *typica joven*" (however fig. 113 corresponds to the *similis* variety)	24c
Pl. VI, fig. 112	"12. *typica joven*" (however fig. 112 corresponds to the *similis* variety)	24d

Table 9. *Voluta angulata ventricosa*, figured by Lahille (1895), with the detail of the inscriptions on their shells and figures here.

Figure of Lahille (1895)	Detail	Figure
Pl. VI, fig.93	"3. *Ventricosa*"	25
Pl. VI, fig.94	"4. *Ventricosa*"	26a
Pl. VI, fig.109	"6. *Ang. nebulosa*" (variety not described, legend on fig. 109 indicates variety *ventricosa*)	26b
Pl. II, fig.78b; pl. VI, fig.92	"2. *Subventricosa*" (variety not described, legends of figs 92 and 78b indicate variety *ventricosa*)	26c
Pl. VI, fig.108	"3. *Ang. nebulosa*" (variety not described, legend of fig. 108 indicates variety *ventricosa*)	26d
Pl. II, fig.78a	–	26e

Voluta angulata ventricosa Lahille, 1895

Syntypes: MLP-Ma 10873, 6 specimens figured by Lahille (1895) (Table 9); 2 other specimens not figured by Lahille. Specimens from 87 to 147 mm long (Figs 25, 26).

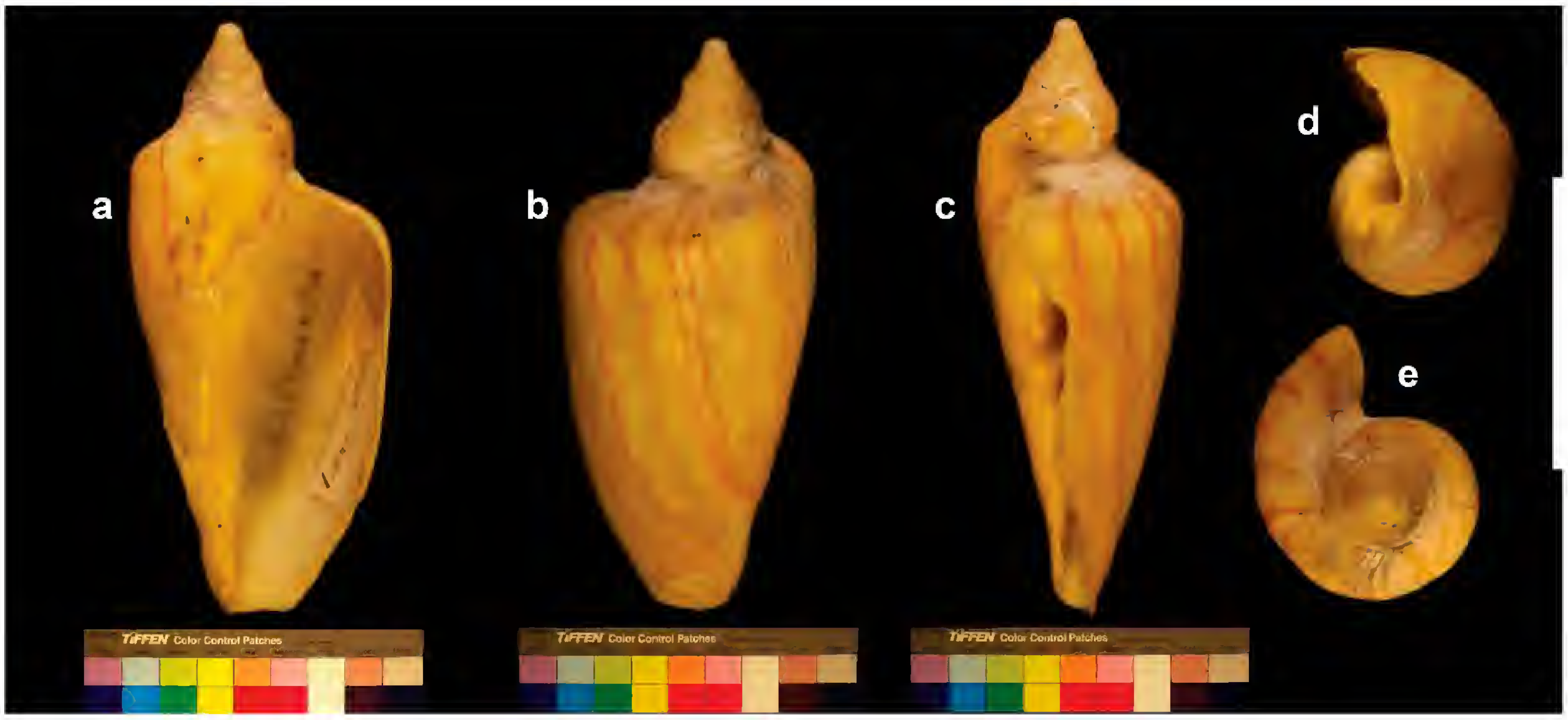

Figure 20. *Voluta angulata luteola*, specimen figured by Lahille (1895: pl. VI, fig. 114). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

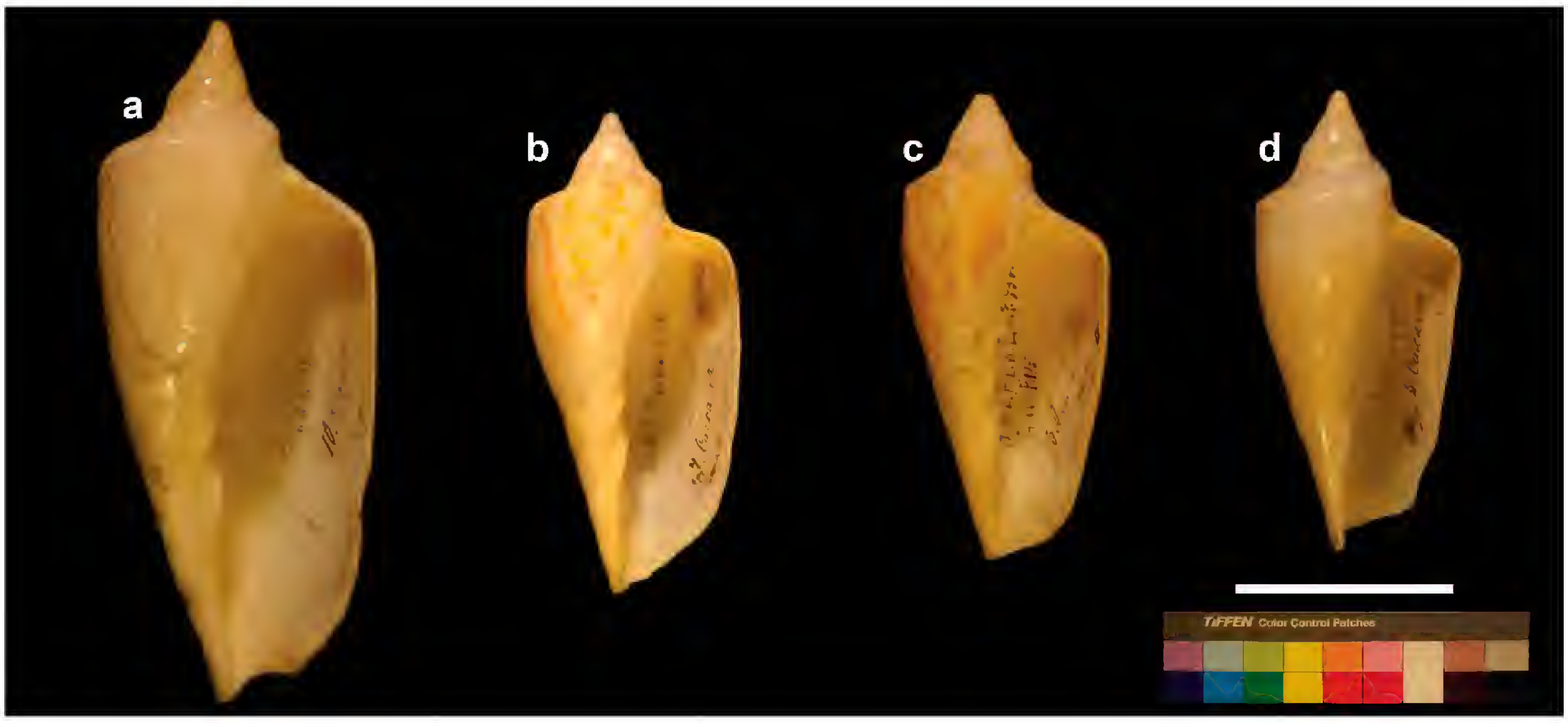

Figure 21. *Voluta angulata luteola*, figured by Lahille (1895). See references on Table 7. Scale bar: 5 cm.

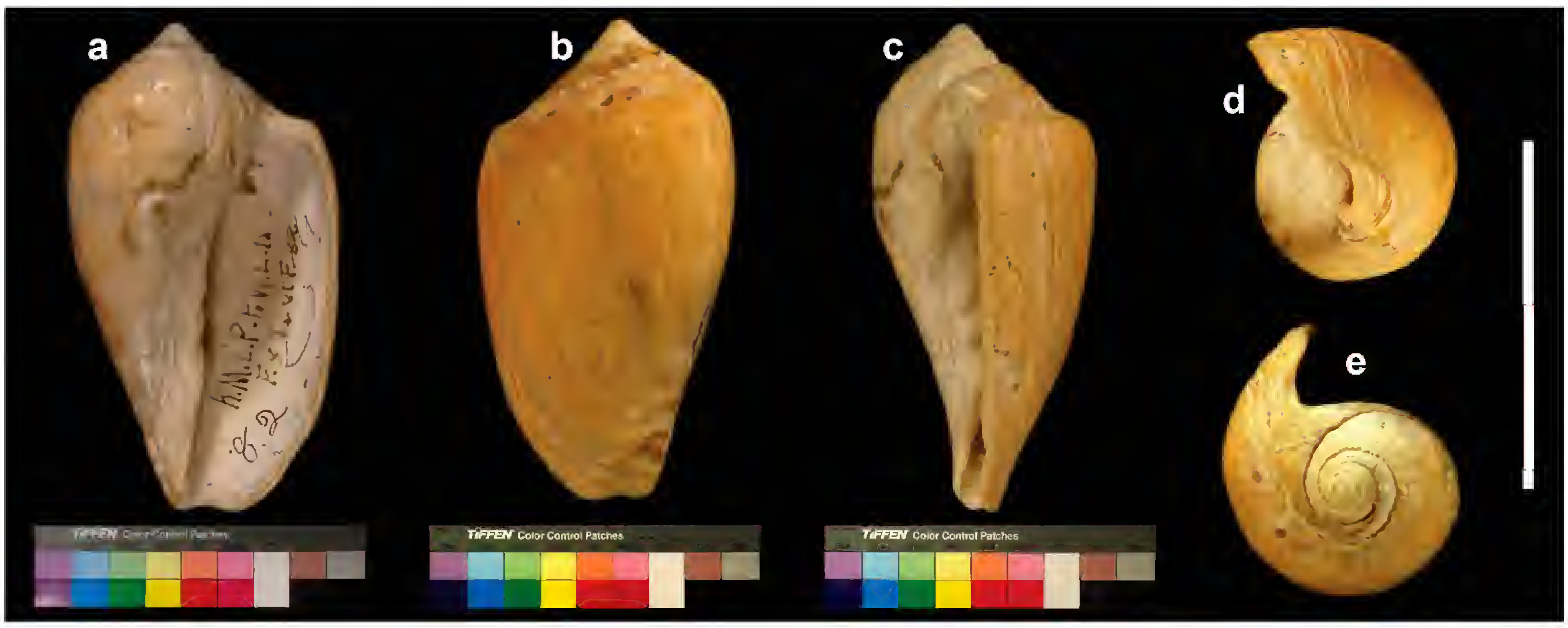

Figure 22. *Voluta angulata mixta*, specimen figured by Lahille (1895: pl. IX, fig. 8; pl. VI, fig. 82). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

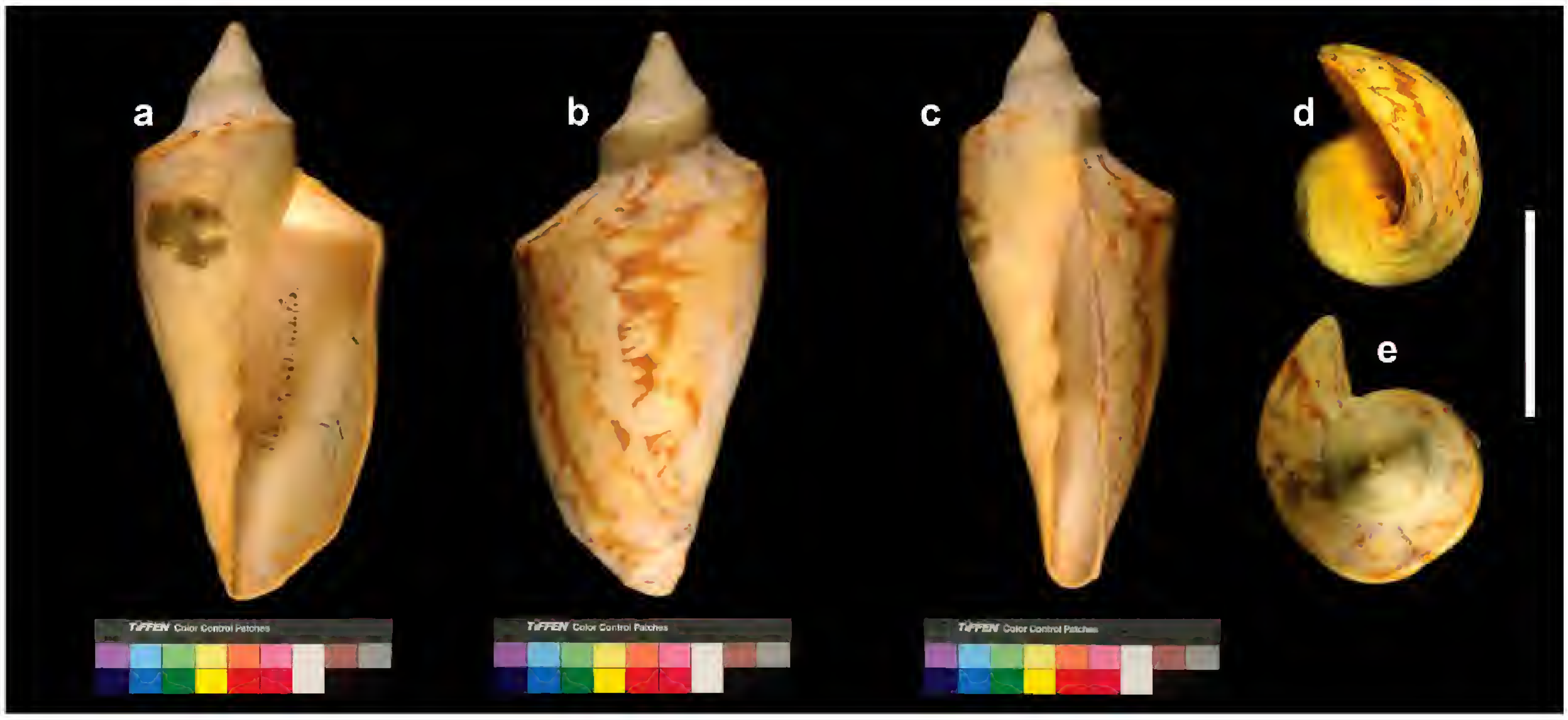

Figure 23. *Voluta angulata similis*, specimen figured by Lahille (1895: pl. IX, fig. 5). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

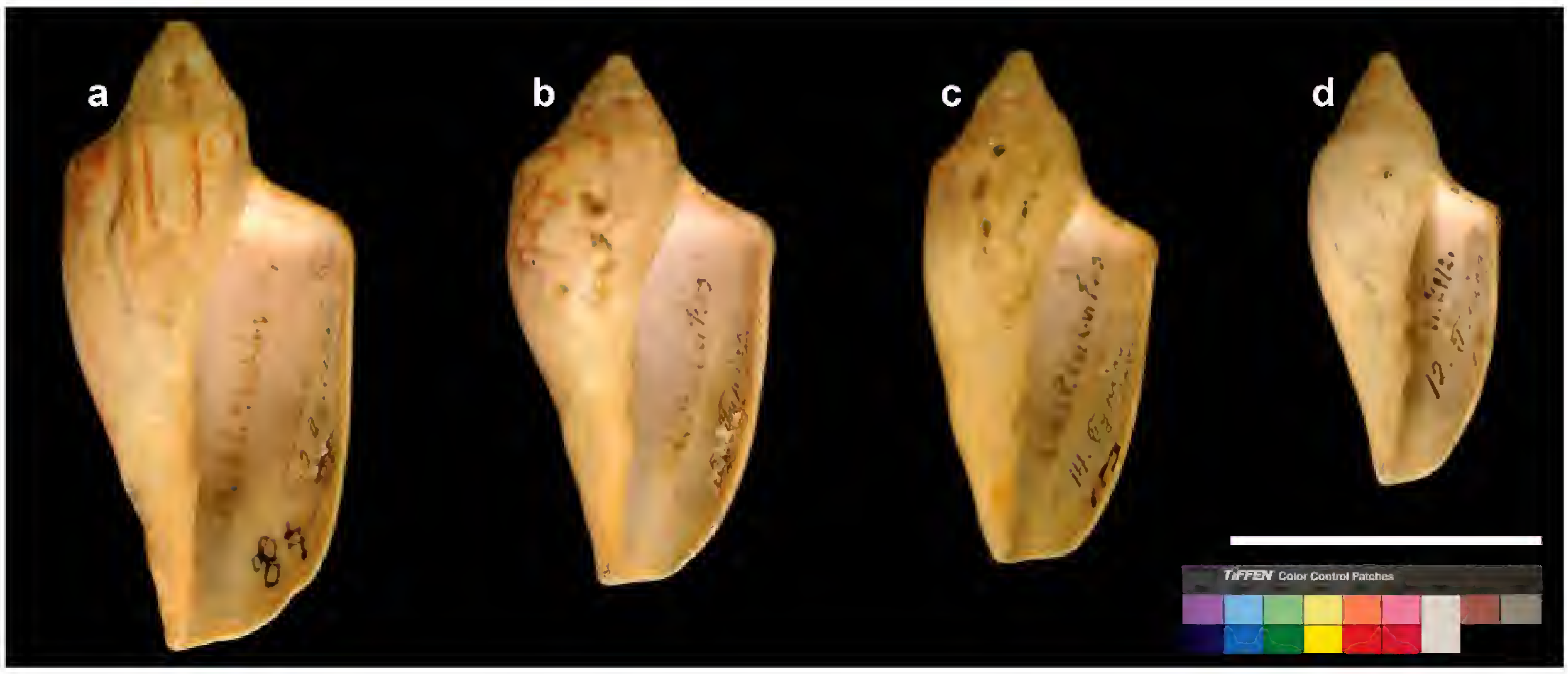

Figure 24. *Voluta angulata similis*, specimens figured by Lahille (1895). See Table 8 for references. Scale bar: 5 cm.

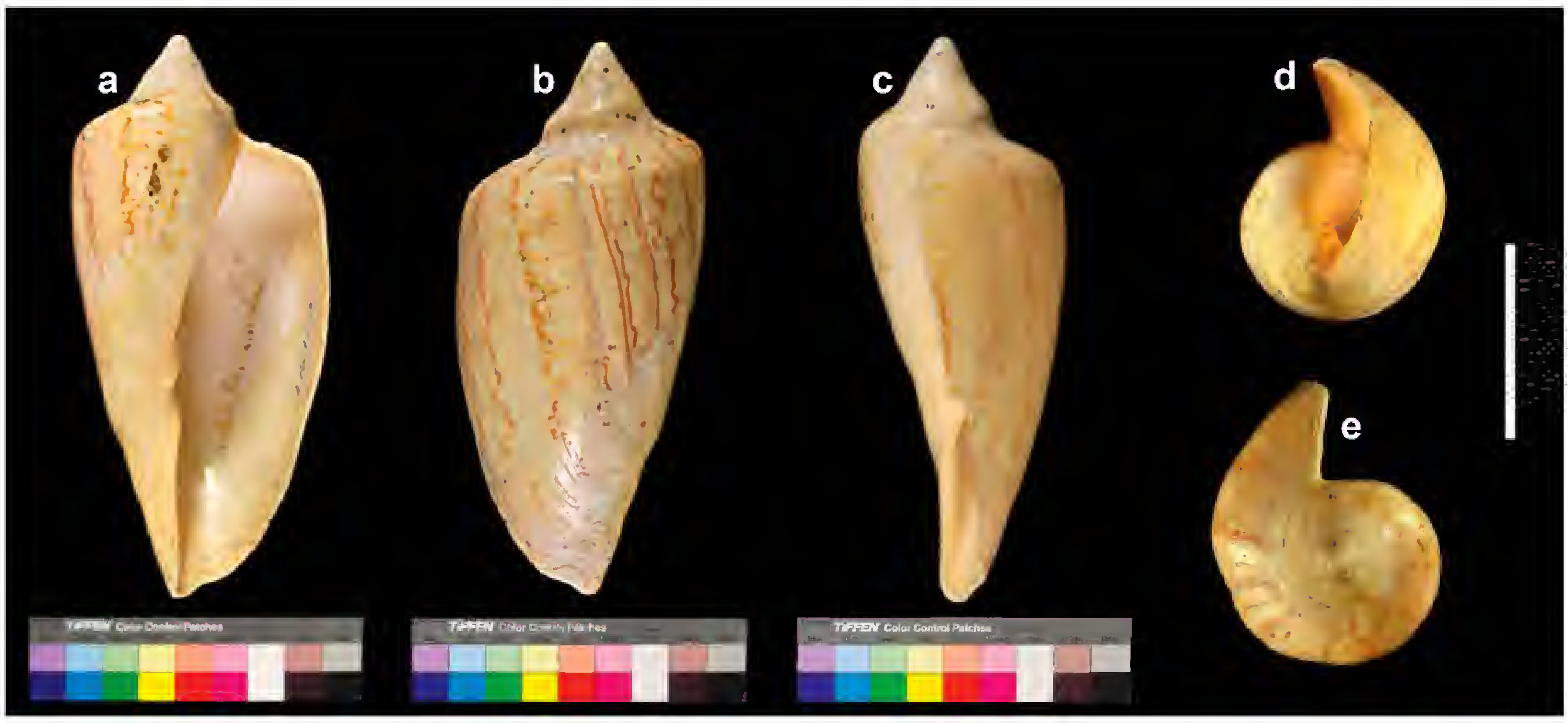

Figure 25. *Voluta angulata ventricosa*, specimen figured by Lahille (1895: pl. VI, fig. 93). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

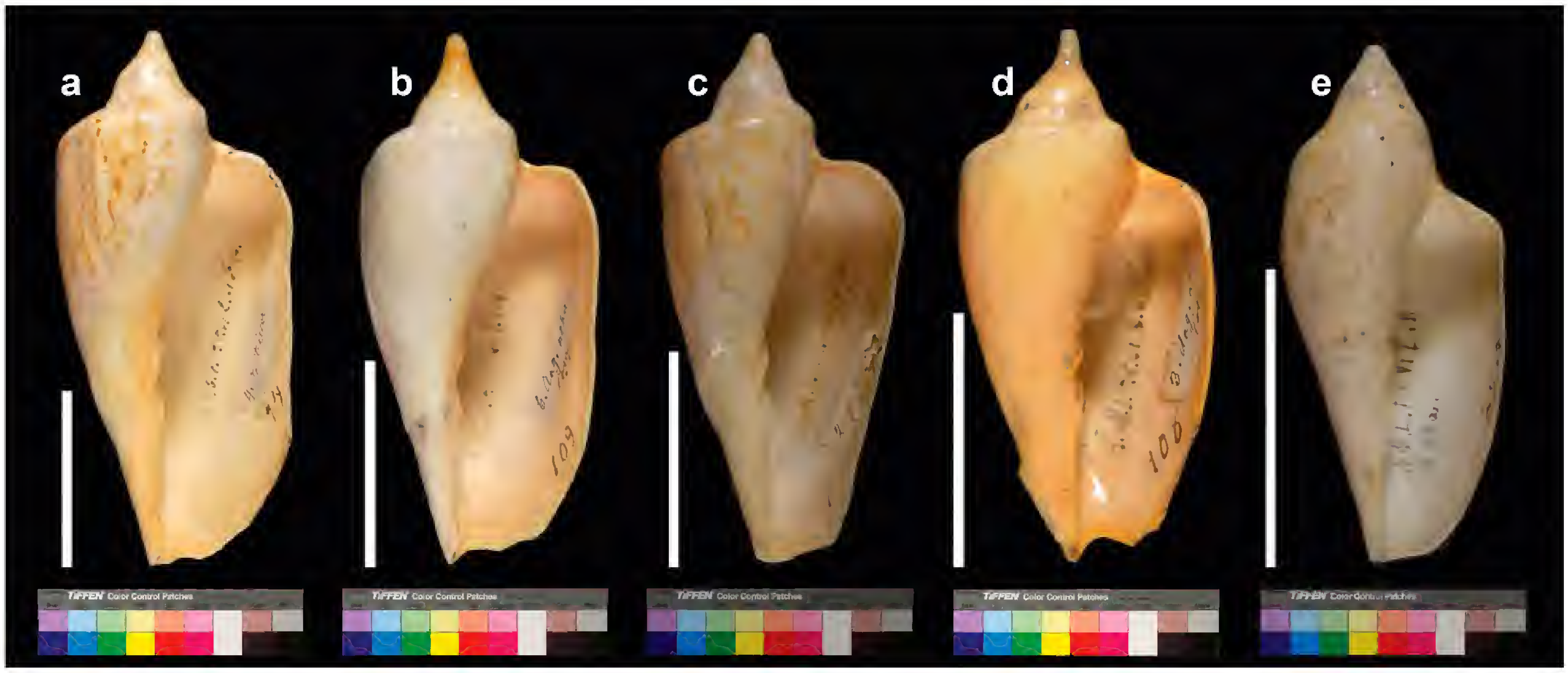

Figure 26. *Voluta angulata ventricosa*, specimens figured by Lahille (1895). See references on Table 9. Scale bars: 5 cm.

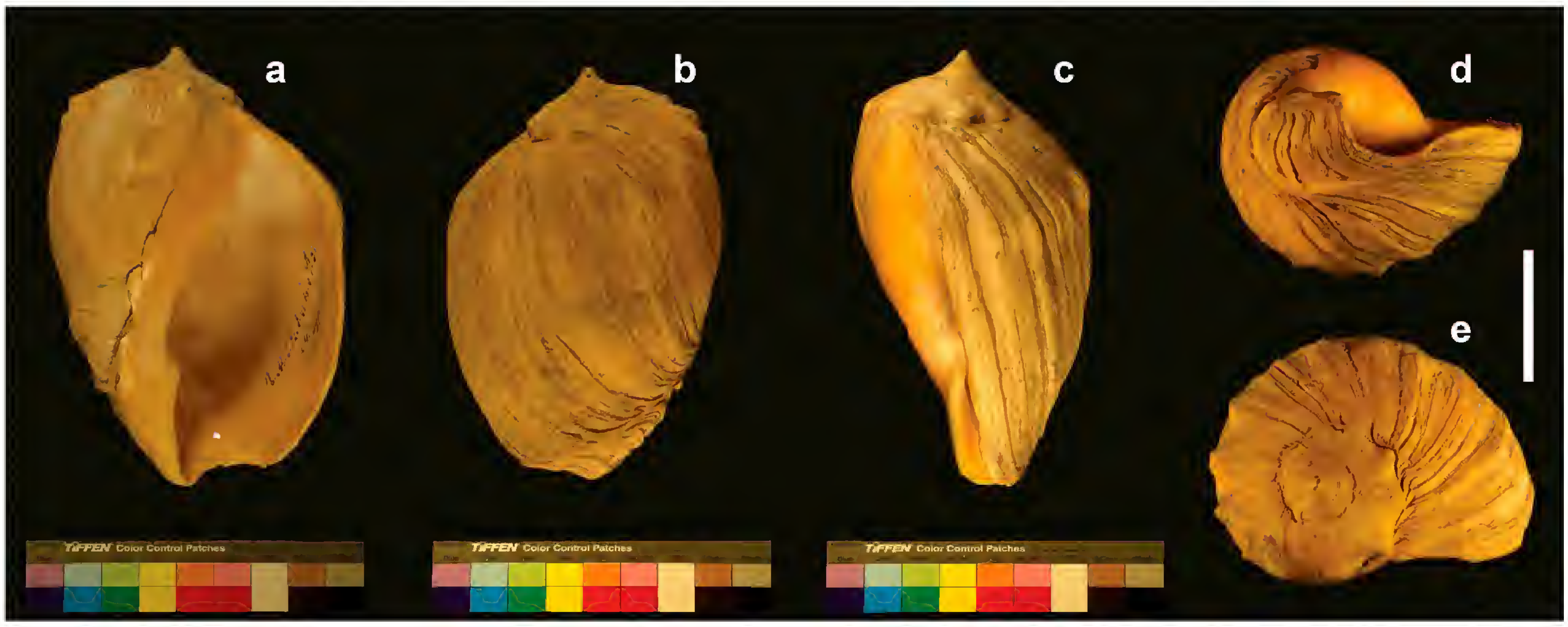

Figure 27. *Voluta colocynthis typica*, specimen figured by Lahille (1895: pl. V, fig. 38) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

This variety is similar to *luteola*, but the last whorl is more expanded and not carinate. The free edge of the aperture forms a curve.

There are five shells that have not been assigned to any variety of this species (MLP-Ma 10872). Two of them were not figured by Lahille (1895). Inscriptions on the remaining three specimens read:

1. "10.*typica jov.*" pl. II, fig. 73 [= *luteola*], pl. VI, fig. 111 [= *similis*].
2. Plate II, fig. 51 [the legend does not indicate the variety].
3. Plate II, fig. 69b [depicts a juvenile specimen].

There are three groups of shells corresponding to *V. angulata* (MLP-Ma 14245). On these shells, are the following inscriptions: "*calcarea*", "*subventricosa*", and "*nebulosa*". These specimens were never described nor figured by Lahille (1895).

Voluta colocynthis (Favane, 1772) Chemnitz

Current name: *Pachycymbiola brasiliana* (Lamarck, 1811).

Lahille (1895) characterised shells of this species as whitish to dark yellow or orange, uniformly coloured, and with juveniles without tubercles. He described nine varieties for this species.

Voluta colocynthis typica Lahille, 1895

Syntypes: MLP-Ma 10876, 11 specimens figured by Lahille (1895) (Table 10), from 45 to 157 mm long; 15 other specimens, adults and juveniles, not figured in Lahille (Figs 27, 28).

According to Lahille (1895), this variety can reach up to 170 mm in length and 130 mm in width. The first three whorls of the spire are smooth; the last whorl covers entirely the tubercles of penultimate whorl. The suture is almost never undulated. The aperture is roughly

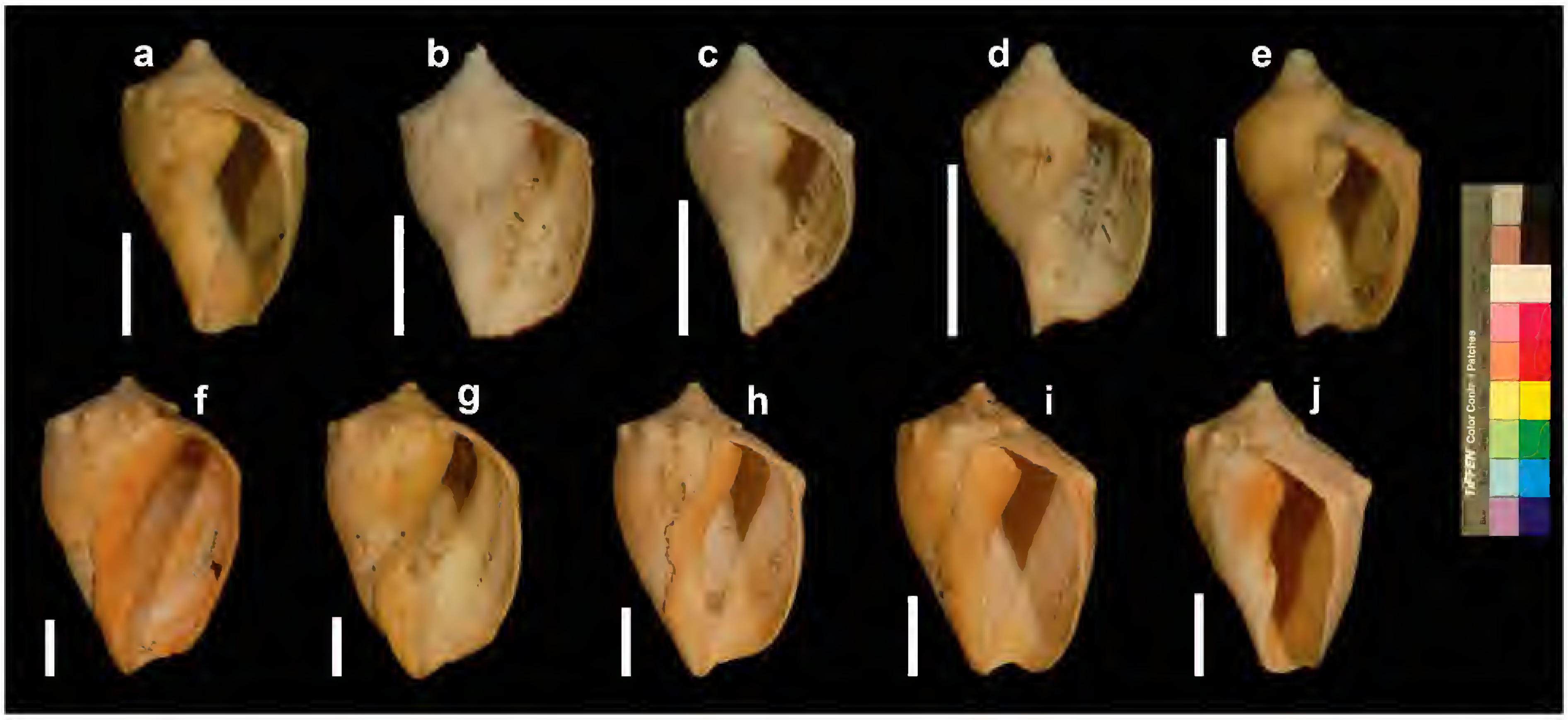

Figure 28. *Voluta colocynthis typica*, specimens figured by Lahille (1895). See references on Table 10. Scale bars: 3 cm.

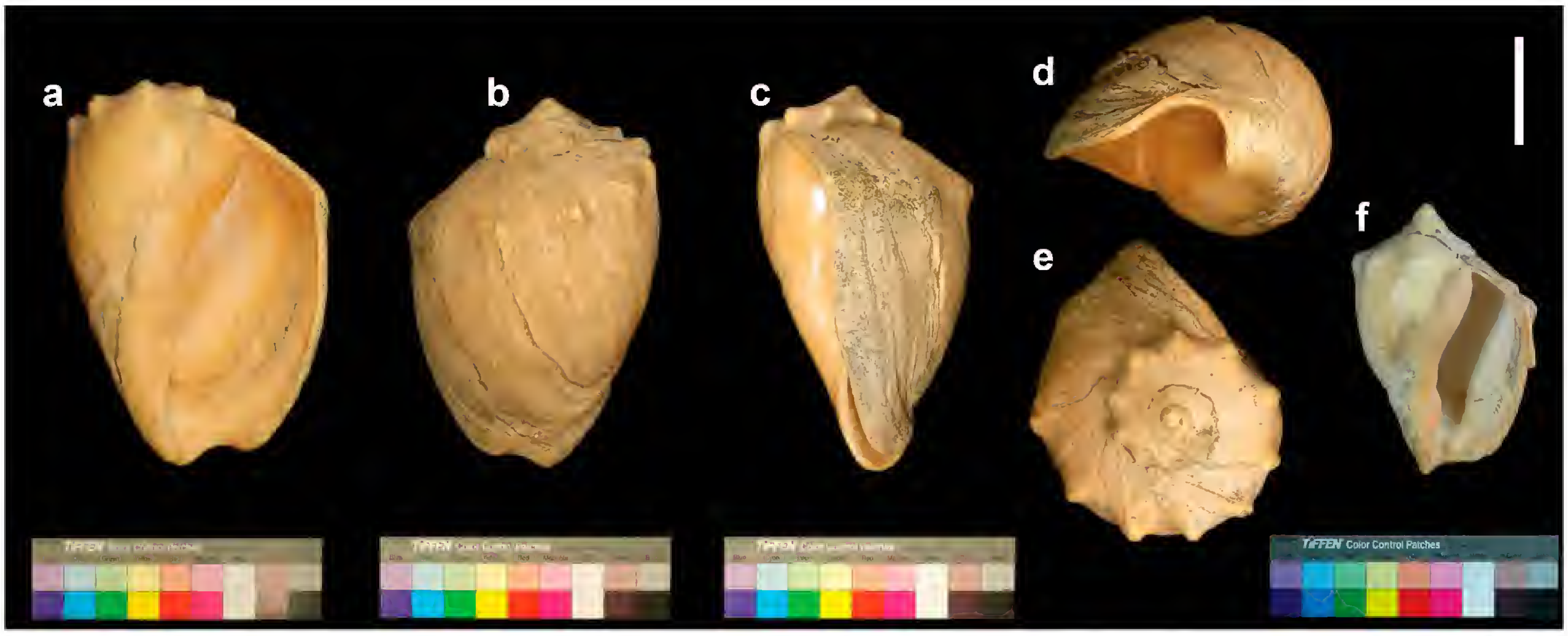

Figure 29. *Voluta colocynthis alternata*, specimens not figured by Lahille (1895). **a–e** Specimen 1 **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Apertural view of specimen 2. Scale bar: 5 cm.

semilunar and white to yellowish-orange. Generally, the shells have two unequal columellar folds. Sometimes the inferior fold fuses with the columella, so it is not visible, while in others, there are two wrinkles on each side of the upper fold. This variety differs from *V. tuberculata* in the absence of zigzag lines on the shell.

Voluta colocynthis alternata Lahille, 1895

Syntypes: MLP-Ma 14247, 2 specimens not figured by Lahille (1895) (Fig. 29).

Lahille described the shells of this variety as more elongated and less conical than those of var. *carinata*. The penultimate whorl is always visible. The nodes of the last two whorls arise usually alternate, giving the name of this variety.

However, this variety was unfigured by Lahille (1895). The only specimen with this name on its shell also has the inscription “L V, F 31”, which indicates its use in plate V, figure 31, which is *typica* according to the plate’s legend.

Voluta colocynthis carinata Lahille, 1895

Holotype: MLP-Ma 10881, 110.5 mm long x 78 mm wide, figured by Lahille (1895: pl. V, fig. 36). Label reads: “511”, “1.*carinata*” (Fig. 30).

Lahille (1895) described this variety as having a conic shell and with the penultimate whorl of the spire almost always separated from the last whorl of the spire. The external edge of the aperture forms an almost straight angle on the upper side, and the tubercles are on the carina.

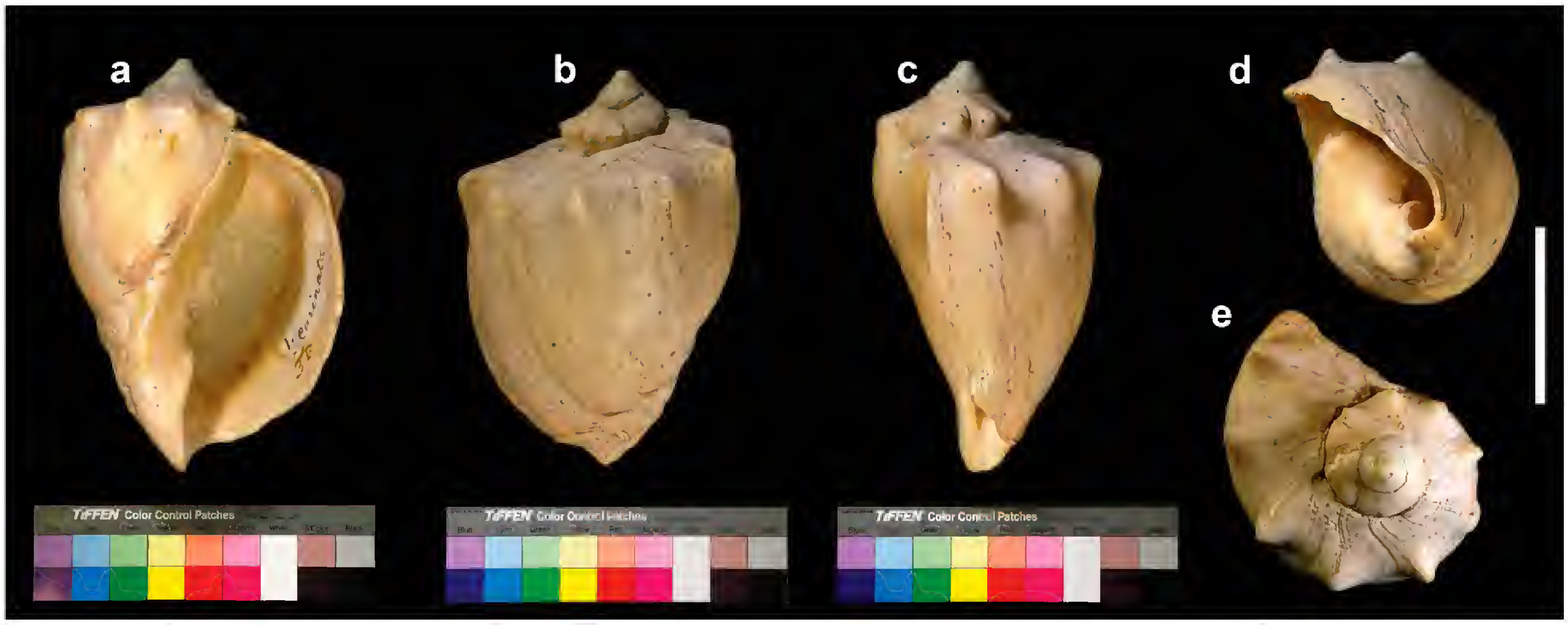

Figure 30. Holotype of *Voluta colocynthis carinata*, figured by Lahille (1895: pl. V, fig. 36) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

Table 10. *Voluta colocynthis typica*, specimens figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. V, fig. 38	"24. *typica*" (figure legend indicates *Voluta colocynthis subtypica*, but this variety is not described in the text)	27
Pl. V, fig. 29	"17. *typica*"	28a
Pl. II, fig. 60; pl. V, fig. 28	"16. *typica*"	28b
Pl. II, fig. 59; pl. V, fig. 27	"4. *typica*"	28c
Pl. II, fig. 58	"13. *typica*"	28d
Pl. II, fig. 57	"11. *typica*"	28e
Pl. V, fig. 35	"12. *typica*"	28f
Pl. V, fig. 34	"11. *typica*"	28g
Pl. V, fig. 33	"457"	28h
Pl. V, fig. 32	"*typica*"	28i
Pl. V, fig. 31	"3. *alternata*"(figure legend indicates *Voluta colocynthis typica*)	28j

Voluta colocynthis depressa Lahille, 1895

Holotype: MLP-Ma 10877, 143.5 mm long × 102 mm wide, figured by Lahille (1895: pl. V, fig. 39). Label reads: "510", "1.*depressa*" (Fig. 31).

According to Lahille (1895), the first few whorls of the spire are small, and form a regularly convex surface. The lower part of the columella has a large inferior fold.

Voluta colocynthis globosa Lahille, 1895

Syntypes: MLP-Ma 10880, 2 specimens figured by Lahille (1895) (Table 11). Specimens over 170 mm long, width approximately 65% of total length (Fig. 32).

Lahille (1895) described this variety as similar to *V. colocynthis intermedia*, but the shells are much more globose and always with tubercles on the last whorl of the spire. The first part of the last whorl rarely has nodes. The specimens are large, up to 200 mm long and 132 mm wide.

Table 11. *Voluta colocynthis globosa*, specimens figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. V, fig. 49	"1. *globosa*" 508	32a-e
Pl. I, fig. 3	"2. *globosa*" 509	32f

Voluta colocynthis intermedia Lahille, 1895

Syntypes: MLP-Ma 10882, 4 specimens figured by Lahille (1895) (Table 12); 4 other specimens not figured by Lahille (Figs 33, 34).

According to Lahille (1895), the shells of this variety are ovoid, up to 160 mm long and 110 mm wide, always without tubercles on the final half the last whorl or with tubercles rudimentary only. The free edge of the aperture is usually rounded. The penultimate whorl of the spire is completely hidden by the last one, the suture is rarely undulated, and there are two columellar folds which are mostly unequal.

Voluta colocynthis lactea Lahille, 1895

Syntypes: MLP-Ma 10878, 2 specimens figured by Lahille (1895) (Table 13), label reads: "*zonaria*", which does not appear in Lahille's publication. Both shells are up to 70 mm long (Fig. 35).

Lahille described *lactea* variety based on five specimens from Mar Chiquita, Buenos Aires Province. The shells are matte white, with a striped appearance due to growth lines. The free edge of the aperture is regularly rounded. The columella is arched, with three equal folds.

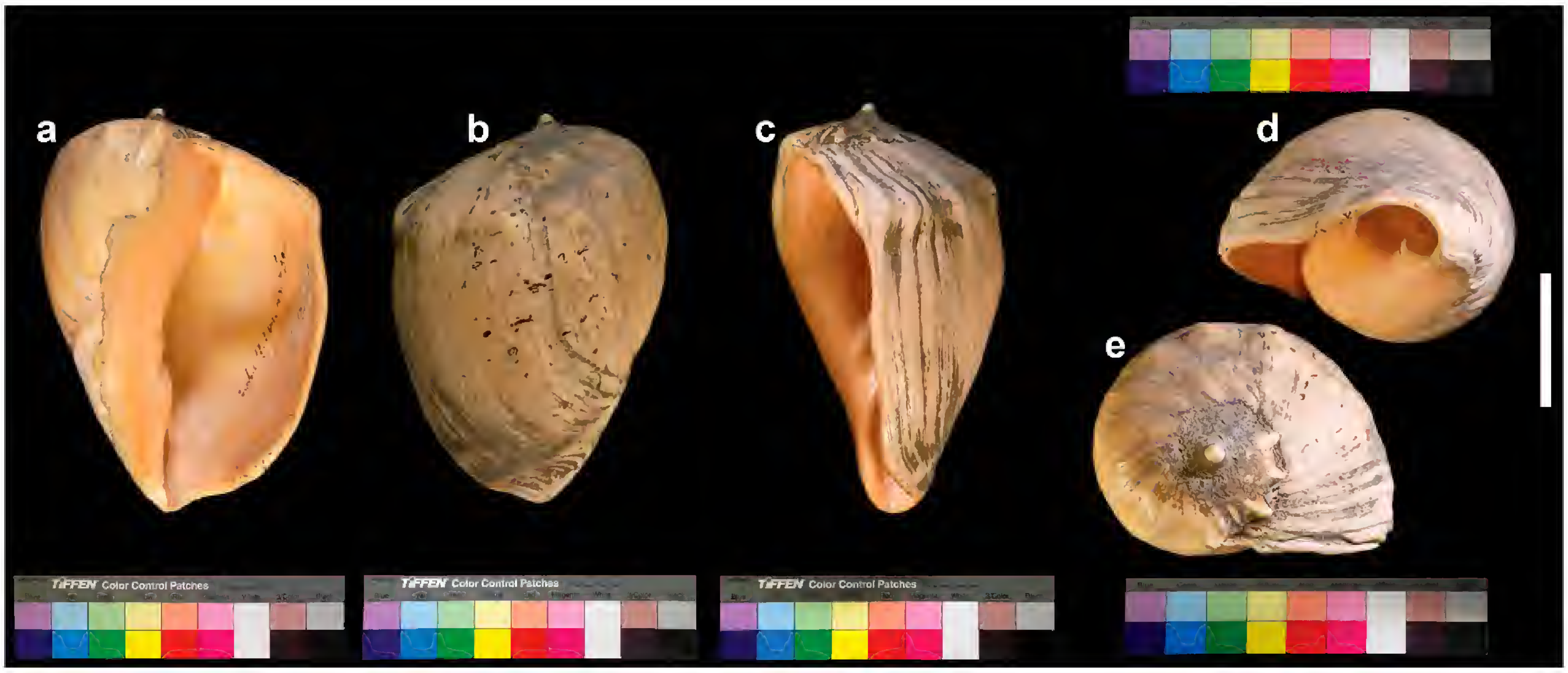

Figure 31. Holotype of *Voluta colocynthis depressa*, figured by Lahille (1895: pl. V, fig. 39) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

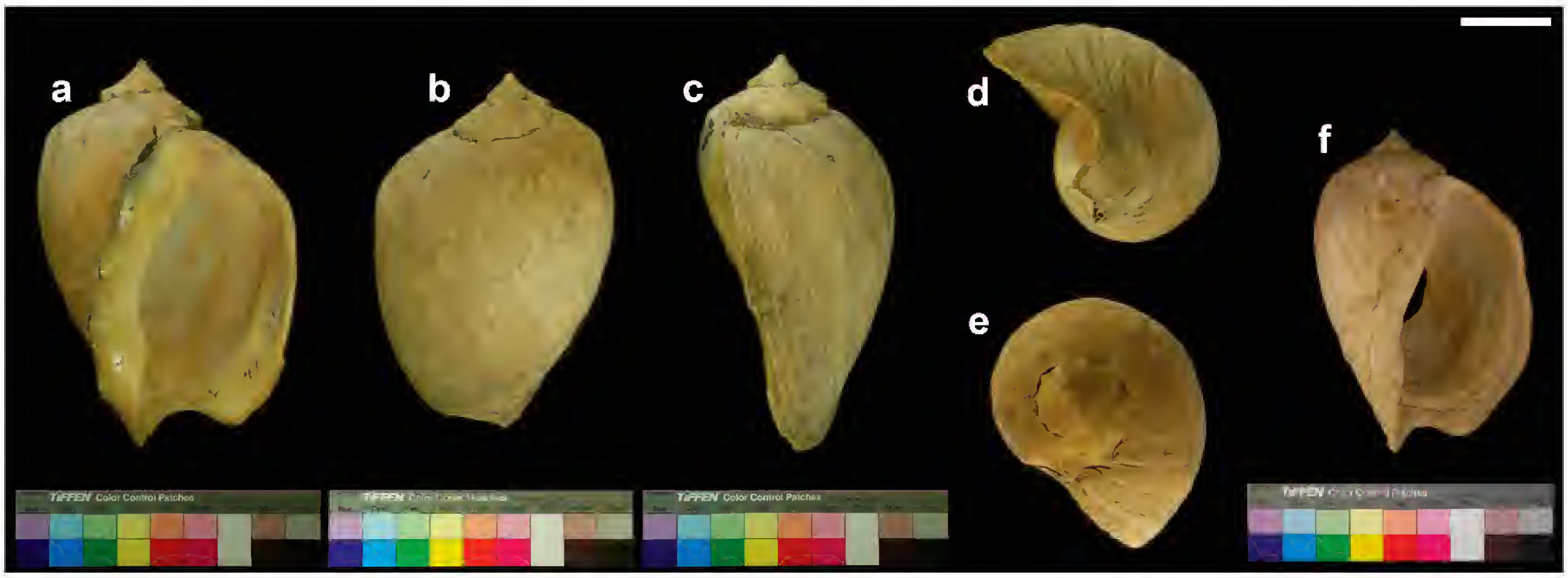

Figure 32. *Voluta colocynthis globosa*. **a–e** Specimen figured by Lahille (1895: pl. V, fig. 49) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. I, fig. 3) in apertural view. Scale bar: 5 cm.

Table 12. *Voluta colocynthis intermedia*, specimens figured by Lahille (1895), with the detail of the inscriptions on their shells and figures here.

Figure of Lahille (1895)	Detail	Figure
Pl. V, fig. 47	"10.*Intermedia*"	33
Pl. V, fig. 46	"9.*Intermedia*"	34a
Pl. V, fig. 44	"5.*Intermedia*"	34b
Pl. V, fig. 42; pl. VII, fig. 138 (this last figure is not mentioned in the legend)	"1.*Intermedia*"	34c

The spire has five whorls, the first two smooth and the last three with strong nodes. The suture is undulate. The last whorl is without a carina but with tubercles from which arise rudimentary longitudinal ribs. The specimens are up to 70 mm long and 45 mm wide and heavier than *V. colocynthis typica*.

Table 13. Specimens of *Voluta colocynthis lactea* figured by Lahille (1895), with the detail of the inscriptions on their shells and figures here.

Figure of Lahille (1895)	Detail	Figure
Pl. X, fig. 3	"2. *zonaria*"	35a–e
Pl. X, fig. 1	"1. *zonaria*"	35f

Voluta colocynthis spirabilis Lahille, 1895

Syntypes: MLP-Ma 10879, 1 specimen figured by Lahille (1895: pl. I, fig. 4; pl. V, fig. 37); 1 other specimen not figured by Lahille, ca 170 mm long × 107 mm wide and labelled: "516" and "2.*spirabilis*" (Fig. 36).

The shells have the spire tall. The nodes on the last whorl of the spire are accentuated and rise above the suture. In large specimens, the upper angle of the aperture is 20–25 mm from the nodes.

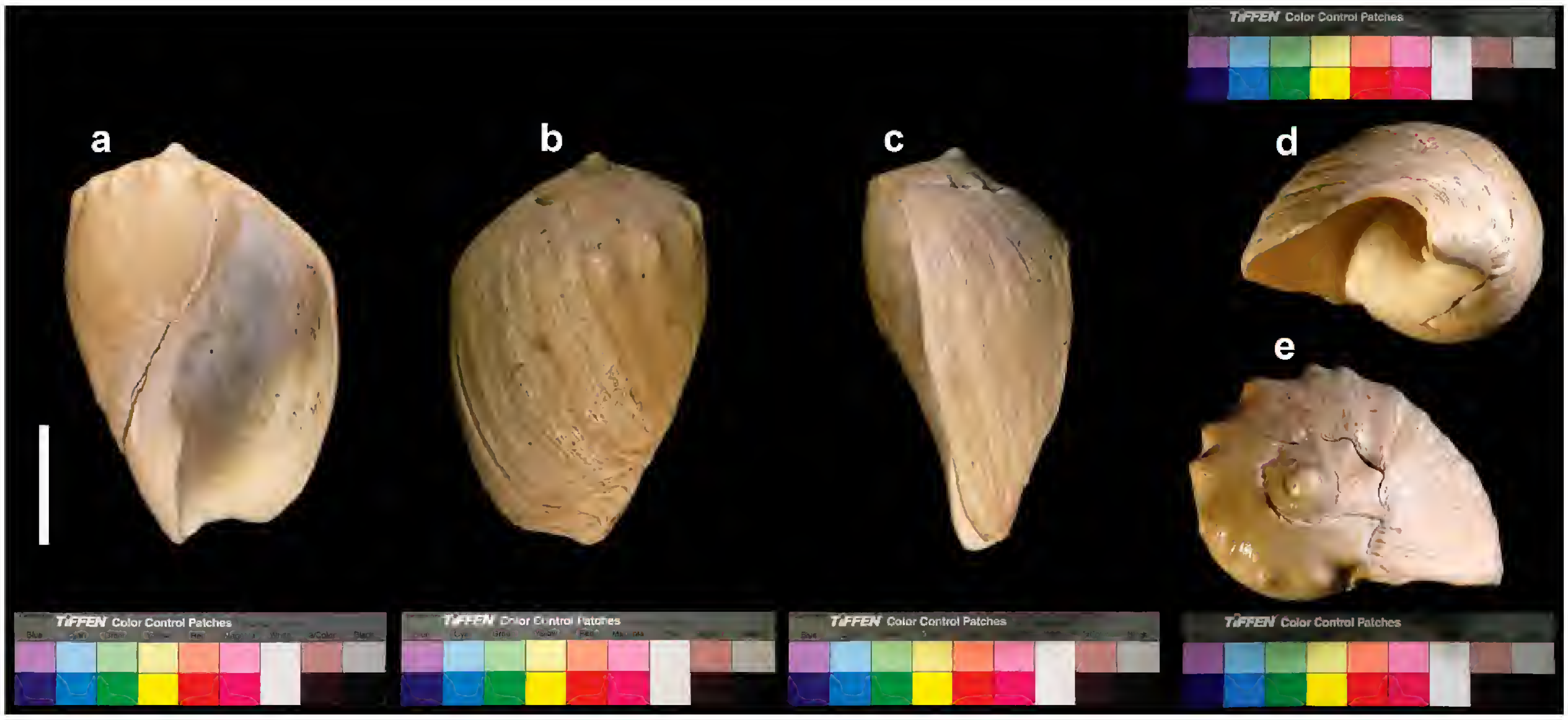

Figure 33. *Voluta colocynthis intermedia*, specimen figured by Lahille (1895: pl. V, fig. 47) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

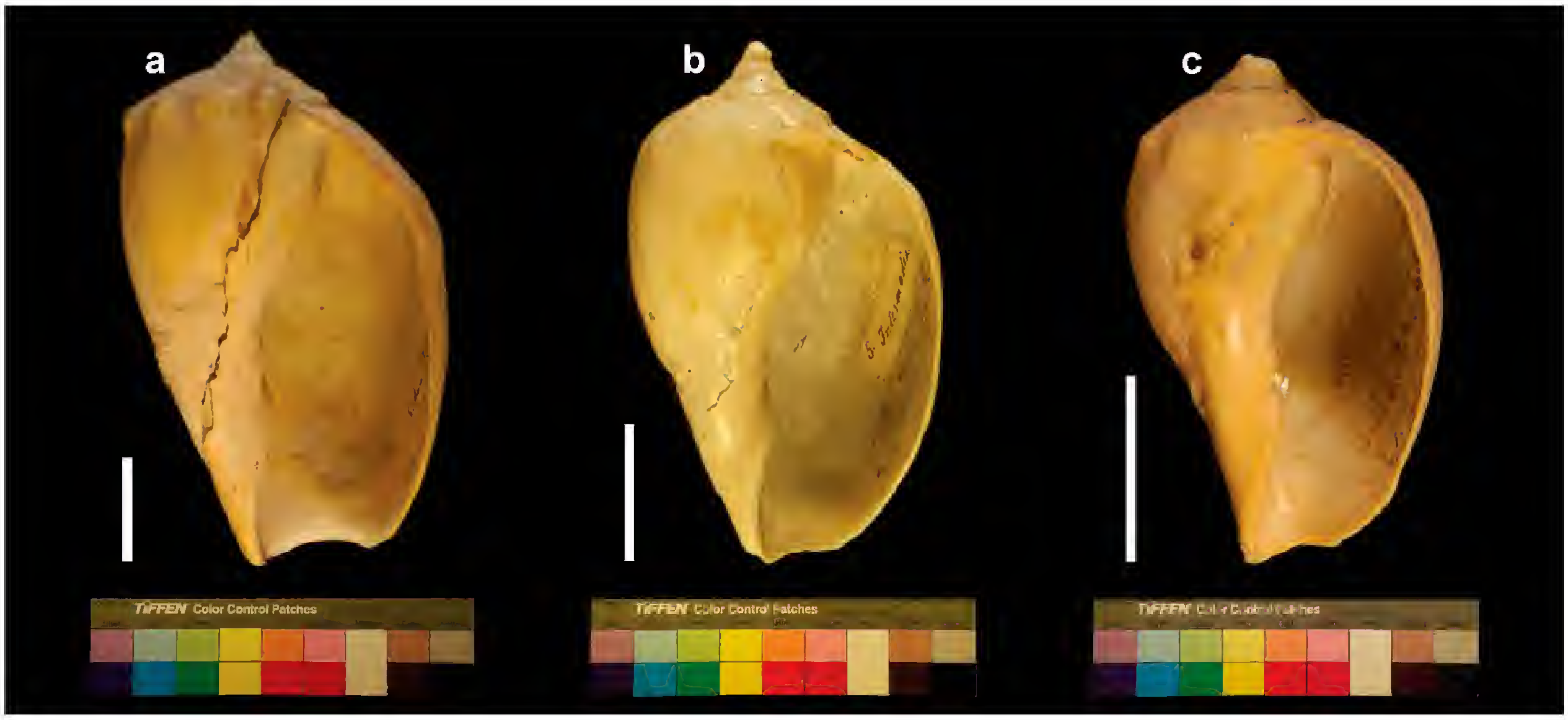

Figure 34. *Voluta colocynthis intermedia*, specimens figured by Lahille (1895). See references on Table 12. Scale bars: 3 cm.

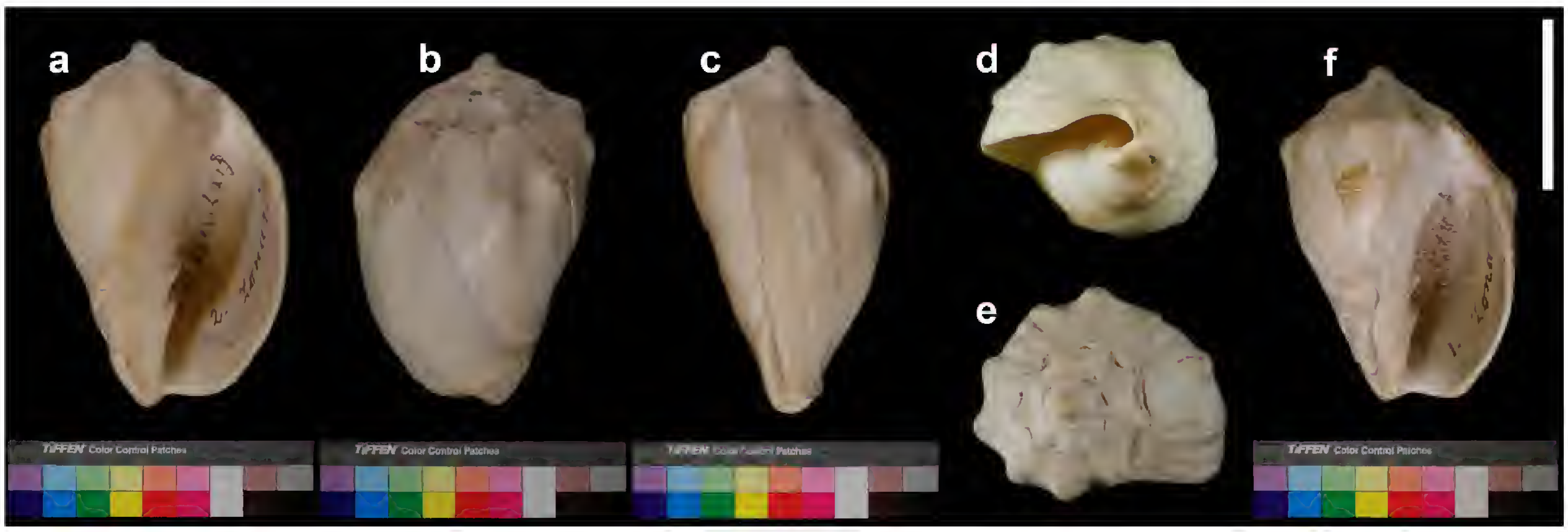

Figure 35. Syntypes of *Voluta colocynthis lactea*. **a–e** Specimen figured by Lahille (1895: pl. X, fig. 3) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. X, fig. 1) in apertural view. Scale bar: 3 cm.

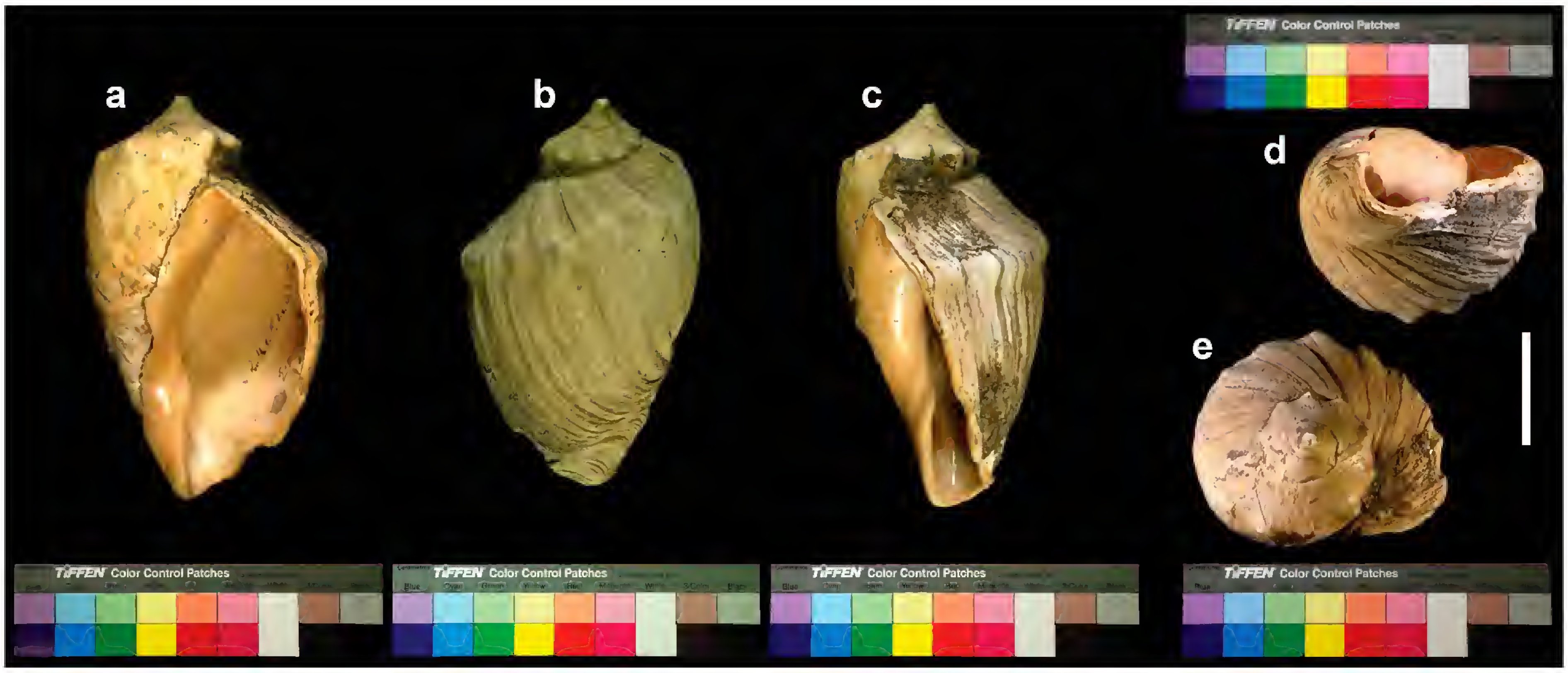

Figure 36. *Voluta colocynthis spirabilis*, specimen figured by Lahille (1895: pl. I, fig. 4; pl. V, fig. 37) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

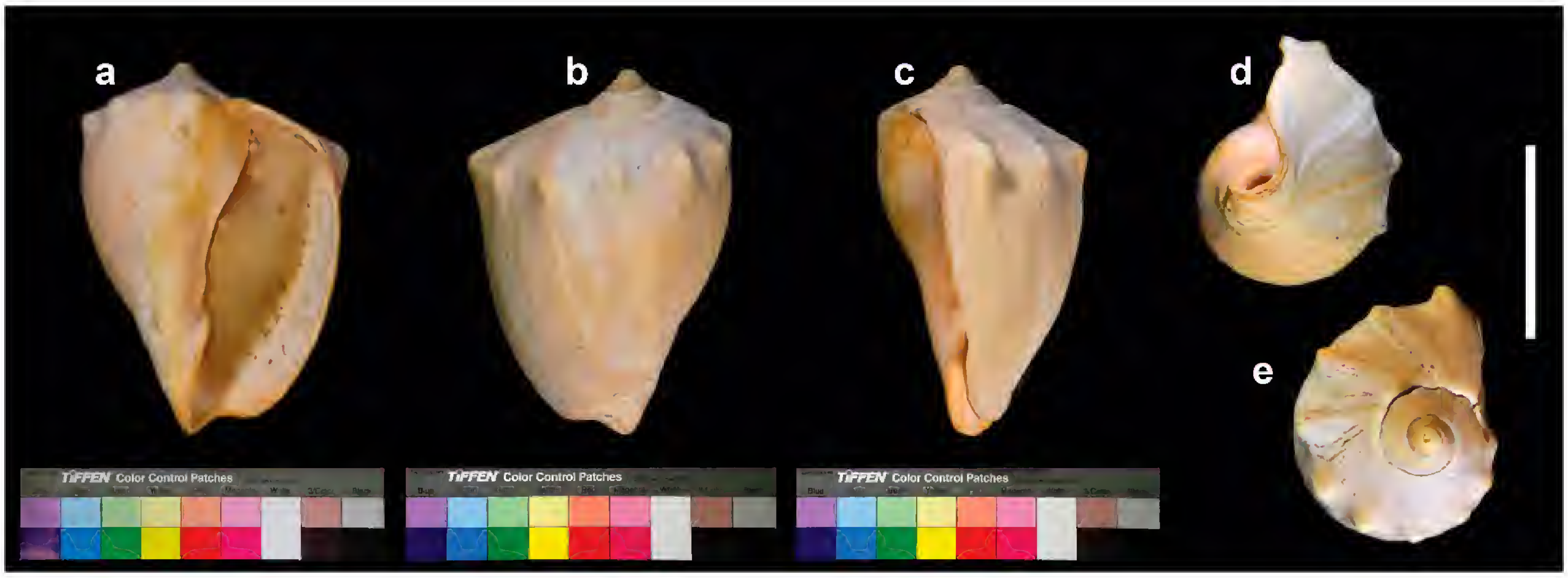

Figure 37. *Voluta colocynthis subcarinata*, specimen figured by Lahille (1895: pl. V, fig. 30) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

Voluta colocynthis subcarinata Lahille, 1895

Holotype: MLP-Ma 10875, 92 mm long × 66 mm wide, figured by Lahille (1895: pl. V, fig. 30). Label reads: Plate V, Fig. 30 "19.*typica*" (Fig. 37).

Lahille (1895) mentioned only that this variety is intermediate between the *typica* and the *carinata* varieties.

Specimens matching *Voluta colocynthis pseudomagellanica* Lahille, 1895 have not been found in the MLP Collection. There are two shells (MLP-Ma 14246) with inscriptions referring to plate II, figure 50 and plate II, figure 69a but not assigned to any variety of this species.

Voluta fusiformis Kiener, 1839

Current name: *Adelomelon beckii* (Broderip, 1836).

Lahille (1895) mentioned that the shells are up to 350 mm long and 170 mm wide, yellow or sometimes very pale, with yellowish-orange longitudinal zigzag lines that align to each node. There are narrow, slightly undulating spiral striae, which are sometimes cut by narrow growth lines. The spire of adults has eight whorls; the first three whorls are generally smooth and form a button. The lower sides of the nodes are prolonged into ribs, which are attenuate or disappear in adults. In large individuals, the nodes of the last whorl form a transverse fold.

Voluta fusiformis typica Lahille, 1895

Syntypes: MLP-Ma 14248, 3 specimens not figured by Lahille (1895). One shell reads "Typos Dr Lahille 502 4.*Typica*", other "Typos Dr Lahille 503", and other "1.*Fusiform. typica*" (Fig. 38).

According to Lahille (1895), the shell of this variety has no tubercles on the last whorl, or rarely, a small carina marks a tubercle line.

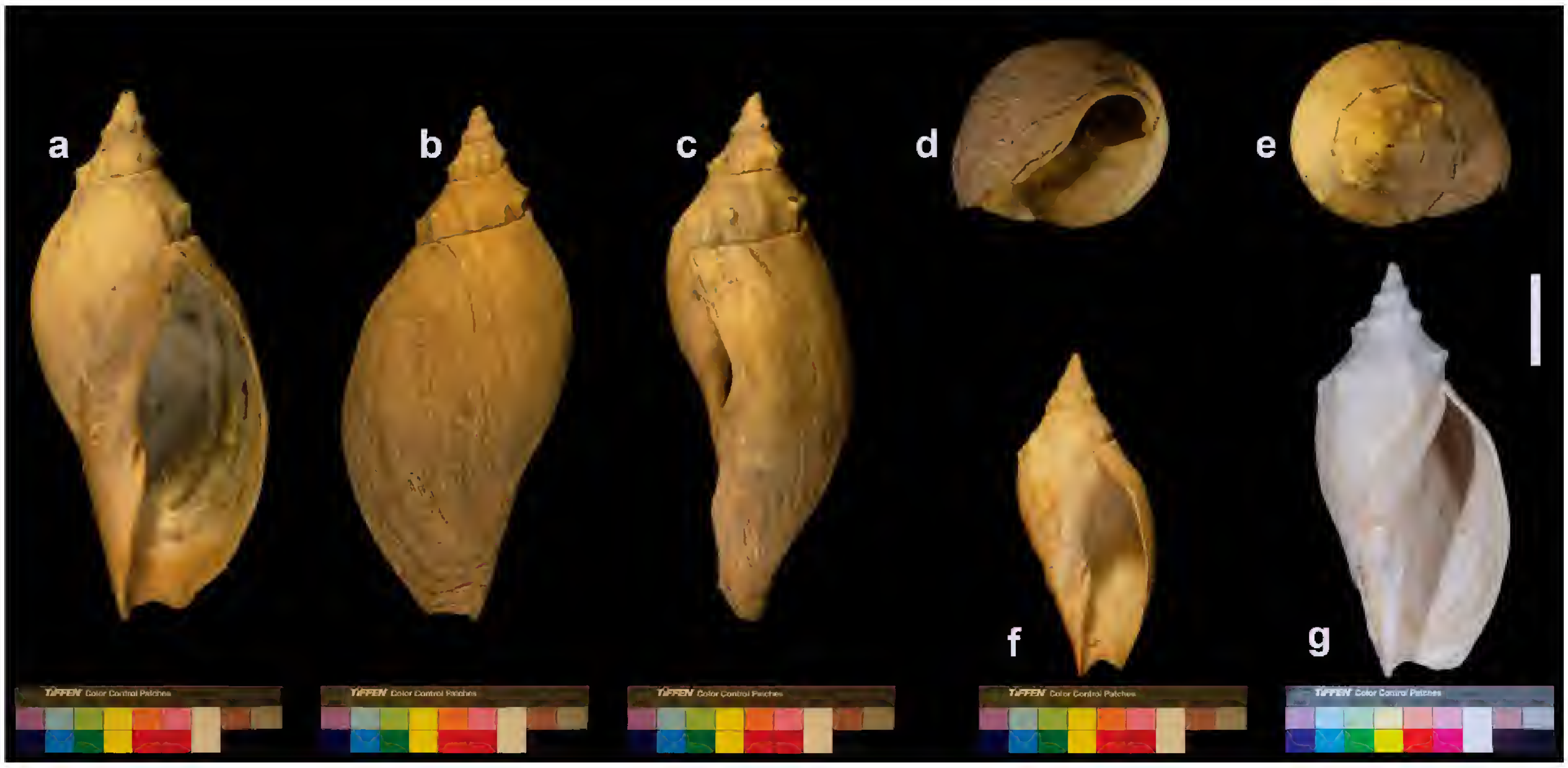

Figure 38. Specimens of *Voluta fusiformis typica*. **a–e** Specimen 1 **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen 2 **g** Specimen 3. Scale bar: 5 cm.

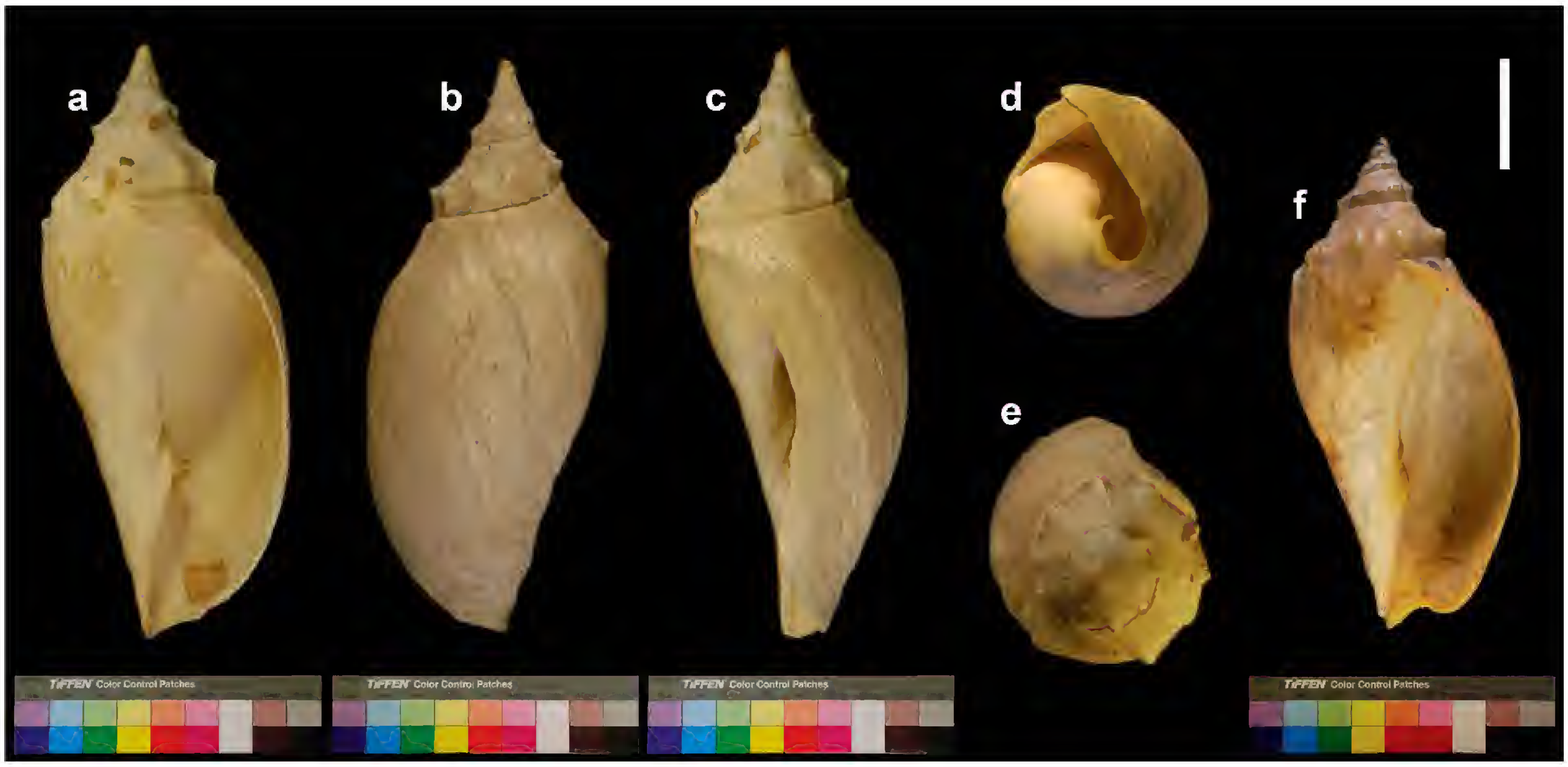

Figure 39. *Voluta fusiformis connexa*. **a–e** Specimen figured by Lahille (1895: pl. III, fig. 20) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. III, fig. 19) in apertural view. Scale bar: 5 cm.

Voluta fusiformis connexa Lahille, 1895

Syntypes: MLP-Ma 10883, 2 specimens figured by Lahille (1895) (Table 14), ca 213 mm and 257 mm long; 2 other specimens not figured by Lahille (Fig. 39).

This variety has few, well-spaced nodes on the last whorl of the spire.

Voluta fusiformis ornata Lahille, 1895

Syntypes: MLP-Ma 10885, 2 specimens figured by Lahille (1895) (Table 15), ca 86 mm long × 41.5 mm wide, and 109 mm long × 55 mm wide ; 4 other specimens not figured by Lahille (Fig. 40).

The shells have very strong tubercles on the last whorl. These are located on a small crest from which rudimentary longitudinal riblets spread out.

Table 14. Specimens of *Voluta fusiformis connexa* figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. III, fig. 20	506 "4.*connexa*"	39a-e
Pl. III, fig. 19	505 "3.*connexa*"	39f

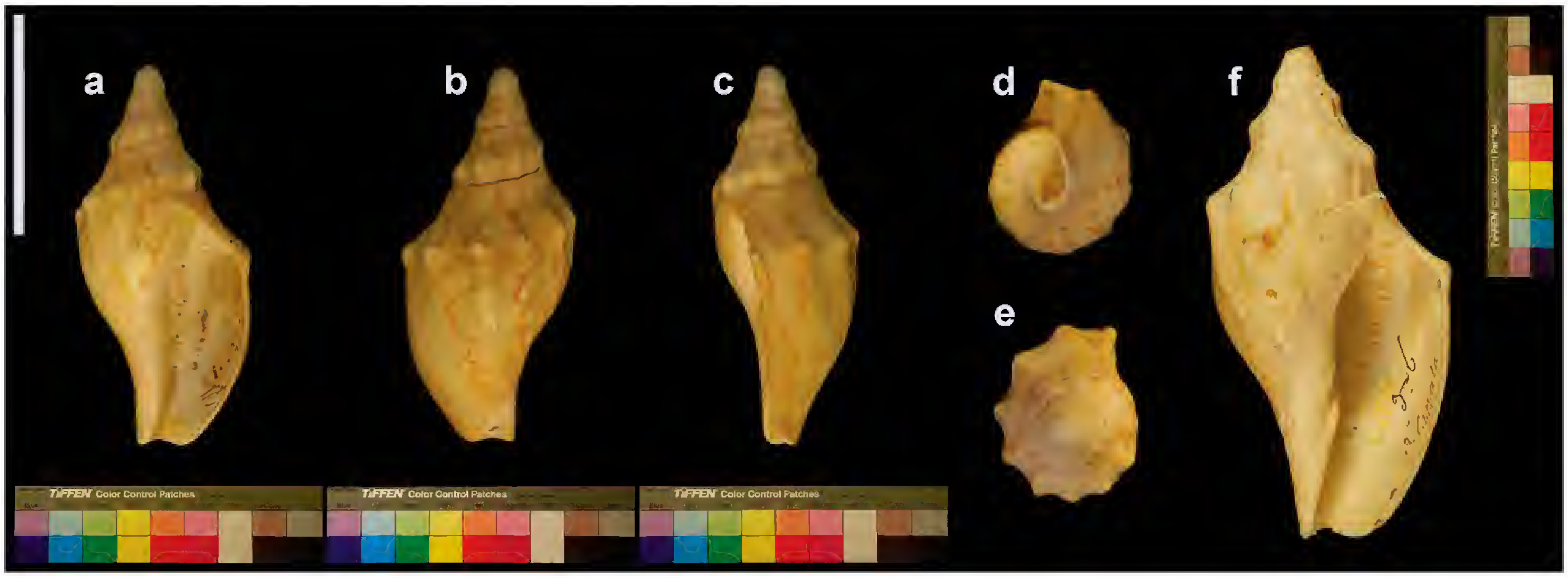

Figure 40. *Voluta fusiformis ornata*. **a–e** Specimen figured by Lahille (1895: pl. III, fig.16; pl. IV figs 24, 25) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. III, fig. 17; pl. IV, fig. 26). Scales bar: 5 cm.

Voluta magellanica Chemnitz, 1788

Current name: *Adelomelon ancilla* (Lightfoot, 1786).

Lahille (1895) remarked on the similarity with *V. ambigua* and *V. ancilla*. *Voluta ambigua* has three coloured longitudinal lines that wide in some points; this character is not present in *V. ancilla*. Lahille (1895) described three varieties.

Voluta magellanica typica Lahille, 1895

Syntypes: MLP-Ma 10888, 3 specimens figured by Lahille (1895) (Table 16), the largest ca 135 mm long × 61 mm wide; 14 other specimens unfigured by Lahille (1895) (Fig. 41).

Lahille (1895) described the shell of this variety as reaching 180 mm long by 90 mm wide, with six convex whorls on the spire. The shells vary from white to pale brown, with prominent dark lines. The aperture is almost oval and orange, pink, or light purple, with thin edges, and the lower columellar fold is not well developed. The juvenile forms have a reticulated surface, without tubercles; they have general aspect of *V. ancilla* but a little wider. The syntypes were divided into two series by Lahille.

Voluta magellanica curta Lahille, 1895

Holotype: MLP-Ma 10886, 134 mm long × 72 mm wide. The specimen could not be matched to any figure by Lahille (1895). Label reads "*curta*" (Fig. 42).

According to Lahille (1895), this variety has a very depressed shell, with the last whorl globose, and with the aperture triangular, wider at the base. Three are strong, horizontal colour bands on the last whorl.

Voluta magellanica taeniolata Lahille, 1895

Holotype: MLP-Ma 10887, 158 mm long × 84.5 mm wide, figured by Lahille (1895: pl. VII, fig. 154) (Fig. 43).

Table 15. Specimens of *Voluta fusiformis ornata* figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. III, fig. 16; pl. IV, figs 24, 25	"1.*ornata*"	40a-e
Pl. III, fig. 17; pl. IV, fig. 26	"3.*ornata*"	40f

Table 16. Specimens of *Voluta magellanica typica* figured in Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. VIII, fig. 175	"17.*Mag.typica* (2°S)"	41a-e
Pl. VIII, fig. 172; pl. XII, Fig. 36	"Chubut"	41f
Pl. II, fig. 65; pl. VIII, fig. 173	"10.*Magellanica typica*"	41g

According with Lahille (1895), this variety is similar to *V. magellanica curta*, but the aperture is semicircular and the columellar edge is deeply indented at the folds. The specimens of this variety can reach up to 150 mm long and 90 mm wide.

Voluta oviformis Lahille, 1895

Current name: *Adelomelon ferussacii* (Donovan, 1824).

Lahille (1895) described this species and three varieties. This material was revised by Wiggers and Veitenheimer-Mendes (2004), who considered it to be a synonym of *Adelomelon ferussacii* (Donovan, 1824).

Voluta oviformis typica Lahille, 1895

Syntypes: MLP-Ma 10890, 19 specimens figured by Lahille (1895) (Table 17); 4 other specimens not figured by Lahille (Figs 44, 45).

Lahille (1895) described this variety as having an ovoid, heavy and smooth, uniformly grey or dark brown shell, with irregular growth lines. The shells become thick, and in

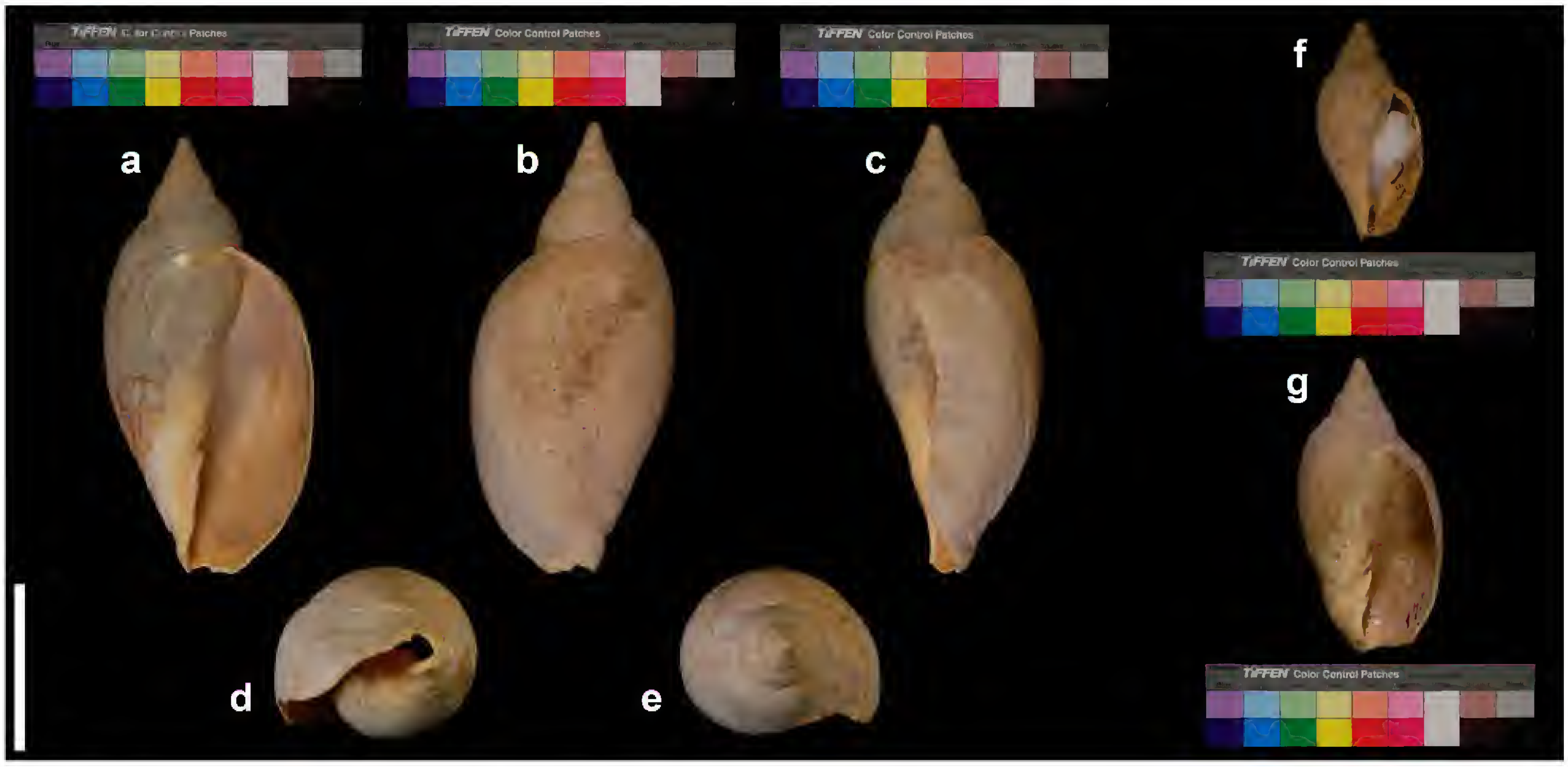

Figure 41. *Voluta magellanica typica*. **a–e:** Specimen figured by Lahille (1895: pl. VIII, fig. 175) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f–g** Apertural view of two other specimens figured by Lahille (1895), see references on Table 16. Scale bar: 5 cm.

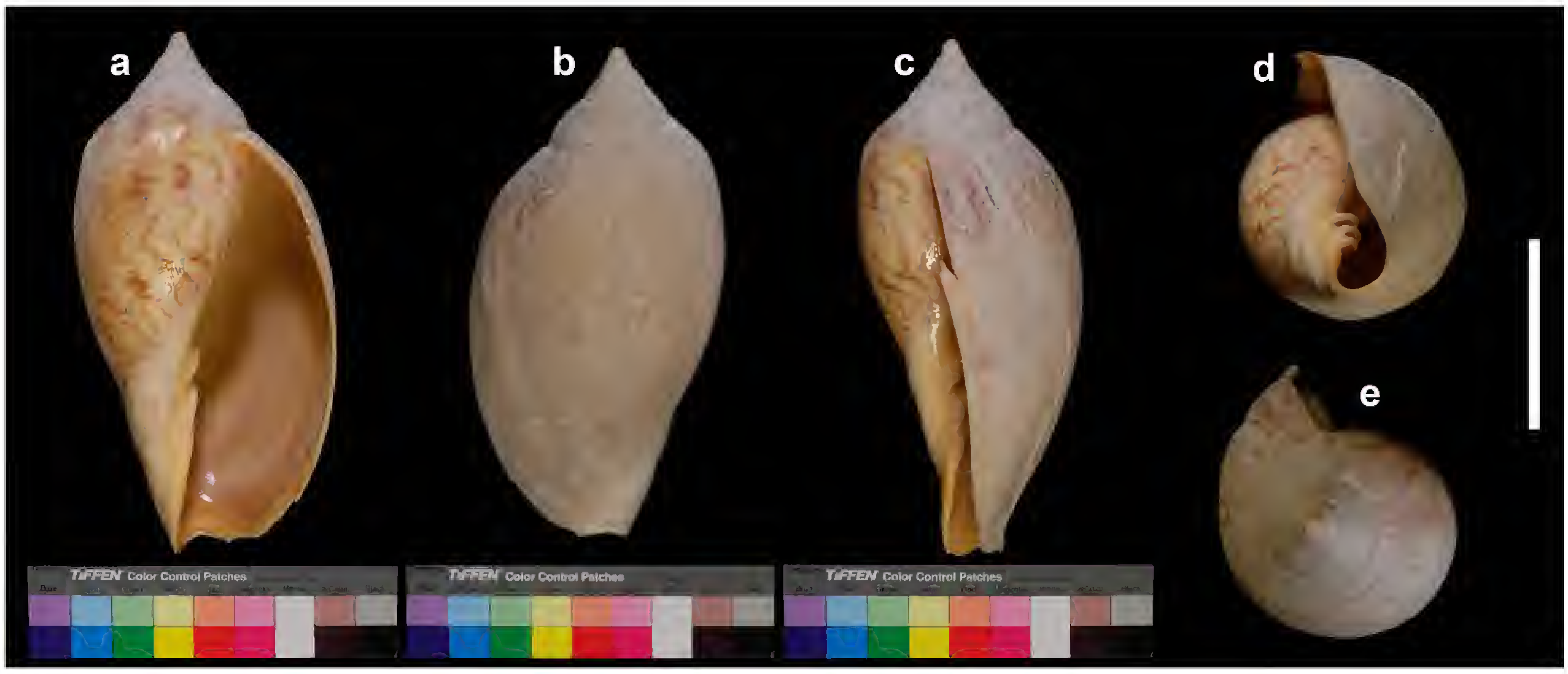

Figure 42. Holotype of *Voluta magellanica curta*. **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

old specimens, the free edge of the aperture is up to 7 mm thick. The largest specimens reach 125 mm long and 85 mm wide and weighing up to 270 g. The spire has five or six whorls. The columella is thick, white or yellowish, and with four to five folds, of which the inferior is more developed.

Voluta oviformis fratercula Lahille, 1895

Syntypes: MLP-Ma 10891, 2 specimens figured by Lahille (1895) (Table 18; Fig. 46).

According to Lahille (1895), this variety lacks tubercles but has a carina on the final part of the last whorl, which results in an angle on the free edge of the aperture, and a less pronounced carine next to the suture.

Voluta oviformis longiuscula Lahille, 1895

Holotype: MLP-Ma 14249, 92 mm long × 55 mm wide, figured by Lahille (1895: pl. VII, fig. 136). Label reads: "1.*Longiuscula*". (Fig. 47).

According to Lahille (1895), this variety has the spire uniformly convex and the last whorl of the spire is very convex. The free edge of the aperture forms a regular curve.

Voluta paradoxa Lahille, 1895

Current name: *Odontocymbiola magellanica* (Gmelin, 1791).

Lahille (1895) described this species without varieties.

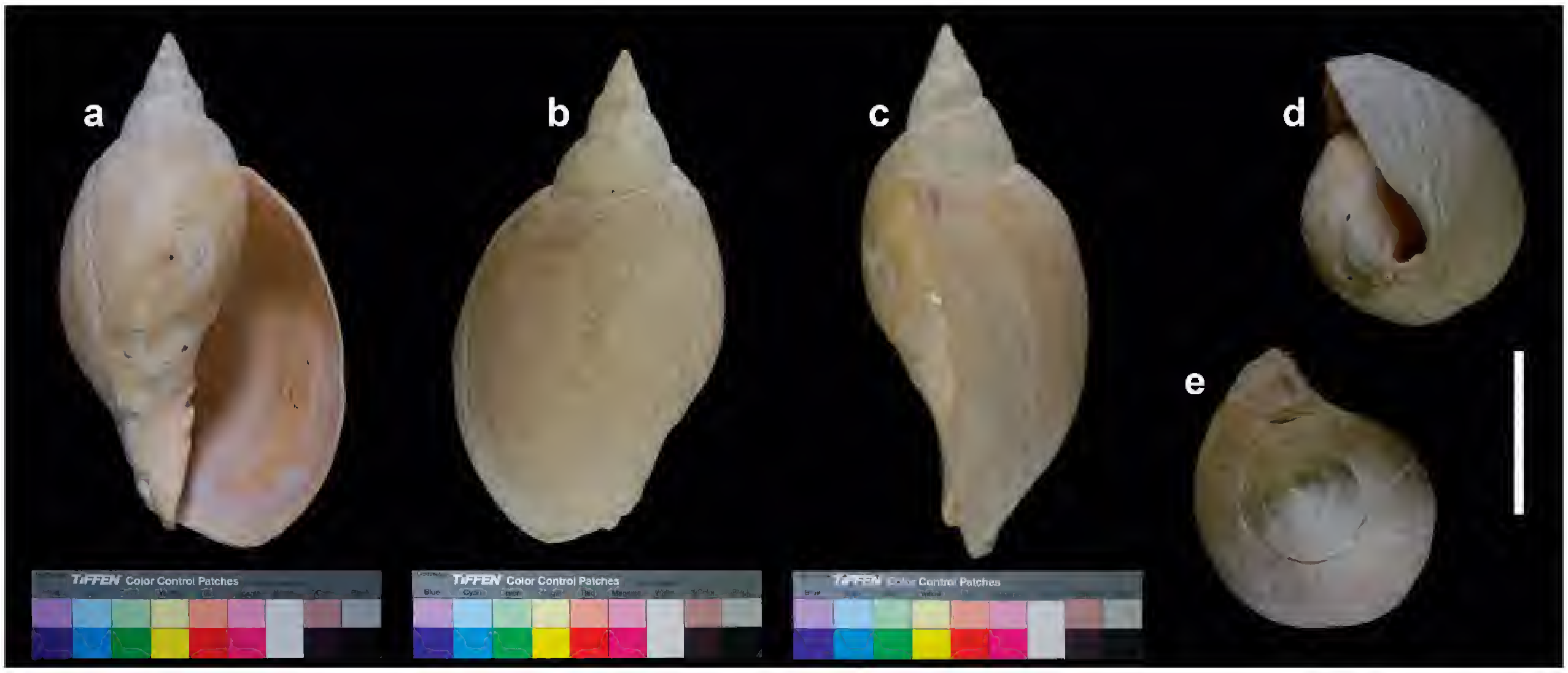

Figure 43. *Voluta magellanica taeniolata*, holotype figured by Lahille (1895: pl. VII, fig. 154) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

Table 17. Specimens of *Voluta oviformis typica* figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. X, fig. 6	269 534	44
Pl. VII, fig. 134	"*Rugosa*" (variety not described)	45a
Pl. I, fig. 1; pl. VII, fig. 133.	"*Rugosa*" (variety not described)	45b
Pl. VII, fig. 132	"*Pseudo-intermedia*" (variety not described)	45c
Pl. X, fig. 5	"8.*typica* 2°s"	45d
Pl. VII, fig. 131	"12.*typica* 2°s"	45e
Pl. VII, fig. 130	"11. *typica*"	45f
Pl. VII, fig. 135	"5. *typica* 2°s"	45g
Pl. II, fig. 56; pl. VII, fig. 129	"10.*typica* 458"	45h
Pl. VII, fig. 137	"1.*typica*"	45i
Pl. VII, fig. 127	"8.*typica* 2°s"	45j
Pl. VII, fig. 128	"9.*typica* 2°s"	45k
Pl. XII, fig. 25	"7.*typica*"	45l
Pl. VII; fig. 126	"6.*typica* 2°s"	45m
Pl. II, fig. 55; pl. VII, fig. 125	"5.*typica* 2°s"	45n
Pl. VII; fig. 124	"3.*typica* 2°s"	45o
Pl. VII, fig. 123; pl. XII, fig. 24	"4.*typica* 2°s"	45p
Pl. II, fig. 54; pl. VII, fig. 122; pl. XII, fig. 23	"2.*typica* 2°s"	45q
Pl. II, Fig. 53;pl. VII, fig. 121; pl. XII, fig. 22	"1.*typica*"	45r

Voluta paradoxa typica Lahille, 1895

Syntypes: MLP-Ma 10892, 8 specimens figured by Lahille (1895) (Table 19); 12 other specimens not figured by Lahille. The largest one is 173 mm long × 77 mm wide (Figs 48, 49).

Lahille (1895) differentiated *V. paradoxa* from *V. colocynthis pseudomagellanica* and *V. magellanica typica* by differences in the juvenile shells. According to him, the shells are thick, similar to *V. colocynthis pseudomagellanica*. The specimens have discontinuous colour lines that can form three bands on the last whorl, similar to *V. magellanica*. The shells lack tubercles. The last whorl is ovoid and globose. Generally, there are three columellar folds, with the inferior fold smaller, and supernumerary folds are sometimes present. The shells are up to 180 mm long and 86 mm wide and can weigh up to 260 g.

This material was revised by Wiggers and Veitenheimer-Mendes (2004), who remarked that all the syntypes illustrated by Lahille (1895) as *V. paradoxa* and deposited in the Museo de La Plata are *Odontocymbiola magellanica* (Gmelin, 1791).

Table 18. Specimens of *Voluta oviformis fratercula* figured in Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. X, fig. 7	230 ½. 535	46a-e
Pl. X, fig. 8	529 "1. *Pseudo-intermedia*" (variety not described)	46f

Table 19. *Voluta paradoxa typica*, specimens figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure en Lahille (1895)	Detail	Figure
Pl. II, fig. 76b; pl. VIII, fig. 161; pl. XII, fig. 20	"11.*paradoxa*"	48
Pl. VIII, fig. 157		49a
Pl. V, fig. 41; pl. VII, fig. 139	"12.*paradoxa* (1°S)"	49b
Pl. XII, fig. 21	343 · 454	49c
Pl. II, fig. 68a; pl. VII, fig. 147; pl. VIII, fig. 166		49d
Pl. XII, fig. 19		49e
Pl. II, fig. 68a; pl. XII, fig. 18		49f
Pl. XII, fig. 17		49g

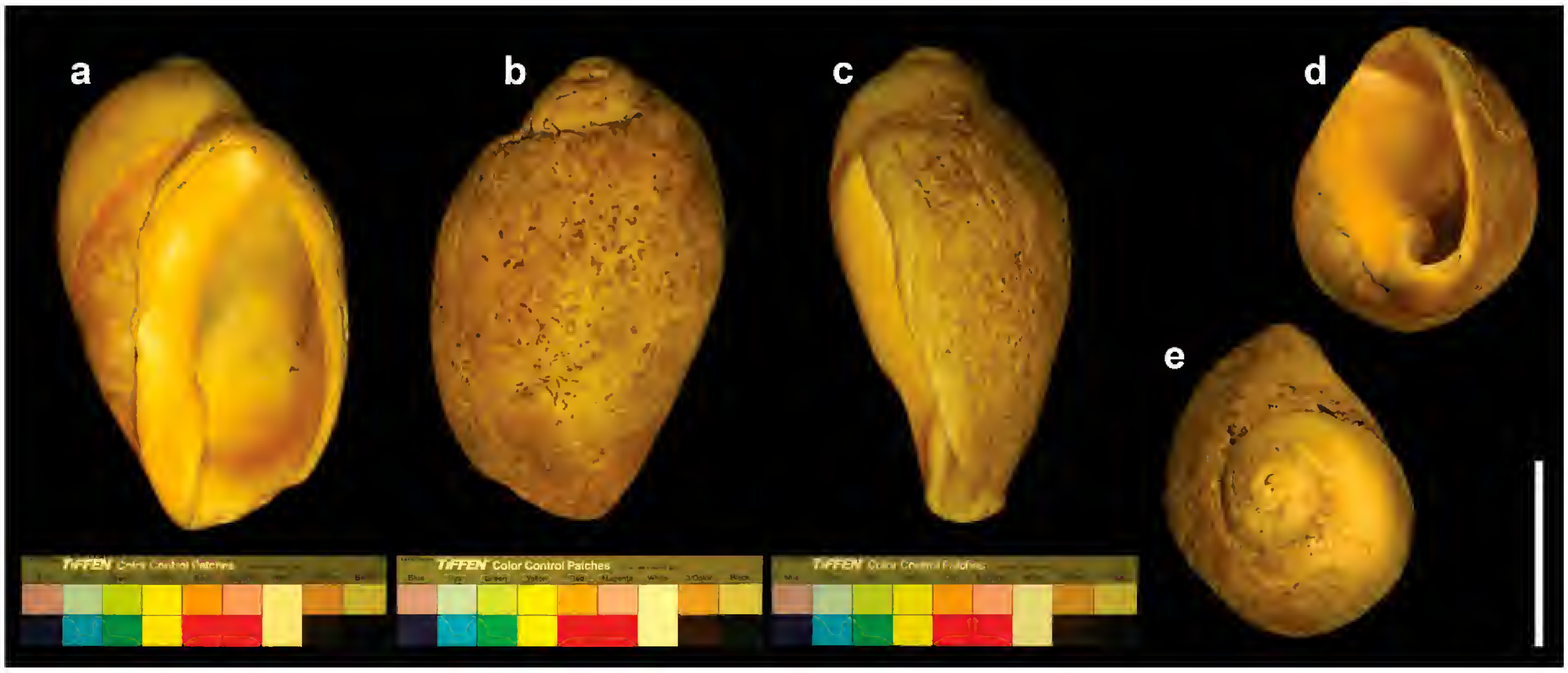

Figure 44. *Voluta oviformis typica*, specimen figured by Lahille (1895: pl. X, fig. 6). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

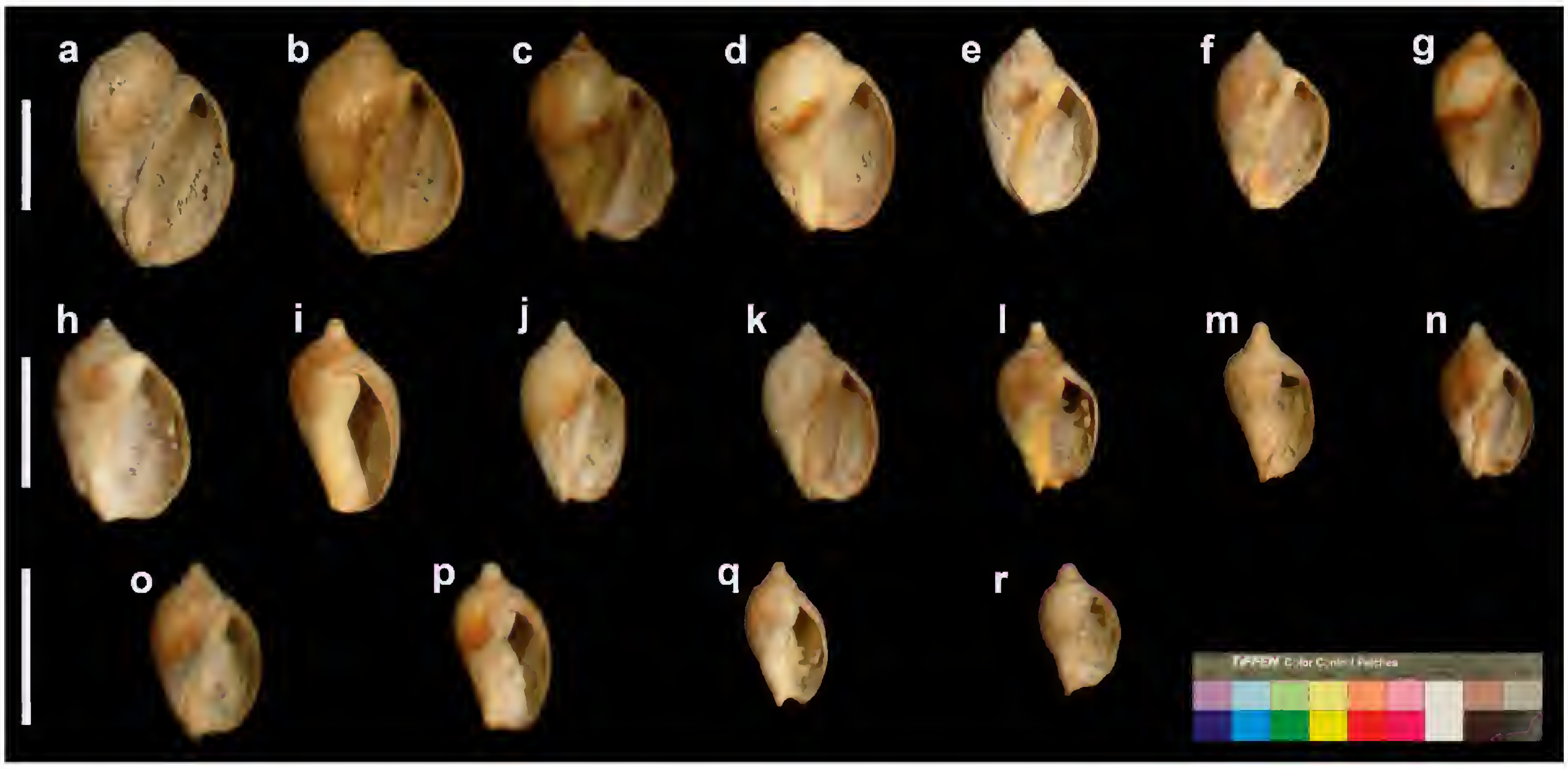

Figure 45. *Voluta oviformis typica*, specimens of figured by Lahille (1895).See references on Table 17. Scale bars: 5 cm.

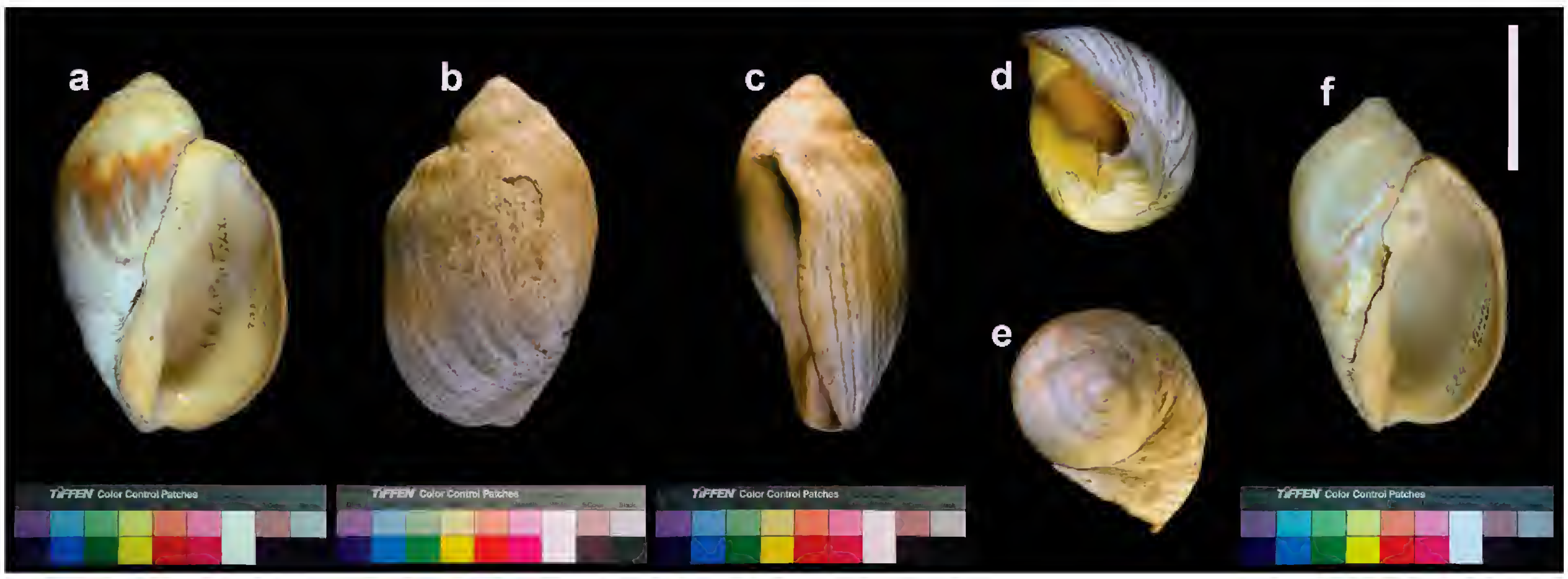

Figure 46. *Voluta oviformis fratercula.* **a–e** Specimen figured by Lahille (1895: pl. X, fig. 7) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. X, fig. 8) in apertural view. Scale bar: 5 cm.

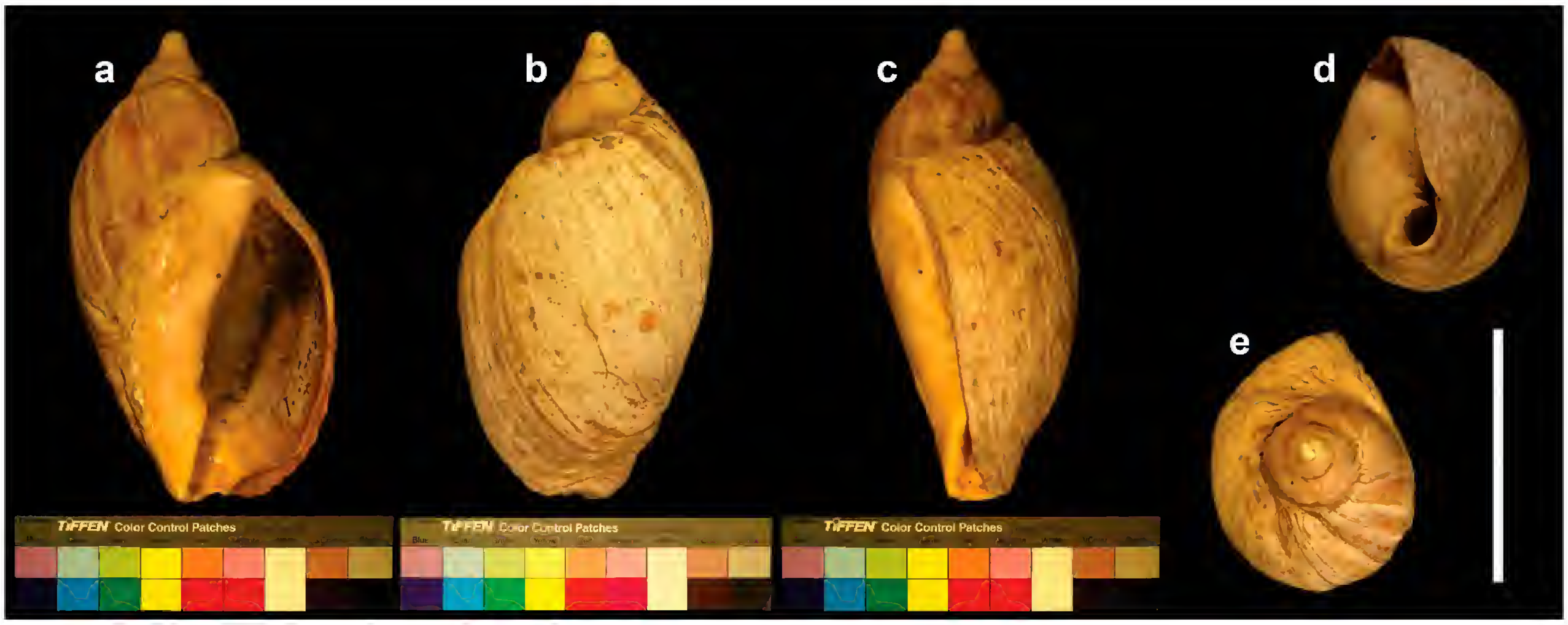

Figure 47. *Voluta oviformis longiuscula*, holotype figured by Lahille (1895: pl. VII, fig. 136) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

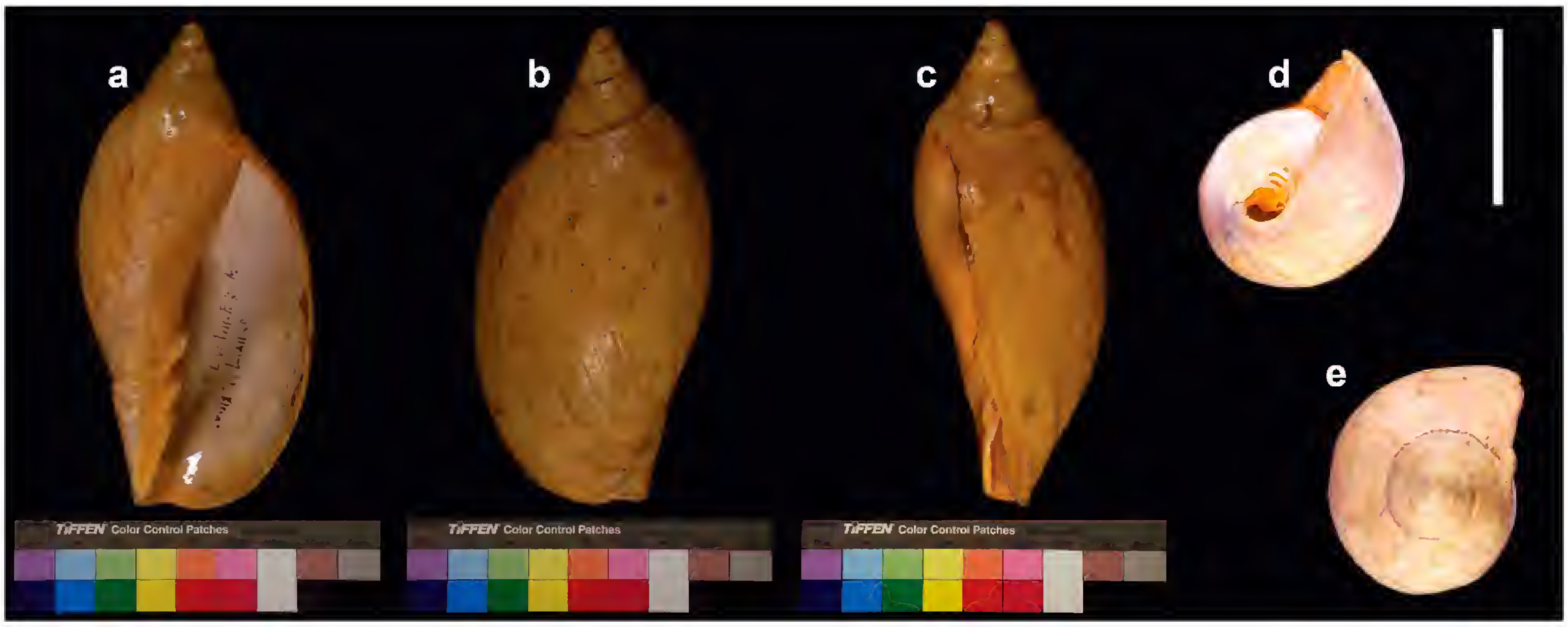

Figure 48. *Voluta paradoxa typica* specimen figured by Lahille (1895: pl. II, fig. 76b; pl. VIII, fig. 161; pl. XII, fig. 20) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

Voluta tuberculata Wood, 1828

Current name: *Odontocymbiola magellanica* (Gmelin, 1791).

Lahille (1895) described five varieties of this species, and mentioned the similarity of this species to *V. colocynthis*. This species is smaller than *V. colocynthis* and always has small lines or flames, usually in three rows.

Voluta tuberculata typica Lahille, 1895

Syntypes: MLP-Ma 10897, 2 specimens figured by Lahille (1895) (Table 20). Shells of 55 mm long × 27 mm wide, and 85.5 mm long × 50 mm wide (Fig. 50).

According to Lahille (1895), adult shells reach up to 120 mm long and 67 mm wide, and are subturbinated. The suture between the penultimate whorl and last whorl is below the carina on the last whorl of the spire. The first two or three whorls of the spire are smooth, and the following three whorls are carinate and have tubercles. Usually, three equal columellar folds are present.

Table 20. Specimens of *Voluta tuberculata typica* figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. VII, fig. 142; pl. XII, fig. 4	"2.*Tuberculata typica*"	50a-e
Pl. XII, fig. 5	"1.*Tuberculata typica*"	50f

Voluta tuberculata decipiens Lahille, 1895

Syntypes MLP-Ma 10896, 2 specimens figured by Lahille (1895) (Table 21); 2 other specimens not figured by Lahille (Fig. 51).

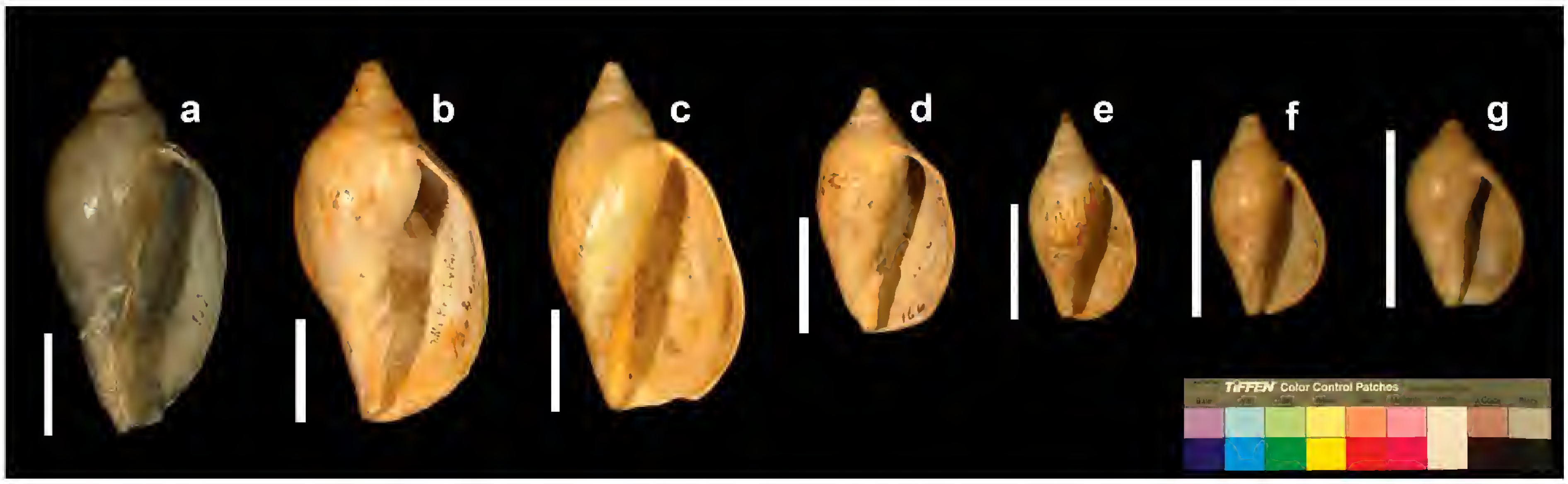

Figure 49. Specimens of *Voluta paradoxa typica* figures by Lahille (1895). See references on Table 19. Scale bars: 5 cm.

Figure 50. *Voluta tuberculata typica*. **a–e** Specimen figured by Lahille (1895: pl. VII, fig. 142; pl. XII, fig. 4) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. XII, fig. 5) in apertural view. Scale bar: 5 cm.

Table 21. Specimens of *Voluta tuberculata decipiens* figured by Lahille (1895) with the detail of the inscriptions on their shells.

Figure in Lahille (1895)	Detail	Figure
Pl. VII, fig. 152; pl. XI, fig. 10	"2.*Decipiens*"	51a-e
Pl. VII, fig. 151; pl. VIII, fig. 162*	"1.*Decipiens*"	51f

*The legend of plate VIII, figure 162 indicates *Voluta magellanica decipiens*, a variety which is never mentioned in the text. No material exists with that name, so it is probably an error.

According to Lahille (1895), this variety is similar to *V. ferruginea* but more elongate (125 mm long × 65 mm wide).

Voluta tuberculata ferruginea Lahille, 1895

Syntypes: MLP-Ma 10898, 3 specimens figured by Lahille (1895) (Table 22); 2 other specimens not figured by Lahille. Specimens are from 90.5 to 133.5 mm long (Fig. 52).

According to Lahille (1895), this variety has a short shell (140 mm long × 90 mm wide), with the last whorl globose, and with an eroded carina. The free edge of the aperture is regularly curved. The inferior columellar fold is small and sometimes with two supplementary upper folds.

Table 22. Specimens of *Voluta tuberculata ferruginea* figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. I, fig. 13; pl. VII, fig. 145; pl. XII, fig. 6	"2.*Ferruginea*"	52a-e
Pl. II, fig. 76a*; pl. VII, fig. 146	"1.*Ferruginea*"	52f
Pl. VII, fig. 144	"1.*Ferruginea*"	52g

*figure 146 of Plate VII indicates variety *fulgurea*, whereas legend on figure 76a of plate II corresponds to *V. paradoxa*. figure 67a only indicates *V. tuberculata*, so it probably corresponds to this shell. On the MLP label, it is assigned to this variety with doubt.

Voluta tuberculata fulgurea Lahille, 1895

Syntypes: MLP-Ma 10893, 3 specimens figured by Lahille (1895) (Table 23); 77–121 mm long (Fig. 53).

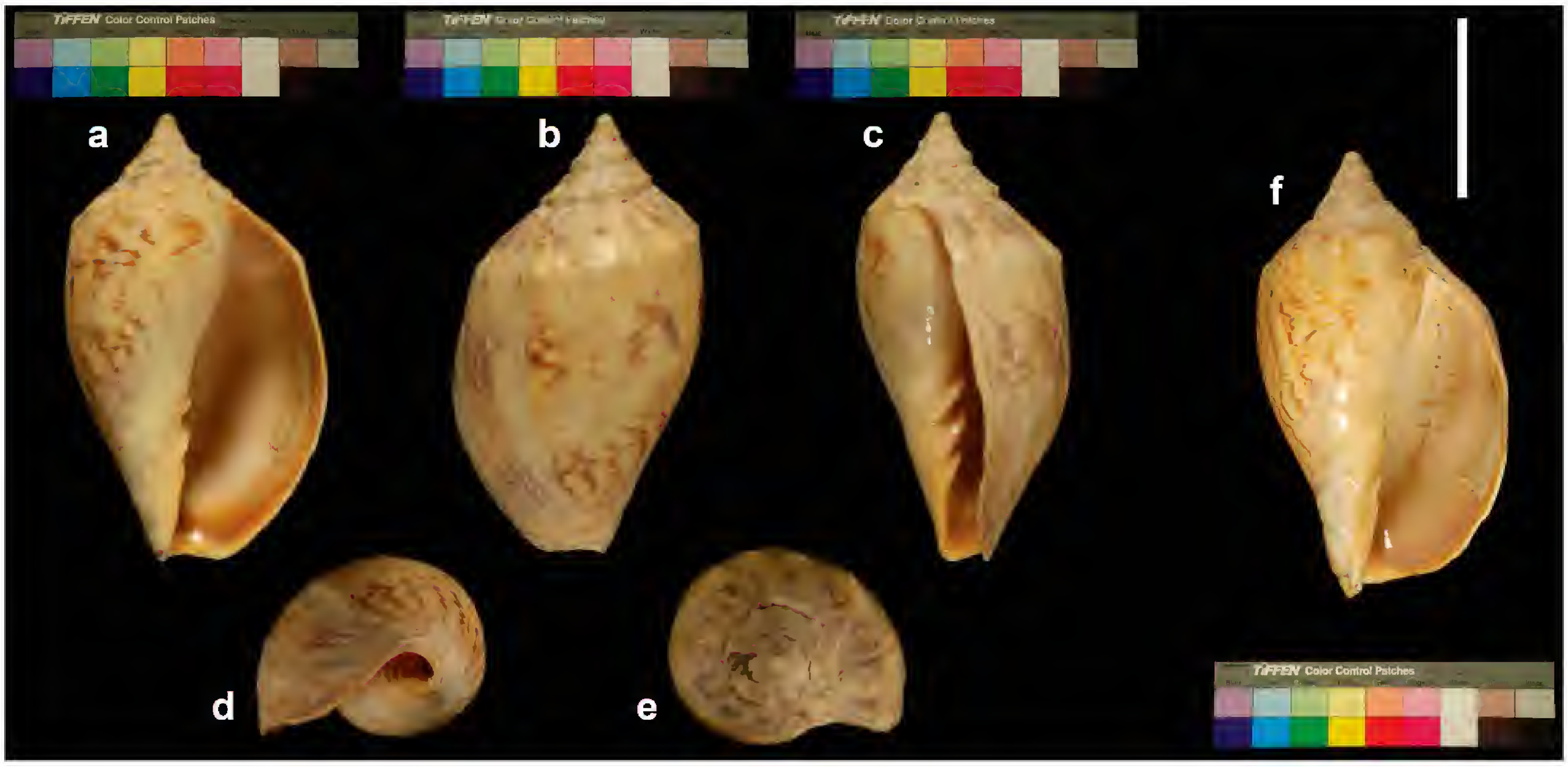

Figure 51. *Voluta tuberculata decipiens*. **a–e** Specimen figured by Lahille (1895: pl. VII, fig. 152; pl. XI, fig. 10) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. VII, fig. 151; pl. VIII, fig. 162) in apertural view. Scale bar: 5 cm.

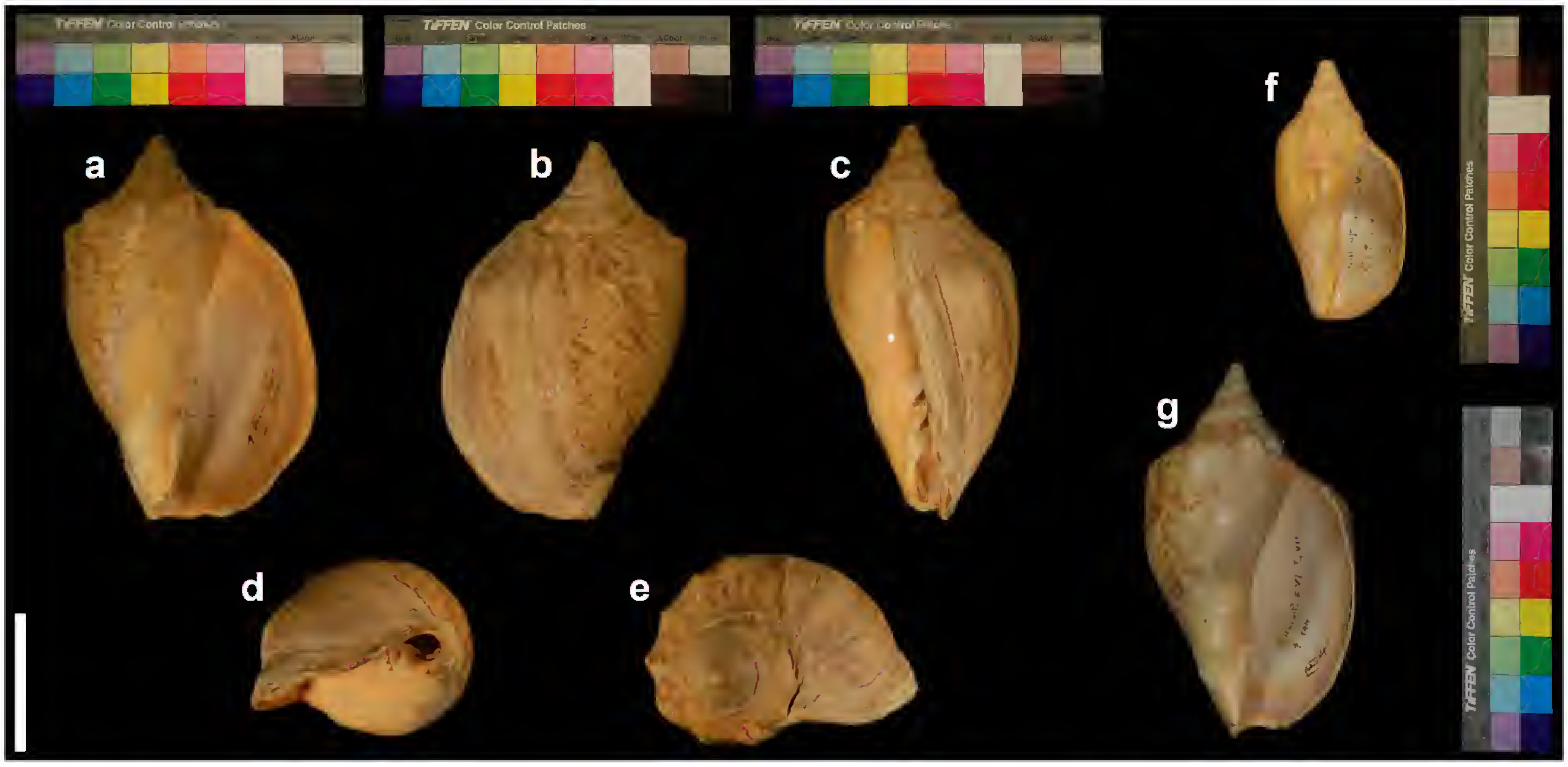

Figure 52. *Voluta tuberculata ferruginea*. **a–e** Specimen figured by Lahille (1895: pl. I, fig. 13; pl. VII, fig. 145; pl. XII, fig. 6) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. VII, fig. 146; pl. II, fig. 76a) in apertural view **g** Specimen figured by Lahille (1895: pl. VII, fig. 144) in apertural view. Scale bar: 5 cm.

Table 23. Specimens of *Voluta tuberculata fulgurea* figured by Lahille (1895) with the detail of the inscriptions on their shells and figures here.

Figure in Lahille (1895)	Detail	Figure
Pl. VII, fig. 153	“3.*Fulgurea*”	53a–e
Pl. VII, fig. 141; pl. XII, fig. 2; pl. II, fig. 67	“1.*Fulgurea*”	53f
Pl. VII, fig. 150; pl. XII, fig. 1	“*Fulgurea*”	53g

Lahille (1895) described the shells as elongate, with the last whorl large and ovoid, and with few tubercles. The penultimate whorl is convex and without tubercles.

Voluta tuberculata pseudofusiformis Lahille, 1895

Holotype: MLP-Ma 10894, 125.5 mm long × 71.5 mm wide, figured by Lahille (1895: pl. XII, fig. 7); label reads: “4.*Pseudo-fusif* (2°S)” (Fig. 54).

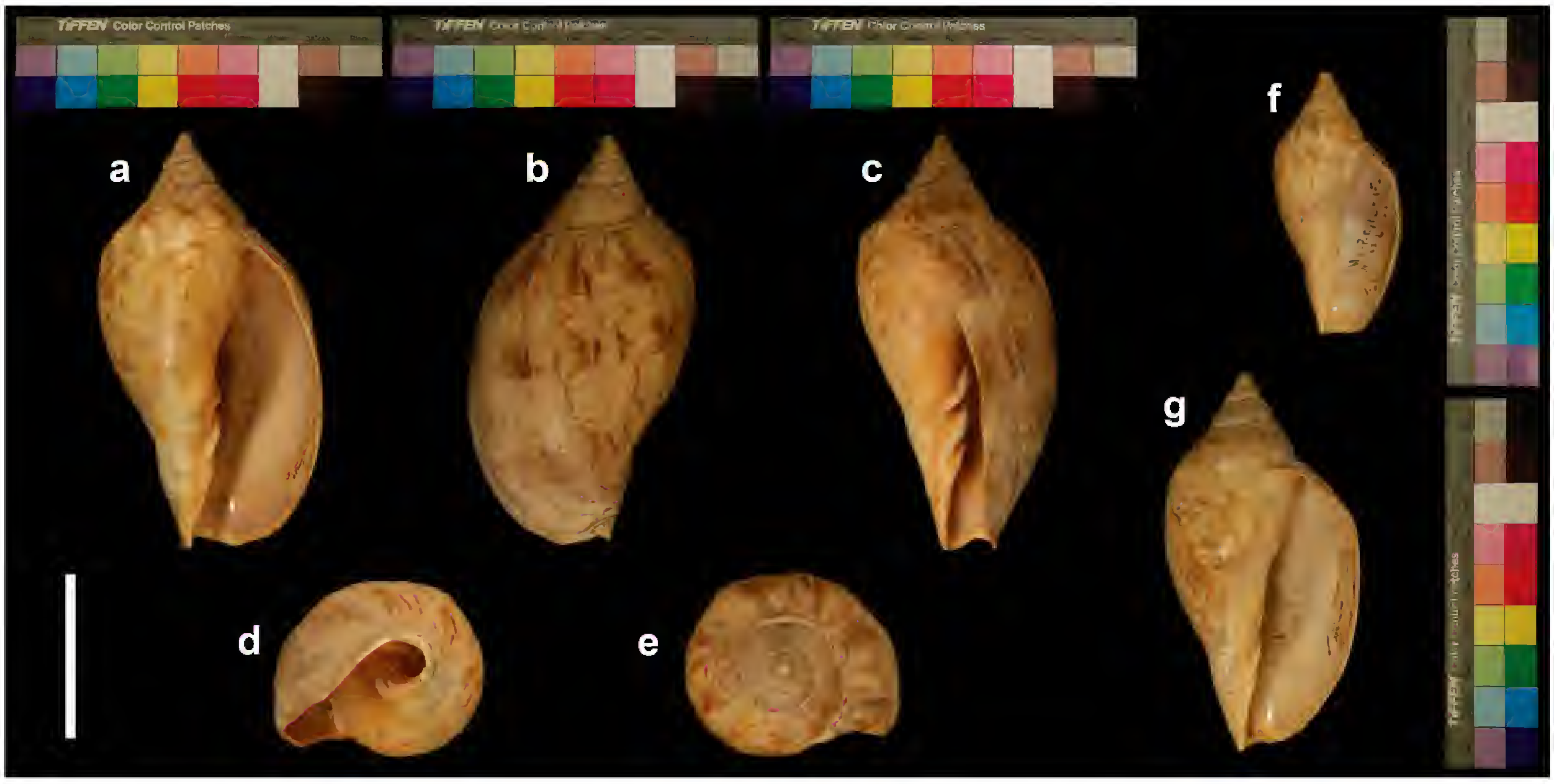

Figure 53. *Voluta tuberculata fulgurea*. **a–e** Specimen figured by Lahille (1895: pl. VII, fig. 153) **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view **f** Specimen figured by Lahille (1895: pl. VII, fig. 141; pl. XII, fig. 2; pl. II, fig. 67) in apertural view **g** Specimen figured by Lahille (1895: pl. VII, fig. 150; pl. XII, fig. 1). Scale bar: 5 cm.

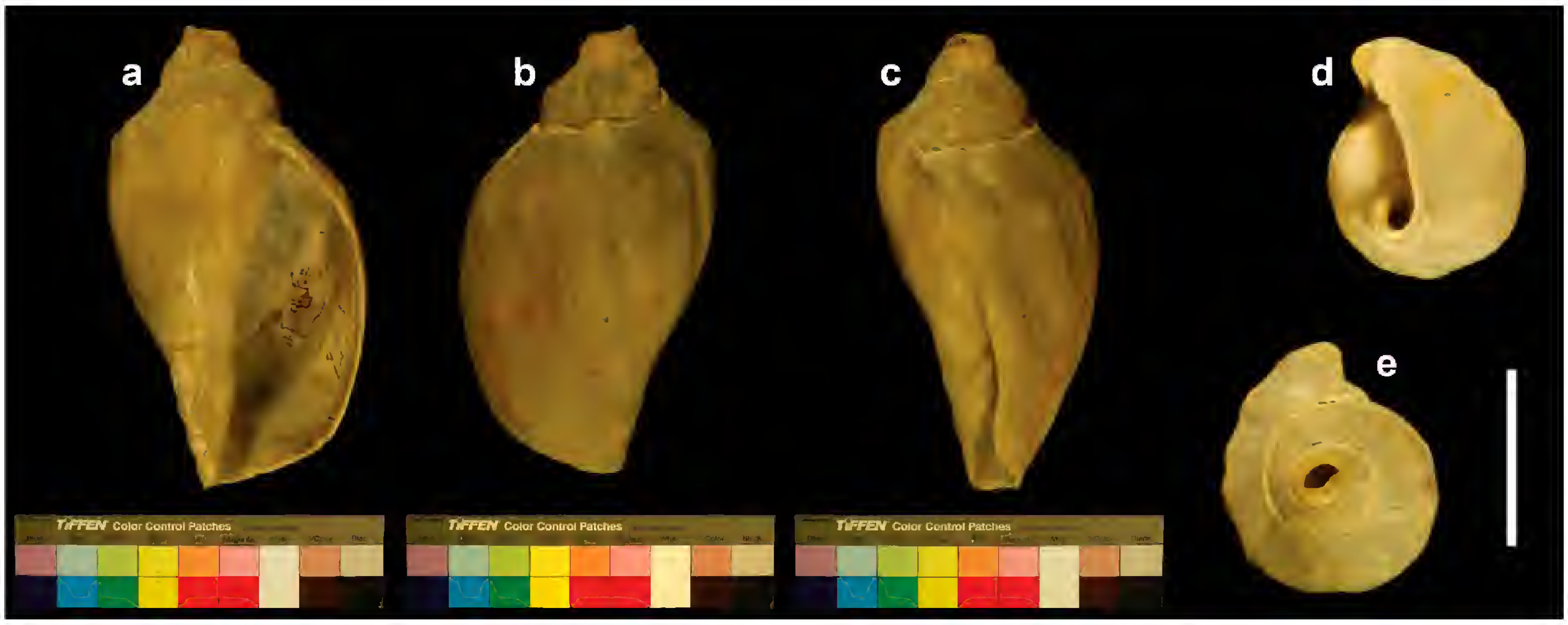

Figure 54. *Voluta tuberculata pseudofusiformis*, holotype figured by Lahille (1985: pl. XII, fig. 7). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

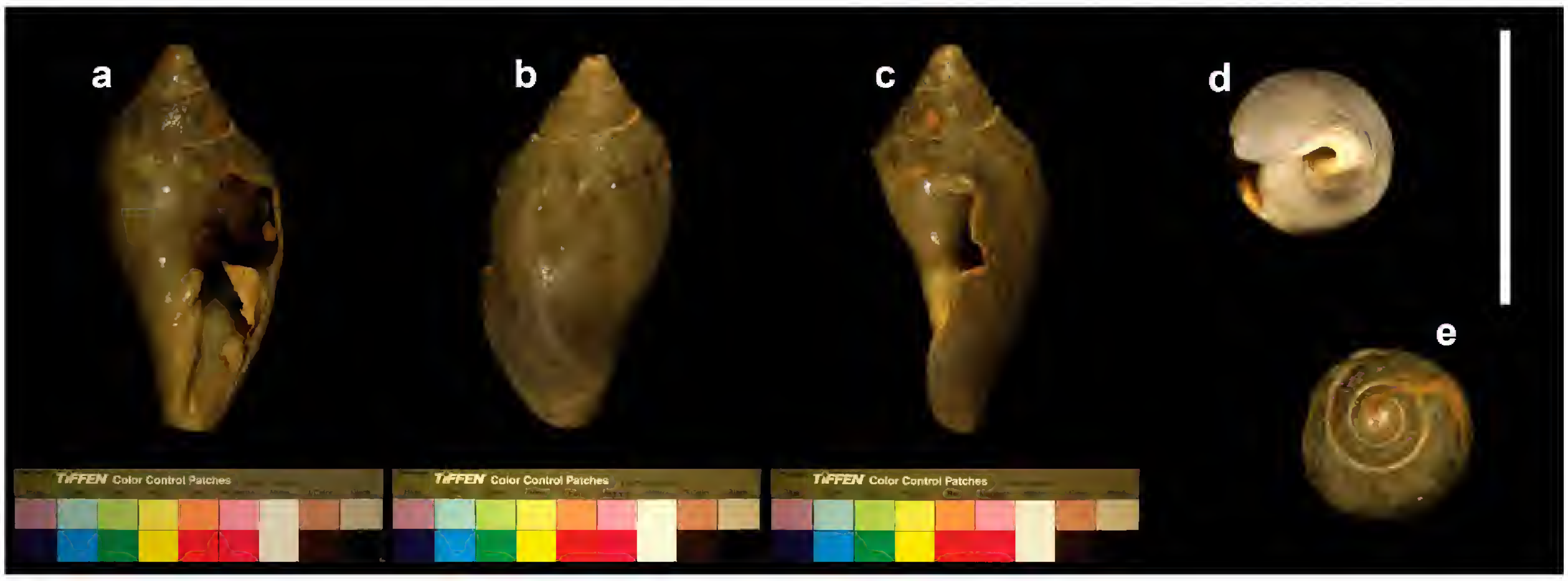

Figure 55. *Voluta tuberculata ambigua*, specimen figured by Lahille (1895: pl. VIII, fig. 155). **a** Apertural view **b** Dorsal view **c** Lateral view **d** Umbilical view **e** Apical view. Scale bar: 5 cm.

According to Lahille (1895), this variety has an elongated shell with three dark lines. The last three whorls are carinate and with tubercles. The columella has four or five folds.

Additional comments

There is a sixth variety, *Voluta tuberculata ambigua*, figured by Lahille (1895: pl. VIII, figs 155, 156) but not described. In the collection there is a specimen (MLP-Ma 10895) of ca 69 mm long, with an inscription: "Plate VIII, fig. 155" (fig. 55). However, the label reads "1.*Ferruginea*").

Twenty one other specimens from Lahille's Collection (MLP-Ma 14250) have not been identified as representatives of any of the previously mentioned varieties.

Along with the material of *Voluta ancilla*, there are 16 other specimens (MLP-Ma 14244) with a label that reads "*crocea*". There is no variety with that name in the publication by Lahille (1895).

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References

Arrozpide RF (1986) Catálogo de tipos de Arácnida (Araneae) del Museo de La Plata. Serie técnica y didáctica. Museo de La Plata 12, 63 pp.

Carcelles AR (1944) Catálogo de los moluscos marinos de Puerto Quequén (República Argentina). Revista del Museo de La Plata (N. S.), Zoología 3: 233–309.

Castellanos ZJA de, Landoni N (1992) Catálogo descriptivo de la malacofauna marina magallánica. Neogastropoda Volutidae, Volutomitridae, Cancellariidae, Olividae y Marginellidae. Comisión de Investigaciones Científicas 10, 43 pp.

César I, Damborenea C (2010) Type and non-type specimens of *Aegla* (Aeglidae: Anomura: Decapoda) housed in the Museo de La Plata, Argentina. Zootaxa 2337: 31–46. https://doi.org/10.11646/zootaxa.4303.1.5

César I, Damborenea C (2016) Catalogue of the specimens of Trichodactylidae (Crustacea, Brachyura) housed in the Museo de La Plata, Argentina. Revista del Museo de La Plata, Sección Zoología 25(184): 1–13.

Díaz AR, Merlo Álvarez VH, Damborenea C (2017) Type material housed in the Carcinological Collection of the Museo de La Plata, Argentina. Zootaxa 4303: 88–102. https://doi.org/10.11646/zootaxa.4303.1.5

Lahille F (1895) Contribución al estudio de las volutas argentinas. Revista del Museo de La Plata, Sección Zoología 6: 293–325.

Lasta ML, Roux A, Bremec C (2000) Caracoles marinos de interés pesquero. Moluscos gasterópodos volutidos. INIDEP Mar del Plata. Informe técnico 31: 1–13.

Lunaschi L, Merlo-Álvarez VH, Damborenea C (2012) Type material housed in the Helminthological Collection of the Museo de La Plata, Buenos Aires, Argentina. Zootaxa 3199: 1–59. https://doi.org/10.11646/zootaxa.3199.1.1

Martín SM, César II (2004) Catálogo de los tipos de moluscos (Gastropoda, Bivalvia, Cephalopoda) del Museo de La Plata. Fundación Museo de La Plata, La Plata, 76 pp.

Morton B (1986) The diet and prey capture mechanism of *Melo melo* (Prosobranchia: Volutidae). Journal of Molluscan Studies 52: 156–160. https://doi.org/10.1093/mollus/52.2.156

Penchaszadeh PP, de Mahieu GG (1976) Reproducción de gasterópodos Prosobranquios del Atlántico sudoccidental. Volutidae. Physis Sección A 35(91): 145–153.

Pereira LA, Ituarte C, Tassara MP (2004) The types of Chilopoda and Diplopoda (Myriapoda) housed at the Museo de La Plata, Argentina. Zootaxa 586: 1–10. https://doi.org/10.11646/zootaxa.586.1.1

Pereira LA, Sutton CA, Ramirez MJ (1999) Catálogo de tipos de Araneae (Arácnida) del Museo de La Plata. Neotropica 45(113–114): 77–100.

Poppe GT, Goto Y (1992) Volutes. Mostra Mondiale Malacologia by L'informatore Piceno, Ancona, 48 pp. [107 pls.]

Rosenberg G (2009) Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca. http://www.malacolog.org [Accessed on: 2018–4–15]

Scarabino V (1977) Moluscos del Golfo San Matías (Provincia de Río Negro, República Argentina). Inventario y claves para su identificación. Comunicaciones de la Sociedad Malacológica del Uruguay 4: 177–285.

Sutton CA, Damborenea C (2000) Colección helmintológica del Museo de La Plata: I. Catálogo de preparaciones microscópicas, material tipo y no tipo. Serie Técnica y Didáctica Museo de La Plata 35: 1–20.

Wiggers F, Veitenheimer-Mendes IL (2008) Taxonomic review of the genus *Adelomelon* (Gastropoda; Volutidae), based on type material. Brazilian Journal of Biology 68(4): 843–850. http://doi.org/10.1590/S1519-69842008000400021

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PENSOFT.

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A new dwarf chameleon, genus *Brookesia*, from the Marojejy massif in northern Madagascar

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Marojejy National Park
Squamata
miniaturisation

Abstract

We describe a new species of dwarf chameleon from the *Brookesia minima* species group. *Brookesia tedi* **sp. n.** occurs above 1300 m above sea level on the Marojejy massif in northeastern Madagascar. It is genetically sister to *B. peyrierasi,* a species occurring in lowlands around the Baie de Antongil, but is genetically strongly divergent from that species in both nuclear (c-mos) and mitochondrial (16S, ND2) genes, and morphologically in its smaller size and distinctly different hemipenis. It is the second species of the *B. minima* species group from Marojejy National Park, but is not known to occur in syntopy with the other species, *B. karchei*, due to elevational segregation.

Introduction

Chameleons, family Chamaeleonidae, are a highly diverse group of lizards, occurring across Africa and Madagascar, with a few species also present in southern Europe and Asia (Tilbury 2018). Body size within the family varies more than tenfold, from the giant species *Furcifer oustaleti* (Mocquard, 1894) at 284 mm maximum snout-vent length (SVL) to the dwarf species *Brookesia micra* Glaw, Köhler, Townsend & Vences, 2012 whose maximum SVL is ca 20 mm snout–vent length (Glaw et al. 2012a; Villeneuve 2017). According to current phylogenetic understanding of the evolution of these lizards (Tolley et al. 2013), chameleons were ancestrally semi-terrestrial, probably roosting above the ground on small twigs and branches at night, and relatively small-bodied, and subsequently evolved fully arboreal habits. Members of the genus *Brookesia* are generally semi-terrestrial (most are terrestrial by day but roosting above the ground at night) and are all comparatively small in size. Most members of the *Brookesia minima* species group are dramatically smaller than other *Brookesia*, and their diversity was long underappreciated because they are difficult to find and due to their miniaturisation and crypsis (Brygoo and Domergue 1975, Glaw et al. 1999). Genetic analysis and more intense fieldwork in northern Madagascar revealed additional species (Glaw et al. 2012a), as has been the trend in other miniaturised Malagasy vertebrate groups (e.g. Rakotoarison et al. 2017).

The *Brookesia minima* species group includes some of the smallest amniotes in the world (Glaw et al. 2012a; Villeneuve 2017). These miniaturised chameleons are dis-

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tributed across the northern half of Madagascar, with one species also occurring in the Tsingy de Bemaraha Massif in the dry west (Schimmenti and Jesu 1996). Glaw et al. (2012a) recognised three clades within the *B. minima* group: Clade A (*B. desperata* Glaw, Köhler, Townsend & Vences, 2012; *B. tristis* Glaw, Köhler, Townsend & Vences, 2012; *B. micra*, *B. confidens* Glaw, Köhler, Townsend & Vences, 2012; *B. tuberculata* Mocquard, 1894) consisting of species distributed primarily in the far north of Madagascar, Clade B (*B. peyrierasi* Brygoo & Domergue, 1975 and *B. karchei* Brygoo, Blanc & Domergue, 1970) consisting of species distributed in northeastern Madagascar, and Clade C (*B. ramanantsoai* Brygoo & Domergue, 1975; *B. exarmata* Schimmenti & Jesu, 1996; *B. dentata* Mocquard, 1900; *B.* sp. 'Betampona') consisting of species distributed in central eastern and western Madagascar, with *B. minima* Boettger, 1893 from the Sambirano region in northwestern Madagascar occupying a position sister to Clade B. Some undescribed diversity is still known within this species group, however.

Brygoo et al. (1974) reported on four specimens (probably MNHN 1986.876–879, formerly all subsumed under the preliminary number 722/C) belonging to the *Brookesia minima* group that they collected at 1300 m above sea level (a.s.l.) in Marojejy, from the humid faces of ravines, where they were found in bushy foliage and among mosses. The colouration of the specimens was briefly described, but their overall morphology was not discussed. A further specimen collected from the region of Sambava (presumably MNHN 1974.251 or 1974.252) was also referred to the species. Brygoo and Domergue (1975) elected not to describe the species due to the lack of sufficient data. A specimen was later illustrated by Brygoo (1978), and he also reported therein that the specimens were closer to *B. tuberculata* than to *B. peyrierasi* in the morphology of their dorsolateral spines and the crests of the dorsal head. According to Brygoo (1978), G. Ramanantsoa had apparently assembled a collection of ca 40 individuals and indicated to Brygoo his intent to describe the species, which presented also hemipenial differences, but this description was never published.

On a recent expedition to Marojejy, we collected new material of this species, and can finally resolve the question of the identity of this population. In the present study we provide a formal taxonomic description of the new species, and provide genetic evidence for its close relationship to *B. peyrierasi*.

Materials and methods

Specimens were found via searching by torchlight at night and photographed the following morning. They were anaesthetised and subsequently euthanised by oral of lidocaine. Tissue samples were taken and stored in pure ethanol. They were then fixed with 90% ethanol and deposited in 75% ethanol for long-term storage. ZCMV and FGZC refer to field numbers of M. Vences and F. Glaw, respectively. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). Reference is also made to the Muséum National d'Histoire Naturelle, Paris, France (MNHN) and University of Michigan Museum of Zoology, Ann Arbor MI, USA (UMMZ).

Morphological analysis was conducted following Glaw et al. (2012a). Measurements were taken by MV to the nearest 0.1 mm using a digital calliper. The following measurements were taken: TL (total length); SVL (snout–vent length); TaL, tail length; HW, maximum head width; HH, maximum head height; ED, eye diameter; FORL, forelimb length.

For molecular analysis, we expanded the DNA sequence data set of Glaw et al. (2012a) for the two mitochondrial genes of NADH dehydrogenase subunit 2 (ND2) and 16S rRNA (16S), and the nuclear gene for oocyte maturation factor mos (c-mos). We added to the existing data sequences for the two individuals of the new species described herein, as well as one additional individual of *B. peyrierasi.* Genomic DNA was extracted and amplified using standard protocols as described in Glaw et al. (2012a). Gene fragments were amplified using the primers ND2F17 (5′-TGACAAAAAATTGCNCC-3′; Macey et al. 2000) and ALAR2 (5′-AAAATRTCTGRGTTGCATTCAG-3′; Macey et al. 1997) for ND2, 16SA-L (5′-CGCCTGTTTATCAAAAACAT-3') and 16S-BH (5'-CCGGTCTGAACTCAGATCACGT-3') for 16S (Palumbi et al. 1991), and CO8 (5′-GCTTGGTGTTCAATAGACTGG-3′) and CO9 (5′-TTGGGAGCATCCAAAGTCTC-3′) for c-mos (Han et al. 2004). PCR products were purified with ExoSAPIT (Thermo Fisher Scientific, Waltham, MA, USA), sequenced on an automated DNA sequencer (ABI 3130 XL; Applied Biosystems). We used the software CodonCode Aligner (CodonCode Corporation) to check and correct errors in the DNA sequences based on the chromatograms, and to trim poor-quality stretches and primer sequences from the beginning and end of the sequences. We verified that none of the sequences of the protein-coding genes (ND2 and c-mos) contained stop codons, and retained hypervariable stretches in the 16S gene, as an exploratory analysis removing these yielded a similar tree topology. All new sequences obtained in the present study were submitted to GenBank (accession numbers MK452364–MK452366, MK457367–MK457369, and MK457452–MK457454); for accession numbers of previously published sequences, see Glaw et al. (2012a).

Alignment and analysis of sequences, separately for each marker, was performed in MEGA7 (Kumar et al. 2016). Sequences were aligned using the Clustal algorithm, and the most suitable substitution models determined under the Bayesian Information Criterion, implemented in MEGA7. Phylogenetic analyses were conducted under the Maximum Likelihood optimality criterion, with subtree-pruning-regrafting branch swapping (SPR level 5) and with 500 heuristic bootstrap replicates. Bootstrap values <50% (suggesting the respective node is recovered by less than half of the replicates) were omitted from the figures. We decided to analyse sequences for each marker separately rather than concatenating them because (1) a concordant signal of markers with different mode of inheritance (nuclear and mitochondrial) provides additional support for distinct evolutionary lineages under the genealogical concordance species criterion (Avise and Ball 1990), and (2) different sets of individuals have been sequenced for the three markers which would inflate a concatenated matrix with missing data, even for the two mitochondrial markers (for which the sequences in part refer to different individuals which we preferred not to combine to form chimera sequences).

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Results

Phylogenetic analysis of the nuclear (c-mos) and mitochondrial (ND2, 16S) markers yielded largely concordant results regarding the phylogenetic placement and molecular divergence of the specimens from Marojejy (Figs 1, 2). While deep relationships among clades of the *Brookesia minima* clade could not be reliably resolved in our single-marker analyses, the Marojejy specimens were in each case placed sister to *B. peyrierasi*, with moderate to strong support from bootstrap analysis (ND2: 99%; 16S: 84%; c-mos: 99%). However, the genetic differentiation between these two lineages were substantial: the Marojejy specimens differed from *B. peyrierasi* by 8.1–9.0% uncorrected pairwise distance (p-distance) in the 16S gene, 17.5–19.3% in the ND2 gene, and 1.7–2.7% in the usually very conserved c-mos gene. Their differentiation to the other species of the *B. minima* clade amounted to 10.8–17.5% for 16S, 26.1–29.2% for ND2, and 2.7–5.5% for c-mos.

Our genetic data confirm for the first time the presence of *B. peyrierasi* in a lowland site on the mainland opposite to its type locality, the islet of Nosy Mangabe (Fig. 3). One specimen from Ambodivoangy clustered with 98–100% bootstrap support with Nosy Mangabe specimens in the analyses of all three gene fragments (Figs 1, 2). Despite a substantial genetic differentiation between the Ambodivoangy and Nosy Mangabe specimens (3.2% in 16S, 7.9% in ND2, 0.7% in c-mos), at present there is no reason to consider them taxonomically distinct. This confirms *B. peyrierasi* as being a species distributed in lowlands of mainland Madagascar near Nosy Mangabe, and we here also assign a specimen from the Masoala peninsula (Fig. 4G, H) to this species based on morphology and biogeography, pending genetic confirmation. Two female specimens from Sambava MNHN 1974.251–252 that were assigned to *B. peyrierasi* based on external morphology by Glaw et al. (1999) and a further uncollected juvenile from Sambava, depicted in Glaw and Vences (1994), are here omitted from further discussion because neither hemipenial nor molecular data are available from these specimens.

Morphological analysis revealed differences between the Marojejy specimens and *B. peyrierasi* in body size (*B. peyrierasi* being slightly larger; see diagnosis below and Table 1). We did not observe additional morphological differences, e.g. in the arrangements of scale rows dorsally on the head, and the two Marojejy individuals differed distinctly from each other in the appearance of their supraocular scales (Fig. 5). However, hemipenial morphology was drastically different between the Marojejy specimens and *B. peyrierasi* (Fig. 6), and the diagnostic characters were constant in all specimens of *B. peyrierasi* studied so far (Glaw et al. 1999) and in the two Marojejy individuals (see below for more details).

In addition, *B. peyrierasi* has so far been collected in lowland localities only (Fig. 3), whereas the two specimens of the Marojejy lineages came from forests ≥ 1300 m a.s.l. Taken together, the concordant and strong differences in mitochondrial and nuclear genes, body size, and hemipenial morphology provide unambiguous evidence for a species-level differentiation of the Marojejy lineage, and we therefore describe and name it as a new species as follows.

Taxonomy

***Brookesia tedi* sp. n.**

http://zoobank.org/8445F2DF-398F-4A6C-BB35-D322A36EDF7B

Figures 5–7; Table 1

Remark. This species has been previously referred to as follows:

B. "*minima*" – Brygoo et al. (1974)
B. minima s. l. – Brygoo and Domergue (1975)
B. aff. *minima* – Brygoo (1978)
B. cf. *minima* – Glaw and Vences (1994)

Possibly also within the definition of *B. minima* by Raxworthy and Nussbaum (1995); see Referred specimens below.

Holotype. ZSM 438/2016 (ZCMV 15262), adult male, collected on 18 November 2016 in Camp 'Simpona' (Camp 3) of Marojejy National Park (ca 14.4366S, 49.7434E, 1325 m a.s.l.), Sava Region, northeastern Madagascar by M.D. Scherz, A. Razafimanantsoa, A. Rakotoarison, M. Bletz, M. Vences, and J.H. Razafindraibe.

Paratype. ZSM 439/2016 (ZCMV 15298), adult male, collected on 20 November 2016 from the same locality and by the same collectors as the holotype.

Referred specimens. Four specimens of *Brookesia* aff. *minima* (MNHN 1986.876–879, formerly all subsumed under the preliminary number 722/C, sex unidentified),

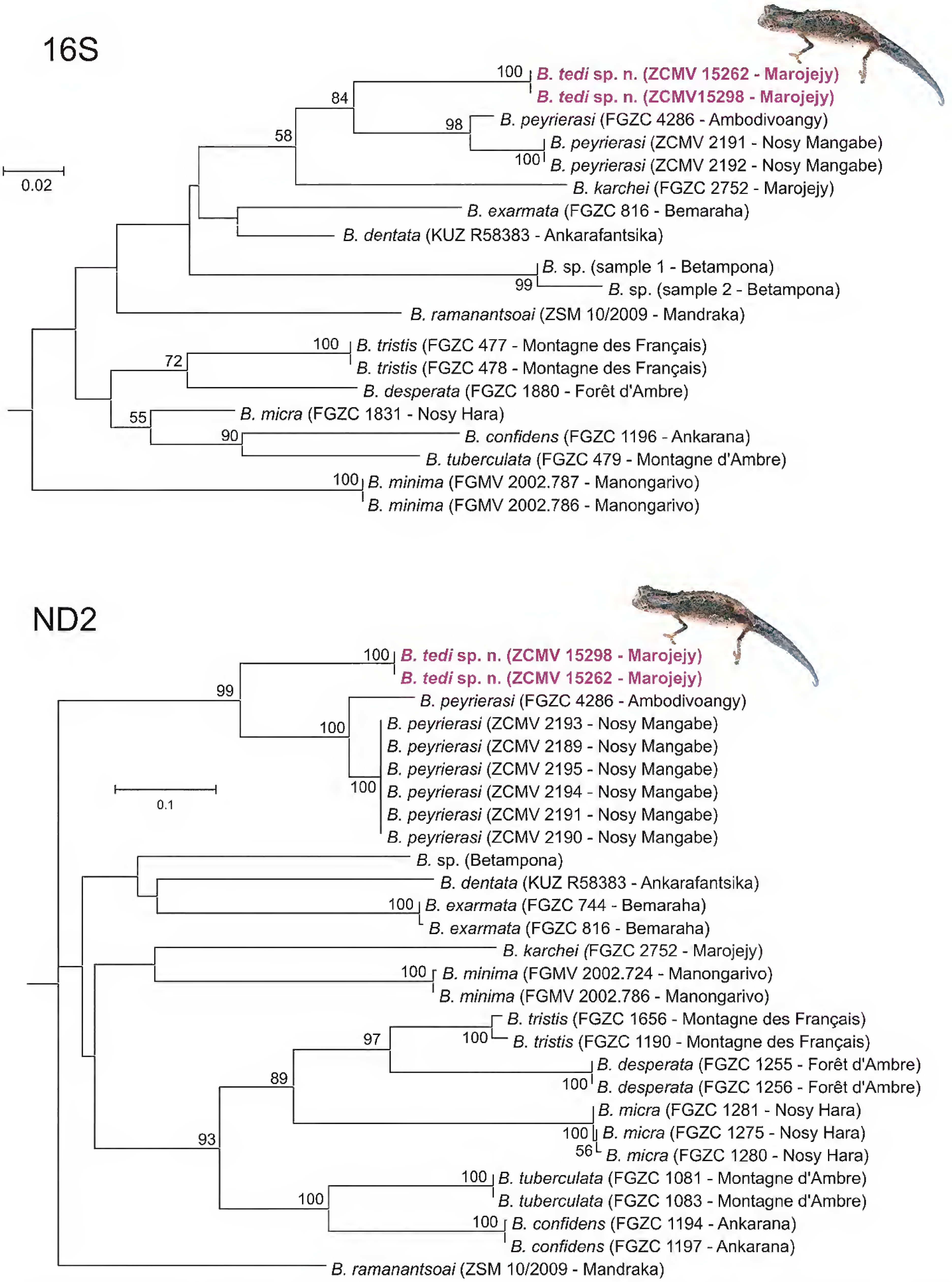

Figure 1. Molecular phylogenetic trees of species in the *Brookesia minima* group, based on sequences of the mitochondrial 16S (480 bp) and ND2 (574 bp) genes, inferred under the Maximum Likelihood optimality criterion, and the GTR+G (16S) and HKY+I+G (ND2) substitution models. Values at nodes are support values from a bootstrap analysis in percent (500 replicates) and are shown only if >50%. The two gene fragments were analysed separately and not concatenated because partly different samples were available for each of them. The trees were rooted with *Brookesia brygooi* (removed for better graphical representation).

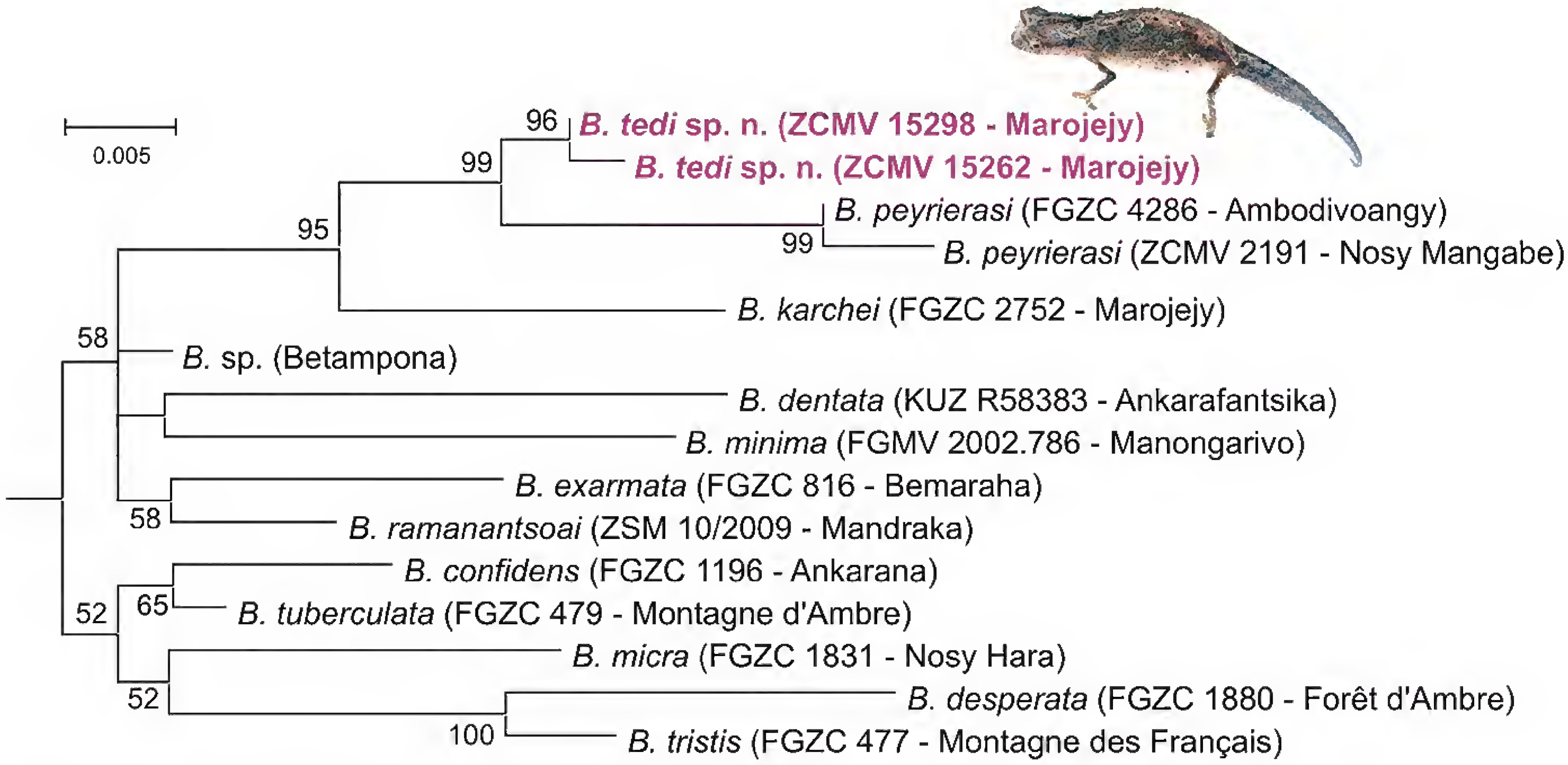

Figure 2. Molecular phylogeny of species in the *Brookesia minima* group, based on the nuclear c-mos gene (405 bp, no missing data) and inferred under the Maximum Likelihood optimality criterion (K2 substitution model). Values at nodes are support values from a bootstrap analysis in percent (500 replicates) and are only shown if >50%. The tree was rooted with *Brookesia brygooi* (removed for better graphical representation).

formerly housed in the Collection of the Institut Pasteur de Madagascar, were apparently collected ('event date') on 4 December 1972 at 'Marojezy' (=Marojejy), 1300 m a.s.l. according to the VertNet database (http://portal.vertnet.org/search, accessed 25 December 2018) and are probably the specimens referred to by Brygoo et al. (1974); we tentatively refer these specimens to this species without having examined them. The whereabouts of additional potential specimens (no. 722 and 723c) and of the ca 40 specimens collected by G. Ramanantsoa reported by Brygoo (1978) is unknown.

Specimens UMMZ 203615–203621 reported by Raxworthy and Nussbaum (1995) to be identical to *B. minima* may also be attributable to this species, but apparently come from lower elevation (200–800 m a.s.l.) and therefore cannot be referred to this species until they are genetically and morphologically investigated. In any case, given the morphological variation of *B. tedi* (see Discussion below) and the presence of one other species of the *B. minima* group at Marojejy (*B. karchei*), the identification of all these additional specimens as *B. tedi* will remain tentative unless molecular data can be obtained or fully diagnostic morphological or osteological characters defined in the future.

Diagnosis. A diminutive chameleon species assigned to the genus *Brookesia* on the basis of its small body size, short tail, crests of the head, dorsolateral spines and molecular relationships. *Brookesia tedi* sp. n. is morphologically characterised by the following unique suite of characters (n = 2 males): (1) SVL 15.3–18.2 mm; (2) TaL/SVL 0.74–0.92; (3) TL 29.5–31.7 mm; (4) HW/SVL 0.20–0.21; (5) 8–10 dorsolateral spines (when countable; sometimes spines are not or are only partly expressed, rendering them difficult to count); (6) distinct pelvic spine; (7) absence of lateral or dorsal spines on the tail; (8) presence of supraocular cone; (9) presence of supranasal cone; and (10) rather globular hemipenis with paired sets of small fleshy apical papillae.

Within the genus *Brookesia*, *B. tedi* sp. n. can easily be distinguished from all species that are not members of the *B. minima* species group based on its diminutive size (SVL 15.3–18.2 mm vs minimum 34 mm). Within the *B. minima* species group, it can be distinguished from males of *B. tristis* by longer relative tail length (TaL/SVL 0.74–0.92 vs 0.71–0.72), presence of supraocular cone (vs. absence); from males of *B. confidens* by slightly smaller body size (SVL 15.3–18.2 vs 18.3–20.1 mm), longer relative tail length (TaL/SVL 0.74–0.92 vs 0.60–0.70), presence of supraocular cone (vs absence), and globular hemipenes (vs tubular); from males of *B. micra* by longer relative tail length (TaL/SVL 0.74–0.92 vs 0.47–0.49), slightly narrower relative head width (HW/SVL 0.20–0.21 vs 0.23), slightly smaller relative head height (HH/SVL 0.16–0.18 vs 0.19–0.20), and globular hemipenes with paired fleshy apical papillae (vs tubular hemipenes with apical combs of papillae); from males of *B. desperata* by smaller body size (SVL 15.3–18.2 vs 25.0–26.7 mm) and total length (TL 29.5–31.7 vs 39.7–42.9 mm), longer relative tail length (TaL/SVL 0.74–0.92 vs 0.59–0.63), absence of lateral tail spines (vs presence), fewer dorsolateral spines (8–10 when countable vs 12–14), and hemipenes with fleshy papillae (vs single spines on strongly bilobed apex); from the male holotype of *B. exarmata* as reported by Schimmen-

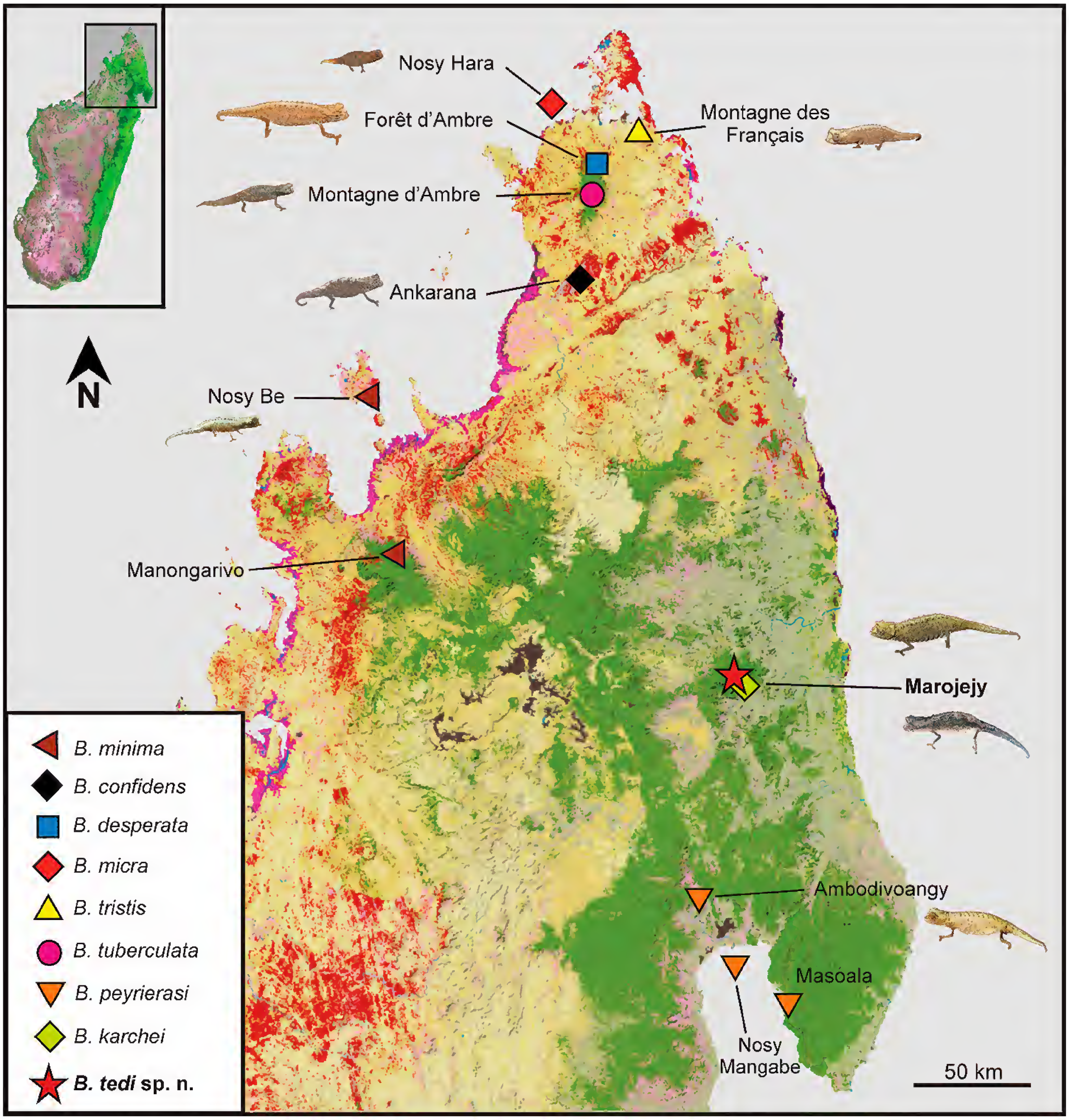

Figure 3. Map of northern Madagascar showing the localities of species of the *Brookesia minima* group in this region, only representing records verified by molecular data (except the *B. peyrierasi* record from Masoala and the *B. minima* record from Nosy Be). Note that *B. dentata, B. exarmata*, and *B. ramanantsoai* occur further south and are not included in the map. Red (dry forest) and green (rainforest) show remaining primary vegetation in 2003–2006, modified from the Madagascar Vegetation Mapping Project (http://www.vegmad.org); see the project for a key to the other colours and the vegetation types they indicate.

ti and Jesu (1996) by the presence of a supraocular cone (vs absence), slightly smaller relative head height (HH/SVL 0.16–0.18 vs 0.23), and slightly smaller total length (TL 29.5–31.7 vs 33.3 mm); from males of *B. minima* by slightly longer relative tail length (TaL/SVL 0.74–0.92 vs 0.65–0.73), slightly wider relative head width (HW/SVL 0.20–0.21 vs 0.16–0.19), presence of supraocular cone (vs absent), and presence of a distinct pelvic spine (vs absent or indistinct); from males of *B. ramanantsoai* by smaller body size (SVL 15.3–18.2 vs 21.7 mm) and total length (TL 29.5–31.7 vs 39.0 mm), and wider relative head width (HW/SVL 0.20–0.21 vs 0.16); from males of *B. dentata* by smaller total length (TL 29.5–31.7 vs 43 mm) and presence of supraocular cone (vs absent); from females of *B. karchei* (as reported by Glaw et al. 2012a; no data from males are available) by longer relative tail length (TaL/SVL 0.74–

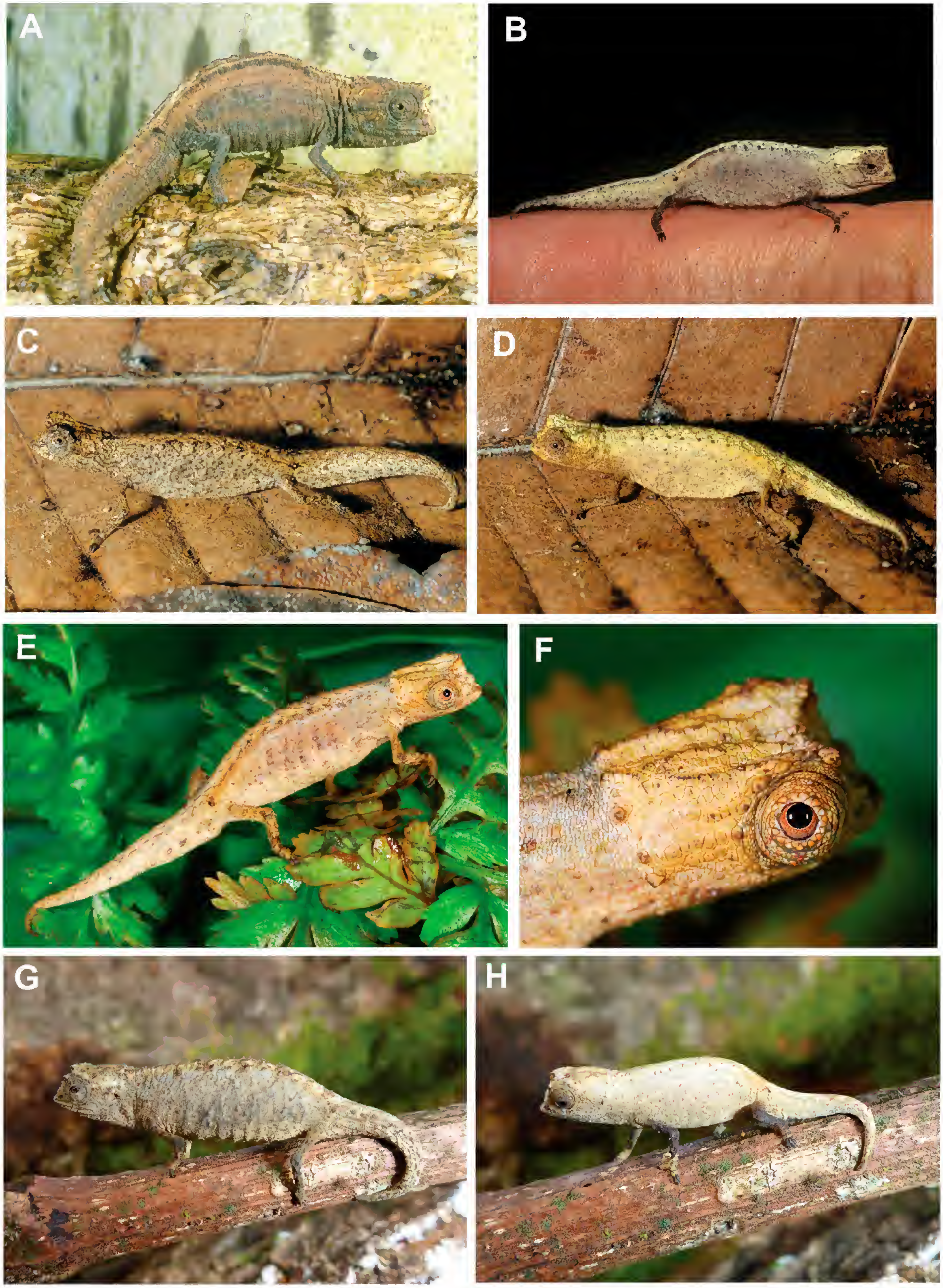

Figure 4. *Brookesia peyrierasi* in life **A–D** Specimens from the type locality Nosy Mangabe (specimen numbers unknown). **E, F** Specimen from Ambodivoangy, ZSM 447/2010 (FGZC 4286) **G, H** Specimens from Masoala (**G**, ZSM 252/2016 [FGZC 5429], **H**, specimen number unknown, species identity not confirmed genetically).

Figure 5. The holotype of *Brookesia tedi* sp. n. from Marojejy in lateral view (above), and dorsal (middle) and lateral (below) views of the heads of the types of *B. tedi* sp. n., in comparison with a representative male specimen of *B. peyrierasi* from the type locality Nosy Mangabe. The lateral view of the holotype (marked with an asterisk) has been mirrored to be in the same orientation as those of the other specimens. Scale bar: 1 mm.

0.92 vs 0.66), slightly wider relative head width (HW/SVL 0.20–0.21 vs 0.17), absence of lateral tail spines (vs presence), and fewer dorsolateral spines (8–10 when countable vs 13); and from males of *B. tuberculata* by smaller supraocular cone and globular hemipenis (vs tubular).

Molecular data clearly identify *B. peyrierasi* as the sister species of *B. tedi* sp. n. (Figs 1, 2); from males of *B. peyrierasi* the new species is distinguished by smaller body size (SVL 15.3–18.2 vs 19.7–22.4 mm) and total length (TL 29.5–31.7 vs 34.2–39.8 mm), more distinct supraocular cone, and rather globular hemipenis lacking apical spines (vs tubular hemipenis with paired sets of apical spines; Fig. 6).

Description of the holotype. Adult male in good state of preservation (Figs 5, 7). Both hemipenes everted. Measurements in Table 1. Lateral crest on head weakly devel-

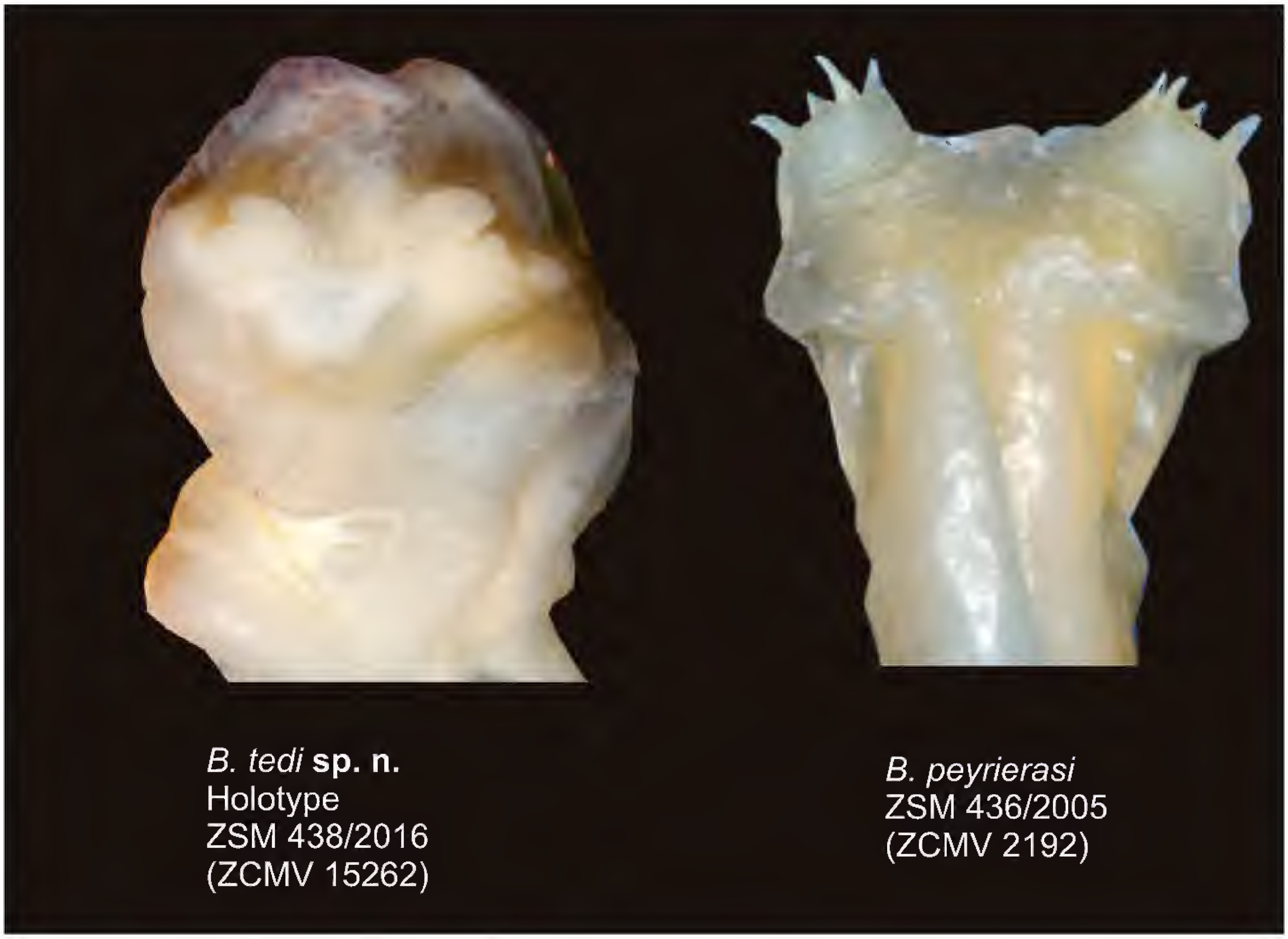

Figure 6. The preserved hemipenes of *Brookesia tedi* sp. n. and its sister species, *B. peyrierasi* in sulcal view. Not to scale. Note that the spines of *B. peyrierasi* are equally visible in asulcal view, and in all studied individuals of this species (see Glaw et al. 1999).

oped, barely recognizable; prominent orbital crests, and a transverse row of enlarged tubercles at the posterior edge of the head that separates the head from the body, no distinct posterior crest; a pair of curved parasagittal crests that start above the eyes and begin to converge before terminating at the transverse row of enlarged tubercles; depression between the eyes with short longitudinal median crest; three pointed tubercles on each side of posterior margin of head; scattered slightly enlarged tubercles on lateral surfaces of head; orbital crest denticulated; distinct supraocular cone present; supranasal cone small, not projecting beyond snout tip; head longer (5.1 mm) than wide (3.2 mm); chin and throat with evenly spaced distinctly enlarged tubercles. Dorsal surface of body without a vertebral ridge or keel; 10/8 (left/right) dorsolateral spines (pointed tubercles) form an almost complete longitudinal line on the body; posteriormost pointed dorsolateral tubercle being largest, above insertion point of hindlimb (the pelvic spine), very slightly projecting backwards; no dorsal pelvic shield in sacral area, but distinct pelvic spine; pointed dorsolateral tubercles almost equally spaced, except for first three tubercles on left side; dorsal surface of tail lacking distinctly enlarged tubercles; scattered enlarged tubercles laterally on anterior third of tail; lateral surface of body with evenly spaced enlarged rounded tubercles; venter with distinctly enlarged rounded tubercles; scattered, distinctly pointed tubercles on limbs; no pointed tubercles around cloaca; longitudinal row of slightly enlarged tubercles lateral on anterior tail; no dorsal, lateral or ventral spines on tail; no enlarged tubercles on ventral surfaces of tail.

The hemipenis is rather globular (though not as globular as that of *B. minima*), short and broad, with a flattened apical end with a clear lip around its circumference (Fig. 6). The whole of the apex is somewhat tilted sulcally. A pair of structures emerge from the apical surface, each of which consists of three fleshy lobes, of which the middle lobe is the shortest. The truncus is smooth and lacks any trace of calyces.

In life, overall colouration light to dark brown, lighter ventrally, the dorsal head and dorsum down to the tail grey. Tubercles and patches of various other colours, including a number of nearly black spots, dot the flanks. Rectangular patches of grey invade the flank from the dorsum. The eye is rayed in shades of brown, with three especially light rays ventrally, the anterior two of which traverse across the upper and lower lips. A brown stripe bordered with cream traverses the supraocular cones.

Figure 7. Different views of the holotype of *Brookesia tedi* sp. n. (ZSM 438/2016; field number ZCMV 15262) in life.

The limbs are distinctly darker than the body. For further detail, see Figure 7. After two years in ethanol, the body colour is muted and more homogeneous. The rays on the eye and stripe between supraocular cones are still distinct, but the grey invading the flanks from the dorsum is less distinct.

Variation. For morphological measurements and proportions see Table 1. The male paratype ZSM 439/2016 differs from the male holotype by a far more prominent supraocular crest, formed by six large pointed tubercles, including a large supraocular cone; by three parallel dorsal crests between parasagittal crests; less prominent enlarged tubercles on throat, chin and venter; indistinct and smaller dorsolateral tubercles (not reliably countable), and a prominent enlarged pointed tubercle on lateral side of head. Its hemipenes are less well extruded than those of the holotype, and the fleshy apical lobes, although present, are difficult to identify.

Etymology. The species name is a patronym dedicated to Ted Townsend, in recognition of his important contributions to the phylogenetics and systematics of squamates, chameleons, and *Brookesia* in particular.

Conservation status. This species is currently only known from relatively high elevation on the Marojejy massif. We follow assessments for other chameleon endemics from this area on Marojejy, specifically *Calumma jejy* and *C. peyrierasi*, which are found somewhat higher but probably have a similar level of microendemism. We consider the species Vulnerable under IUCN Red List criterion Vulnerable D2: as far as is known, *B. tedi* has a highly restricted area of occupancy (= extent of occurrence) of under 150 km^2 (this is the area of 1200 m a.s.l. and above in Marojejy), and is known from a single threat-defined location at 1300 m a.s.l. and above in Marojejy National Park. Two plausible future threats, namely decrease in efficacy of protection on Marojejy, and fire, could rapidly drive the species to becoming Critically Endangered.

Table 1. Morphometric measurements of holotype and paratype of *Brookesia tedi* sp. n. (all in mm). See Materials and methods for abbreviations.

	ZSM 438/2016 ZCMV 15262 Holotype	ZSM 439/2016 ZCMV 15298 Paratype
Sex	M	M
TL	29.5	31.7
SVL	15.3	18.2
TaL	14.2	13.5
HW	3.2	3.6
HH	2.7	2.9
ED	1.6	1.8
FORL	5.3	5.3

Discussion

The new species *Brookesia tedi* is a distinctive, new, and comparatively high-elevation member of the *Brookesia minima* species group. Despite being the sister species of *B. peyrierasi*, the two species differ strongly in their hemipenis morphology. Indeed, hemipenis morphology is a particularly valuable taxonomic character in this species group (Glaw et al. 1999), with characters of several members manifesting as novel structures, such as the arrays of spines of *B. peyrierasi* (Fig. 6), single spines of *B. desperata*, symmetrical short papillae of *B. micra*, and the small structures of the apex of *B. tuberculata* (Brygoo and Domergue 1975; Glaw et al. 1999, 2012a). The apical papillae of *B. tedi* are again different, and the hemipenes of this species resemble somewhat those of *B. ramanatsoai* and *B. minima* in their globular construction and apical lobes (Glaw et al. 1999, 2012a). The evolutionary significance of this variability among species of *Brookesia* remains unclear, but it is a promising area for future research.

Brookesia tedi joins the ranks of species from the Marojejy massif—an assemblage that has been growing rapidly in recent years. The majority of the species that have recently been described from Camp Simpona at 1325 m a.s.l. are amphibians (Glaw and Vences 2000, 2011; Glaw et al. 2011, 2012b; Scherz et al. 2014, 2016, 2017; Rakotoarison et al. 2017) and only one is a reptile (Prötzel et al. 2018). Some of these species have shown an interesting biogeographic connection with similar elevations on the Sorata massif, which we have discussed elsewhere (Scherz et al. 2018b). Data from miniaturised frogs of the genus *Stumpffia* suggest that this pattern can occur also in miniaturised species with supposedly low vagility, but most species of that genus show closer relationships with taxa from areas to the south and east of Marojejy (Rakotoarison et al. in press). The close affinities of *B. tedi* with *B. peyrierasi* from Masoala, Nosy Mangabe, and Ambodivoangy conform rather to this latter pattern.

The two type specimens of *B. tedi* showcase the intraspecific variability that can be present in members of the *B. minima* species group. The holotype has only low tubercles on its head and relatively low supraocular cones, whereas the paratype has pronounced spiny tubercles, and an especially large supraocular cone (Fig. 5). Some morphological variability is present in other members of the group as well; characters such as dorsolateral spines can be present or absent within a single species (Glaw et al. 2012a). Substantial variation in several characters also characterizes other, larger-bodied members of the genus *Brookesia*, e.g. regarding the form of the pelvic shield or the number of dorsolateral spines (see Scherz et al. 2018a for an extreme example). However, there are no *Brookesia* outside the *B. minima* species group where the dorsolateral spines can be present or absent. It is probable that the miniaturisation of this group has resulted in increased morphological variability of adults, as is often seen in miniaturised animals (Hanken and Wake 1993).

Apart from Montagne d'Ambre, at present, Marojejy is the only other known locality where two species of the *B. minima* species group occur. Despite this, and similar to the situation on Montagne d'Ambre, *B. tedi* and *B. karchei* possibly do not occur syntopically, the former being known from at and above 1300 m a.s.l. and the latter from under 1000 m a.s.l. However, still unidentified *Brookesia minima*-group specimens are known from lower altitudes of Marojejy (Raxworthy and Nussbaum 1995; Raselimanana et al. 2000) and future studies need to clarify their taxonomic status. Other populations from the vicinity of Sambava (Glaw and Vences 1994) must also be investigated, as these may represent further undescribed diversity within this group.

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References

Avise JC, Ball RM (1990) Principles of genealogical concordance in species concepts and biological taxonomy. In: Futuyma D, Antonovics J (Eds) Oxford Surveys in Evolutionary Biology. Oxford University Press, Oxford, 45–67.

Brygoo ÉR (1978) Reptiles sauriens Chamaeleonidae genre *Brookesia* et complément pour le genre *Chamaeleo*. Faune de Madagascar 47: 1–173.

Brygoo ÉR, Blanc CP, Domergue CA (1974) Notes sur les *Brookesia* de Madagascar VII [VIII]. *Brookesia* du Marojezy. *B. betschi* et *B. griveaudi* n. sp. (Reptilia, Squamata, Chamaeleonidae). Bulletin de l'Académie Malgache 51(1): 167–184.

Brygoo ÉR, Domergue CA (1975) Notes sur les *Brookesia* de Madagascar. IX. Observations sur *B. tuberculata* Mocquard, 1894, *B. ramanantsoai* sp. nov. et *B. peyrierasi* nom. nov. Bulletin du Muséum national d'Histoire naturelle, Paris 267(189): 1769–1782.

Glaw F, Köhler J, Townsend TM, Vences M (2012a) Rivaling the world's smallest reptiles: discovery of miniaturized and microendemic new species of leaf chameleons (*Brookesia*) from northern Madagascar. PLoS ONE 7(2): e31314. https://doi.org/10.1371/journal.pone.0031314

Glaw F, Köhler J, Vences M (2011) New species of *Gephyromantis* from Marojejy National Park, northeast Madagascar. Journal of Herpetology 45(2): 155–160. https://doi.org/10.1670/10-058.1

Glaw F, Köhler J, Vences M (2012b) A tiny new species of *Platypelis* from the Marojejy National Park in northeastern Madagascar (Amphibia: Microhylidae). European Journal of Taxonomy 9: 1–9. https://doi.org/10.5852/ejt.2012.9

Glaw F, Vences M (1994) A Fieldguide to the Amphibians and Reptiles of Madagascar (2nd edn). Vences & Glaw Verlags, Cologne, 478 pp.

Glaw F, Vences M (2000) A new species of *Mantidactylus* from northeastern Madagascar (Amphibia, Anura, Ranidae) with resurrection of *Mantidactylus blanci* (Guibé, 1974). Spixiana 23(1): 71–83.

Glaw F, Vences M (2011) Description of a new frog species of *Gephyromantis* (subgenus *Laurentomantis*) with tibial glands from Madagascar. Spixiana 34(1): 121–127.

Glaw F, Vences M, Ziegler T, Böhme W, Köhler J (1999) Specific distinctness and biogeography of the dwarf chameleons *Brookesia minima*, *B. peyrierasi* and *B. tuberculata* (Reptilia: Chamaeleonidae): evidence from hemipenial and external morphology. Journal of Zoology 247: 225–238. https://doi.org/10.1111/j.1469-7998.1999.tb00986.x

Han D, Zhou K, Bauer AM (2004) Phylogenetic relationships among gekkotan lizards inferred from C-mos nuclear DNA sequences and a new classification of the Gekkota. Biological Journal of the Linnean Society 83: 353–368. https://doi.org/10.1111/j.1095-8312.2004.00393.x

Hanken J, Wake DB (1993) Miniaturization of body size: organismal consequences and evolutionary significance. Annual Review of Ecology and Systematics 24: 501–519. https://doi.org/10.1146/annurev.es.24.110193.002441

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Macey JR, Larson A, Ananjeva NB, Fang Z, Papenfuss TJ (1997) Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. Molecular Biology and Evolution 14(1): 91–104. https://doi.org/10.1093/oxfordjournals.molbev.a025706

Macey JR, Schulte JA, Larson A, Ananjeva NB, Wang Y, Pethiyagoda R, Rastegar-Pouyani N, Papenfuss TJ (2000) Evaluating trans-tethys migration: an example using acrodont lizard phylogenetics. Systematic Biology 49: 233–256. https://doi.org/10.1093/sysbio/49.2.233

Palumbi SR, Martin A, Romano S, McMillan WO, Stice L, Grabowski G (1991) The Simple Fool's Guide to PCR, Version 2.0. Privately published, University of Hawaii, 45 pp.

Prötzel D, Vences M, Hawlitschek O, Scherz MD, Ratsoavina FM, Glaw F (2018) Endangered beauties: micro-CT cranial osteology, molecular genetics and external morphology reveal three new species of chameleons in the *Calumma boettgeri* complex (Squamata: Chamaeleonidae). Zoological Journal of the Linnean Society 184(2): 471–498. https://doi.org/10.1093/zoolinnean/zlx112

Rakotoarison A, Scherz MD, Bletz MC, Razafindraibe JH, Glaw F, Vences M (in press) Diversity, elevational variation, and phylogenetic origin of stump-toed frogs (Microhylidae, Cophylinae, *Stumpffia*) on the Marojejy massif, northern Madagascar. Salamandra.

Rakotoarison A, Scherz MD, Glaw F, Köhler J, Andreone F, Franzen M, Glos J, Hawlitschek O, Jono T, Mori A, Ndriantsoa SH, Raminosoa Rasoamampionona N, Riemann JC, Rödel M-O, Rosa GM, Vieites DR, Crottini A, Vences M (2017) Describing the smaller majority: integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar. Vertebrate Zoology 67(3): 271–398.

Raselimanana AP, Raxworthy CJ, Nussbaum RA (2000) Herpetofaunal species diversity and elevational distribution within the Parc National de Marojejy, Mad[a]gascar. Fieldiana Zoology (New Series) 97: 157–174. https://biodiversitylibrary.org/page/2838065

Raxworthy CJ, Nussbaum RA (1995) Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. Journal of Zoology 235: 525–558. https://doi.org/10.1111/j.1469-7998.1995.tb01767.x

Scherz MD, Glaw F, Rakotoarison A, Wagler M, Vences M (2018a) Polymorphism and synonymy of *Brookesia antakarana* and *B. ambreensis*, leaf chameleons from Montagne d'Ambre in north Madagascar. Salamandra 54(4): 259–268.

Scherz MD, Glaw F, Vences M, Andreone F, Crottini A (2016) Two new species of terrestrial microhylid frogs (Microhylidae: Cophylinae: *Rhombophryne*) from northeastern Madagascar. Salamandra 52(2): 91–106.

Scherz MD, Hawlitschek O, Razafindraibe JH, Megson S, Ratsoavina FM, Rakotoarison A, Bletz MC, Glaw F, Vences M (2018b) A distinctive new frog species (Anura, Mantellidae) supports the biogeographic linkage of the montane rainforest massifs of northern Madagascar. Zoosystematics and Evolution 94(2): 247–261. https://doi.org/10.3897/zse.94.21037

Scherz MD, Razafindraibe JH, Rakotoarison A, Bletz MC, Glaw F, Vences M (2017) Yet another small brown frog from high altitude on the Marojejy Massif, northeastern Madagascar. Zootaxa 4347(3): 572–582. https://doi.org/10.11646/zootaxa.4347.3.9

Scherz MD, Ruthensteiner B, Vences M, Glaw F (2014) A new microhylid frog, genus *Rhombophryne*, from northeastern Madagascar, and a re-description of *R. serratopalpebrosa* using micro-computed tomography. Zootaxa 3860(6): 547–560. https://doi.org/10.11646/zootaxa.3860.6.3

Schimmenti G, Jesu R (1996) *Brookesia exarmata* sp. nov. (Reptilia, Chamaeleonidae): a new dwarf chameleon from the limestone outcrops of western Madagascar. Italian Journal of Zoology 63(2): 193–197. https://doi.org/10.1080/11250009609356129

Tilbury CR (2018) Chameleons of Africa: An Atlas, Including the Chameleons of Europe, the Middle East and Asia. Chimaira Buchhandelsgesellschaft, Frankfurt am Main, Germany, 643 pp.

Tolley KA, Townsend TM, Vences M (2013) Large-scale phylogeny of chameleons suggests African origins and Eocene diversification. Proceedings of the Royal Society of London B 280(1759): 20130184. https://doi.org/10.1098/rspb.2013.0184

Villeneuve AR (2017) Habitat selection and population density of the world's smallest chameleon, *Brookesia micra*, on Nosy Hara, Madagascar. Herpetological Conservation and Biology 12(2): 334–341.

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A new stiletto snake (Lamprophiidae, Atractaspidinae, *Atractaspis*) from Liberia and Guinea, West Africa

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Abstract

We describe a new stiletto snake, *Atractaspis*, from western Liberia and southeastern Guinea. The new species shares with morphologically similar western African *Atractaspis* species, *A. reticulata* and *A. corpulenta*, the fusion of the 2nd infralabial with the infra-maxillary. From *A. corpulenta* the new species differs by a more slender body (276–288 ventrals and 19 or 20 dorsal scale rows versus 178–208 ventrals with 23–29 dorsal scale rows), a divided anal plate and divided subcaudal scales (both non-divided in *A. corpulenta*). The new species differs from most *A. reticulata* by having 19 or 20 dorsal scale rows at midbody (versus 21–23, rarely 19), and a lower ventral count (276–288 versus 304–370). The new species thus has a relatively longer tail: snout-vent-length / tail-length in the female holotype (15.7) and paratype (21.5) versus a mean of 23.6 in seven female *A. reticulata*. The new *Atractaspis* likely is endemic to the western part of the Upper Guinea forest zone and thus adds to the uniqueness of this diverse and threatened biogeographic region.

Introduction

The stiletto snakes or burrowing asps, genus *Atractaspis* Smith, 1849, currently comprise 22 (Wallach et al. 2014), or 21 (Uetz et al. 2018) valid species. Most species are restricted to sub-Saharan Africa where they occur in a wide range of habitats from semi-deserts to rainforests (Spawls and Branch 1995); only two occur in the Middle East and Arabia (Wallach et al. 2014; Grossmann et al. 2018). These fossorial and venomous snakes are famous for their unique skull anatomy and venom delivery system, enabling them to use a single fang to bite, with closed mouth, in a lateral stabbing movement (Broadley 1990; Greene 1997; Cundall and Irish 2008; McDowell 2008). Various herpetologists have already been suffering from this behavior, making it impossible to hold the snakes in the usual way behind the head without being bitten (see Wagner et al. 2009). Their systematic position was matter of a constant debate and the snakes have been placed for instance within Viperidae, within Aparallactinae as subfamily of Colubridae, as a separate family Atractaspididae, and most recently as a subfamily Atractaspidinae within the Lamprophiidae (Broadley 1990; Vidal et al. 2007; Wallach et al. 2014; Uetz et al. 2018; Portillo et al. 2018).

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From West and western Central Africa 11 *Atractaspis* species are known: *A. aterrima* Günther, 1863, *A. boulengeri* Mocquard, 1897, *A. coalescens* Perret, 1960, *A. congica* Peters, 1877, *A. corpulenta* (Hallowell, 1854), *A. dahomeyensis* Bocage, 1887, *A. irregularis* (Reinhardt, 1843), *A. microlepidota* Günther, 1866, *A. micropholis* Günther, 1872, *A. reticulata* Sjöstedt, 1896, and *A. watsoni* Boulenger, 1908 (Chippaux 2001; Chirio and LeBreton 2007). On recent surveys in north-western Liberia and south-eastern Guinea, we collected stiletto snakes deviating from all other known *Atractaspis* species. These snakes are described here as a species new to science. In addition, we redescribe the holotype of *A. reticulata,* the species which is morphologically most similar to our new species, and summarize its known distribution.

Material and methods

The holotype was euthanized by smearing a benzocaine cream into its mouth. The paratype and one additional specimen were found dead. From the holotype and paratype we collected tissue samples, which were preserved in 97% ethanol. The snakes were preserved in 75% ethanol and are inventoried in the herpetological collections of the Museum für Naturkunde, Berlin, Germany (ZMB; holotype), the Museo di Storia naturale del Salento, Calimera, Italy (MSNS; paratype), or will be inventoried at the Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB; additional specimen, see below). Measurements and assessment of morphological characters of the new species and comparative material, including its pholidosis, has been done by one person (CK). Ct-scanning and measurements of skull bones have been compiled by KM. Dorsal scale rows were counted at three points along the trunk, i.e. at one head length posterior to the end of the head, at midbody (at half of the snout-vent length), and at one head length anterior to the anal scale. Dorsal scale row reduction formulae were based on Dowling (1951a), the formulae for the supracaudal scales are analogous to this procedure. We added a 'x' to the formulae if no fusion or reduction takes place. Ventral counts are according to Dowling (1951b). Preventrals are the scales anterior to the ventrals, characterized as being broader than long. The terminal scale was not included in the subcaudal count and is given as '+1'. Values for symmetric characters are given as left/right. Measurements of snout-vent length and tail length were rounded to the nearest millimeter, all other to the nearest 0.1 millimeter. Sex was determined by a small incision at the base of the tail. Comparative measures have been compiled from the literature, material housed at ZMB and the holotype of *A. reticulata* from the Naturhistoriska Rijkmuseet, Section for Vertebrate Zoology, Stockholm, Sweden (NRM 1796 collected in "Kamerun, Ekundu" by Sjöstedt; Tables 1, 2). Wallach et al. (2014) and Uetz et al. (2018) erroneously cited the Zoological Museum of the University of Uppsåla, Sweden (ZMUU), as the repository of the holotype of *A. reticulata.*

The heads of the holotype and paratype of the new species, the *A. reticulata* holotype and further comparative material were subjected to micro-tomographic analysis at the Museum für Naturkunde Berlin, using a Phoenix nanotom X-ray|s tube at 80–100 kV and 100–230 µA, generating 1000–1440 projections with 750 ms per scan. The different kV-settings depended on the respective specimen size. Effective voxel size, i.e. resolution in three-dimensional space, ranged from 5.71–15.67 µm. The cone beam reconstruction was performed using the phoenix|x-ray datos|x version 2.2 software (GE Sensing and Inspection Technologies GMBH) and the data were visualized in VG Studio Max, version 3.1.

We sequenced 509 bp of the 16S ribosomal RNA of the types of the new species, following the procedures and using the primers as described in Portillo et al. (2018). We compared the two sequences to each other and to the sequences of the other *Atractaspis* species from which 16S have been published (Portillo et al. 2018): *Atractaspis boulengeri* (IPMB J355; GenBank AY611833), *A. corpulenta* (IPMB J369; GenBank AY611837), *A. irregularis* (UTEP 21655; GenBank MG746901) and *A. micropholis* (IPMB J283; GenBank AY611823). We also received an unpublished 16S sequence from *A. reticulata heterochilus* (UTEP 21664; Democratic Republic of the Congo, Tshopo Province: road between Nia Nia and Kisangani; Portillo et al. submitted) for comparison. The sequences of the new species have been deposited at GenBank.

Results

Species description

***Atractaspis branchi* sp. n.**

http://zoobank.org/990E7C05-947C-4ED7-A8A8-97BFCD77A29F

Figures 1–4; Tables 1–3

Holotype. ZMB 88529 (field and tissue number RG97; 16S GenBank MK501382), female, Liberia, Lofa region, Foya Forest, 08°01'16.2"N, 010°25'31.4"W, 317 m a.s.l., near a small rocky creek in primary lowland rainforest, 6 April 2018, coll. M.-O. Rödel, G. Sambolah & J. Glos.

Paratype. MSNS Rept 280 (field number 9294X, skull broken; 16S GenBank MK501383), female, Guinea, Nzérékoré Region, Koyakoélé, 07°44'54"N, 009°11'28"W, 393 m a.s.l., 26 December 2011, coll. L. Chirio.

Additional material. IRSNB not yet accessioned (field number 9314X), Guinea, Nzérékoré Region, Belefanin, 07°55'28"N, 009°01'33"W, 486 m a.s.l., coll. L. Chirio (voucher, only head and anterior part of body; snake still in Africa and thus not available to us).

Diagnosis. External morphology, skull anatomy and molecular data (see below) clearly supports the position within the genus *Atractaspis*. The new species can be only mistaken morphologically with species from

Table 1. Morphology and pholidosis of *A. branchi* sp. n. and the three subspecies of *Atractaspis reticulata*, based on literature data, the *A. branchi* and *A. reticulata* types and vouchers from ZMB collection; SVL = snout-vent length; TL = tail length; na = no data available; measures in mm, for scale counts see material & method section; museum acronyms: AMNH = American Museum of Natural History, New York, USA; KUZ= Department of Zoology, Kyoto University, Kyoto, Japan; MBG = Mission Biologique au Gabon, Makokou, Gabon; MNHN = Museum National d'Histoire Naturelle, Paris, France; MSNS = Museo di Storia naturale del Salento, Calimera, Italy; NRM = Naturhistoriska Rijkmuseet, Stockholm, Sweden; RGMC= Musée Royal de l'Afrique Centrale, Tervuren, Belgium (now MRAC); SMF = Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt am Main, Germany; USNM = Smithsonian Institution, National Museum of Natural History, Washington, USA; ZMB = Museum für Naturkunde, Berlin, Germany; ZMH = Zoologisches Museum Hamburg, Hamburg, Germany; ZSM = Zoologische Staatssammlung München, Munich, Germany; * = error according to Laurent (1950).

Taxon	Accession number	Status	Sex	SVL	TL	Dorsals	Ventrals	Subcaudals	Source
A. branchi sp. n.	ZMB 88529	Holotype	♀	267	17	17-19-17	3+276	25/25+1	this study
	MSNS Rept 280	Paratype	♀	689	32	19-20-19	5+288	19/19+1	this study
A. r. reticulata	NRM 1796	Holotype	na	765	35	?-19-?	308	21/21	Sjöstedt 1897
			♀	712	33	17-19-17	4+304+1/2	21/21+1	this study
	ZMB 14724		na	1095	40	?-21-?	328	19/19	Werner 1899
			♂	1075	40	19-21-17	1+327	20/19+1	this study
	ZMB 21725		♀	855	37	17-21-17	6+322	21/21+1	this study
	ZMB 28500		♀	483	5+?	19-21-17	5+320	4/4+?	this study
	ZMB 30714		♀	600	23	17-21-17	3+338	21/21+1	this study
	ZMB ? (not found)		na	na	na	?-21-?	330	20	Sternfeld 1908
	ZMH R11274		♂	485	25	?-21-?	327	27/28+1	Werner 1913
A. r. brieni	RGMC 2706	Syntype	♂	na	na	19-23-19	345	28	Laurent 1945 / 1956a
	RGMC 2694	Syntype	♀	na	na	19-23-19	370	22 (1× simple)	Laurent 1945 / 1956a
	RGMC 21577		♂	717	35	23-23-19	347	25 (2× simple)	Laurent 1960
	AMNH 11901		♂	786	30	19-23-19	353	23	Schmidt 1923
A. r. heterochilus	KUZ R8330		na	273	13	19-23-19	327	22/22	Ota et al. 1987
	MBG 0644		♂	507	23	?-23-?	339	22	Knoepffler 1966
	MNHN 1964.566		♀	706	30	19-23-?	337	21/21	Roux-Estève 1965
	MNHN 1963.899		♀	783	39	19-23-?	344	23/23	Roux-Estève 1965
	RGMC 608	Holotype	♀	497	23	19-23-?	341	22	Boulenger 1901/1919
		Holotype	♀	na	na	19-23-19	342	21	Laurent 1945
	RGMC 1686		♀	na	na	?-23-?	359	21	Boulenger 1919
			♀	na	na	19-23-19	350	21	Laurent 1945
	RGMC 6614		♀	na	na	19-23-19	344	na	Laurent 1945
	RGMC 8003		♀	na	na	19-23-19	346	na	Laurent 1945
	RGMC 8252		♀	na	na	19-23-19	349	24	Laurent 1945
	RGMC 8764		♀	na	na	19-23-19	350	23	Laurent 1945
	RGMC 8767		♀	na	na	19-23-19	355	24	Laurent 1945
	RGMC 16214		♂	na	na	19-23-19	319	26	Laurent 1956a
	? (Cameroon)		♀	na	na	?-21-?	336	21	Boulenger 1919
	BMNH (Cameroon)		♀	na	na	?-21-?	356*	20	Boulenger 1919
	? (Cameroon)		♀	na	na	?-23-?	339	22	Boulenger 1919
	SMF 52361		♂	na	na	?-23-?	319	24/24+1	Perret and Mertens 1957
	USNM 565138		♂	730	45	19-23-19	4+318	2/2+1+26/26	Pauwels and Sallé 2009
	ZMH R11275		♀	730	25	?-23-?	326	4/4+2+11/11+1	Werner 1913
	ZSM 111/1954		♂	640	31	19-23-21	328	1+25/25+1	Hellmich 1957
			♂	564	32	19-23-19	6+331	1+25/25+1	this study
	Summary data		♂♂				313-327		Laurent 1956a
	Summary data		♀♀				326-353		Laurent 1956a

Laurent's (1950) section 'D', his *reticulata*-group. In particular it differs from all other species of the genus, except *A. reticulata* and *A. corpulenta* (including the West African *A. c. leucura*), by the fusion of the 2nd infralabial with the inframaxillary. From *A. corpulenta* it differs by a much higher ventral count (276–288 vs 178–208), lower number of dorsal scale rows at midbody (19 vs 23–29), divided anal plate and subcaudals, and the absence of a white colored tail tip (present in *A. c. leucura*); from *A. reticulata* it can be distinguished by a lower ventral count (276–288 vs 304–370), and 19 (the paratype has mostly 19 scale rows, but 20 at midbody) dorsal scales rows at midbody (19 scale rows present in the *A. reticulata* holotype, other vouchers having 21–23 rows) (Table 1). The new species further differs from *A. corpulenta* by a more slender body and from *A. reticulata* by a longer tail compared to body length.

Table 2. Morphological ratios in some *Atractaspis* species. SVL = snout-vent length; TL = tail length; EM / VE = distance lower eye margin to mouth / vertical eye diameter; EN / HE = distance anterior eye margin to nostril / horizontal eye diameter; HW / VE = head width (distance of outer margins of supraoculars) at mid eye level / vertical eye diameter; * head damaged, no measures possible; measures in mm.

Taxon	Accession number	sex	SVL / TL	HW / VE	EM / VE	EN / HE
A. branchi sp. n.	ZMB 88529 (Holotype)	♀	267.0 / 17.0 = 15.7	4.5	2.5	1.9
	MSNS Rept 280 (Paratype)	♀	689.0 / 32.0 = 21.5	6.2	3.6	2.4
A. r. reticulata (Cameroon, Ekundu)	NRM 1796 (Holotype)	♀	712.0 / 33.0 = 21.6	6.4	4.2	2.3
A. r. reticulata (Cameroon, Johann-Albrechtshöhe)	ZMB 28500	♀	483.0 / 5+ = ?	6.3	3.6	2.6
A. r. reticulata (Cameroon, Victoria)	ZMB 21725	♀	855.0 / 37.0 = 23.1	6.1	3.8	2.9
A. r. reticulata (Cameroon, Ajoshöhe)	ZMB 30714	♀	600.0 / 23.0 = 26.1	6.4	3.5	3.0
A. r. reticulata (Cameroon, Yaoundé)	ZMB 14724	♂	1075.0 / 40.0 = 26.9	*	*	*
A. r. heterochilus (Angola, Piri Dembos)	ZSM 111/1954	♂	564.0 / 32.0 = 17.6	4.9	2.6	2.1
A. bibronii rostrata (Mozambique)	ZMB 2821	♀	565.0 / 33.0 = 17.1	5.5	3.0	2.2
A. bibronii rostrata (Tanzania)	ZMB 16799	♀	177.0 / 13.0 = 13.6	4.5	1.8	2.0
A. bibronii rostrata (Tanzania, Sanya)	ZSM 60/1993	♀	272.0 / 17.0 = 16.0	4.6	2.0	1.9
A. bibronii rostrata (Tanzania, Sanya)	ZSM 60/1993	♀	432.0 / 25.0 = 17.3	5.0	2.4	2.4
A. c. congica (Angola, Belavista)	ZSM 113/1954	♂	395.0 / 32.0 = 12.3	5.7	2.7	2.2
A. c. congica (Angola, Piri Dembos)	ZSM 112/1954/2	♂	508.0 / 36.0 = 14.1	5.4	2.7	2.4
A. i. irregularis (Liberia, Nimba County)	ZMB 88015	♀	241.0 / 18.0 = 13.4	4.6	1.7	1.8
A. i. irregularis (Liberia, Nimba County)	ZMB 87809	♀	550.0 / 41.0 = 13.4	5.1	2.4	1.8

Holotype description. Subadult female; slender snake with moderately robust body and short and rounded head; no constriction between head and body; snout-vent length 267 mm; tail length 17 mm (ratio snout-vent length / tail length = 15.7); head length 7.7 mm (tip of snout to angle of jaws) / 7.1 mm (tip of snout to end of parietal suture); head width 5.7 mm (at widest point) / 3.6 mm (distance between the outer margins of supraocular at the level of mid eye); nostrils directed laterally; dorsally measured distance between nostrils 2.9 mm; small eyes directed dorsolaterally; eye diameter 1.0 mm (horizontal) / 0.8 mm (vertical), pupil roundish; distance from lower border of eye to mouth 2.0 mm; distance between anterior edge of eye to posterior edge of nostril 1.9 mm; 5 supralabials, the 4^{th} being the largest, the 3^{rd} and 4^{th} in contact with eye; 5 infralabials, the 1^{st} and 3^{rd} touching the inframaxillary, the 2^{nd} fused with the inframaxillary, the 3^{rd} being the largest; the 1^{st} pair of infralabials in contact behind mental; rostral visible from above, rounded in lateral and dorsal views; nasal divided, touching 1^{st} to 3^{rd} supralabial and preocular, nostril nearly completely situated in the anterior part of nasal; loreal absent; 1 small preocular, not in contact with frontal, touching 3^{rd} supralabial; 1 postocular distinctly larger than preocular, touching temporal and 4^{th} supralabial; 1 small supraocular (length 1.6 mm); 1 very large anterior temporal (length 2.7 mm) followed by 2 posterior temporals; beside the temporals only 3 further scales touching the posterior borders of parietals; 1 pair of distinctive inframaxillaries touched by 3 gular scales; mental groove present; top of head covered by 9 scales; suture of internasals 0.7 mm long; suture of prefrontals 0.8 mm long; frontal slightly longer than wide (3.1 mm vs 2.8 mm); suture of parietals 1.8 mm long; dorsal scales smooth, rhombic shaped, decreasing gradually in size dorsally, apical pits absent, but all dorsal scales with a single little pore near the center of the scale; 3 preventrals, 276 rounded ventral scales; anal plate divided; subcaudals divided, 25/25+1; ratio ventrals / subcaudals: 11.0; dorsal scale rows straight.

Dorsal scale row reduction:

$$19\,\frac{4+5(8)}{4+5(8)}\,17\,\frac{6\rightarrow 6+7(66)}{6\rightarrow 6+7(64)}\,19\,\frac{5+6(240)}{6+7(239)}\,17(276)$$

Supracaudal scale row reduction:

$$14\,\frac{2+3(2)}{3+4(4)}\,12\,\frac{-4(5)}{5+6(5)}\,10\,\frac{4+5(17)}{4+5(16)}\,8\,\frac{3+4(22)}{3+4(22)}\,6\,\frac{-3(25)}{-3(24)}\,4(25)$$

Color in life: dorsal scales of uniform, shiny, purple-brown with light grey margins, venter marginally lighter, broad tongue fleshy (Fig. 1). Color in preservation: dorsally uniform dark grey with a purplish hue; all scales with lighter margins, venter lighter; mental, first pair of infralabials and lower margin of the rostral pale.

Paratype description. Adult female, skull broken; slender snake with moderately robust body and short and rounded head; no constriction between head and body; snout-vent length 689 mm; tail length 32 mm (ratio snout-vent length / tail length = 21.5); head length 7.7 mm (tip of snout to angle of jaws) / 11.7 mm (tip of snout to end of parietal suture); head width 10.3 mm (at widest point) / 6.2 mm (distance between the outer margins of supraocular at the level of mid eye); nostrils directed laterally; dorsally measured distance between nostrils 4.7 mm; small eyes directed dorsolaterally; eye diameter 1.5 mm (horizontal) / 1.0 mm (vertical), pupil roundish; distance from lower border of eye to mouth 3.6 mm; dis-

Figure 1. Life coloration of the *Atractaspis branchi* sp. n. holotype (ZMB 88529).

tance between anterior edge of eye to posterior edge of nostril 3.6 mm; 5 supralabials, the 4th being the largest, the 3rd and 4th in contact with eye; 5 infralabials, the 1st and 3rd touching the inframaxillary, the 2nd fused with the inframaxillary, the 3rd being the largest; the 1st pair of infralabials in contact behind mental; rostral visible from above, rounded in lateral and dorsal views; nasal divided, touching 1st to 3rd supralabial and preocular on the right side (left side preocular is fused with the prefrontal), nostril nearly completely situated in the anterior part of nasal; loreal absent; 1 small preocular on the right side (left side missing), not in contact with frontal, touching 3rd supralabial; 1 postocular little larger than preocular, touching temporal and 4th supralabial; 1 small supraocular (length 2.6 mm); 1 very large anterior temporal (length 5.2 mm) followed by 2 posterior temporals; beside the temporals only 3 further scales touching the posterior borders of parietals; 1 pair of distinctive inframaxillaries touched by 3 gular scales; mental groove present; top of head covered by 9 scales; suture of internasals 1.4 mm long; suture of prefrontals 1.6 mm long; frontal slightly longer than wide (4.9 mm vs 4.8 mm); suture of parietals 2.8 mm long; dorsal scales smooth, rhombic shaped, decreasing gradually in size dorsally, apical pits absent, but all dorsal scales with a single little pore near the center of the scale; 5 preventrals, 288 rounded ventral scales; anal plate divided; subcaudals divided, 19/19+1; ratio ventrals/subcaudals: 15.6; dorsal scale rows oblique.

Dorsal scale row reduction:

$$19\underset{4+5(10)}{\overset{4+5(14)}{\text{———}}}17\underset{5\to5+6(59)}{\overset{5\to5+6(64)}{\text{———}}}19\underset{6\to6+7(128)}{\overset{x}{\text{———}}}20\underset{6+7(137)}{\overset{x}{\text{———}}}19\underset{6\to6+7(139)}{\overset{x}{\text{———}}}20\underset{6+7(149)}{\overset{x}{\text{———}}}19\underset{5+6(272)}{\overset{5+6(274)}{\text{———}}}17$$

Supracaudal scale row reduction:

$$14\underset{4+5(1)}{\overset{5+6(2)}{\text{———}}}12-\mathrm{PV+PV}(3)-11\underset{4+5(4)}{\overset{x}{\text{———}}}10\underset{4+5(9)}{\overset{4+5(10)}{\text{———}}}8\underset{3+4(15)}{\overset{-4(15)}{\text{———}}}6-\mathrm{PV+PV}(18)-5-\text{-V}(19)-4(19)$$

Color: Dorsal and ventral scales of freshly dead individual a dark grey with lighter grey to almost white margins; dorsal scales with slight rainbow shimmer (Fig. 2).

Additional material. The only available data, collected in the field, of this specimen (Fig. 2; only head and anterior body left), were sublinguals fused on each side with the 2nd infralabials; 4/4 infralabials (including the ones fused with the sublinguals); 2 preventrals + > 56 ventrals).

Skull anatomy. The skull anatomy of most *Atractaspis* species is unknown, as is the phylogenetic relationships of our new species. We here compare ct-scans and measurements of the holotype and paratype of *Atractaspis branchi* sp. n. to the morphologically most similar *Atractaspis* species, *A. reticulata* (NRM 1796, holotype of *A. r. reticulata*; and ZMB 28500), and two other *Atractaspis* species, *A. boulengeri matschiensis* (ZMB 11040) and *A. aterrima* (ZMB 8016). In general, skull shape was very similar (Figs 3–5; Table 3). However, the short and stout skull of the new species can be distinguished from the representatives of the three other species by shorter frontals compared to skull length with only a shallow inclusion of the nasals (ratio length of frontals to skull length: 0.25–0.26 vs 0.28–0.31) and a higher number of palatine teeth (3 vs 0 or 2). Furthermore *A. branchi* sp. n. differs from *A. boulengeri matschiensis* and *A. aterrima* by the extension of the nasals anteriorly, being longer than level of premaxilla (vs nasals shorter than level of premaxilla), and from *A. boulengeri matschiensis* by a transverse anterior border of the premaxilla in dorsal view (vs a convex anterior border). However, we examined only one or two (*A. branchi* and *A. reticulata*) individuals of each taxon, and intraspecific variability so far has not been investigated in any *Atractaspis* species, but it might be expected. For instance, the measurements and scans of the two types of *A. branchi* sp. n. indicate that smaller specimens may have shorter fangs and larger eyes (Table 2).

Figure 2. *Atractaspis branchi* sp. n. paratype (MSNS Rept 280) and head and anterior part of body of a further, not yet accessioned specimen (field number 9314X) from south-eastern Guinea.

Table 3. Skull anatomy of some *Atractaspis* species; given are measures and ratios of bones, collected from ct-scans; *Atractaspis branchi* sp. n. has a comparatively short frontale; measures in mm (compare Material and methods and Figs 3–5).

Species / character	*branchi* sp. n. (Holotype)	*branchi* sp. n. (Paratype)	*reticulata* (Holotype)	*reticulata*	*aterrima*	*boulengeri matschiensis*
Accession number	ZMB 88529	MSNS Rept 280	NRM 1796	ZMB 28500	ZMB 8016	ZMB 11040
Head length	8.46	14.74	13.17	9.98	12.89	14.22
Nasale length	1.88	3.43	3.22	2.43	3.3	2.91
Nasale width	1.83	2.96	2.64	2.41	2.15	2.82
Frontale length	2.15	3.88	4.01	3.09	3.67	4.14
Vomer length	1.41	2.43	2.3	1.82	2.1	2.53
Vomer width	0.99	1.52	1.35	1.15	1.28	1.71
Lower jaw length	8.24	15.85	15.29	11.09	14.62	17.44
Length of fang	2.98	7.14	7.42	4.02	6.02	5.51
Quadratum length	2.45	5.66	4.49	3.79	5.67	6.6
Angulare length	1.46	2.84	2.77	2.13	3.27	3.16
Spleniale length	1.31	3.08	2.28	2.08	2.45	2.71
Nasale / head length	0.22	0.23	0.24	0.24	0.26	0.20
Frontale / head length	0.25	0.26	0.30	0.31	0.28	0.29
Nasale width / length	0.97	0.86	0.82	0.99	0.65	0.97
Vomer width / length	0.70	0.63	0.59	0.63	0.61	0.68
Lower jaw / head length	0.97	1.08	1.16	1.11	1.13	1.23
Fang / head length	0.35	0.48	0.56	0.40	0.47	0.39
Quadratum / head length	0.29	0.38	0.34	0.38	0.44	0.46
Angulare / Spleniale	0.90	1.08	0.82	0.98	0.75	0.86

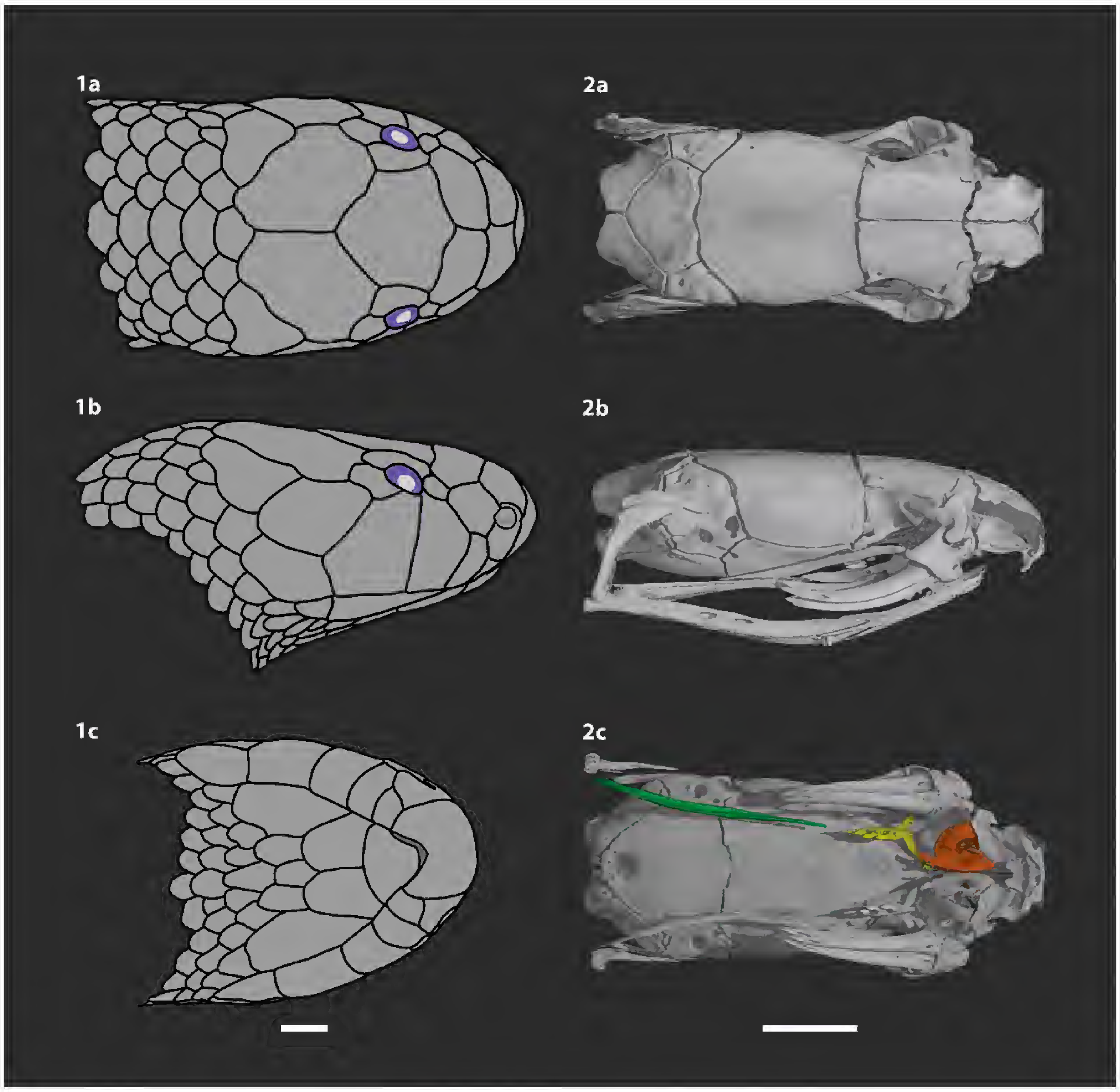

Figure 3. Holotype of *Atractaspis branchi* sp. n. (ZMB 88529) **1** head scalation in dorsal (**a**), lateral (**b**), and ventral (**c**) views **2** ct-scan of skull in dorsal (**a**), lateral (**b**), and ventral (**c**) views; lower jaw virtually removed; green: pterygoid, yellow: palatine, orange: vomer. Scale bar: 1 mm.

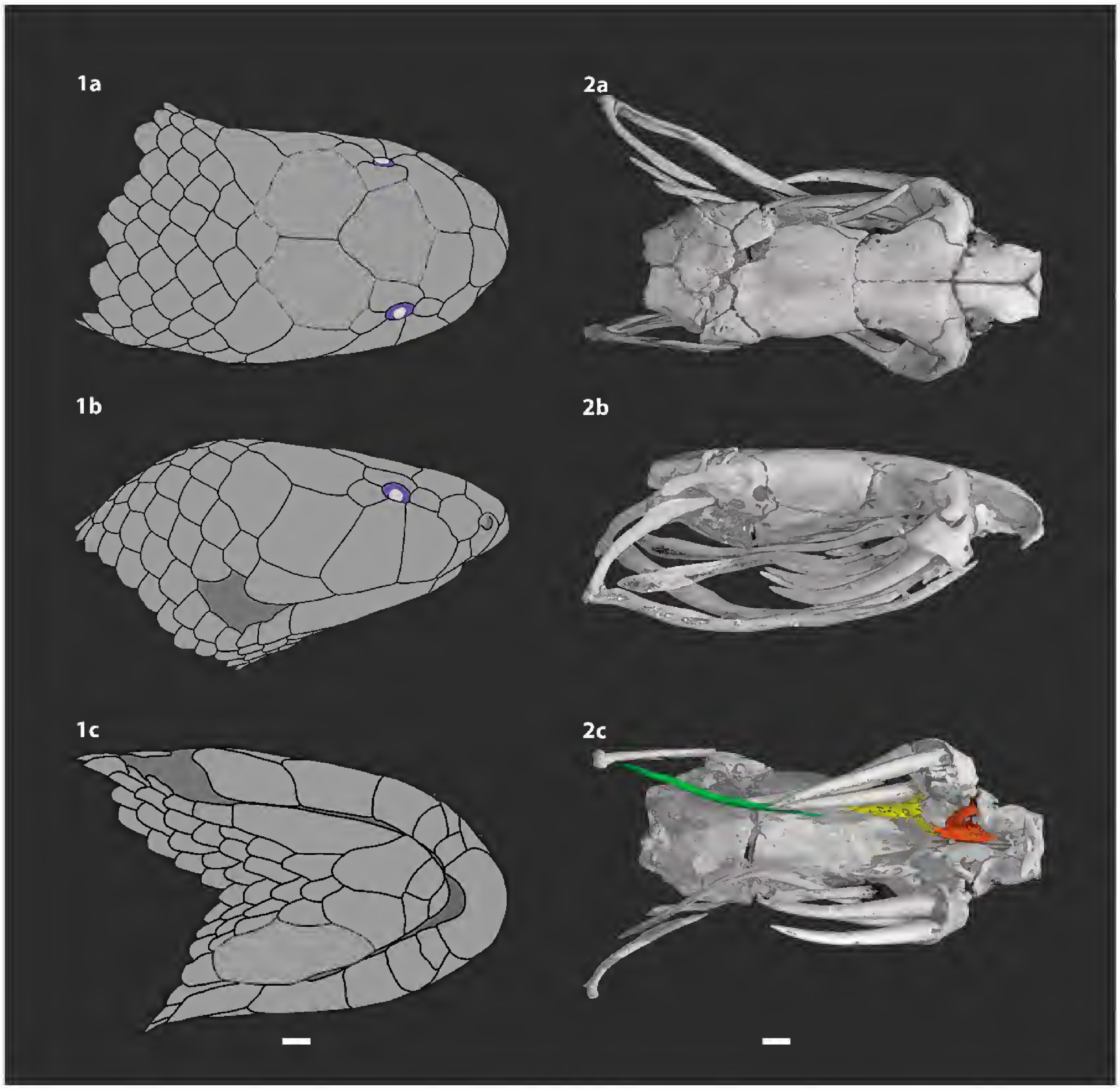

Figure 4. Paratype of *Atractaspis branchi* sp. n. (MSNS Rept 280) **1** head scalation in dorsal (**a**), lateral (**b**), and ventral (**c**) views; **2** ct-scan of skull in dorsal (**a**), lateral (**b**), and ventral (**c**) views; lower jaw virtually removed; green: pterygoid, yellow: palatine, orange: vomer. Scale bar: 1 mm.

Broadley (1990: fig. 121) figured an *A. bibronii* Smith, 1849 that possesses one fang (no replacement teeth) on each maxilla, but small teeth on palatine (4) and dental (3) bones. Cundall and Irish (2008: fig. 2.87D) figured functional and replacement fangs and two palatine teeth.

Molecular data. The 16S sequences of the two type specimens of *Atractaspis branchi* sp. n. were almost identical (1% difference, 509 bp used for comparisons). Uncorrected pairwise comparisons to the respective part of 16S sequences of other *Atractaspis* revealed the following differences (first number refers to comparison with *A. branchi* holotype, the second to the paratype): *Atractaspis boulengeri* (4–3%, 499 bp, 485 bp), *A. corpulenta* (7–6%, 501 bp, 487 bp), *A. irregularis* (8–7%, 509 bp, 505 bp), *A. micropholis* (5%, 502 bp, 488 bp), and *A. reticulata heterochilus* (7–6%, 521 bp, 505 bp).

Natural history. We found the holotype at night. It was slowly moving along the steep slope of the bank of a small rocky creek in primary lowland evergreen rainforest (Fig. 6). When handled, the snake first tried to hide its head below body loops; the head was bend down at an almost right angle and with fangs partly visible outside of the mouth. In this head position, the snake repeatedly tried to strike. Either it tried to move slowly away from the human observers or it abruptly coiled and uncoiled, often jumping distances equaling almost its entire body length, similar to wolf snakes of the genus *Lycophidion* (Rödel et al. 1995; Greene 1997). The two snakes from south-eastern Guinea were collected in plantations of banana, manioc and coffee, which were planted under the few remaining high trees of the former forest. No other data on biology and ecology of the new species are known.

Distribution. So far the new species is known from the type locality and two additional sites in south-eastern Guinea. These latter two sites are about 27 km apart (Fig. 7).

Etymology. We name this new snake to honor our recently deceased friend and colleague, William Roy "Bill"

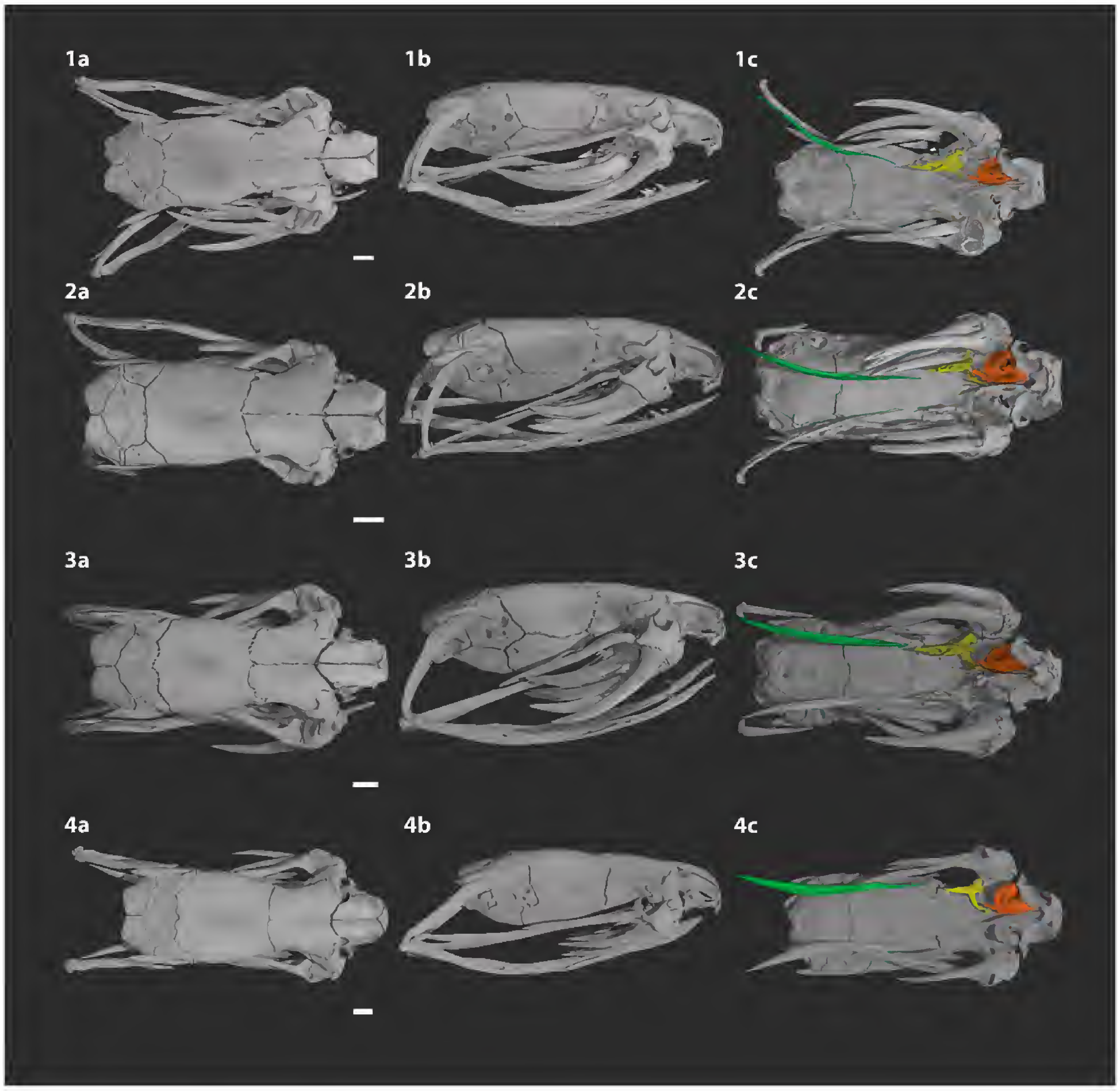

Figure 5. Dorsal (**a**), lateral (**b**) and ventral (**c**) views (lower jaw removed virtually, green: pterygoid, yellow: palatine, orange: vomer) of the skulls of **1** *Atractaspis reticulata* (NRM 1796, holotype); **2** *Atractaspis reticulata* (ZMB 28500); **3** *Atractaspis aterrima* (ZMB 8016); and **4** *Atractaspis boulengeri matschiensis* (ZMB 11040). Scale bar: 1 mm.

Branch, for his outstanding contributions to African herpetology. MOR and OSGP are particularly pleased to name the species in memory of Bill. We remember our outstanding field trips with him, unforgettable discussions with a large portion of special humor, and his friendship. The dedication of this species of stiletto snake to Bill is particularly appropriate. After Bill turned from cancer research to herpetology (see "William R. Branch" in Li Vigni 2013), the subject of his first herpetological research, on the serotaxonomy and hemipeneal morphology of stiletto snakes, was presented in two contributions at a symposium of herpetology and ichthyology in Kruger National Park in 1975 (Branch 1975a, b). As the vernacular name, we suggest Branch's Stiletto Snake.

Redescription of the holotype of *Atractaspis reticulata reticulata* Sjöstedt, 1896 (NRM 1796) (Fig. 8)

Adult female; slender snake with moderately robust body and short and rounded head; no constriction between head and body; snout-vent length 712 mm; tail length 33 mm (ratio SVL / TailL = 21.6); head length 16.4 mm (tip of snout to angle of jaws) / 11.7 mm (tip of snout to end of parietal suture); head width 13.8 mm (at widest point) / 5.8 mm (distance between outer margins of supraoculars at the level of mid eye); nostrils directed laterally; dorsally measured distance between nostrils 4.5 mm; small eyes directed dorsolaterally; eye diameter 1.3 mm (horizontal) / 0.9 mm (vertical), pupil roundish; distance from lower border of eye to mouth 3.8 mm; distance between anterior edge of eye to posterior edge of nostril 3.0 mm; 5 supralabials, the 4th being the largest, the 3rd and 4th in contact with eye; 5 infralabials, the 1st and 3rd touching the inframaxillary, the 2nd fused with the inframaxillary, the 3rd being the largest; the 1st pair of infralabials in contact behind mental; rostral visible from above, rounded in lateral and dorsal views; nasal divided, touching 1st to 3rd supralabial and preocular, nostril nearly completely situated in the anterior part of nasal; loreal absent; 1 small preocular, not in contact with frontal, touching 3rd supralabial; 1 postoc-

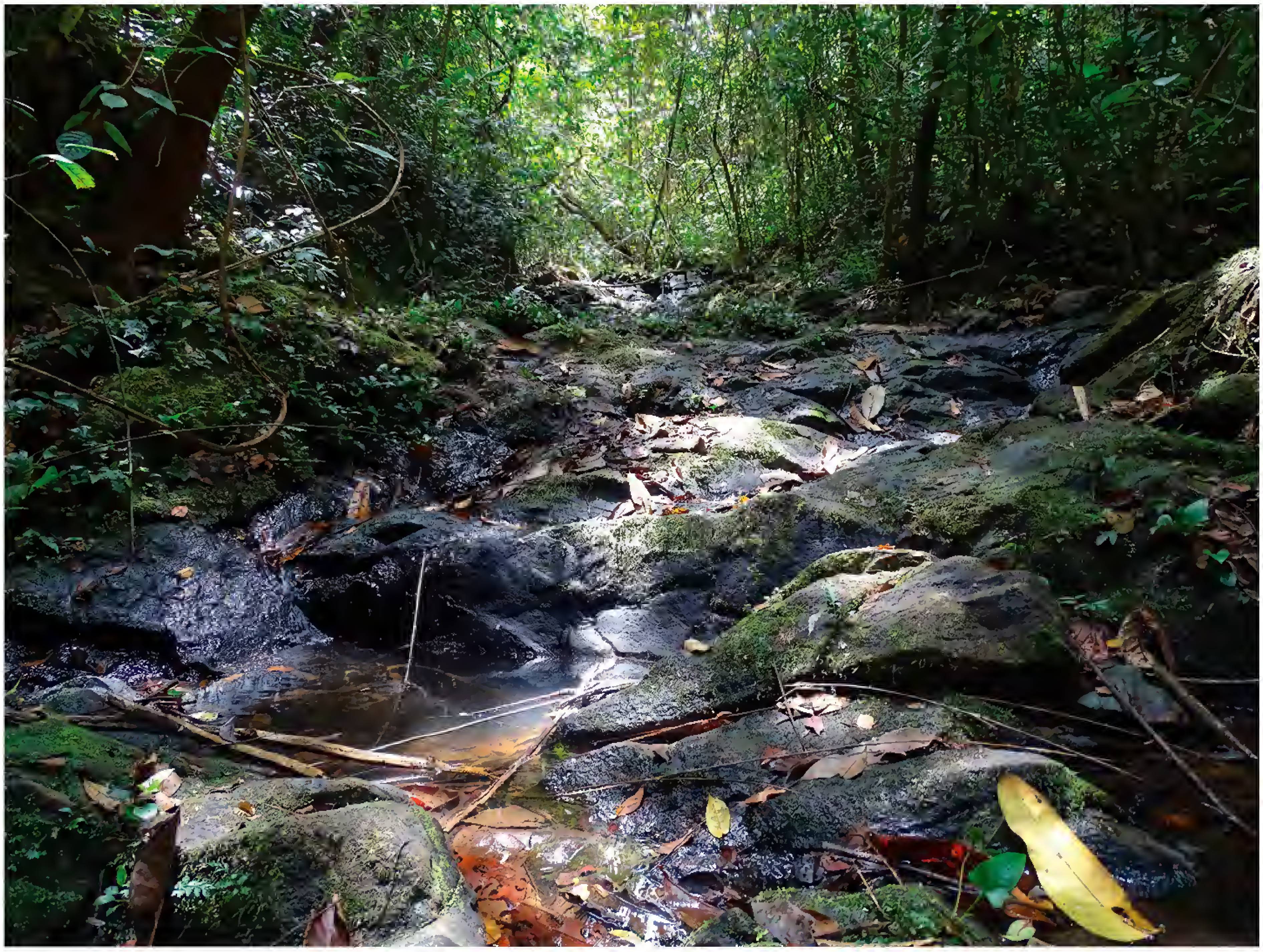

Figure 6. Type locality of *Atractaspis branchi* sp. n. in north-western Liberia. The holotype specimen was found at night. It was moving along the steep slope on the left bank of the small creek.

ular only slightly larger than preocular, touching temporal and 4th supralabial; 1 small supraocular (length 2.4 mm); 1 very large anterior temporal (length 5.0 mm) followed by 2 posterior temporals; other than the temporals only 3 further scales touching the posterior borders of parietals; 1 pair of inframaxillaries, mental groove present; top of head covered by 9 scales; suture of internasals 1.4 mm long; suture of prefrontals 1.3 mm long; frontal slightly longer than wide (5.1 mm vs 4.5 mm); suture of parietals 2.9 mm long; dorsal scales smooth, rhombic shaped, decreasing gradually in size dorsally; apical pits absent, but all dorsal scales with a single little pore near the center of the scale; 4 preventrals, 304+1/2 rounded ventral scales; anal divided; subcaudals divided, 21/21+1; ratio ventrals/subcaudals: 14.5; dorsal scale rows oblique.

Dorsal scale row reduction:

$$19 \frac{3+4(2)}{4+5(4.\ \mathrm{PreV})} 17 \frac{5\rightarrow 5+6(70)}{5\rightarrow 5+6(68)} 19 \frac{-5(268)}{5+6(263)} 17 \frac{5\rightarrow 5+6(268)}{x} 18 \frac{4+5(272)}{x} 17(304)$$

Supracaudal scale row reduction:

$$15 \frac{1+2(1)}{3+4/6+7(1)} 12 \frac{2+3(2)}{3+4(2)} 10 \frac{4+5(6)}{4+5(5)} 8 \frac{3+4(13)}{3+4(13)} 6 \frac{2+3(19)}{2+3(18)} 4(21)$$

Color in preservation: Dorsally uniform dark greyish blue, all scales with thin lighter margins; venter and head appear slightly lighter with a olive hue; most of the mental, and lower margin of the rostral pale.

Distribution of *Atractaspis reticulata* subspecies

Three subspecies of *A. reticulata* are currently recognized (Wallach et al. 2014): the nominate form *A. reticulata reticulata* Sjöstedt, 1896, *A. reticulata heterochilus* Boulenger, 1901, and *A. reticulata brieni* Laurent, 1956.

The definitions of these subspecies are still unclear. The holotype of *A. r. reticulata* is the only known specimen with 19 midbody dorsal scale rows. Boulenger (1901) described *A. heterochilus* based on 23 midbody dorsal scale rows and more ventrals (341 vs “308” [304 according to method of Dowling 1951b]). Laurent (1950) assigned *A. heterochilus* as a subspecies to *A. reticulata*. Laurent (1956a) described *A. r. brieni* based on higher ventral counts in both sexes. The taxonomic classification of specimens with 21 dorsal scale rows at midbody remains difficult. All of them were found in southern Cameroon (ZMB material; Werner 1913; Boulenger 1919). The four examined ZMB specimens (ZMB 14724,

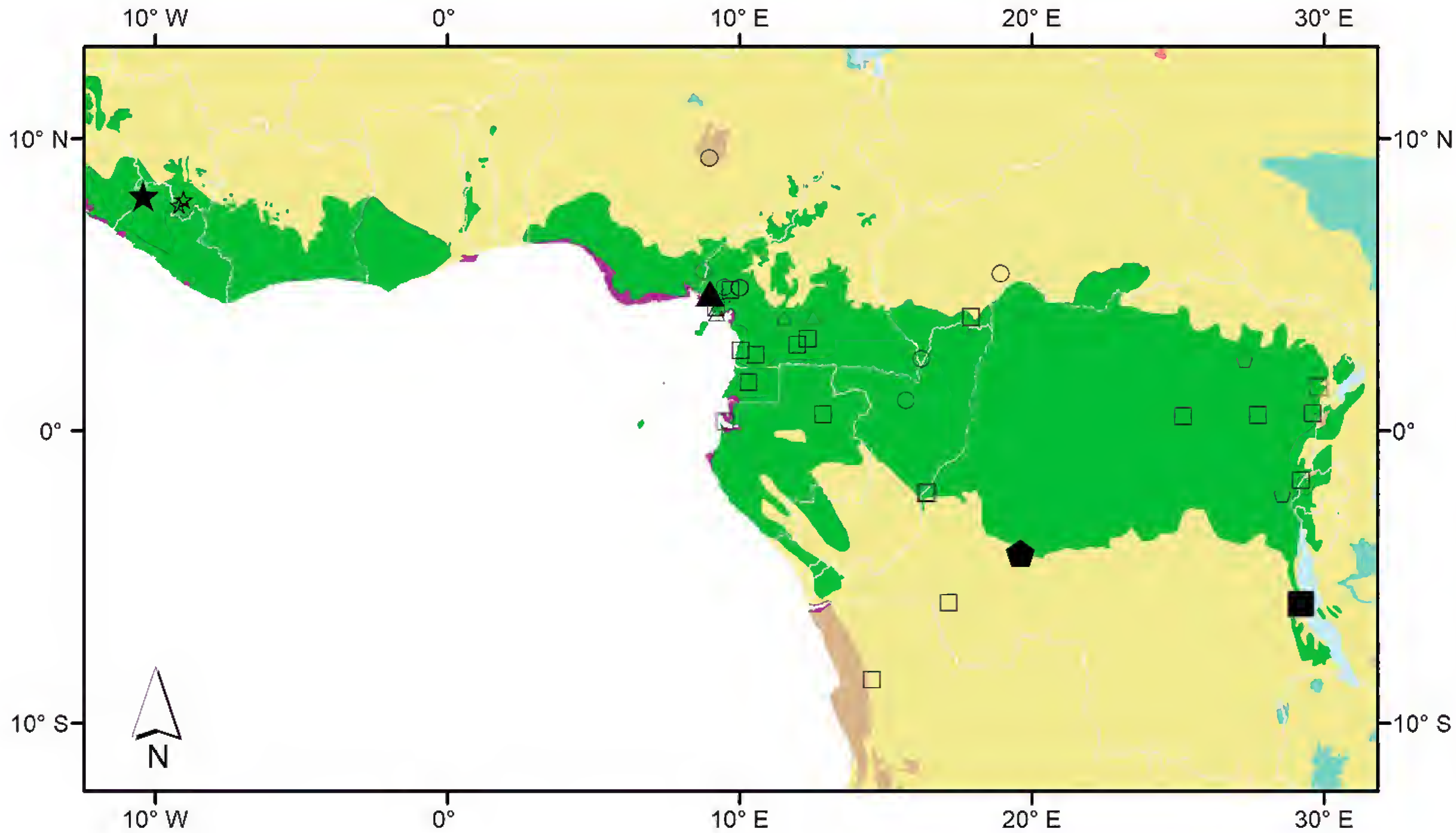

Figure 7. Localities of *Atractaspis branchi* sp. n. and *A. reticulata* ssp. Records are based on museum specimens, literature and database (GBIF) records; large closed symbols represent the type localities of the different taxa, stars: *A. branchi* sp. n., circles: *A. reticulata* records without reference to subspecies; triangles: *A. r. reticulata*; quadrats: *A. r. heterochilus*; diamonds: *A. r. brieni*; country borders indicted as white lines; background of map: major biomes based on Olson et al. (2001).

21725, 28500, 30714) were determined as *A. r. reticulata*. Based on the published data (23 midbody scale rows), the record of the nominate subspecies *A. r. reticulata* from the Republic of Congo by Ota et al. (1987) is recognized here as *A. r. heterochilus*. The *A. r. heterochilus* record in Schmidt (1923) from Medje, Haut-Uele Province, Democratic Republic of Congo, is identifiable as *A. r. brieni* (female with 353 ventrals).

We here summarize data from the literature, GBIF database, and some museum records of *A. reticulata* (Fig. 7). *Atractaspis reticulata* is a terrestrial forest snake (Hughes 1983; Lasso et al. 2002; Herrmann et al. 2005). Data for altitudinal range are given for Cameroon: 0–1800 m a.s.l. (Herrmann et al. 2005; Chirio and LeBreton 2007; Gonwouo et al. 2007), and Gabon: 0–500 m a.s.l. (Pauwels and Vande weghe 2008). According to Frétey and Blanc (2004), this species occurs in Cameroon, the Central African Republic, Equatorial Guinea, Gabon, Republic of Congo, and the Democratic Republic of the Congo. Hughes (1983, 1988) listed this species also for Ghana and Nigeria, however without locality or collection data. Barry Hughes wrote in an email to OSGP, “The mention of *Atractaspis reticulata* from Ghana is based on the examination of a single individual in poor condition, whose head scalation corresponds with the description of that species” (B. Hughes pers. comm. September 2018). Unfortunately, we could not examine that specimen, and the record for Ghana must be regarded as doubtful (see Discussion). In addition to recent records of four specimens from south-eastern Nigeria (Eniang and Ijeomah 2011), there is one voucher from the Bauchi plateau in Central Nigeria in the British Museum of Natural History (BMNH 1934.7.7.45, don. Hamilton Liddiard). Furthermore, this species was recorded from Angola (Hellmich 1957). Pitman (1938) included *Atractaspis reticulata* and *A. heterochilus* in a key to Ugandan snakes because of records from the neighboring northeast Democratic Republic of Congo. However, until now, no voucher of these snakes has become known from east of the African rift valley. Here we summarize the records which have been published, using the subspecies affiliation as mentioned in the respective literature (Fig. 7). In various cases the subspecies mentioned in the respective papers cannot be verified with the presented data or figures!

Atractaspis reticulata ssp. records without reference to subspecies and without published scalation data are from **Ghana**: without precise locality (Hughes 1983, 1988); **Nigeria**: without precise locality (Hughes 1983; Butler and Reid 1990); Cross River Province: Oban Division of Cross River National Park (Eniang and Ijeomah 2011); Plateau Province: “Bauchi” (GBIF: BMNH 1934.7.7.45); **Cameroon**: Sud-West Province: Kumba-Nguti road,

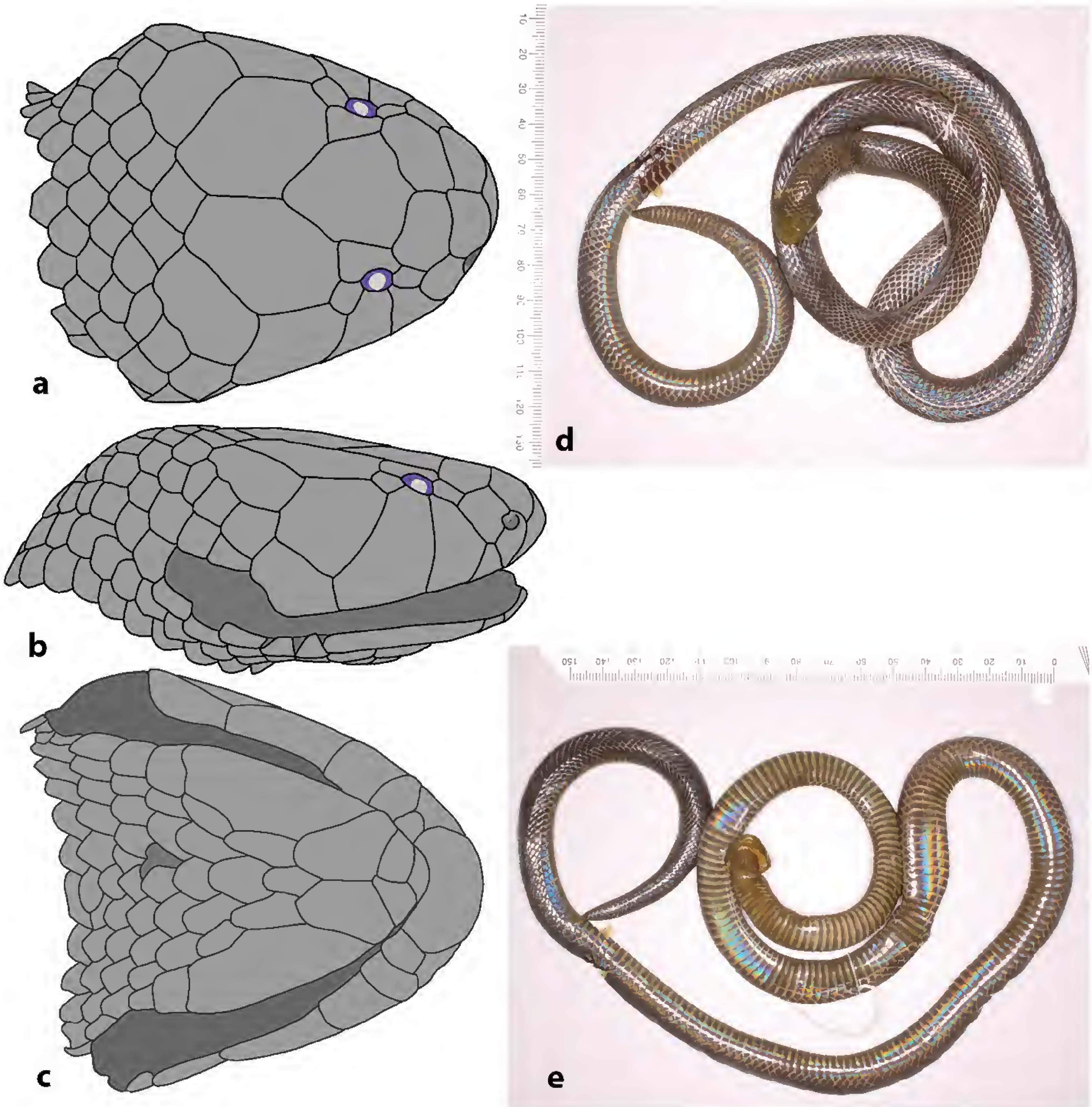

Figure 8. Dorsal (**a**), lateral (**b**) and ventral (**c**) views of the head *Atractaspis reticulata* (NRM 1796, holotype); dorsal (**d**) and ventral (**e**) views of the entire snake.

58.3 km south of Nguti (Lawson 1993: UTA R 31311); Littoral Province: Nguéngué (1140 m a.s.l.) and Mount Nlonako (Herrmann et al. 2005: ZFMK 75261, HWH [private collection Herrmann] 639, 714, 765); **Central African Republic**: Sangha-Mbaéré Province, Parc National de Dzangha-Ndoki (GBIF: MNHN 2011.281); **Republic of Congo**: Sangha Province: Liouesso (Trape and Roux-Estève 1995); **Democratic Republic of Congo**: Kwilu Province: Kafumba (GBIF: SDNHM 63850).

Atractaspis reticulata reticulata records are restricted to southern and south-western **Cameroon** (between sea level and ca 700 m a.s.l.): Sud-West Province: "Ekundu" [= Ekundu Titi] (Sjöstedt 1896: NRM 1796, type locality; locality according to map in Mertens 1938); Buea (Werner 1913: ZMH R11274); Victoria (Sternfeld 1908: ZMB ? no identifiable voucher present, ZMB 21725); Johann-Albrechtshöhe (ZMB 28500); Central Province: "Ajoshöhe am Nyong" [= Ayos] (ZMB 30714); Yaoundé (Sternfeld 1908: ZMB 14724).

Atractaspis reticulata heterochilus was likewise reported from **Cameroon:** Sud-West Province: Nyasoso (photographic record in Dobiey and Vogel 2007); Mount Cameroon area (Gonwouo et al. 2007); Sud Province: "Ngam" [= Ngan] (Perret and Mertens 1957: SMF 52361); Bitye (Laurent 1950, but 21 midbody scale rows); Campo Reserve (Ota et al. 1987: KUZ R8330); **Central African Republic**: Lobaye Province: Boukoko, (Roux-Estève 1965: MNHN 1963.899, MNHN 1964.566); **Equatorial Guinea**: Centro-Sur Province: Monte Alén, (Lasso et al. 2002); **Gabon**: Ogooué-Maritime Province: Yenzi, Gamba, Ndougou Department (Pauwels and Sallé 2009: USNM 565138); Ogooué-Ivindo Province: Makokou (Knoepffler 1966: MBG 0644); Estuaire Province: "Gabun" [= probably Gabon estuary] (Werner 1913: ZMH R11275); **Democratic Republic of the Congo**: Tshopo Province: "Stanleyville" [= Kisangani] (Laurent 1945: RGMC 6614, 8003, 8252); Tanganyika Province: "Albertville" [= Kalemie] (Boulenger 1901: RGMC 608, type locality); Ituri Province: "Makele" [= Makala, according to Christy 1915], (Boulenger 1919; Laurent 1945: RGMC 1686); Irumu (de Witte 1953); North Kivu Province: "N'Goma" [= Goma], (Schouteden 1933; de Witte 1941: RGMC 4068); "Kartoushi" [= near Oicha, according to map in Gyldenstolpe 1924] (de Witte 1941); Mai-Ndombe Province: "Ndwa" [= Bolobo, according to Chapin 1954] (Laurent 1956a: RGMC 16214); "Kunungu" [= Bolobo, according to Chapin 1954] (Laurent 1945: RGMC 8764, 8767); Kwango Province: "Imbela" [= Kimbele] (GBIF: RBINS 12278); **Angola**: Cuanza Norte Province: Piri Dembos (Hellmich 1957: ZSM 111/1954). The Angolan record of Hellmich (1957) was doubted by Branch (2018). However, the specimen was re-examined by us and could be confirmed as being *A. reticulata heterochilus*.

Atractaspis reticulata brieni was reported from **Democratic Republic of the Congo**: Kwilu Province: Ipamu, (Laurent 1945, 1956a: RGMC 2694, 2706, type locality); South Kivu Province: Mushofi (1300 m asl), near Bunyakiri, (Laurent 1960: RGMC 21577); Haut-Uele Province: Medje (Schmidt 1923: AMNH 11901).

It is apparent from this list and Figure 7 that the distributions of the *A. reticulata* "subspecies", and in particular the nominate form and *A. r. heterochilus*, are not in accordance with any logical pattern of biogeographic regions or barriers. We would not be surprised if *A. reticulata* proves to be actually a complex of various cryptic species, but proofing this hypothesis is beyond the goal of the present study.

Discussion

The phylogenetic relationships within the genus *Atractaspis* are still unclear. Two recent contributions included only some species of *Atractapis* (Underwood and Kochva 1993; Moyer and Jackson 2011). The study by Underwood and Kochva (1993) deviates in its phylogenetic conclusions partly from Laurent's (1950) species grouping. However, for morphological comparisons between species Laurent's (1950) paper is still the most useful. Our new species morphologically falls within Laurent's (1950) section "D" (*reticulata* group) of the genus. Together with *A. reticulata* and *A. corpulenta* it shares the fusion of the 2nd infralabial with the inframaxillary. This character likewise distinguishes these two species and *A. branchi* sp. n. from all other congeners.

Atractaspis corpulenta is a comparatively very robust, heavily built snake (only 178–208 ventrals with 23–29 dorsal scale rows at midbody vs 276–288 ventrals and 19 or 20 dorsal scale rows in *A. branchi*) and has a non-divided anal plate and subcaudal scales (both divided in *A. branchi*). Its West African rainforest subspecies, *A. corpulenta leucura*, has a white tail tip (see fig. 3 in Rödel and Mahsberg 2000), which is lacking in *A. branchi*. *Atractaspis branchi* thus can be only confused with *A. reticulata*, from which it differs by a lower ventral count while having simultaneously a higher number of subcaudals and, thus, a relatively longer tail: snout-vent length / tail length in *A. branchi*: 15.7 and 21.5; in *A. reticulata*: mean = 22.3, minimum = 16.2, maximum = 29.2 (N = 15). The two *A. reticulata* with the comparatively longest tails (16.2 and 17.6) originate from Gabon and Angola, respectively, and are both males. The seven *A. reticulata* females, for which we could calculate a snout-vent length / tail length ratio, had a mean of 23.6 (Tables 1, 2).

The new species has 19 dorsal scales rows at midbody (the paratype has mostly 19 rows but rarely 20 around midbody) and thus differs from almost all *A. reticulata* vouchers investigated by us and reported in the literature by having 21–23 rows (Table 1). However, the holotype of *A. reticulata reticulata* has only 19 scale rows and mid-body scale rows. thus numbers of scales at mid-body is not diagnostic for these two taxa. Apart from ventral and subcaudal scale counts, differences in skull anatomy between the new species and *A. reticulata* are a shorter frontale and a greater number of palatine teeth in the new species. An additional diagnostic character might be larger eyes in *A. branchi* compared to *A. reticulata* (Table 2). However, the holotype is a young female and relative eye size seems to diminish with body size, as indicated by the two types and our measurements of other differently sized *Atractaspis*, including variously sized *A. reticulata* (Table 2). The types of the new species indicate other potential ontogenetic changes in characters, i.e. body colour changing from brown to grey, fang length increasing with body length, and rows of the dorsal body scales changing from perfectly straight in the smaller holotype to oblique in the larger, and presumably older, paratype.

However, confusion of *A. branchi* with *A. reticulata* taxa seems unlikely, as they most probably do not overlap geographically. From West Africa sensu stricto (Senegal to the Nigerian Cross River; see Penner et al. 2011 for discussion), *A. reticulata* has been reported from Nigeria (Eniang and Ijeomah 2011: Oban Division, Cross River National Park, Cross River Province; Butler and Reid 1990 and Hughes 1983: without further details) and Ghana (Hughes 1983). The Ghanaian record is of particular interest, as it might be conspecific, based on biogeographic arguments, with the new species. Unfortunately, this snake could not be investigated.

The Cross River area is zoogeographically part of the Lower Guinea forest zone. It is not yet clear where the zoogeographic barrier between the West and Central African fauna exactly runs: at the Cross River, the Niger Delta, or the Dahomey Gap. Nor has it been clarified what exact processes are responsible for the separation of fauna and flora, and what is the time scale during which taxa in both areas evolved (see Penner et al. 2011; Jongsma et al. 2018 and studies cited therein). The geographic scale, processes and time most likely varies between taxa (see Bell et al. 2017 for Central African examples). However, it is becoming more evident that there is only very little to almost no overlap in occurrences between forest species of the Upper and Lower Guinea realms. Indeed, many studies, mostly recent, either have discovered related but distinct species in both forest blocs or have shown that "widespread" taxa actually comprise cryptic species complexes, including species that either occur in West or Central African rainforests. Examples of recent discoveries of species pairs within amphibians are *Sclerophrys taiensis* and *S. tuberosus* (Bufonidae; Rödel and Ernst 2000); *Acanthixalus sonjae* and *A. spinosus* (Hyperoliidae; Rödel et al. 2003); *Cardioglossa occidentalis* and *C. leucomystax* (Arthroleptidae; Blackburn et al. 2008); and *Amnirana* "albolabris-West" and *Amnirana albolabris* (Ranidae; Jongsma et al. 2018). Among reptiles different species in West and Central Africa have been discovered in the crocodile genera *Mecistops* and *Osteolaemus* (Crocodylidae; Shirley et al. 2014); the turtles *Pelusios cupulatta* and *P. gabonensis* (Pelomedusidae; Rhodin et al. 2017); the cobras *Naja guineensis* and *N. melanoleuca* (Elapidae; Wüster et al. 2018); and the vipers *Atheris hirsuta* and *A. squamigera* (Viperidae; Ernst and Rödel 2002). Among birds there are for instance *Picathartes gymnocephalus* and *P. oreas* (Picathartidae; Treplin 2006); and among mammals there are different West and Central African species within the antelope genera (*Neotragus* spp., *Tragelaphus* spp.; *Philantomba* spp.; Hernández Fernández and Vrba 2005; Moodley and Bruford 2007; Colyn et al. 2010), within small carnivores (*Genetta johnstoni* and *G. piscivora*; Gaubert et al. 2004), otter shrews (*Micropotamogale* spp.), or within various bats such as the genus *Rhinolophus* (Fahr et al. 2002). Many more examples have been published (Huntley et al. 2019) and several more examples, still unpublished, are known to us.

Apart from a species-level uniqueness of Upper Guinean forest assemblages, it is also evident, that this region is an important area for old endemic lineages. Prominent herpetological examples comprise the frog family Odontobatrachidae (Barej et al. 2014), and the frog genera *Pseudhymenochirus* (Pipidae; Evans et al. 2004) and *Morerella* (Hyperoliidae; Rödel et al. 2009). Therefore, the discovery of a new and presumably endemic species of fossorial snake from the western Upper Guinea forests is not very surprising. However, further surveys are needed to determine the geographic range of the new snake species and to gather more information about its ecological needs and biological properties.

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References

Barej MF, Schmitz A, Günther R, Loader SP, Mahlow K, Rödel M-O (2014) The first endemic West African vertebrate family – a new anuran family highlighting the uniqueness of the Upper Guinean biodiversity hotspot. Frontiers in Zoology 11: 8. https://doi.org/10.1186/1742-9994-11-8

Bell RC, Parra JL, Badjedjea G, Barej MF, Blackburn DC, Burger M, Channing A, Dehling JM, Greenbaum E, Gvoždík V, Kielgast J, Kusamba C, Lötters S, McLaughlin PJ, Nagy ZT, Rödel M-O, Portik DM, Stuart BL, VanDerWal J, Zassi-Boulou AG, Zamudio KR (2017) Idiosyncratic responses to climate-driven forest fragmentation and marine incursions in reed frogs from Central Africa and the Gulf of Guinea Islands. Molecular Ecology 26: 5223–5244. https://doi.org/10.1111/mec.14260

Blackburn DC, Kosuch J, Schmitz A, Burger M, Wagner P, Gonwouo LN, Hillers A, Rödel M-O (2008) A new species of *Cardioglossa* (Anura: Arthroleptidae) from the Upper Guinean forests of West Africa. Copeia 2008: 603–612. https://doi.org/10.1643/CH-06-233

Boulenger GA (1901) Matériaux pour la faune du Congo. Reptiles nouveaux. Annales du Musée du Congo (Zoologie, Série 1) 2: 7–14. [pls 3–5]

Boulenger GA (1919) Batraciens et reptiles recueillis par le Dr. C. Christy au Congo Belge dans les districts de Stanleyville, Haut-

Uelé et Ituri en 1912–1914. Revue zoologique Africaine 7: 1–29. https://doi.org/10.5962/bhl.part.15108

Branch WR (1975a) Serotaxonomic studies on southern African snakes, with particular reference to the status of the genus *Atractaspis*. Abstract of a contribution presented at the 'Symposium of Herpetology and Ichthyology', Kruger National Park, 1–5 Sept 1975. Journal of the Herpetological Association of Africa 14: 7–8. https://doi.org/10.1080/04416651.1975.9650872

Branch WR (1975b) Hemipeneal morphology of southern African snakes: a taxonomic review. Abstract of a contribution presented at the 'Symposium of Herpetology and Ichthyology', Kruger National Park, 1–5 Sept 1975. Journal of the Herpetological Association of Africa 14: 10. https://doi.org/10.1080/04416651.1975.9650877

Branch WR (2018) Snakes of Angola: an annotated checklist. Amphibian & Reptile Conservation 12: 41–82.

Broadley DG (1990) Fitzsimons' Snakes of Southern Africa. Jonathan Ball & AD Donker Publishers, Parklands, South Africa, 423 pp.

Butler JA, Reid JC (1990) Records of snakes from Nigeria. The Nigerian Field 55: 19–40.

Chippaux J-P (2001) Les Serpents d'Afrique Occidentale et Centrale. Collection Faune et Flore tropicales 35. IRD éditions, Paris, 292 pp.

Chirio L, LeBreton M (2007) Atlas des reptiles du Cameroun. Patrimoines naturels 67. Muséum national d'Histoire naturelle/IRD éditions, Paris, 688 pp.

Chapin JP (1954) Gazetteer for "The Birds of the Belgian Congo". Bulletin of the American Museum of Natural History 75B: 638–738.

Christy C (1915) The Ituri river, forest, and pygmies. The Geographical Journal 46: 200–213. https://doi.org/10.2307/1779389

Colyn M, Hulselmans J, Sonet G, Oudé P, De Winter J, Natta A, Nagy ZT, Verheyen E (2010) Discovery of a new duiker species (Bovidae: Cephalophinae) from the Dahomey Gap, West Africa. Zootaxa 2637: 1–30. https://doi.org/10.11646/zootaxa.2637.1.1

Cundall D, Irish F (2008) The snake skull. In: Gans C, Gaunt AS, Adler K (Eds) Biology of the Reptilia, Volume 20, Morphology H, The Skull of Lepidosauria. Society for the Study of Amphibians and Reptiles, Ithaca, New York, 349–692.

Dobiey M, Vogel G (2007) Venomous snakes of Africa / Giftschlangen Afrikas. Edition Chimaira, Terralog 15, Frankfurt am Main, 149 pp.

Dowling HG (1951a) A proposed method of expressing scale reductions in snakes. Copeia 1951: 131–134. https://doi.org/10.2307/1437542

Dowling HG (1951b) A proposed standard of counting ventrals in snakes. British Journal of Herpetology 1: 97–99.

Eniang EA, Ijeomah HM (2011) Diversity of ophidian species in Oban Division of the Cross River National Park, Nigeria. Production Agriculture and Technology Journal 7: 188–201.

Ernst R, Rödel M-O (2002) A new *Atheris* species (Serpentes: Viperidae), from Taï National Park, Ivory Coast. Herpetological Journal 12: 55–61.

Evans BJ, Kelley DB, Tinsley RC, Melnick DJ, Cannatella DC (2004) A mitochondrial DNA phylogeny of African clawed frogs: phylogeography and implications for polyploid evolution. Molecular Phylogenetics and Evolution 33: 197–213. https://doi.org/10.1016/j.ympev.2004.04.018

Fahr J, Vierhaus H, Hutterer R, Kock D (2002) A revision of the *Rhinolophus maclaudi* species group with the description of a new species from West Africa (Chiroptera: Rhinolophidae). Myotis 40: 95–126.

Frétey, T, Blanc CP (2004) Liste des reptiles d'Afrique centrale. Les dossiers de l'ADIE, Serie Biodiversité "2" [= 3]: 1–73.

Gaubert P, Fernandes CA, Bruford MW, Veron G (2004) Genets (Carnivora, Viverridae) in Africa: an evolutionary synthesis based on cytochrome b sequences and morphological characters. Biological Journal of the Linnean Society 81: 589–610. https://doi.org/10.1111/j.1095-8312.2004.00309.x

Gonwouo NL, LeBreton M, Chirio L, Ineich I, Tchamba NM, Ngassam P, Dzikouk G, Diffo JL (2007) Biodiversity and conservation of the reptiles of the Mount Cameroon Area. African Journal of Herpetology 56: 149–161. https://doi.org/10.1080/21564574.2007.9635560

Greene HW (1997) Snakes: the Evolution of Mystery in Nature. University of California Press, Berkeley, 351 pp.

Grossmann W, Zwanzig BM, Kowalski T, Zilger HJ, Colacicco F, Ballandat S (2018) Die Erdviper *Atractaspis andersonii* Boulenger, 1905 im Sultanat Oman. Sauria 40: 3–19.

Gyldenstolpe N (1924) Zoological results of the Swedish Expedition to Central Africa 1921. Vertebrata. I. Birds. Kungliga Svenska Vetenskapsakademiens handlingar (3. Ser.) 1(3): 1–326. [1 pl., 1 map]

Hellmich W (1957) Die Reptilienausbeute der Hamburgischen Angola-Expedition. Mitteilungen aus dem Hamburger Zoologischen Museum und Institut 55: 39–80.

Hernández Fernández M, Vrba ES (2005) A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. Biological Reviews of the Cambridge Philosophical Society 80: 269–302. https://doi.org/10.1017/S1464793104006670

Herrmann H-W, Böhme W, Euskirchen O, Herrmann PA, Schmitz A (2005) African biodiversity hotspots: the reptiles of Mt Nlonako, Cameroon. Revue Suisse de Zoologie 112: 1045–1069. https://doi.org/10.5962/bhl.part.80336

Hughes B (1983) African snake faunas. Bonner zoologische Beiträge 34: 311–356.

Hughes B (1988) Herpetology in Ghana (West Africa). British Herpetological Society Bulletin 25: 29–38.

Huntley JW, Keith KD, Castellanos AA, Musher LJ, Voelker G (2019) Underestimated and cryptic diversification patterns across Afrotropical lowland forests. Journal of Biogeography early view. https://doi.org/10.1111/jbi.13505

Jongsma GFM, Barej MF, Barratt CD, Burger M, Conradie W, Ernst R, Greenbaum E, Hirschfeld M, Leaché AD, Penner J, Portik DM, Zassi-Boulou A-G, Rödel M-O, Blackburn DC (2018) Diversity and biogeography of frogs in the genus *Amnirana* (Anura: Ranidae) across sub-Saharan Africa. Molecular Phylogenetics and Evolution 120: 274–285. https://doi.org/10.1016/j.ympev.2017.12.006

Knoepffler L-P (1966) Faune du Gabon (amphibiens et reptiles). I. Ophidiens de l'Ogooué-Ivindo et du Woleu N'tem. Biologia Gabonica 2(1): 3–23.

Lasso CA, Rial AI, Castroviejo J, De la Riva I (2002) Herpetofauna del Parque Nacional de Monte Alén (Rio Muni, Guinea Ecuatorial). Graellsia 58(2): 21–34. https://doi.org/10.3989/graellsia.2002.v58.i2.276

Laurent RF (1945) Contribution à la connaissance du Genre *Atractaspis* A. Smith. Revue de Zoologie et de Botanique Africaines 38: 312–343.

Laurent RF (1950) Révision du genre *Atractaspis* A. Smith. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 38: 1–49.

Laurent RF (1956a) Notes herpétologiques africaines. Revue de Zoologique et de Botanique Africaines 53: 229–256.

Laurent RF (1956b) Contribution à l'herpétologie de la région des Grands Lacs de l'Afrique centrale. Annales du Musée Royal du Congo belge (Sciences Zoologiques) 48: 1–390.

Laurent RF (1960) Notes complémentaires sur les chéloniens et les ophidiens du Congo oriental. Annales du Musée Royal du Congo Belge (Sciences Zoologiques) 84: 1–86.

Lawson DP (1993) The reptiles and amphibians of the Korup National Park project, Cameroon. Herpetological Natural History 1(2): 27–90.

Li Vigni F (2013) A Life for Reptiles and Amphibians, Vol. 1. Edition Chimaira, Frankfurt am Main, 495 pp.

McDowell SB (2008) The skull of Serpentes. In: Gans C, Gaunt AS, Adler K (Eds) Biology of the Reptilia, Volume 21, Morphology I, The Skull and Appendicular Locomotor Apparatus of Lepidosauria. Society for the Study of Amphibians and Reptiles, Ithaca, New York, 467–620.

Mertens R (1938) Herpetologische Ergebnisse einer Reise nach Kamerun. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 442: 1–52. [10 pls.]

Moodley Y, Bruford MW (2007) Molecular biogeography: towards an integrated framework for conserving Pan-African biodiversity. PLoS ONE 2(5): e454. https://doi.org/10.1371/journal.pone.0000454

Moyer K, Jackson K (2011) Phylogenetic relationships among the stiletto snakes (genus *Atractaspis*) based on external morphology. African Journal of Herpetology 60: 30–46. https://doi.org/10.1080/21564574.2010.520034

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the World: a new map of life on Earth. BioScience 51: 933–938.

Ota H, Hikida T, Barcelo J (1987) On a small collection of lizards and snakes from Cameroon, West Africa. African Study Monographs 8: 111–123.

Pauwels OSG, Sallé B (2009) Miscellanea Herpetologica Gabonica III. Hamadryad 34: 22–27.

Pauwels OSG, Vande Weghe JP (2008) Les Reptiles du Gabon. Smithsonian Institution, Washington DC, 272 pp.

Penner J, Wegmann M, Hillers A, Schmidt M, Rödel M-O (2011) A hotspot revisited – a biogeographical analysis of West African amphibians. Diversity and Distributions 17: 1077–1088. https://doi.org/10.1111/j.1472-4642.2011.00801.x

Perret J-L (1960) Une nouvelle et remarquable espèce d'*Atractaspis* (Viperidae) et quelques autres serpents d'Afrique. Revue Suisse de Zoologie 67: 129–139. https://doi.org/10.5962/bhl.part.75262

Perret JL, Mertens R (1957) Etude d'une collection herpétologique faite au Cameroun de 1952–1955. Bulletin de l'Institut Français d'Afrique Noire, Série A, Sciences Naturelles 19: 548–601.

Pitman CRS (1938) A guide to the snakes of Uganda – part XI. The Uganda Journal 5(3): 160–244.

Portillo F, Branch WR, Conradie W, Rödel M-O, Penner J, Barej MF, Kusamba C, Muninga WM, Aristote MM, Bauer AM, Trape JF, Nagy ZT, Carlino P, Pauwels OSG, Menegon M, Burger M, Mazuch T, Jackson K, Hughes DF, Behangana M, Zassi-Boulou A-G, Greenbaum E (2018) Phylogeny and biogeography of the African burrowing snake subfamily Aparallactinae (Squamata: Lamprophiidae). Molecular Phylogenetics and Evolution 127: 288–303. https://doi.org/10.1016/j.ympev.2018.03.019

Rhodin AGJ, Iverson JB., Bour R, Fritz U, Georges A, Shaffer HB, van Dijk PP (2017) Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Edition). Chelonian Research Foundation, Lunenburg, 292 pp.

Rödel M-O, Ernst E (2000) *Bufo taiensis* n. sp., eine neue Kröte aus dem Taï-Nationalpark, Elfenbeinküste. herpetofauna 22(125): 9–16.

Rödel M-O, Grabow K, Böckheler C, Mahsberg D (1995) Die Schlangen des Comoé-Nationalparks, Elfenbeinküste (Reptilia: Squamata: Serpentes). Stuttgarter Beiträge zur Naturkunde, Serie A 528: 1–18.

Rödel M-O, Kosuch J, Grafe TU, Boistel R, Assemian NE, Kouamé NG, Tohé B, Gourène G, Perret J-L, Henle K, Tafforeau P, Pollet N, Veith M (2009) A new tree-frog genus and species from Ivory Coast, West Africa (Amphibia: Anura: Hyperoliidae). Zootaxa 2044: 23–45.

Rödel M-O, Kosuch J, Veith M, Ernst R (2003) First record of the genus *Acanthixalus* Laurent, 1944 from the Upper Guinean rain forest, West Africa, with the description of a new species. Journal of Herpetology 37: 43–52.

Rödel M-O, Mahsberg D (2000) Vorläufige Liste der Schlangen des Tai-Nationalparks / Elfenbeinküste und angrenzender Gebiete. Salamandra 36: 25–38.

Roux-Estève R (1965) Les serpents de la région de La Maboké–Boukoko. Cahiers de la Maboké 3: 51–92.

Schmidt KP (1923) Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915. Part II. Snakes, with field notes by Herbert Lang and James P. Chapin. Bulletin of the American Museum of Natural History 49: 1–146.

Schouteden H (1933) Contribution á la faune des reptiles et des batraciens de la région méridionale du Parc Albert (Kivu). Revue de Zoologique et de Botanique Africaines 23: 233–238.

Shirley MH, Vliet KA, Carr AN, Austin JD (2014) Rigorous approaches to species delimitation have significant implications for African crocodilian systematics and conservation. Proceedings of the Royal Society B 281: 20132483. https://doi.org/10.1098/rspb.2013.2483

Sjöstedt Y (1896) *Atractaspis reticulata*, eine neue Schlange aus Kamerun. Zoologischer Anzeiger 19: 516–517.

Sjöstedt Y (1897) Reptilien aus Kamerun West-Afrika. Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar 23(4): 1–29. [pls 1–3]

Spawls S, Branch B (1995) The Dangerous Snakes of Africa. Natural history. Species Directory. Venoms and Snakebite. Blandford, London, 192 pp.

Sternfeld R (1908) Die Schlangenfauna von Kamerun. Mitteilungen aus dem Zoologischen Museum in Berlin 3: 397–432.

Trape JF, Roux-Estève R (1995) Les serpents du Congo: liste commentée et clé de détermination. Journal of African Zoology 109: 31–50.

Treplin S (2006) Inference of phylogenetic relationships in passerine birds (Aves: Passeriformes) using new molecular markers. Dissertation, University of Potsdam, Germany, 131 pp.

Vidal N, Delmas A-S, David P, Cruaud C, Couloux A, Hedges SB (2007) The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. Comptes Rendus Biologies 330: 182–187. https://doi.org/10.1016/j.crvi.2006.10.001

Uetz P, Freed P, Hošek J (2018) The Reptile Database. http://www.reptile-database.org [Accessed on: 2018-9-14]

Underwood G, Kochva E (1993) On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). Zoological Journal of the Linnean Society 107: 3–64. https://doi.org/10.1111/j.1096-3642.1993.tb01252.x

Wagner P, Townsend E, Barej M, Rödder D, Spawls S (2009) First record of human envenomation by *Atractaspis congica* Peters, 1877 (Squamata: Atractaspididae). Toxicon 54: 368–372. https://doi.org/10.1016/j.toxicon.2009.04.019

Wallach V, Williams KL, Boundy J (2014) Snakes of the World: A Catalogue of Living and Extinct Species. Taylor & Francis, CRC Press, London, New York, Boca Raton, 1209 pp. https://doi.org/10.1201/b16901

Werner F (1899) Ueber Reptilien und Batrachier aus Togoland, Kamerun und Deutsch-Neu-Guinea grösstentheils aus dem k. Museum für Naturkunde in Berlin. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 49: 132–157.

Werner F ("1912" [1913]) Neue oder seltene Reptilien und Frösche des Naturhistorischen Museums in Hamburg. Reptilien der Ostafrika-Expedition der Hamburger Geographischen Gesellschaft 1911/12. Leiter: Dr. E. Obst. Reptilien und Amphibien von Formosa. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 30 2. Beiheft: 1–39, 40–45, 45–51.

de Witte GF (1941) Exploration du Parc National Albert. Batraciens et reptiles. Institut des Parcs Nationaux du Congo Belge, Brussels, xviii + 261 pp. [+ xxvi pls]

de Witte GF (1953) Exploration du Parc National de l'Upemba. Reptiles. Institut des Parcs Nationaux du Congo Belge, Brussels, 322 pp. [+ xli pls +1 map]

de Witte GF (1962) Genera des serpents du Congo et du Ruanda-Urundi. Annales du Musée Royal d'Afrique Centrale 104: 1–203.

Wüster W, Chirio L, Trape J-F, Ineich I, Jackson K, Greenbaum E, Barron C, Kusamba C, Nagy ZT, Storey R, Hall C, Wüster CE, Barlow A, Broadley DG (2018) Integration of nuclear and mitochondrial gene sequences and morphology reveals unexpected diversity in the forest cobra (*Naja melanoleuca*) species complex in Central and West Africa (Serpentes: Elapidae). Zootaxa 4455: 68–98. https://doi.org/10.11646/zootaxa.4455.1.3

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Chevreuxiopsis franki gen. n., sp. n. (Crustacea, Amphipoda, Thoriellidae) from the deep sea southwest of Tasmania

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Abstract

A new amphipod species and genus, *Chevreuxiopsis franki*, found in a pelagic sediment trap southwest of Tasmania is described. The new species can be recognized by its unique antenna 2, which consists of a narrow peduncle, and a 4-articulate flagellum, which has a massively developed, article 1, large, posteriorly drawn out articles 2 and 3, and an elongate lanceolate 4th article. The pereopod 1 basis surrounds large maxillipedal plates. Pereopod 3 to 6 are equipped with subchelate propodus dactylus arrangements. The bases of pereopods 5–7 are narrow.

Key Words

Aristioidea
Australia
Indian Ocean
new species
pelagic sediment trap
Tasmania
taxonomy

Introduction

An unusual amphipod was found in a pelagic sediment trap in the Indian sector of the Southern Ocean, southwest of Tasmania, Australia. Careful examination allowed us to identify it as a member of the family Thoriellidae Lowry & Stoddart, 2011. The Thoriellidae consists of four genera: *Chevreuxiella* Stephensen, 1915, *Danaella* Stephensen, 1925, *Parachevreuxiella* Andres, 1987, and *Thoriella* Stephensen, 1915. The morphological diversity in this family is very high. The two *Danaella* species, *Danaella mimonectes* Stephensen, 1925 and *Danaella obensis* (Birstein & Vinogradov, 1962) (initially described as *Chevreuxiella obensis*) have inflated bodies that are more reminescent of hyperiid amphipods than of other Aristioidea Lowry & Stoddart, 1997. In contrast to *Danaella,* the genus *Thoriella*, represented by the slender *Thoriella islandica* Stephensen, 1915, has rather small coxal plates. *Chevreuxiella* and *Parachevreuxiella* are very similar, only differing by the length of uropods 1 and 2, their shape and the presence/absence of an inner ramus on both appendages. As the new species does not fit in any of the known thoriellid genera we are erecting the new genus *Chevreuxiopsis* herein.

Material and methods

The material was collected by a McLane 21-cup sediment trap at 1,000 m depth in the subantarctic Southern Ocean, southwest of Tasmania. The conical sediment trap has a surface of 0.5 m² and is filled with unfiltered water from the region (49°S, 153°E at 1,200 m), which was treated with sodium chloride (5 g/L) to increase the solution density,

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sodium tetracarborate (1 g/L) as a pH buffer, and mercuric chloride (3 g/L) for preservation (Roberts et al. 2008). The sample was filtered through a 1 mm screen and the specimen was found in the fraction > 1 mm, which contains plankton and micronekton organisms (Roberts et al. 2008).

For taxonomic study, we transferred the material in a graded series of ethanol-glycerol mixes into pure glycerol and then mounted the specimen or dissected parts on slides for the preparation of the drawings. Pencil drawings of the habitus were made with on a Leica M 205c dissecting microscope and details of the appendages and mouthparts on a Leica DMLB compound microscope. Both microscopes were equipped with a camera lucida. The line drawings were made following the technique described in Coleman (2003, 2009). Measurements were made along the dorsal outline of the animals, from the rostrum to the end of the urosome.

The material is held in the collections of the Leibniz Institute for Evolution and Biodiversity Science, Museum für Naturkunde Berlin (ZMB).

Systematics

Thoriellidae Lowry & Stoddart, 2011

Species list:

Chevreuxiella metopoides Stephensen, 1915
Chevreuxiopsis franki gen. n., sp. n.
Danaella mimonectes Stephensen, 1925
Danaella obensis (Birstein & Vinogradov, 1962)
Parachevreuxiella justi Lowry & Stoddart, 2011
Parachevreuxiella lobata Andres, 1987
Thoriella islandica Stephensen, 1915

Key to the species of the Thoriellidae

1 Coxae small and separate from each other, in uropods 1 and 2 both rami subequal in length .... *Thoriella islandica*
– Coxae large and overlapping each other, uropods 1 and 2 inner ramus short, vestigial or absent............................... 2
2 Pereonites 3–6 grossly swollen 3
– Pereonites 3–6 ordinary... 4
3 Posterior margin of urosome straight .... *Danaella mimonectes*
– Posterior margin of urosome incised .... *Danaella obensis*
4 Antenna 2 with flagellum consisting of subequal articles 5
– Antenna 2 flagellum consisting of 4 massive articles, article 1 expanded, articles 2 and 3 drawn out posteriorly, article 4 lanceolate ....*Chevreuxiopsis franki* gen. n. sp. n.
5 Uropods 1 and 2 with spine-like inner rami...*Chevreuxiella metopoides*
– Uropods 1 and 2 without inner rami 6
6 Uropods 1 and 2 rami much longer than peduncle... *Parachevreuxiella lobata*
– Uropods 1 and 2 rami subequal or shorter than peduncle... *Parachevreuxiella justi*

***Chevreuxiopsis* gen. n.**

http://zoobank.org/444F2A88-72B7-472B-BCE0-B5B70FA92ED3

Diagnosis. *Body* slender, pereon not inflated. *Antenna 1* slender, with normal flagellum. *Antenna 2* flagellum 4-articulate, much wider than peduncle, massively developed; article 1 enlarged, weakly drawn out posteriorly; articles 2 and 3 strongly drawn out posteriorly; article 4 lanceolate. *Maxilla 1* inner plate with 2 terminal plumose setae; outer plate with 6+1 apical spine-like setae; palp 2-articulate; article 2 inflated, lanceolate. *Maxilla 2* ordinary. *Pereopod 1* basis ovoid, expanded, with anteromarginal nose-like process; dactylus knob-like. *Pereopods 3–6* propodus subchelate; dactylus falcate (probably prehensile). *Pereopod 3* coxa slightly longer than that of peropod 2. *Pereopod 4* coxa enlarged, posteromarginally straight. *Pereopods 5–7* basis slender. *Urosome* segments 2 and 3 fused; uropods 2 pairs, each with lanceolate outer ramus and spine-like inner ramus. *Telson* absent.

Type species. *Chevreuxiopsis franki* sp. n., monotypic.

***Chevreuxiopsis franki* sp. n.**

http://zoobank.org/A8EDC94F-9584-46B7-B33A-21F489AEE688
Figures 1–5

Material examined. Holotype: female (the specimen appears to have unsetose oostegites), 12 mm.

Type locality. The specimen was collected with a McLane 21-cup sediment trap at 1,000 m depth between the 11 and 26 August 1998 at the Southern Ocean Time Series site (SOTS, 46°45.52′S, 142°5.38′E), southwest of Tasmania, Australia (ZMB Crust 31700).

Etymology. The species is named for Frank Halfter, the father of the first author.

Diagnosis. As for generic diagnosis.

Description (based on holotype, 12 mm).

Body (Fig. 1c). Head deeper than long, shorter than pereonite 1. Pereonite 2 slightly longer than 1. Pereonites

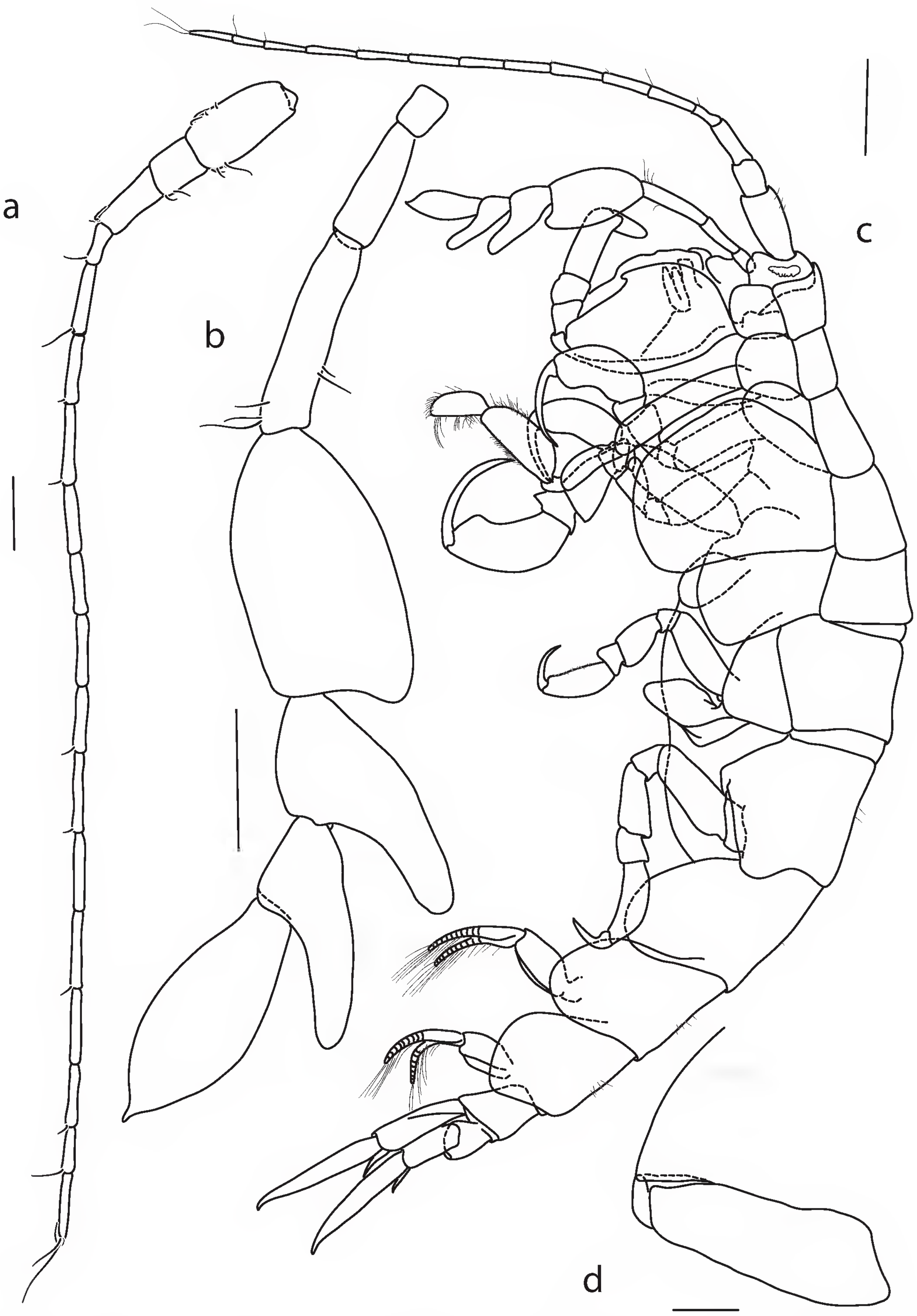

Figure 1. *Chevreuxiopsis franki* gen. n., sp. n., holotype 12 mm. **a** Antenna 1 **b** Antenna 2, peduncular articles 1–2 missing **c** Habitus **d** Labrum and mandible, lateral view. Scale bars: 500 µm (a, b); 1 mm (c); 100 m (d).

3 and 4 subequal in length. Pereonite 5 as long as pereonite 2. Pleonites subequal in length, posteroventrally rounded. Urosomite 1 longer than the fused urosomites 2 and 3. Telson absent.

Head (Fig. 1c) with anterior rounded lobe between insertion of antenna 1 and 2. Eyes present, dark pigments visible in alcohol; weakly reniform, extended dorsoventrally. *Antenna 1* (Fig. 1a, c) about 2× as long as antenna 2; peduncular article ratios 1 : 0.4 : 0.6, width successively smaller; 15 flagellum articles, slender, with very few slender setae. *Antenna 2* (Figs 1b, 6) peduncle articles slender, with 2 minute basal articles (which were damaged during dissection), article 3 short; article 4 about 2× as long as article 3; article 5 as long as article 1–4 combined; flagellum article 1 distally expanded, about 3× as wide as basal articles, posterodistally lobate; article 2 and 3 proximally as wide as peduncular article 3 and posterodistally drawn out into long narrow lobes; article 4 lanceolate, distally pointed and inside with a dense mass of tissue. *Mouthparts* (Figs 1c, 2f) extended ventrally, all covered by large outer plates of maxilliped, which leave an anteriorly and ventrally slit-like opening and additionally surrounded posteriorly by wide bases of pereopods 1. Mandibles to maxilla 2 directed anteriorly; ventrally of these mouthparts is a dense tissue mass (dashed in Fig. 2f, 3a), that might represent the inner maxillipedal plates. Both *mandibles* slender without molar, setal rows or palp (Fig. 2a, b). *Labrum* without pronounced epistome, rounded from lateral view (Fig. 1d). *Lower lip* (Fig. 2e) with rather long rounded apices with few setae in the hypopharyngeal gap and with slender mandibular lobes. *Maxilla 1* (Fig. 2c, d) inner plate with 2 plumose apical

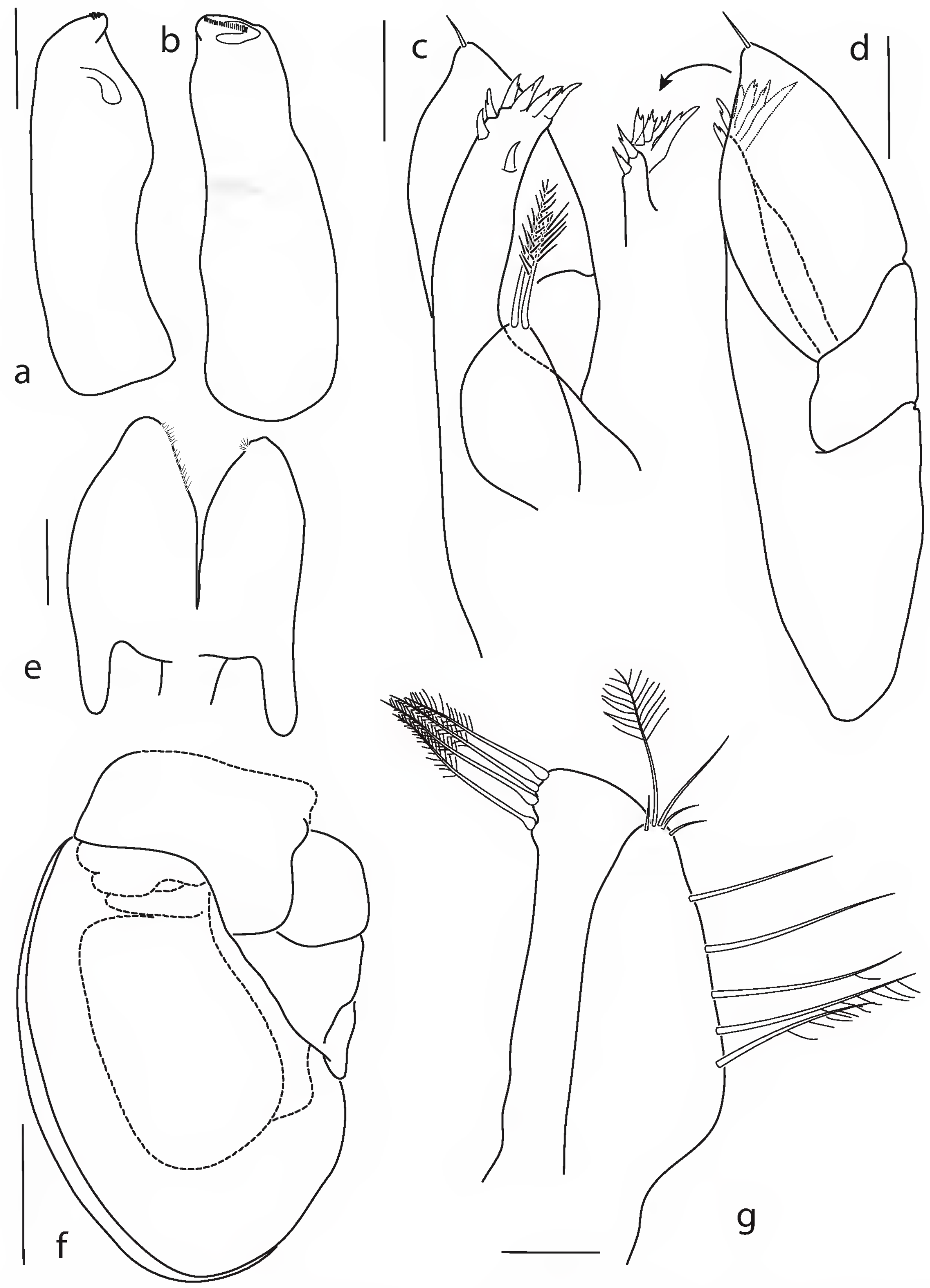

Figure 2. *Chevreuxiopsis franki* gen. n., sp. n., holotype 12 mm. **a** Right mandible **b** Left mandible **c, d** Maxilla 1 **e** Lower lip **f** Mouthparts, left aspect **g** Maxilla 2. Scale bars: 100 µm (a–e); 500 µm (f).

setae; outer plate with 6 plus 1 apical robust setae; palp 2-articulate, line between both articles barely visible, distal article lanceolate, with 1 short seta on tapering tip. *Maxilla 2* (Fig. 2g) inner plate with some medial setae; outer plate with 4 distolateral plumose setae.

Pereon. *Pereopod 1* (Fig. 3b) dark purple/black pigmented in ethanol; coxa subquadrate; basis anteromarginally expanded with short nose-shaped protrusion; ischium and merus subequal; carpus weakly expanded distally 2.2× as long as wide; propodus slightly tapering distally with distal knob-like dactylus. *Pereopod 2* (Fig. 3d, e) basis elongate and slender; ischium 2.7× as long as wide; merus short, distally pointed; carpus longer than propodus with cushions of slender, hair-like setae on anterior and posterior margins; propodus anteromarginally rounded with similar setation as carpus; dactylus subapically, accompanied with long several long setulated setae and with few setae on the inner curvature. *Pereopod 3* (Fig. 3c) coxa subrectangular, slightly directed anteriorly; basis as long as coxa; ischium 0.6× the width of basis; merus relatively short, distally expanded; carpus wider than long, distally expanded; carpus curved posteriorly, distally oblique; dactylus with proximal rounded joint, weakly curved, slender; propodus and dactylus form subchelate complex. *Pereopod 4* (Fig. 4a) coxa largest, about 4× as long as coxa 1, surpassing basis, ischium and part of merus, anteriorly convex, posteriorly straight; basis to dactylus subequal to pereopod 3, except for the slightly longer carpus. *Pereopod 5* (Fig. 4b) coxa bilobed; basis to merus subequal to pereopod 4; carpus shorter than wide, with anterior process; propodus curved anteriorly with oblique distal margin; carpus and long, slender, weakly curved dactylus form a very large subchela.

Pereopod 6 (Fig. 5a, d) coxa wide, weakly bilobate, posterior lobe slightly longer than anterior one; basis about half as long as coxa width; ischium longer than wide; merus expanded posterodistally; carpus short, distally expanded, with some small teeth anteromarginally; propodus, relatively slender, convex posteromarginally, anteromarginally straight, with marginal small teeth, especially on the medial face; dactylus falcate.

Pereopod 7 (Fig. 4c) coxa shorter than wide, subrectangular; basis posteroproximally weakly expanded,

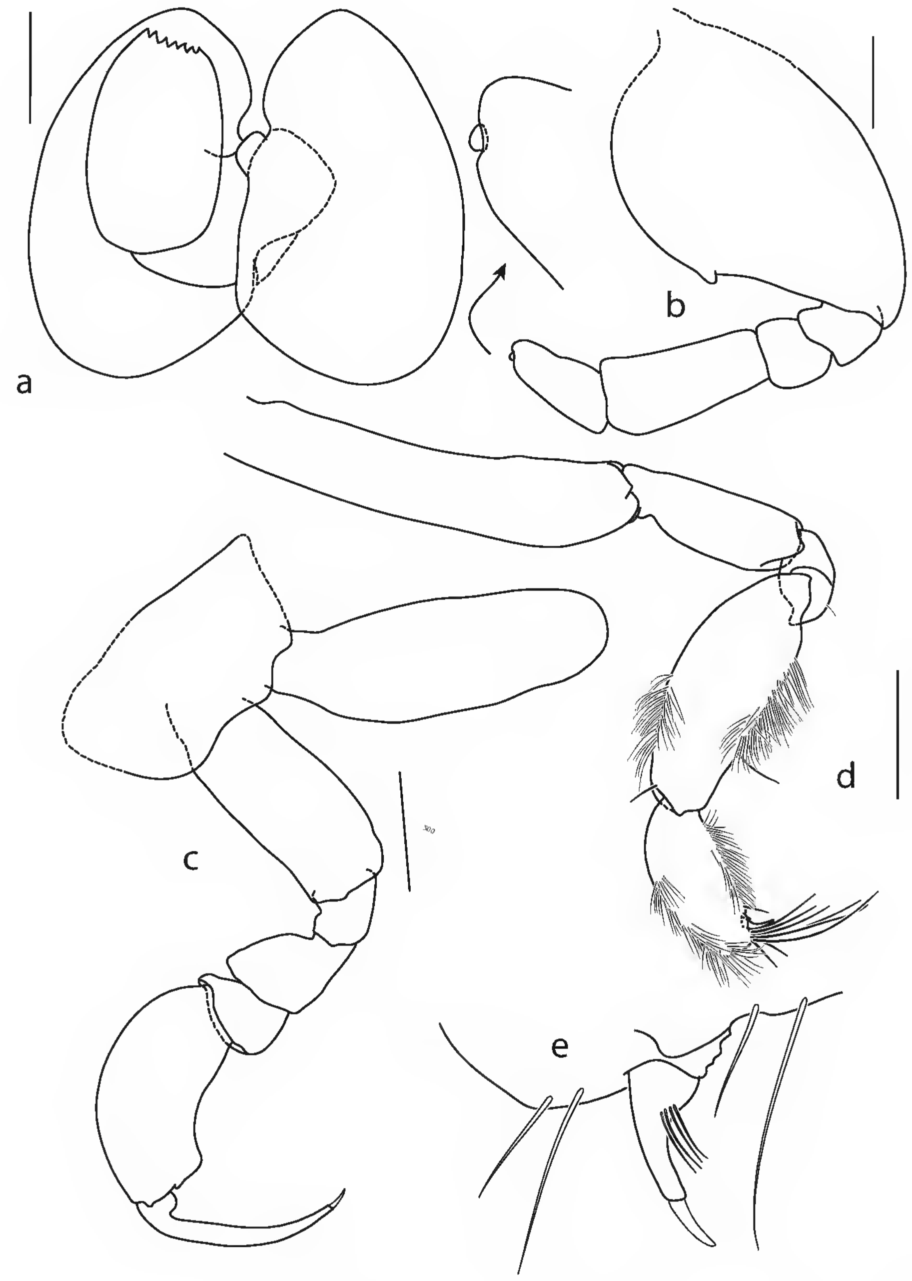

Figure 3. *Chevreuxiopsis franki* gen. n., sp. n., holotype 12 mm. **a** Maxilliped, opened up **b** Pereopod 1, basis to dactylus; detail shows knob-like dactylus **c** Pereopod 3 **d** Pereopod 2, without coxa **e** Dactylus of pereopod 2. Scale bar: 500 µm (a–d).

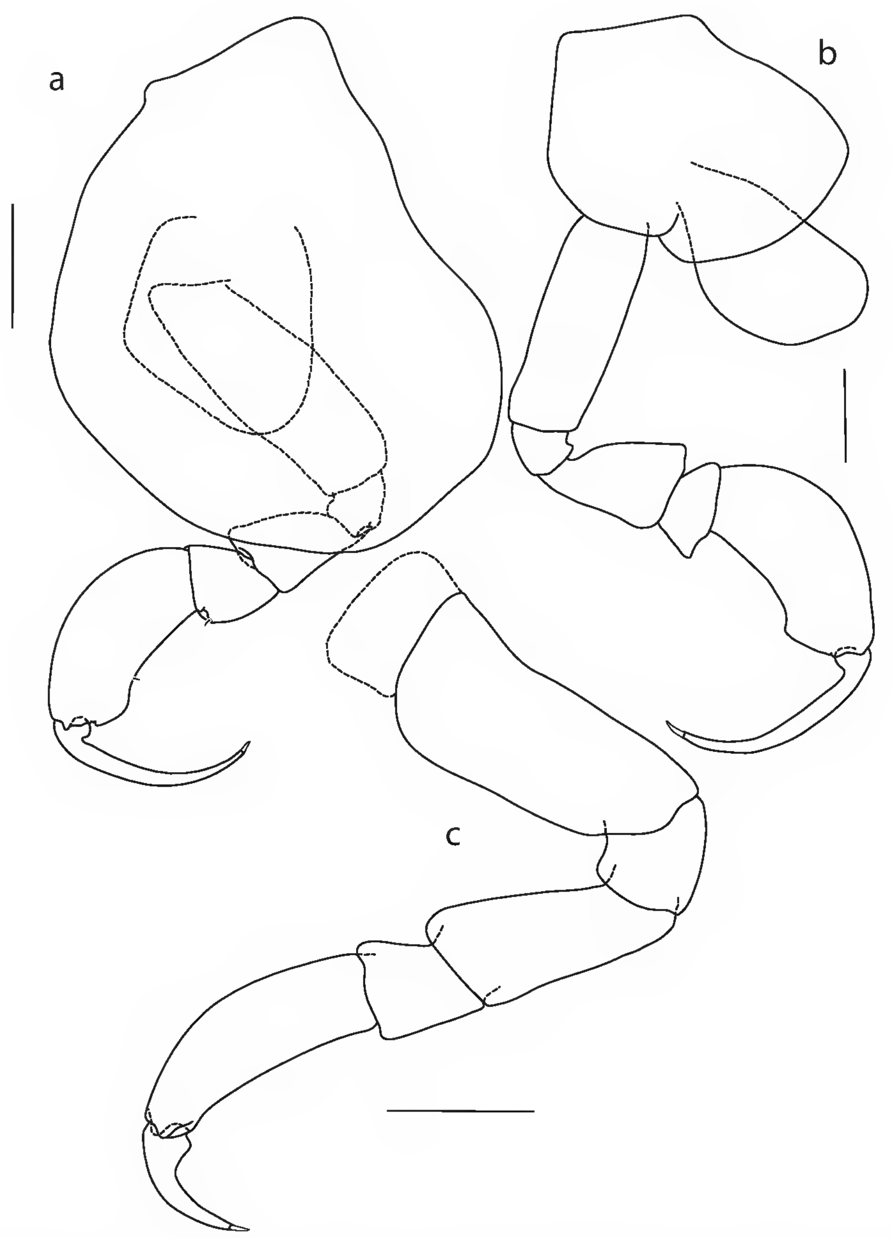

Figure 4. *Chevreuxiopsis franki* gen. n., sp. n., holotype 12 mm. **a** Pereopod 4 **b** Pereopod 5 **c** Pereopod 7, medial aspect. Scale bar: 500 µm (a–c).

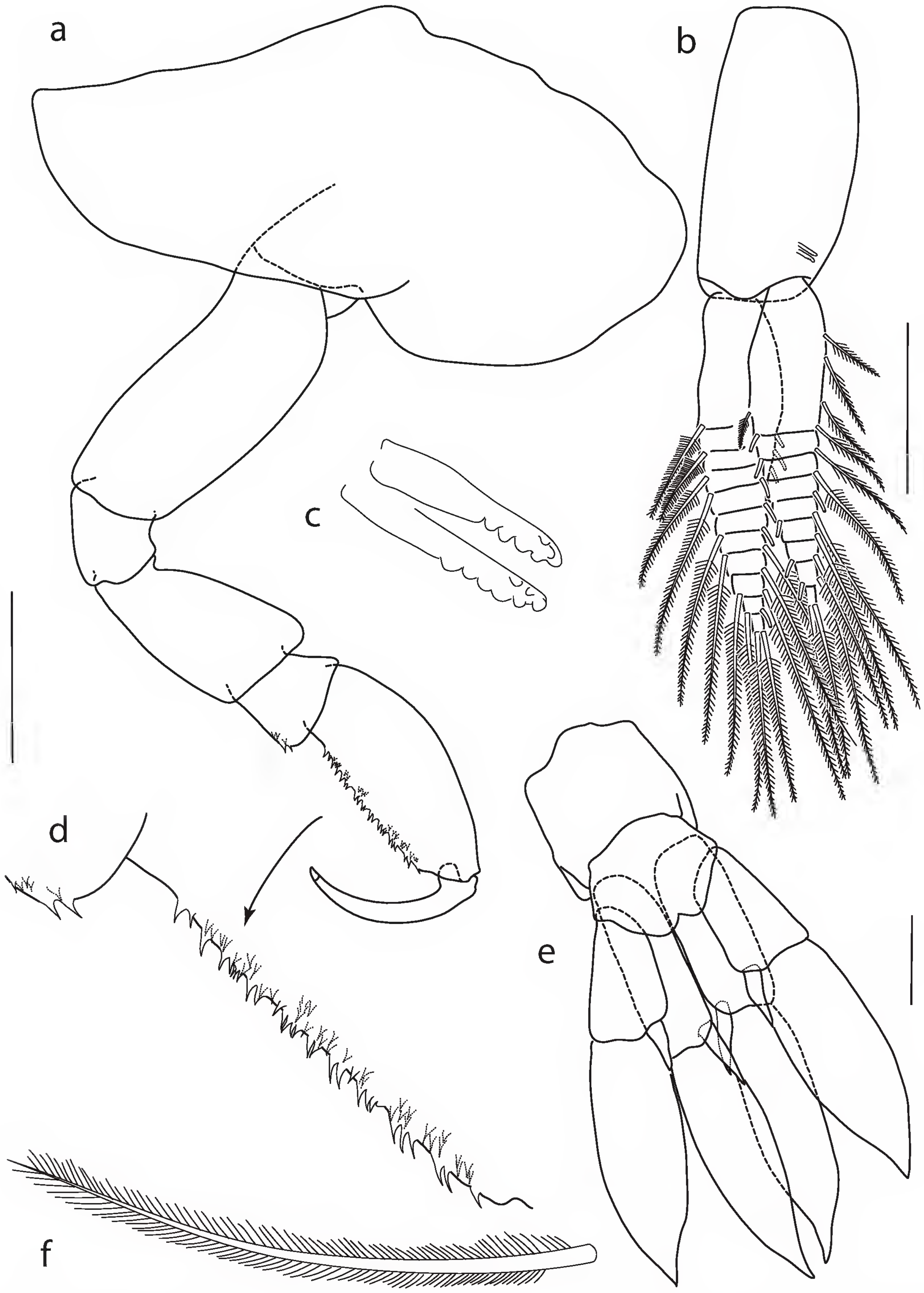

Figure 5. *Chevreuxiopsis franki* gen. n., sp. n., holotype 12 mm. **a** Pereopod 6 **b** Pleopod 1; **c** Coupling hooks of pleopod **d** Anterior margin of propodus **e** Urosome, dorsal view **f** Setulated seta of pleopod. Scale bar: 500 µm (a, b, e).

somewhat tapering distally; ischium subquadrate; merus weakly expanded posterodistally; carpus subquadrate; propodus convex posteromarginally, straight anteromarginally; dactylus much shorter than preceding appendages.

Pleon. *Pleopod 1* (Fig. 5b, c) peduncle 2× as long as wide; coupling hooks (Fig. 5c) long with rows of protrusions ventrally; both rami slightly longer than peduncle, inner ramus somewhat shorter than outer ramus; swimming setae moderately long with dense setulation (Fig. 5f).

Urosome. First urosomite longer than the fused second and third segment; urosomite 2 expanded midlaterally and weakly incised posteromarginally forming 2 short rounded lobes; peduncle of uropod 1 2.5× as long as wide; outer ramus lanceolate; inner ramus spine-like, 25% of outer ramus length; uropod 2 peduncle shorter than that of uropod 1 and weakly expanded distally; outer ramus slightly wider compared to that of uropod 1; inner ramus 23% of outer ramus. Telson absent.

Distribution. The species is so far only known from the type locality.

Discussion

We classified the new species in a new genus, *Chevreuxiopsis*. This genus is related to *Chevreuxiella* (represented by *C. metopoides*, the only species) and both genera share

Figure 6. *Chevreuxiopsis franki* gen. n., sp. n., holotype 12 mm. Photo of head, antennae, maxillipeds and anterior pereopods. Note the dark purple/black colour of the 1st pereopods. Scale bar: 500 µm.

the following: pereon not inflated (cf. *Danaella*); coxa 4 enlarged; similarities in the mouthparts: rather underived maxilla 1 and 2 and the morphology of the maxilliped; urosome and both uropods are very similar in the lanceolate shape of the rami and the dimensions of the inner rami.

However, there are also strong differences between the new species and *C. metopoides*. *Chevreuxiopsis franki* gen. n. sp. n. has a differently shaped, slender antenna 1 (vs expanded and elongate first flagellar article. This is perhaps a sexually dimorphic character, as *C. metopoides* was described on a male specimen) and especially antenna 2 flagellum, which has an enlarged article 1, large, posteriorly drawn out articles 2 and 3 and a lanceolate article 4 (vs normally shaped and multiarticulate); maxilla 1 with inflated palp article 2 (vs normal), inner plate with 2 plumose setae (vs 4 setae); basis of pereopod 1 ovoid expanded with anteromarginal nose-like process (vs weakly expanded and without nose-like process); coxa 3 slightly longer than coxa 2 (vs much longer and wider); coxa 4 posteromarginally straight (vs posteroventally lobate); basis of pereopods 5–7 slender (vs expanded); pereopod 3–6 probably prehensile due to their subchelate arrangement of propodus and falcate dactylus (vs simple).

The maxilliped is of a unique shape in thoriellids. Large plates surround the mouthparts and leave a small slit anteriorly and ventrally. However, due to its derived morphology it is very difficult to homologize the parts. For example, Stephensen (1915: 41, fig. 24) labelled the massive maxillipedal plates, that surround the mouthparts, as the first palp articles, but we think they are the outer plates of the maxilliped. These plates are overlapped by the huge bases of the first pereopod, which has dark purple/black pigmentation and may act as a shutter (see below).

Due to the few records in literature, knowledge about the biology of the Thoriellidae is limited (Lowry and Stoddart 2011). Stephensen (1915) suggested a semiparasitic lifestyle for *Chevreuxiella* and *Thoriella*, and Andres (1987) found *Parachevreuxiella lobata* attached to a wound of a bathypelagic fish. However, it is difficult to draw conclusions about the lifestyle of *Chevreuxiopsis franki* sp. n. Due to the relatively good preservation of the body, an active entering of the specimen into the sediment trap is assumed. The long-term deployment of the sediment trap prevents analyses of potential differences in day vs night distribution due to diurnal vertical migration. Hence, no additional information on the vertical distribution of this species can be concluded.

The specimen is of transparent appearance apart from the dark purple gnathopod 1, which covers the maxilliped

(Fig. 6). Herring (1981: 171) already noted a blue-green bioluminescence in the genera *Chevreuxiella* and *Danaella* in the thoriellid family while handling, which "almost extinguished when the maxilliped plate was withdrawn between the two densely pigmented expanded basal articles of the first pair of gnathopods". Also, Parker (1999) studied the luminescence of an unidentified thoriellid juvenile and found the expanded fifth articles of the second antennae to act as reflectors of the luminescent maxilliped. He assumed that rather than having a communication or defensive function, light flashes could be used to catch prey. Similarly, this could be the case in our specimen. Additional to the dark purple/black shutter, we also note enlarged articles of the second antenna, which could function as reflector of the emitted bioluminescence and lead potential prey towards the maxillipeds. However, this has to be further investigated in behavioural studies.

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References

Andres H (1987) Die Gammaridea der 76. Reise von FFS „Walther Herwig“ mit Beschreibung von *Parachevreuxiella lobata* gen. n. und sp. n. (Crustacea: Amphipoda). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 84: 95–103.

Birstein JA, Vinogradov ME (1962) [Pelagic Gammaridea (Amphipoda, Gammaridea) collected by the Soviet Antarctic Expedition on the M/V "Ob", south of 40°S]. Akademiya Nauk SSSR, Issledovaniya Fauny Morei 1(10): 33–56.

Coleman CO (2003) "Digital inking": How to make perfect line drawings on computers. Organisms Diversity & Evolution, Electronic Supplement 14: 1–14. http://senckenberg.uni-frankfurt.de/odes/03-14.pdf

Coleman CO (2009) Drawing setae the digital way. Zoosystematics and Evolution 85: 305–310. https://doi.org/10.1002/zoos.200900008

Herring PJ (1981) Studies on bioluminescent marine amphipods. Journal of the Marine Biological Association of the United Kingdom 61(1): 161–176. https://doi.org/10.1017/S0025315400045999

Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO, Corbari L, Costello MJ, Daneliya M, Dauvin J-C, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Hughes L, Jaume D, Jazdzewski K, Kim Y-H, King, R, Krapp-Schickel T, LeCroy S, Lörz A-N, Mamos T, Senna AR, Serejo C, Sket B, Souza-Filho JF, Tandberg AH, Thomas J, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (2018) World Amphipoda Database. Thoriellidae Lowry & Stoddart, 2011. World Register of Marine Species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=558702. [Accessed on: 2018-12-14]

Lowry KJ, Stoddart EH (1997) Amphipoda Crustacea IV., Families Aristiidae, Cyphocarididae, Endevouridae, Lysianassidae, Scopelocheiridae, Uristidae. Memoirs of the Hourglass Cruises 10: 1– 148.

Lowry J, Stoddart H (2011) The new deep-sea families Cebocaridae fam. nov., Cyclocaridae fam. nov. and Thoriellidae fam. nov. (Crustacea: Amphipoda: Lysianassoidea). Zootaxa 2747(1): 53–68. https://doi.org/10.11646/zootaxa.2747.1.4

Parker A (1999) An unusually isolated reflector for host bioluminescence on the second antenna of a lysianassoid (Amphipoda: Gammaridea). Schram FR, von Vaupel Klein JC (Eds) Crustaceans and the Biodiversity Crisis (Crustaceana). Brill, Leiden, 879–887.

Roberts D, Howard W, Moy A, Roberts J, Trull T, Bray S, Hopcroft, R (2008) Interannual variability of pteropod shell weights in the high-CO 2 Southern Ocean. Biogeosciences Discussions 6: 4453–4480. https://doi.org/10.5194/bgd-5-4453-2008

Stephensen K (1915) Isopoda, Tanaidacea, Cumacea, Amphipoda (excl. Hyperiidea). Report on the Danish Oceanographical Expeditions 1908–10 to the Mediterranean and Adjacent Seas 2, Biology (D1): 1–53.

Stephensen K (1925) *Danaella mimonectes* (n. gen., n. sp.), a new bathypelagic gammarid (Fam. Lysianassidae) from South Greenland waters. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjöbenhavn 80: 423–428.

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Tadpoles of three western African frog genera: *Astylosternus* Werner, 1898, *Nyctibates* Boulenger, 1904, and *Scotobleps* Boulenger, 1900 (Amphibia, Anura, Arthroleptidae)

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Abstract

Herein, we describe the tadpoles of six *Astylosternus* species, *A. fallax*, *A.* cf. *fallax*, *A. laurenti*, *A. montanus*, *A. perreti*, *A. ranoides*, and *Scotobleps gabonicus*, and redescribe the tadpoles of *A. batesi*, *A. diadematus*, *A. laticephalus*, *A. occidentalis*, *A. rheophilus*, and *Nyctibates corrugatus*. All *Astylosternus* tadpoles are adapted to torrent currents and share a long, oval body, slightly flattened in lateral view, with very long muscular tails with narrow fins. The jaws are massive, serrated, and often show a tooth-like medial projection (fang) in the upper jaw. Body proportions of *Astylosternus* tadpoles are extremely similar. The best characters to distinguish species might be life coloration and potentially the shape of labial papillae. The tadpole of *Scotobleps gabonicus* is similar to *Astylosternus* and differs only slightly by a narrower body with a shorter and rounder head. The upper jaw of *Scotobleps* carries two or three lateral fangs instead of one medial one. The tadpole of *Nyctibates corrugatus* is easily distinguishable from the other two genera on the basis of their very long, eel-shaped body and tail and the bluish-black color.

Introduction

The anuran family Arthroleptidae comprises eight genera, all being endemic to sub-Saharan Africa (Frost 2018). The species-rich genera, *Arthroleptis* Smith, 1849 and *Leptopelis* Günther, 1859, are widespread and occur in forest and open habitats (Blackburn 2008; Schiøtz 1999). Whereas all *Arthroleptis* seem to reproduce by terrestrial, direct development (Guibé and Lamotte 1958a; Lamotte and Perret 1963; Wager 1986; Schweiger et al. 2017), *Leptopelis* deposit their clutches in soil, from where the hatched, long and slender, exotrophic tadpoles move into lentic or lotic waters (Rödel 2000; Channing 2008; Barej et al. 2015). The genus *Cardioglossa* Boulenger, 1900 is restricted to western and central Africa and has stream-dwelling tadpoles with special morphological characteristics like an eel-shaped body and an elongated spiraculum (Hirschfeld et al. 2012). The genus *Leptodactylodon* Andersson, 1903, is restricted to the western part of central Africa. The tadpoles are likewise stream dwellers, but presumably live in the interstitial spaces between pebbles and have special funnel mouths (Mapouyat et al. 2014). The tadpoles of the Hairy Frog, *Trichobatrachus* Boulenger, 1900, live in torrent, mountainous streams from eastern Nigeria, south to northern Angola (Ernst et al. 2014). They are comparatively short and robust with a huge oral sucker and numerous rows of keratodonts (Mertens 1938; Channing et al. 2012).

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Two of the three remaining genera, *Astylosternus* Werner, 1898 and *Nyctibates* Boulenger, 1904, have large, long and very muscular stream-dwelling tadpoles, as far as is known (Amiet 1971; Channing et al. 2012). The tadpole of *Scotobleps* Boulenger, 1900, a monotypic genus ranging from south-eastern Nigeria to Gabon and the Republic of the Congo (Portik et al. 2017) is unknown, as are the tadpoles of various *Astylosternus* species.

During the last 15 years we collected numerous tadpoles of morphologically similar, torrenticolous arthroleptid tadpoles, apparently belonging to 10 species of *Astylosternus*, *Nyctibates corrugatus,* and *Scotobleps gabonicus*. We present re-descriptions of tadpoles of six species (*A. batesi*, *A. diadematus*, *A. laticephalus*, *A. occidentalis*, *A. rheophilus*, and *N. corrugatus*) and new tadpole descriptions for six additional species, amongst them the first from the genus *Scotobleps*.

Material and methods

Collection, preservation, deposition and barcodes

Tadpoles were collected with dip nets and anesthetized in chlorobutanol solutions before being either preserved in formalin (5–10%) or ethanol (75%). All were finally stored in 75% ethanol. Prior to preservation tail tips of representative specimens were preserved separately in 96% ethanol for genetic investigations. All tadpole vouchers and tissue samples are deposited at the collection of the Museum für Naturkunde Berlin (ZMB; see descriptions). For comparisons we examined further adult frogs and corresponding sequences from the collections of Natural History Museum of Geneva (MHNG; Geneva, Switzerland) and the Zoological Research Museum A. Koenig (ZFMK; Bonn, Germany). Tadpoles were assigned to species by DNA-barcoding, using up to 558 bp of the mitochondrial 16S rRNA gene; for exact laboratory procedures see Mapouyat et al. (2014) and Barej et al. (2015). All sequences of tadpoles and adults have been produced for this study and deposited at GenBank (for accession numbers see tadpole descriptions). Comparisons between sequences were carried out using BioEdit 7.0.9.0 (Hall 1999).

Character assessment

All measurements were taken by FG and MR. Measurements of randomly chosen vouchers were measured by both persons and the entire dataset only put together after these measures did not differ. Measures were taken with a digital caliper (accuracy ± 0.1 mm) and a measuring ocular on a Leica MZ95 dissecting microscope (accuracy ± 0.02 mm).

The following measurements were taken: TL (total length), BL (body length), TAL (tail length), BH (body height at the point of the spiracle insertion), BW (maximum body width), TMW (tail muscle width at tail base), TMH (maximum tail muscle height), VFH (maximum height of ventral fin), DFH (maximum height of dorsal fin), MTH (maximum tail height), ED (horizontal eye diameter), ND (horizontal nostril diameter), IOD (interorbital distance), IND (inter-nasal distance), SN (nostril-snout distance), EN (eye-nostril distance), ES (eye-snout distance), MW (mouth width), SP (spiracle length) and SSD (snout-spiracle distance). Based on these measures the following proportions were calculated: BL/TL, BH/BL, BW/BL, BH/MTH, TMW/BW, TMH/MTH, VFH/DFH, IND/IOD, ED/BL. All measurements are provided in Appendix 1.

In the text, measurements or ratios are usually summarized (for $N \geq 3$) and given as: mean ± standard deviation and range (min–max). As we tried to predominately use genotyped specimens for the descriptions and the tail tips were missing in most of them (see above), the total length was either determined in comparison with alternative specimens of the same series and developmental stage or estimated based on the usual tail shape of the group. The mouthpart formulae are in accordance with Dubois (1995). In addition, the number, form and arrangement of the labial papillae were accessed and described. We further checked for a lateral line system. As all tadpoles proved to possess such organs in an identical arrangement, we excluded it from the species-specific tadpole descriptions and instead present a summary description at the end of the result section. The terminology of lateral lines follows Escher (1925). The staging of tadpoles was according to Gosner (1960). Whenever possible we tried to choose tadpoles of Gosner stages 25–30 for descriptions. Descriptions of life coloration are based on photos taken in the field.

Illustrations

Photos of entire tadpoles were taken with a Canon EOS 50D digital camera and a 50 mm 1:2.5 lens. Mouthpart pictures were taken with a stacking camera (Leica DFC490) on a Leica Z16 APO A microscope. Single exposures were combined using the Automontage® software v. 5.03.0061 (Syncroscopy). All pictures were edited with Adobe Photoshop v. 18.1.0. Schematic sketches of the keratodont formulae are usually based on several individuals of the respective species.

Analysis of morphological differences

To test, if and how the tadpoles of the different species can be distinguishable, we plotted indices of our various measures against each other and ran a Principle Component Analysis (PCA) using qti-Plot and Past 3.18 (Hammer et al. 2001). Before running the PCA, all measures were standardized against the respective body lengths.

Results

Tadpole descriptions

Astylosternus batesi (Boulenger, 1900)

Material examined. ZMB 82863 (GenBank MK318840), Gosner stage 25, Cameroon, Mt Kala, 899 m, 3°50'27.66"N, 11°20'52.44"E, 9 November 2011, leg. M.F. Barej, H.C. Liedtke & N.L. Gonwouo; ZMB 82864 (GenBank MK318841), Gosner stage 25, Cameroon, Ebo Forest, Bekob, 893 m, 4°21'51.96"N, 10°25'10.26"E, 30 September 2011, leg. M. Dahmen; ZMB 82865 (GenBank MK318842), Gosner stage 25, Cameroon, Ebo Forest, Bekob, 852 m, 4°21'54.36"N, 10°25'17.22"E, 1 September 2011, leg. M. Dahmen; ZMB 82866 (GenBank MK318843), 2 tadpoles, Gosner stage 25, Cameroon, Ebo Forest, Bekob, 917 m, 4°21'27.42"N, 10°25'5.94"E, 9 January 2011, leg. M. Hirschfeld & F. Grözinger; ZMB 82784 (GenBank MK318844), Gosner stage 36, Cameroon, Ebo Forest, Bekob, 807 m, 4°21'54.3"N, 10°25'24.54"E, 10 January 2011, leg. M. Hirschfeld & F. Grözinger.

All tadpoles were caught in small to medium-sized streams. The description is mainly based on ZMB 82865 and ZMB 82784. Genotyped tadpoles have been compared with an adult frog (MC11_205; GenBank MK318905) from Mount Kala, near Kala village, Cameroon. The genotyped individuals were genetically almost identical, the maximum uncorrected p-differences in pairwise comparisons was 0.2% (1 bp).

Description. Long slender tadpole with long, muscular tail and narrow fins (Fig. 1); body oblong oval in dorsal and lateral view; back with a medial longitudinal-depression; snout rounded in dorsal view, more narrow-rounded in lateral view; body length approximately 0.3 (31.3–36.7%, $N = 3$) of total length; body height 46.3 ± 5.6% of body length; body width 60.5 ± 6.0% of body length; eyes positioned dorsolaterally, eye diameter 11.3 ± 1.4% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 75.2 ± 9.7% of interorbital distance; tail fins narrow, dorsal and

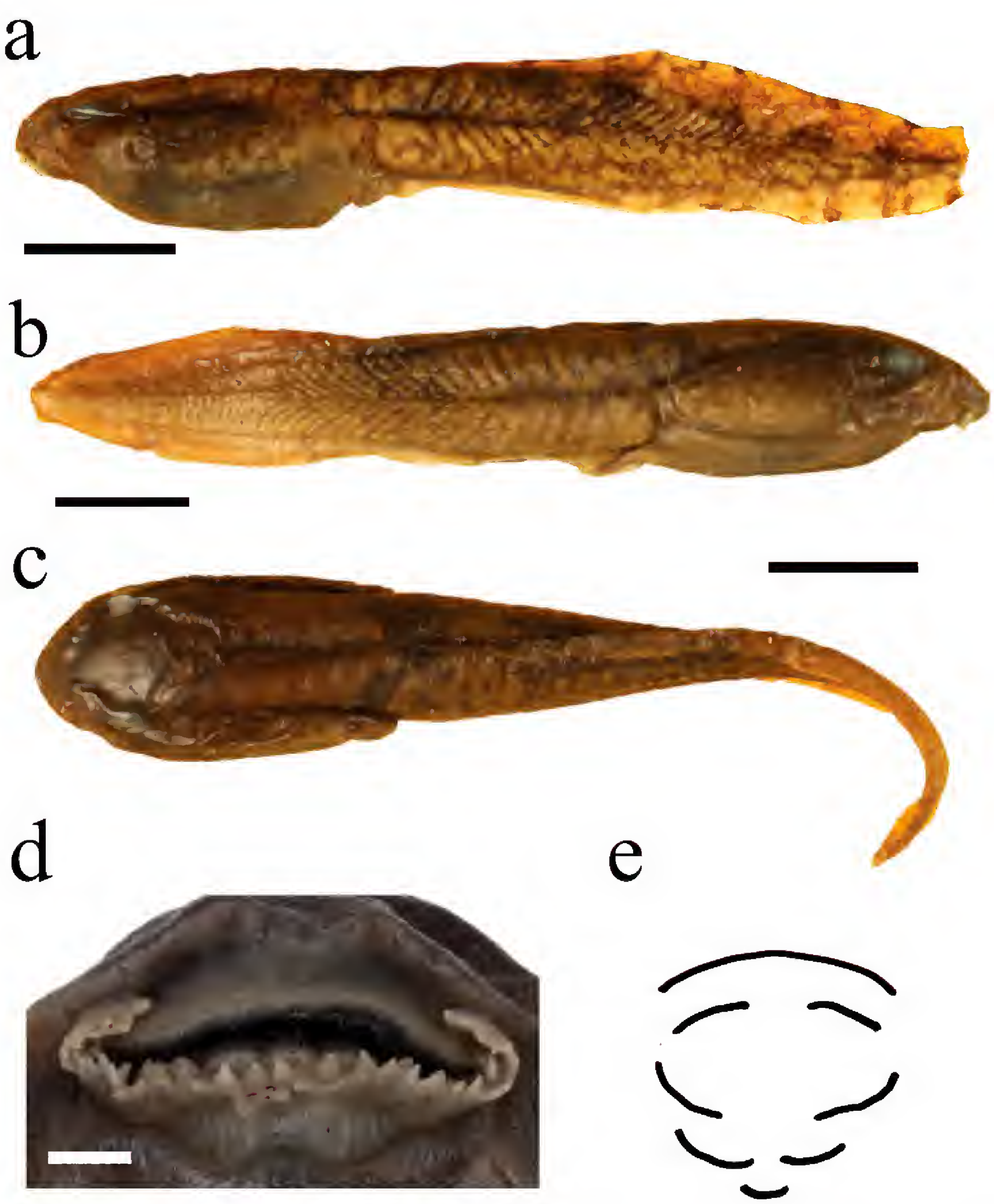

Figure 1. *Astylosternus batesi* tadpoles; **a** ZMB 82865 (Gosner stage 25) and **b–d** ZMB 82784 (Gosner stage 36); **a–b** lateral, and **c** dorsal view; **d** oral disc; **e** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

ventral fin originating from tail base, ventral fin height narrow, reaching 70.7 ± 4.7% of dorsal fin height; highest part of tail approximately in the middle of the tail; body height 91.7 ± 11.5% of maximum tail height; tail axis width 41.3 ± 11.4% of body width; tail axis height 59.8 ± 13.9% of maximum tail height; tail tip rounded; vent tube dextral; body with large lateral air sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, very close to snout, narrower than interorbital distance; keratodont formula 1:2/2+2:1; anterior lip only lateral with papillae, large rostral gap; posterior lip with 2–3 rows of approximately 20 uniform papillae, papillae triangular and approximately as long as broad (Fig. 1d); black jaw sheaths massive and serrated; upper jaw with a big medial projection (fang); lower jaw U-shaped with a medial notch.

The largest tadpole, still Gosner stage 25 (ZMB 82865), measured 25 mm body length. The most developed specimen (ZMB 82784, Gosner stage 36) had similar body length of 24.7 mm. When reconstructing the tail tip of the largest specimens by the shape of tails in smaller specimens we estimate the maximum total length of *A. batesi* tadpoles to be 60–80 mm.

Coloration in preservation. Brown, slightly fading from snout to tail; dorsal surfaces with irregular dark speckles; ventral surfaces without or only few darker markings; tail fins sometimes with dark blotches or speckles, partly transparent. Life color of very small specimens with much yolk, were much lighter than larger specimens (Fig. 2), showing distinct black blotches on body and tail axis, tail fins completely transparent.

Variation. According to Channing et al. (2012) the anterior lip has three rows of keratodonts, 1:2+2/2+2:1. We cannot exclude that our specimens lost the very short third row, likewise it is possible that populations vary in this character. Channing et al. (2012) describe coloration to be partly yellowish or reddish on back and flanks, ventrally bluish to violet, dark spots on all surfaces, less-so on the venter. Angel (1930) described a tadpole as *Gampsosteonyx batesi.* As this tadpole originated from an area that is outside the present day range of *A. batesi*, the description might have be based on another *Astylosternus* species (Channing et al. 2012).

Taxonomic remark. Whereas all genotyped tadpoles were genetically almost identical amongst each other and an adult from Mount Kala, Cameroon, further genetic comparisons with specimens from across the range of the species revealed three distinct genetic lineages (results not shown). Our tadpoles originated from Cameroon. All genetic samples from Gabon and the Republic of Congo, fell into a different clade. As the type locality of *A. batesi* however, is

Figure 2. Young *Astylosternus batesi* tadpoles (ZMB 82863) in life, Gosner stage 25 at a total length of about 15 mm, still with large amounts of yolk.

"Benito River, Gaboon" (Boulenger 1900), the tadpoles on which our descriptions is based may thus actually belong to an undescribed species within the *A. batesi*-complex.

Astylosternus diadematus Werner, 1898

Material examined. ZMB 82799 (GenBank MK318845), 1 tadpole, Gosner stage 25, Cameroon, Mt Manengouba, Nkikok, 1328 m, 5°5'34.5"N, 9°49'3.8"E, 8 September 2011, leg. M. Hirschfeld; ZMB 82870 (GenBank MK318846), 1 tadpole, Gosner stage 25, Cameroon, Mt Manengouba, M'Bourouko, 1459 m, 5°4'3.48"N, 9°51'56.22"E, 1 December 2010, leg. M. Hirschfeld; ZMB 88345, 1 tadpole, Gosner stage 25, Cameroon, near Korup National Park, Mokango, 621 m, 5°8'11.29"N, 9°4'37.43"E, 9 May 2014, leg. F. Mühlberger; ZMB 88346, 1 tadpole, Gosner stage 36, Cameroon, near Korup National Park, Mokango, 502 m, 5°7'36.51"N, 9°4'9.49"E, 10 May 2014, leg. F. Mühlberger.

The two specimens from Mount Manengouba were caught in medium-sized streams in gallery forest; the Korup specimens were from small creeks in rainforest. The description is mainly based on ZMB 82799 and ZMB 88346. Genotyped tadpoles have been compared with two adults from Mount Nlonako, Cameroon (ZFMK 81585 and ZFMK 81702; GenBank MK318847, MK318848). The uncorrected pairwise p-difference between the tadpoles and between the tadpoles and the adults ranged from 0.2–0.7% (1–3 bp).

Description. Long robust tadpole with muscular tail (Fig. 3); body oval in dorsal and lateral view; snout rounded in dorsal view, slightly more pointed in lateral view; body length approximately 0.3 (32.8–32.9%, $N = 2$) of total length; body height 46.7 ± 4.5% of body length;

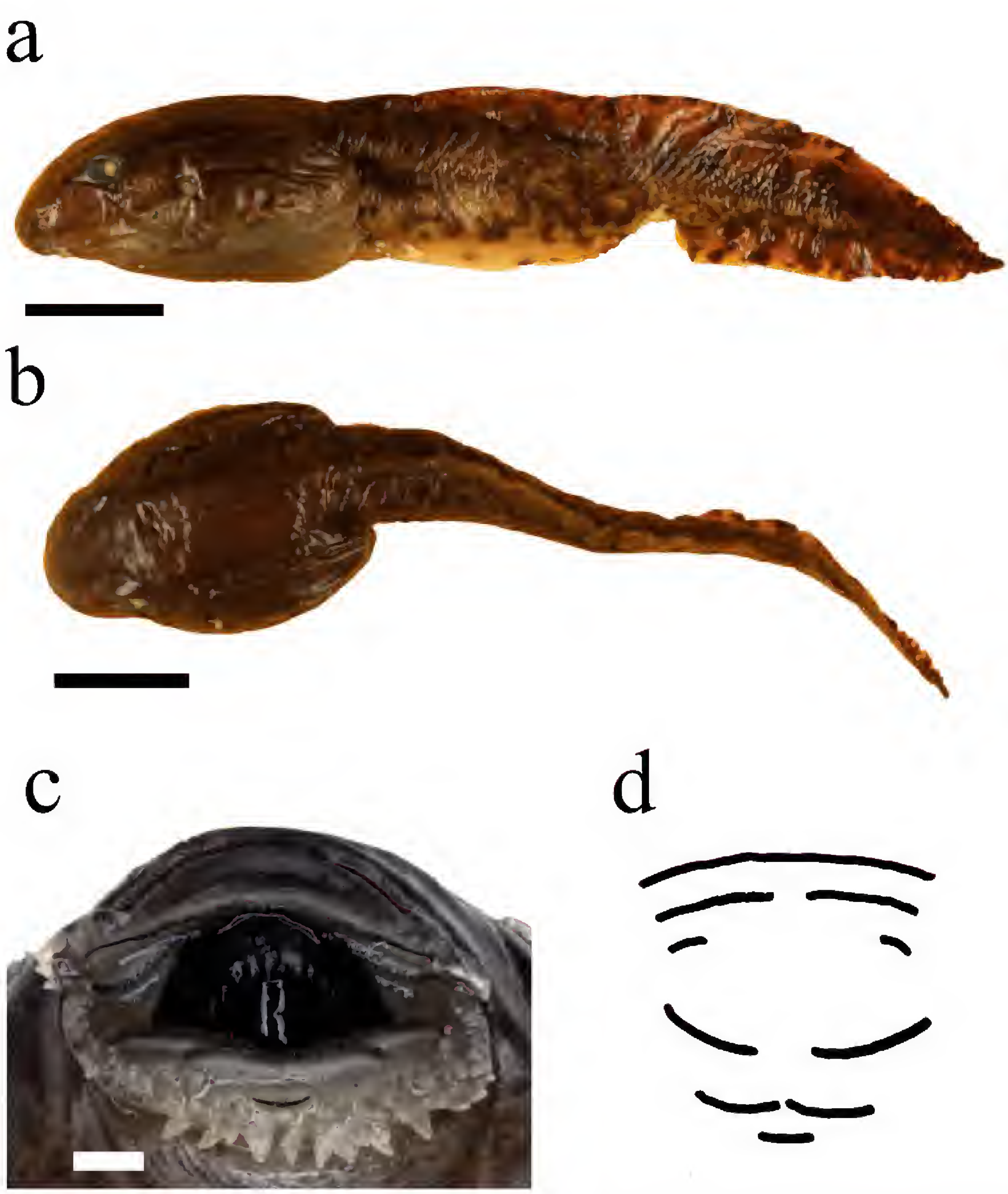

Figure 3. *Astylosternus diadematus* tadpole (ZMB 88346) at Gosner stage 36; **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

body width 60.7 ± 7.8% of body length; eyes positioned dorsolaterally, eye diameter 11.5 ± 1.0% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 70.9 ± 3.5% of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base, ventral fin height 67.7 ± 3.2% smaller than dorsal fin height; highest part of tail axis approximately in the middle of the tail; body height 82.2–85.7% (N = 2) of maximum tail height; tail axis width 47.4 ± 4.8% of body width; tail axis height 69.8 ± 5.4% of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, very close to snout, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip only with lateral papillae and large rostral gap; posterior lip with two rows of around 20 papillae, central papillae long and narrow, papillae becoming smaller towards angles of the mouth (Fig. 3c); black jaw sheaths massive and serrated; upper jaw with a medial fang, lower jaw U-shaped with medial notch.

The largest tadpole (ZMB 88346, Gosner stage 36) had 72 mm total length (body length: 23 mm).

Coloration in preservation. Brown to dark brown, dorsal surfaces darker, venter lighter and more grayish; flanks densely beset with diffuse and small brown spots; intensity of patterning deceases from back to vent; tail fins slightly transparent, dorsal fin with dark patterning, ventral fin with fewer dark spots.

Variation. ZMB 88346 had a particularly high body (95.4% of maximum tail height) and a keratodont formula of 1:2+2/1+1:2. Channing et al. (2012) report the keratodont formulae 3+3/2+2:1 and 3+3/1+1:2, as well as lighter coloration and less dark spots. The latter differences possibly are due to preservation differences.

Astylosternus fallax Amiet, 1978

Material examined. ZMB 82868 (GenBank MK318849), 3 tadpoles, Gosner stage 25, Cameroon, Ebo Forest, Njuma, 373 m, 4°20'54.66"N, 10°14'24.3"E, 16 July 2011, leg. M. Dahmen & M. Hirschfeld; ZMB 82869 (GenBank MK318850), 1 tadpole, Gosner stage 25, Cameroon, Ebo Forest, Njuma, 306 m, 4°20'35.64"N, 10°14'0.54"E, 29 September 2010, leg. M. Hirschfeld & M.-O. Rödel.

All tadpoles were caught in forest streams. The description is mainly based on ZMB 82868. Genotyped tadpoles have been compared with an adult from Bekop, Ebo forest, Cameroon (ZMB 82787; GenBank MK318851). The two tadpoles and the adult were genetically identical.

Description. Long slender tadpole with long, muscular tail (Fig. 4); body oval in dorsal and lateral view; snout rounded in dorsal and lateral view; body length 36.3 ± 2.6% of total length; body height 40.3 ± 3.3% of body length; body width 56.2 ± 4.4% of body length; eyes positioned dorsolaterally, eye diameter 11.4 ± 0.5% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 74.1 ± 7.0% of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base; ventral fin height narrower, 68.9 ± 11.5%, than dorsal fin height; highest part of tail approximately in the middle of the tail; body height 96.6 ± 14.8% of maximum tail height; tail axis width 45.6% ± 10.0% of body width; tail axis height 69.3 ± 4.7% of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth positioned rostroventral, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with lateral papillae and big rostral gap; posterior lip with 2 or 3 rows of app. 20 triangular papillae (Fig. 4c), papillae of inner row (or rows) shorter than in the marginal row; black jaw sheaths massive and serrated; upper jaw sheath with a small medial fang, lower jaw U-shaped with a broad medial notch.

The tadpoles (all Gosner stage 25) ranged from 45 mm to 74 mm total length.

Coloration in preservation. Basic color light brown, the dorsal surfaces darker; back and tail with irregular, big, dark brown spots or blotches; venter light with few or no dark speckling; tail fins beige, semitransparent with dark brown spots.

Taxonomic remarks. Morphologically and genetically tadpoles of this species were very similar to *A. laurenti* and a taxon (here termed *A.* cf. *fallax*) which genetically was intermediate between *A. fallax* and *A. laurenti* (for respective tadpole descriptions see below). The uncorrected pairwise p-difference between *A. fallax* and *A. laurenti* was 2.55%, between *A. fallax* and *A.* cf. *fallax* it was 1.85%, and between *A. laurenti* and *A.* cf. *fallax* the distance was 1.99%. Further morphological and genetically research is necessary to conform if these three lineages represent distinct species or merely are representatives of one, genetically variable species.

Astylosternus cf. *fallax* Amiet, 1978

Material examined. ZMB 82867 (GenBank MK318852), Gosner stage 25, Cameroon, foot of Mt Nlonako, Ekomtolo, 477 m, 4°49'58.46"N, 9°55'33.42"E, 24 November 2011, leg. M.F. Barej, H.C. Liedtke, N.L. Gonwouo & M. Hirschfeld.

The tadpole was caught in a forest stream. The genotyped tadpole has been compared with the two adults from Mount Nlonako, Cameroon (ZFMK 81164 and ZFMK 81608; GenBank MK318853, MK318854). The tadpole was genetically identical to these adults (compare Taxonomic remarks in the description of the *A. fallax* tadpole).

Description. Long slender tadpole with long, muscular tail (Fig. 5); body oval in dorsal view, bullet-shaped in

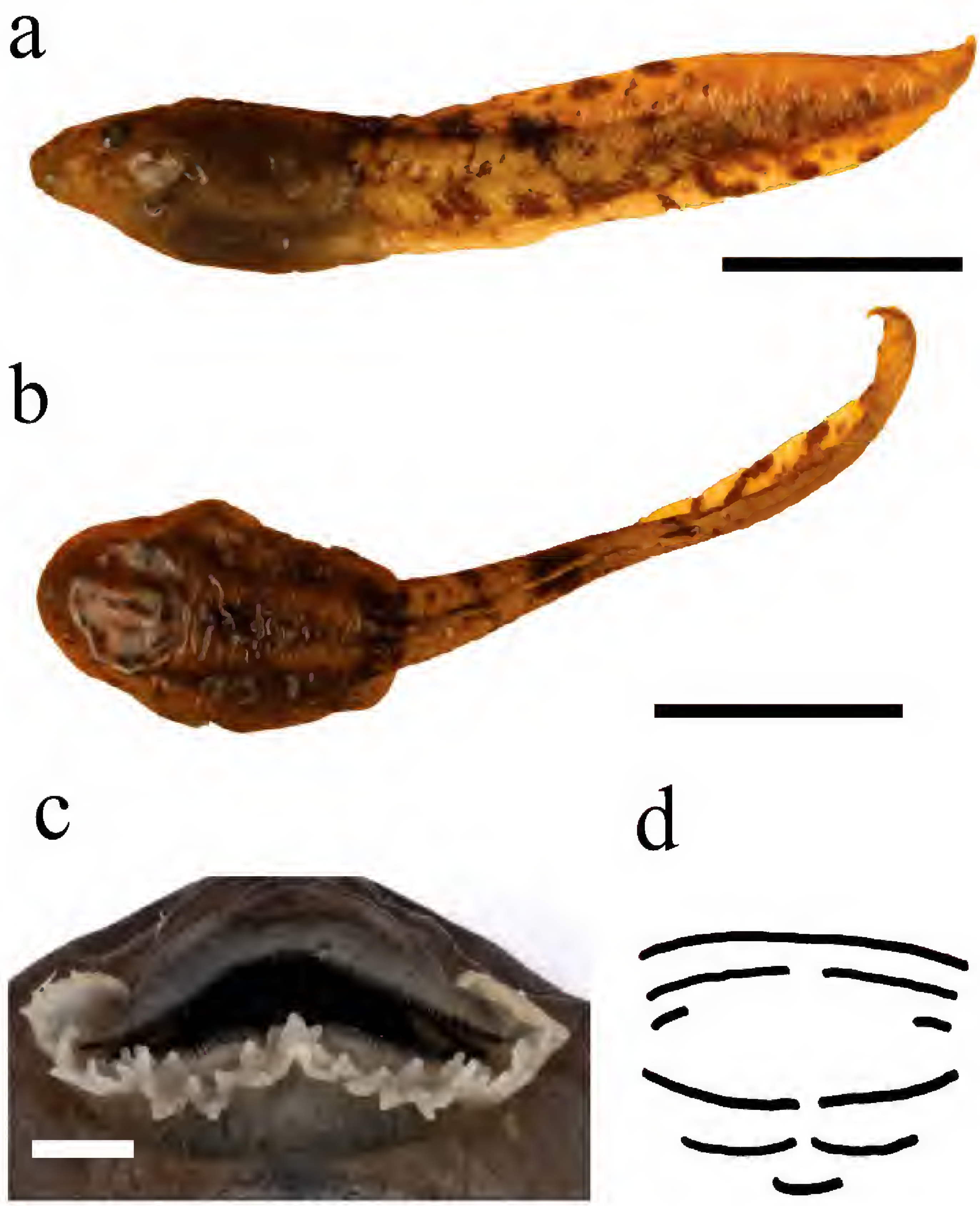

Figure 4. *Astylosternus fallax* (ZMB 82868 B; Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

lateral view; snout rounded in dorsal and lateral view; body length 31.7% of total length; body height 34.9% of body length; body width 48.4% of body length; eyes positioned dorsolaterally, eye diameter 10.7% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 86.7% of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base; ventral fin height narrower, 73.2% of dorsal fin height; highest part of tail approximately at two-thirds of the tail; body height 72.3% of maximum tail height; tail axis width 52.6% of body width; tail axis height 65.3% of maximum tail height; tail tip pointed; vent tube dextral; body with lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth positioned rostroventral, narrower than interorbital distance; keratodont formula 1:2+2+2/2+2:1; anterior lip with lateral papillae and big rostral gap; posterior lip with 2 or 3 rows of ca 20 massive papillae, papillae of marginal row are distinctly longer than of inner rows (Fig. 5c); black jaw sheaths massive and serrated; upper jaw sheath with a small medial fang, lower jaw U-shaped with a broad medial notch.

The tadpole (Gosner stage 25) measures 97.4 mm in total length.

Coloration in preservation. Basic color light brown with darker and speckled dorsal surface; venter light and grayish with few or no dark speckling; tail fins beige, semitransparent with irregular tiny dark brown spots. In life the color was of a duller, darker brown (Fig. 6).

Astylosternus laurenti Amiet, 1978

Material examined. ZMB 88353 (GenBank MK318855), 1 tadpole, Gosner stage 25, Cameroon, Korup National

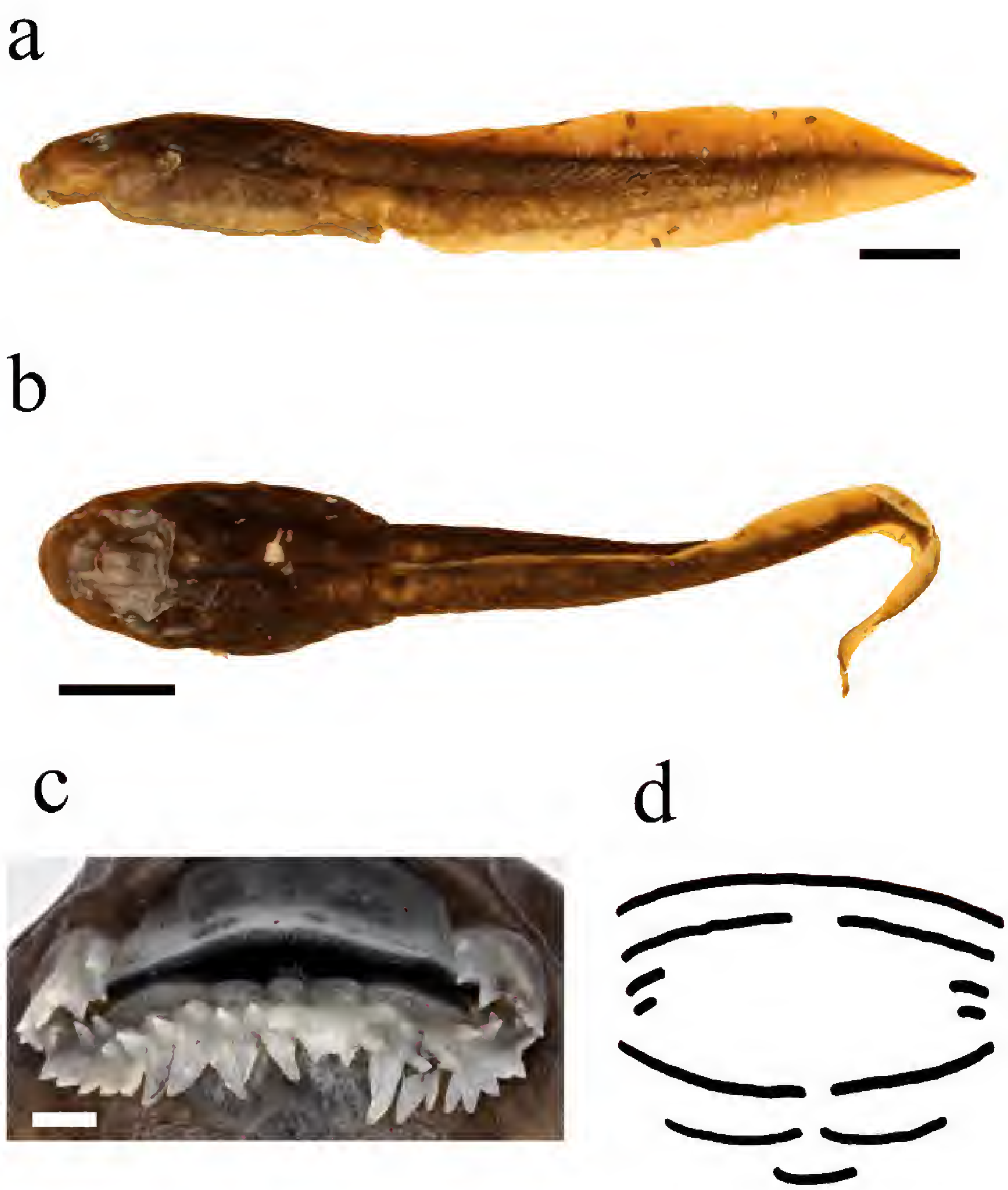

Figure 5. *Astylosternus* cf. *fallax* (ZMB 82867, Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; compare Fig. 6; black bars = 1 cm, white bar = 1 mm.

Park, Bera, 564 m, 5°21'59.57"N, 8°59'45.6"E, 22 May 2014, leg. F. Mühlberger.

The tadpole was caught in a forest stream. It was genotyped and compared with an adult from east of Ntale village, Banyang-Mbo, Cameroon (MCZ A-136785; GenBank MK318856); the uncorrected p-difference was 0.2% (1 bp) (compare Taxonomic remarks in the description of the *A. fallax* tadpole).

Description. Long slender tadpole with long, muscular tail (Fig. 7); body oval in dorsal view, bullet-shaped in lateral view; snout rounded in dorsal view, more narrowly rounded in lateral view; body length 34.2% of total length; body height 41.8% of body length; body width 54.8% of body length; eyes positioned dorsolaterally, eye diameter 13.0% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 77.1% of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base; ventral fin height narrower, measuring 72.2% of dorsal fin height; highest part of tail slightly behind the middle of the tail; body height 77.1% of maximum tail height; tail axis width 47.4% of body width; tail axis height 61.5% of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth positioned rostroventral, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with lateral papillae and big rostral gap; posterior lip with 2 or 3 rows of ca 20 triangular papillae (Fig. 7c), papillae of inner row (or rows) shorter than in the marginal row; black jaw sheaths massive and serrated; upper jaw sheath with a small medial fang, lower jaw U-shaped with a broad medial notch.

The tadpole (Gosner stage 25) measures 51.7 mm in total length.

Figure 6. *Astylosternus* cf. *fallax* in life coloration (ZMB 82867, Gosner stage 25).

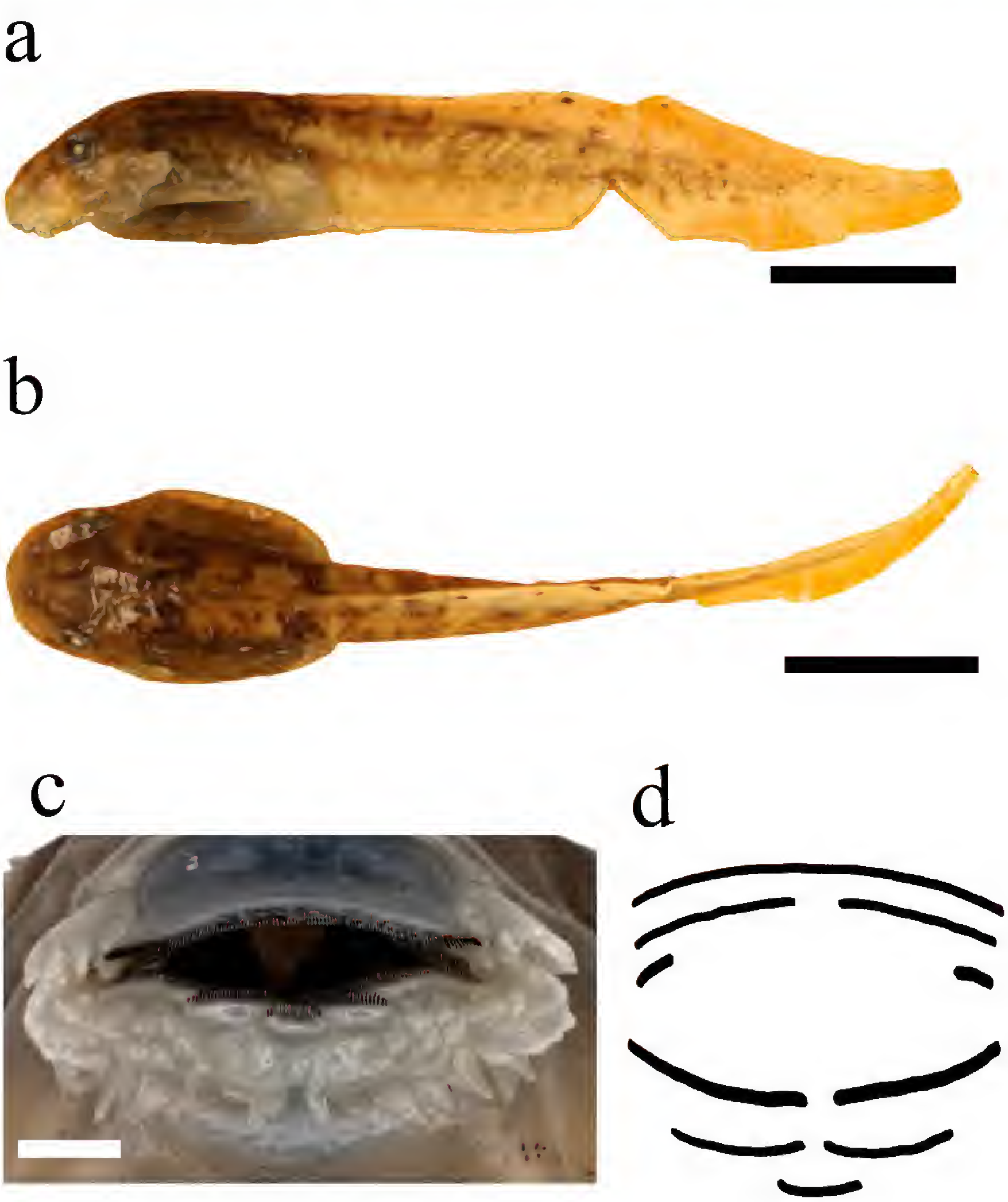

Figure 7. *Astylosternus laurenti* (ZMB 88353; Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

Coloration in preservation. Basic color light brown, the dorsal surfaces darker; back and tail axis with irregular, dark brown spotted patterns; ventral surfaces light with few or no dark speckling; tail fins beige, semitransparent with tiny dark brown spots on dorsal fin.

Astylosternus laticephalus Rödel, Hillers, Leaché, Kouamé, Ofori-Boateng, Diaz & Sandberger, 2012

Material examined. ZMB 75460 (Gosner stage 39, Ghana, Afao Hills, 531 m, 6°15'19.36"N, 2°17'37.14"W, 28 March 2007, leg. C.O. Boateng & A. Hillers). This tadpole was already assigned to *A. laticephalus* and described in Rödel et al. (2012) and in Channing et al. (2012). The tail tip is lost, so total length was taken from Rödel et al. (2012). This specimen has various preservation artifacts.

Description. Long tadpole with muscular tail; body oval in dorsal and lateral view (Fig. 8); snout broadly rounded in dorsal view, almost truncated in lateral view; body length 36.4% of total length; body height 29.5% of body length; body width 69.6% of body length; eyes positioned dorsolaterally, eye diameter 11.0% of body length; nostrils positioned dorsally, closer to snout tip than to eyes; inter-nostril distance 34.4% of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base, ventral fin narrower, 82.6% of dorsal fin height; body height around 130% of maximum tail height; tail axis width 35.4% of body width; tail axis height 65.1% of maximum tail height; vent tube dextral, body with huge lateral sacs, extending from halfway in between eye level and spiracle to end of body; short spiracle (almost impossible to see), sinistral; mouth ventral and close to snout, mouth smaller than interorbital distance; labial tooth formula 1:1+1/1+1:2, the

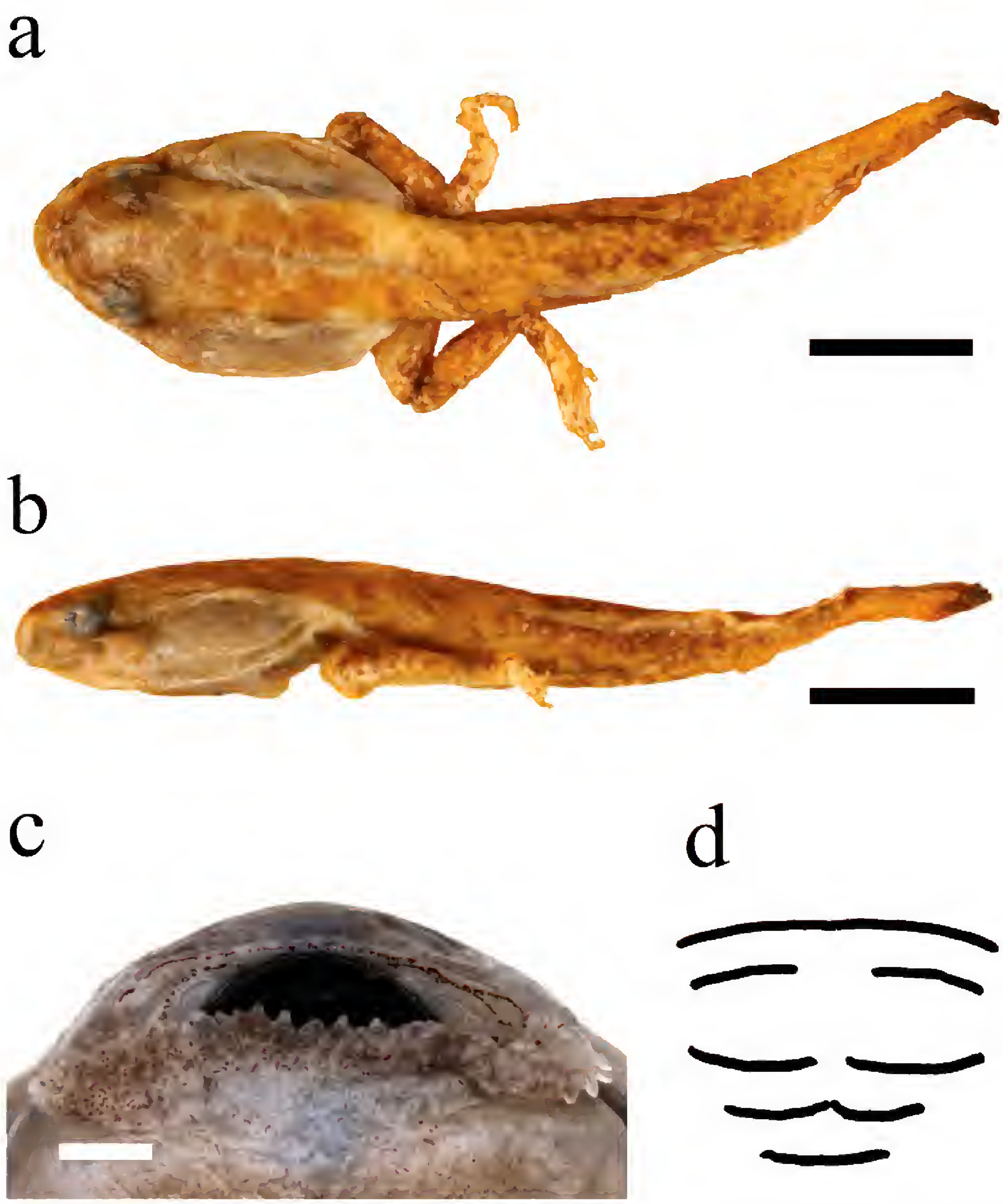

Figure 8. *Astylosternus laticephalus* (ZMB 75460, Gosner stage 39); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

first pair rows in the lower lip are very close to each other (Rödel et al. 2012 interpreted this as being 1:1+1/3); anterior lip with lateral papillae and large rostral gap; posterior lip with 1 or 2 rows of small, uniformly rounded papillae (Fig. 8c), which are as long as they are wide; black, massive, serrated jaws; upper jaw broadly arched with a small medial fang, lower jaw broadly V-shaped.

The maximum size of *A. laticephalus* tadpoles is estimated to be around 60–70 mm. The total length of ZMB 75460 is 62.1 mm.

Coloration in preservation. General color light brown or beige, with irregular small brown spots covering body and tail; ventral surfaces of body more grayish, dark speckling almost absent; tail tip darker.

Astylosternus montanus Amiet, 1978

Material examined. ZMB 82871 (GenBank MK318857), 2 tadpoles, Gosner stage 28 (A) and stage 25 (B), Cameroon, Mt Manengouba, 1290 m, 4°58'23.76"N, 9°52'31.8"E, 21 November 2010, leg. M. Hirschfeld; ZMB 82872, Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1365 m, 5°0'33"N, 9°46'30"E, 14 December 2010, leg. M. Hirschfeld; ZMB 82873, 2 tadpoles, Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.5"N, 9°46'5.82"E, 16 December 2010, leg. M. Hirschfeld; ZMB 82874 (GenBank MK318860), 2 tadpoles, Gosner stage 35, Cameroon, Mt Manengouba, Ebonemin, 1417 m, 5°1'27.6"N, 9°45'53.2"E, 15 August 2011, leg. M. Hirschfeld; ZMB 82875 (GenBank MK318861), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1356 m, 5°1'33.4"N, 9°45'46.7"E, 16 August 2011, leg. M. Hirschfeld; ZMB 82876 (GenBank MK318862), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.5"N, 9°46'5.8"E, 7 October 2011, leg. M. Hirschfeld.

All tadpoles were caught in small to medium-sized streams. The description is mainly based on ZMB 82875. The genotyped tadpoles have been compared with an adult from Mount Rata, Rumpi Hills, Cameroon (MHNG 2715.35; GenBank MK318863). The uncorrected pairwise p-difference between tadpoles and between tadpoles and the adult ranged from 0.20–0.71% (1–4 bp).

Description. Robust tadpole with long muscular tail (Fig. 9); body bullet-shaped in dorsal view, more oval in lateral view; back with a longitudinal medial depression; snout broadly rounded in dorsal view, more narrowly rounded in lateral view; body length 33.3 ± 1.0% of total length; body height 43.8 ± 4.5% of body length; body width 55.8 ± 5.0% of body length; eyes positioned dorsolaterally, eye diameter 10.5 ± 0.8% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 81.8 ± 11.5% of interorbital distance; tail fins narrow; ventral fin originating from tail base, dorsal fin slightly behind, ventral fin height 70.7 ± 6.8% of dorsal fin height; highest part of tail at about middle of tail length; body height 104.6 ± 12.2% of maximum tail height; tail axis width 47.9 ± 9.3% of body width; tail axis height 70.2 ± 10.2% of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, close to snout, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with large rostral gap, only few small papillae anterior to angles of mouth; posterior lip with two rows of around 30 triangular papillae, slightly longer than wide with rounded tips (Fig. 9c); black, massive, serrated jaw sheaths; upper jaw arched with a small medial projection (fang), lower jaw V-shaped.

The largest tadpole in Gosner stage 25 has a body length of 22.5 mm; the longest one (Gosner stage 28) had a total length of 73.2 mm.

Coloration in preservation. Basic color brownish, dorsal surfaces darker than ventral ones, turning into yellow, tail lighter brown; tail axis with few dark speckles; tail fins very light brown, semitransparent and with a longitudinal row of small spots on the margin of dorsal fin.

Taxonomic remarks. As in *A. batesi* and *A. fallax*, we have molecular evidence for cryptic diversity in *A. montanus*. Apart from the above listed material, we had access to further samples which represented an additional genetic lineage. The distances between the two clades reached an uncorrected pairwise distance of 2.5%.

Astylosternus occidentalis Parker, 1931

Material examined. ZMB 77317, 2 tadpoles, Gosner stage 25, Guinea, Déré, 419 m, 7°36'20.0"N, 8°15'36.5"W, 7 August 2010, leg. M. Hirschfeld; ZMB 77440, Gosner stage 25, Guinea, Ziama, 664 m, 8°23'99.3"N, 9°17'13.7"W, leg. M. Hirschfeld; ZMB 77438, Gosner stage 26, Guinea, Fouta Djallon, Chûte Saala, 939 m, 11°17'26.2"N, 12°29'58.0"W, July 2010, leg. C. Brede & J. Doumbia; ZMB 77439, Gosner stage 25, Guinea, Fouta Djallon, Chûte Dintin, 760 m, 10°49'13.1"N, 12°11'30.7"W, 24 July 2010, leg. C. Brede & J. Doumbia; ZMB 75368 2 tadpoles, Gosner stage 41 (A) and 37 (B), Sierra Leone, Gola North, leg. J. van der Winden; ZMB 37564, Gosner stage 26, Guinea, Mt Nimba, leg. M. Lamotte.

The description is mainly based on the two tadpoles accessioned as ZMB 77317. These and ZMB 77440 have been already described by Rödel et al. (2012), who also provide genetic sequences for specimens across the entire range of the species.

Description. Long slender tadpole with strong, muscular tail (Fig. 10); body oval in dorsal and lateral view; snout broadly rounded in dorsal view, more narrowly rounded in lateral view; body length 31.1 ± 2.8% of total length;

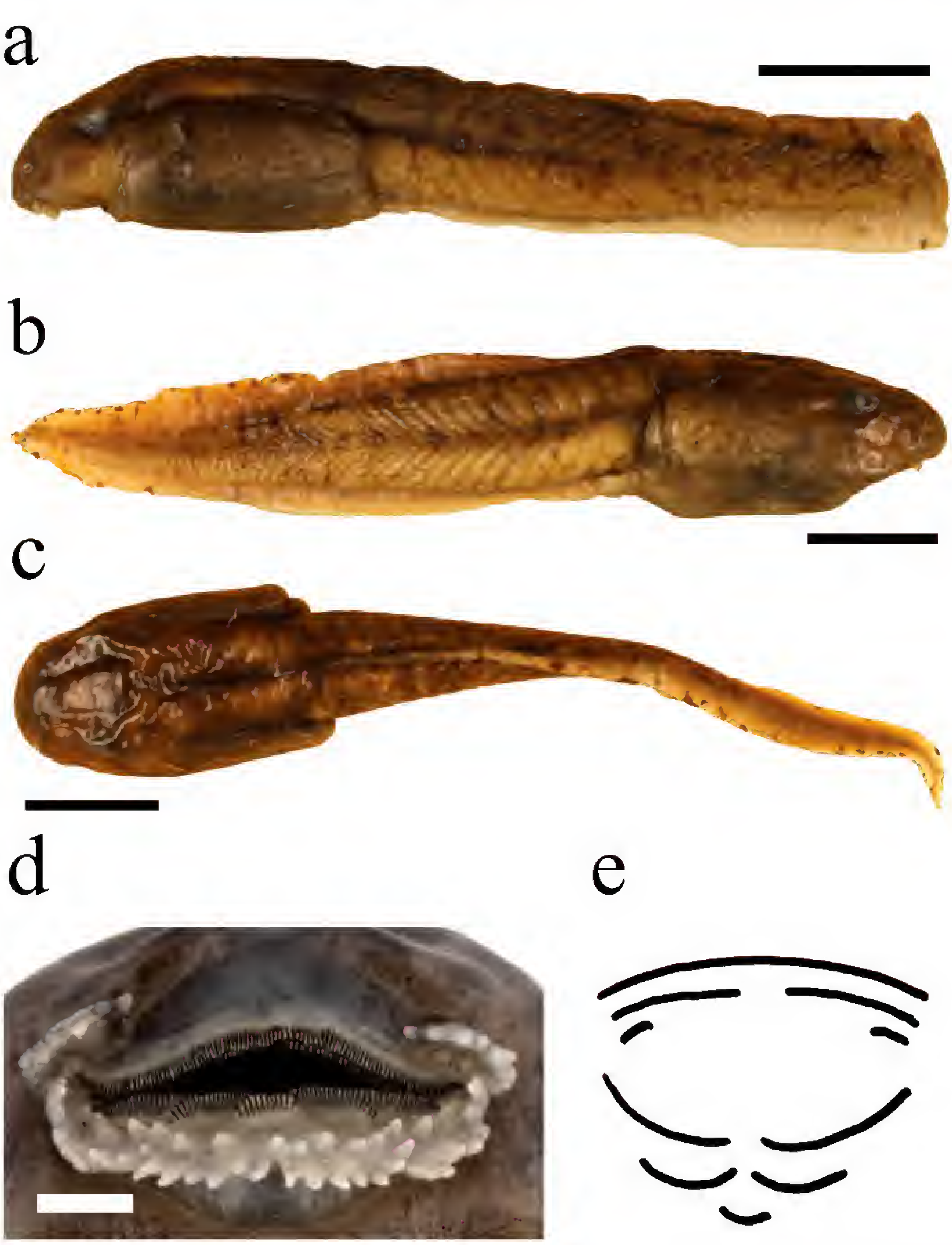

Figure 9. *Astylosternus montanus* tadpoles, **a, c, d** ZMB 82875 (Gosner stage 25), and **b** ZMB 82871 (Gosner stage 28); **a–b** lateral, and **c** dorsal view; **d** oral disc; **e** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

body height 40.2 ± 2.2% of body length; body width 56.1 ± 4.9% of body length; eyes positioned dorsolaterally, eye diameter 11.5 ± 2.3% of body length; nostrils positioned dorsally, closer to snout tip than to eyes; inter-nostril distance 62.2 ± 2.7% of interorbital distance; tail fins narrow; ventral fin originating from tail base, dorsal fin insertion a bit posterior to tail base; ventral fin height 71.6 ± 13.7% of dorsal fin height; highest part of tail approximately in the middle of the tail; body height 84.8 ± 9.4% of maximum tail height; tail axis width 53.1 ± 8.6% of body width; tail axis height 71.9 ± 14.2% of maximum tail height; tail tip broadly pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, very close to snout, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with a few lateral papillae and large rostral gap; posterior lip with 2–3 rows of about 30 short and triangular papillae (Fig. 10c); papillae of inner row smaller than those of marginal row; black, massive, serrated jaw sheaths; upper jaw broadly arched with a small medial projection (fang), lower jaw narrowly U-shaped.

The largest tadpole in Gosner stage 25 measured 95.9 mm total length. Gosner stage 41 tadpole measured 77.5 mm. Tadpoles with more than 10 cm total length have been caught (Guibé and Lamotte 1958b; MOR unpubl. data).

Coloration in preservation. Body more or less uniform dark brown; ventral lighter, slightly grayish; tail fin margins are missing dark pigmentation; last third of tail darker to almost black (Fig. 10). In life, ventral surfaces grayish; lateral and dorsal parts, as well as tail, with a small but very dense yellow and brown speckling (Fig. 11). This pattern progressively becomes denser and darker towards tail tip.

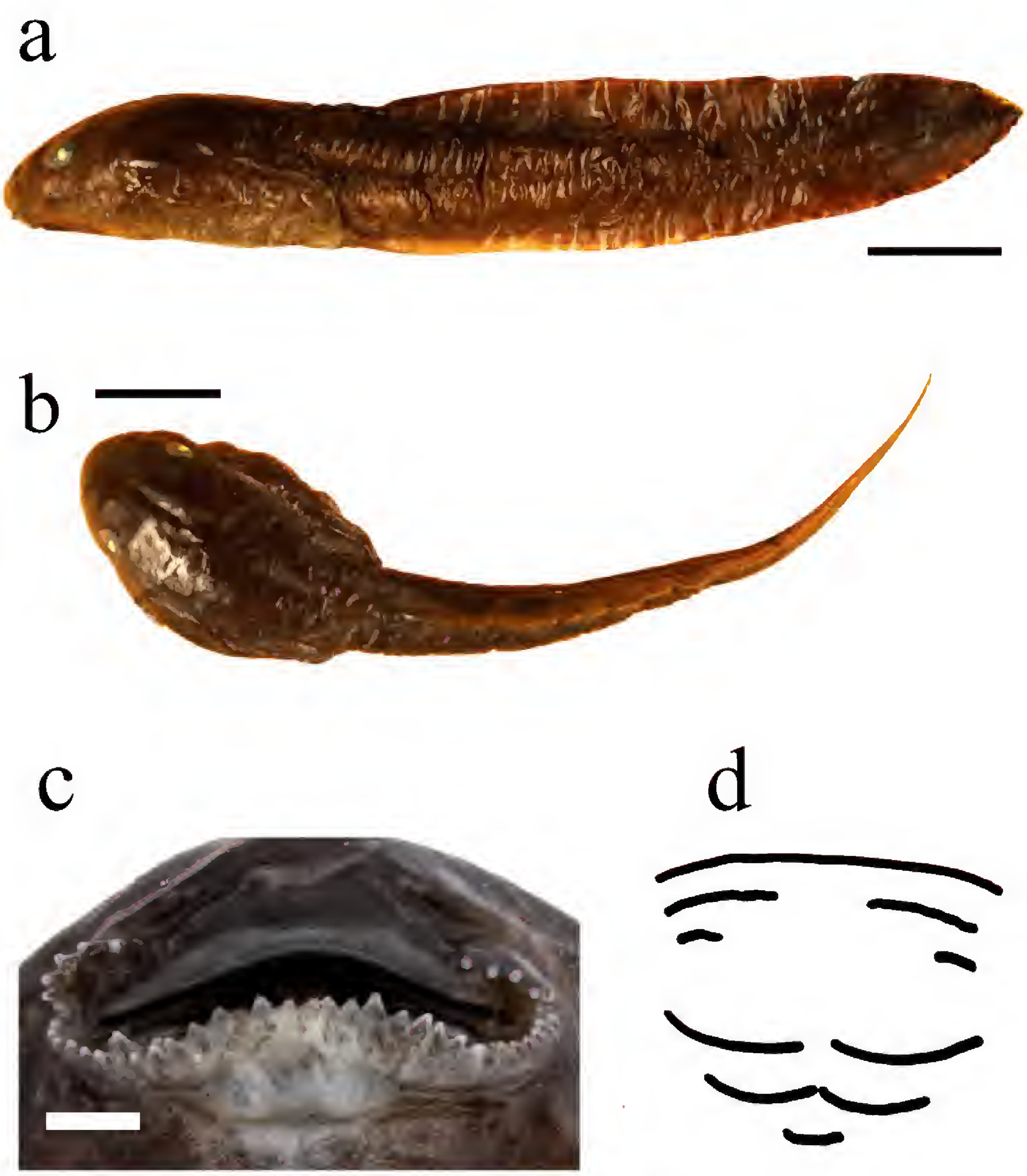

Figure 10. *Astylosternus occidentalis* tadpole, ZMB 77317A (Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

Variation. ZMB 75368 (Gosner stage 41) is very light brown in comparison to other specimens. According to Lamotte (1985), tooth row P2 is continuous and not divided, thus tooth row formula would be 1:2+2/1+1:2. According to Lamotte, the body is almost evenly pigmented, with lighter lateral sacs and lightly speckled tail. The tadpole of this species was first described by Lamotte and Zuber-Vogeli (1954) as *A. diademamus.* Parker (1936) mentioned *A. occidentalis* tadpoles from Liberia. More recent descriptions have been published by Channing et al. (2012) and Rödel et al. (2012).

Astylosternus perreti Amiet, 1978

Material examined. ZMB 82877 (GenBank MK318864), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1365 m, 5°0'33"N, 9°46'30"E, 14 December 2010, leg. M. Hirschfeld; ZMB 82879 (GenBank MK318865), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.5"N, 9°46'5.82"E, 16 December 2010, leg. M. Hirschfeld; ZMB 82880 (GenBank MK318866), Gosner stage 25, Cameroon, Mt Manengouba, near Pastoral Nkongsamba, 1457 m, 4°59'13.26"N, 9°52'45.9"E, 18 January 2011, leg. M. Hirschfeld & F. Grözinger; ZMB 82881 (GenBank MK318867), 2 tadpoles, 1 genotyped, both Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1356 m, 5°1'33.4"N, 9°45'46.7"E, 16 August 2011, leg. M. Hirschfeld; ZMB 82882 (GenBank MK318868), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.45"N, 9°46'5.82"E, 7 October 2011, leg. M. Hirschfeld; ZMB 82883 (GenBank MK318869), 2 tadpoles, 1 genotyped, both Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.5"N,

Figure 11. Life coloration of an *Astylosternus occidentalis* tadpole (ZMB 88550, Gosner stage 25), Foya forest, Liberia, 96.9 mm total length.

9°46'5.8"E, 7 October 2011, leg. M. Hirschfeld; ZMB 82884A, Gosner stage 28, ZMB 82884B (GenBank MK318870), Gosner stage 27, Cameroon, Mt Manengouba, Ebonemin, 1342 m, 5°0'46.5"N, 9°46'30.9"E, 8 October 2011, leg. M. Hirschfeld; ZMB 82816 (GenBank MK318871), Gosner stage 26, Cameroon, Mt Manengouba, Ebonemin, 1356 m, 5°1'33.42"N, 9°45'46.74"E, 13 December 2010, leg. M. Hirschfeld.

All tadpoles were caught in small to medium-sized streams and rivers in secondary and very degraded forests. The description is mainly based on ZMB 82881B and ZMB 82884B. Genotyped tadpoles have been compared with an adult from Mount Kupe, Cameroon (MHNG 2715.38; GenBank MK318872). The uncorrected pairwise p-difference between tadpoles and between tadpoles and the adult ranged from 0–0.4% (0–2 bp).

Description. Long slender tadpole with strong and muscular tail (Fig. 12); longish oval in dorsal view, slightly flatter in lateral view; back with medial, longitudinal depression; snout broadly rounded in dorsal view, more narrowly rounded in lateral view; body length 31.2 ± 2.2% of total length; body height 43.4 ± 4.5% of body length; body width 54.7 ± 5.9% of body length; eyes positioned dorsolaterally, eye diameter 12.0 ± 1.5% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 87.7 ± 5.1% of interorbital distance; tail fins narrow; dorsal and ventral fin originating from tail base; ventral fin height 79.9 ± 6.8% of dorsal fin height; highest part of tail approximately in the middle of the tail; body height 98.8 ± 11.2% of maximum tail height; tail axis width 48.5 ± 10.3% of body width; tail axis height 72.3 ± 7.3% of maximum tail height; tail tip very narrow, filamentous; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout and narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with only a few lateral papillae and large rostral gap; posterior lip with 2 or 3 rows of ca 20–30 small, broadly triangular (shark tooth-shaped) papillae (Fig. 12c), medial papillae bigger than lateral ones; black, massive, serrated jaw sheaths; upper jaw broadly arched with a small medial projection (fang), lower jaw narrow U- to V-shaped.

The largest tadpole in Gosner stage 25 measured 26.2 mm body length and had an approximate total length of 78 mm. The most advanced specimen at Gosner stage 28 had a total length of 108.1 mm.

Coloration in preservation. Body dark brown; tail very light brown to beige; lateral sacs and ventrum lighter brown or dark gray; a broad dark brown longitudinal band on tail axis reaching about middle to two-thirds of tail length, proximate end of tail with smaller dark speckles; fins light yellowish beige (Fig. 12). In life body and tail light brown with black blotches on back and broad black bands and spots on tail axis; lateral sacks light grayish brown; tail fins transparent greyish brown (Fig. 13).

Variation. In larger specimens (Fig. 12b, c) the dark pattern on body and tail axis seems to fade, base color becomes darker. Size and arrangement of dark marks differ between specimens (Figs 12b, c, 13).

Taxonomic remarks. Whereas all genotyped tadpoles and the comparative adult were genetically almost identical, a single specimen (MHNG 2715.40 from Mofako Balue, Rumpi Hills) differed genetically by about 2%, indicating intraspecific genetic variability or cryptic diversity. The tadpoles used for the description are from the area of the type locality (Mouandong) of *A. perreti*.

Astylosternus ranoides Amiet, 1978

Material examined. ZMB 82823 (GenBank MK318873), Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2135 m, 5°0'35.4"N, 9°51'24.8"E, 7 August 2011, leg. M. Hirschfeld.

The tadpole was caught in a medium-sized river within a heavily degraded forest fragment. The tail tip had been taken as tissue sample; the continuation of the tail tip was thus reconstructed based on the generalized tail shape of the genus, and total length estimated (compare Fig. 14a).

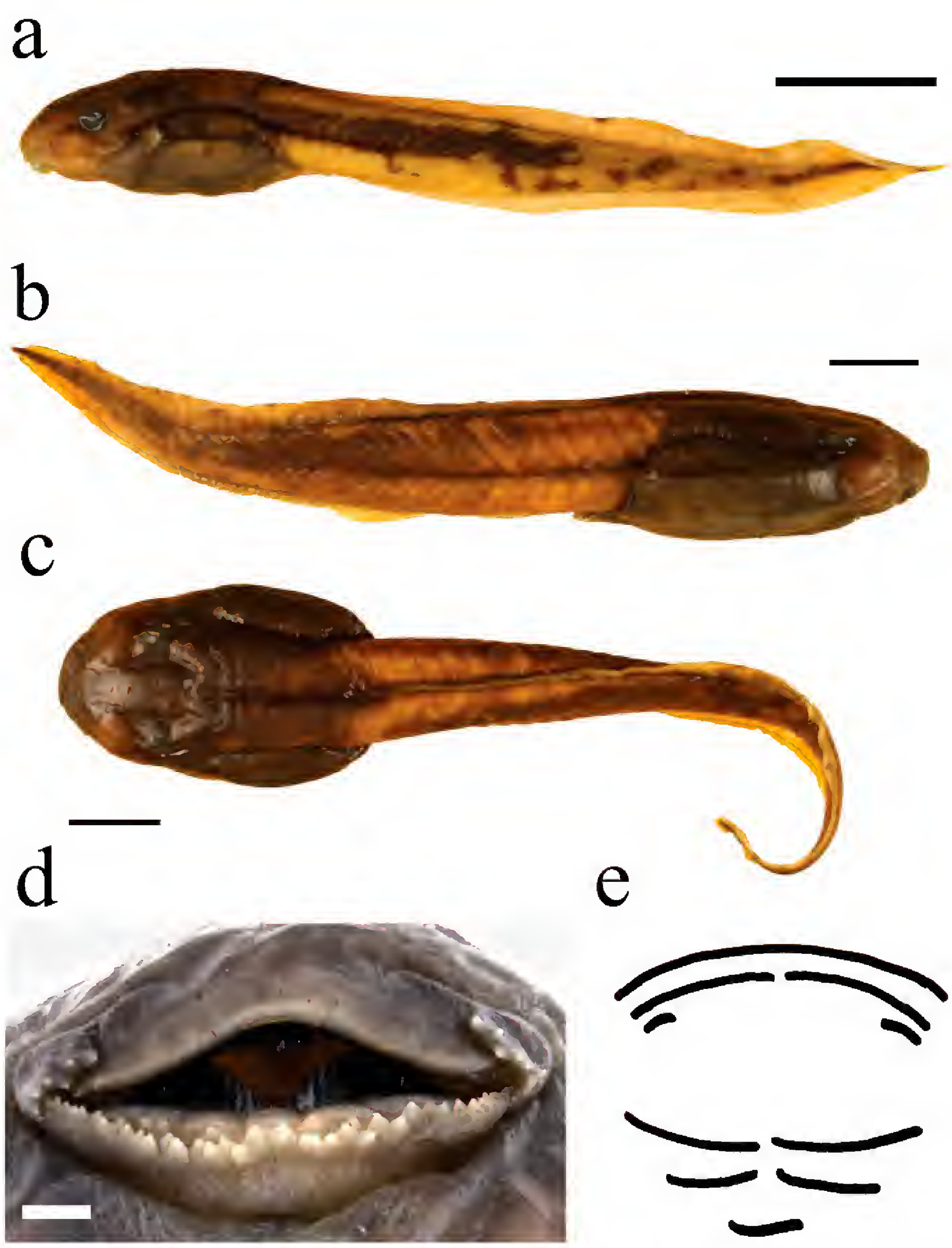

Figure 12. *Astylosternus perreti* tadpoles, **a** ZMB 82881 (Gosner stage 25), and **b–d** ZMB 82884A (Gosner stage 28); **a–b** lateral view; **c** dorsal view; **d** oral disc; **e** sketch of keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

Figure 13. Life coloration of an *Astylosternus perreti* tadpole from Mount Manengouba, Cameroon (ZMB 82816, Gosner stage 25–27).

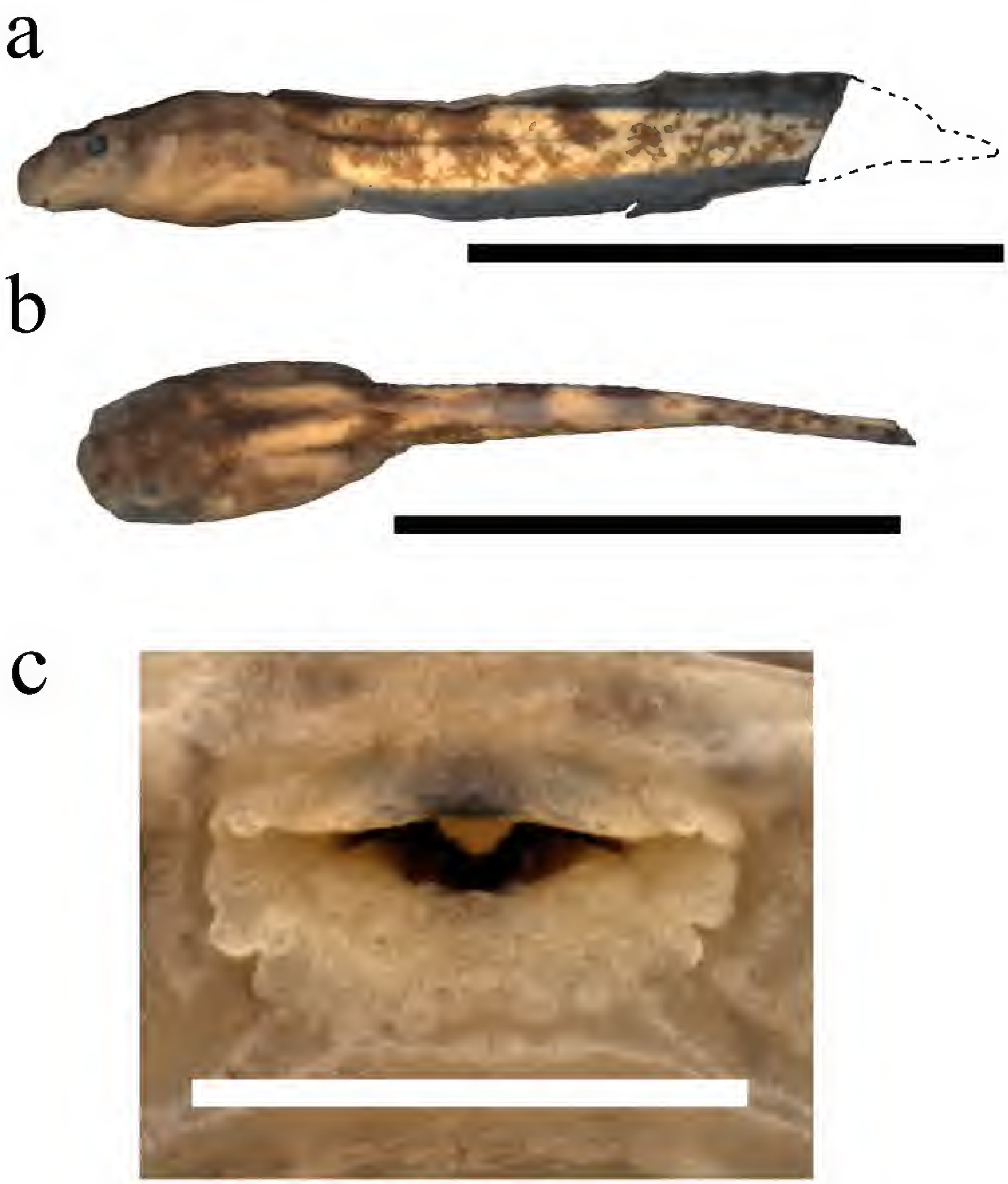

Figure 14. *Astylosternus ranoides* tadpole, ZMB 82823 (Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; the black color of the fins on the figure is due to the black background, the fins are light grey and transparent with little dark patterning; black bars = 1 cm, white bar = 1 mm.

The tadpole's sequence has been compared with an adult from Kodmin, Cameroon (ZFMK 67364; GenBank MK318874). The two sequences were identical.

Description. Long slender tadpole with narrow, muscular tail (Fig. 14); body longish oval in dorsal view, more flattened in lateral view; snout broadly rounded in dorsal view, almost truncate in lateral view; body length 34.1% of total length; body height 45.2% of body length; body width 58.1% of body length; eyes positioned dorsolaterally, eye diameter 9.6% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 83.3% of interorbital distance; tail fins narrow; dorsal and ventral fin originating at tail base; ventral fin height 81.8% of dorsal fin height; highest part of tail approximately in the last third of the tail; body height 82.4% of maximum tail height; tail axis width 33.3% of body width; tail axis height 61.8% of maximum tail height; exact form of tail tip unknown; vent tube dextral; body with lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout tip, narrower than interorbital distance; no keratodonts; anterior lip with large rostral gap, only two papillae on each side, close to angles of jaw; posterior lip with about 15 short roundish papillae (Fig. 14c); massive black, serrated jaws, both more or less U-shaped.

Total length of this tadpole was estimated to be about 18 mm (Fig. 14a). The absence of keratodonts implies that the tadpole is in a very early stage of development.

Coloration in preservation. Body light brown to beige, slightly speckled; tail axis yellowish with large dark brown blotches; tail fins with dark patterning, but predominately transparent (in Fig. 14a the background was black).

Astylosternus rheophilus Amiet, 1978

Material examined. ZMB 82885 (GenBank MK318875), Gosner stage 25, ZMB 82886 (GenBank MK318876), Gosner stage 39 and ZMB 82886A, Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2114 m, 5°0'51.78"N, 9°49'24.24"E, 8 November 2010, leg. M. Hirschfeld; ZMB 82887 (GenBank MK318877) and ZMB 82887A, Gosner stage 36, Cameroon, Mt Manengouba, Pola, 1719 m, 5°3'27.96"N, 9°49'39"E, 2 December 2010, leg. M. Hirschfeld; ZMB 82888 (GenBank MK318878), Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 2088 m, 5°2'7.6"N, 9°50'46.8"E, 3 August 2011, leg. M. Hirschfeld; ZMB 82889 (GenBank MK318879) and ZMB 82889A, Gosner stage 26, Cameroon, Mt Manengouba, near Abdou, 5°2'13"N, 9°51'24.5"E, 4 August 2011, leg. M. Hirschfeld; ZMB 82890 (GenBank MK318880), Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2100 m, 5°1'4.6"N, 9°51'54.9"E, 5 August 2011, leg. M. Hirschfeld; ZMB 82891 (GenBank MK318881), Gosner stage 25, Cameroon, Mt Manengouba, near Caldera, 1889 m, 5°2'26.2"N, 9°48'30"E, 6 August 2011, leg. M. Hirschfeld; ZMB 82892 (GenBank MK318882), Gosner stage 25, Cameroon, Mt Manengouba, Pola, 1788 m, 5°3'26.6"N, 9°50'10.2"E, 2 September 2011, leg. M. Hirschfeld; ZMB 82893 (GenBank MK318883), Gosner stage 25, Cameroon, Mt Manengouba, Pola, 1719 m, 5°3'27.9"N, 9°49'39"E, 6 September 2011, leg. M. Hirschfeld; ZMB 82894 (GenBank MK318884), Gosner stage 25, Cameroon, Mt Manengouba, Nkikok, 1328 m, 5°5'34.5"N, 9°49'3.8"E, 8 September 2011, leg. M. Hirschfeld; ZMB 82895 (GenBank MK318885) and ZMB 82895A, Gosner stage 25, Cameroon, Mt Manengouba, M'Bouroukou, 1518 m, 5°3'48.2"N, 9°52'0.1"E, 22 September 2011, leg. M. Hirschfeld; ZMB 82896 (GenBank MK318886), Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 2042 m, 5°2'26.3"N, 9°51'18.9"E, 23 September 2011, leg. M. Hirschfeld; ZMB 82897 (GenBank MK318887) and ZMB 82897A, Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 1992 m, 5°2'13"N, 9°51'24.5"E, 24 September 2011, leg. M. Hirschfeld; ZMB 82898 (GenBank MK318888), Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 2088 m, 5°2'7.6"N, 9°50'46.8"E, 25 September 20011, leg. M. Hirschfeld; ZMB 82899 (GenBank MK318889), Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2135 m, 5°0'35.4"N, 9°51'24.8"E, 28 September 2011, leg. M. Hirschfeld; ZMB 82900 (GenBank MK318890), Gosner stage 25, Cameroon, Mt Manengouba, Nkack, 1466 m, 5°2'17.4"N, 9°46'27.3"E, 13 October 2011, leg. M. Hirschfeld; ZMB 82901 (GenBank MK318891), Gosner stage 27, ZMB 82901A, Gosner stage 26, ZMB 82901B, Gosner stage 25, Cameroon, Mt Manengouba, near Caldera, 1889 m, 5°2'26.2"N, 9°48'30"E, 17 October 2011, leg. M. Hirschfeld; ZMB 82902 (GenBank MK318892), Gosner stage 25, Cameroon, Mt Manengouba, Pola, 1788 m, 5°3'26.6"N, 9°50'10.2"E, 20 October 2011, leg. M. Hirschfeld; ZMB 82828 (GenBank MK318893), Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 2012 m, 5°2'24"N, 9°51'39.3"E, 26 September 2011, leg. M. Hirschfeld; ZMB 79241, Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2042 m, 5°2'26.3"N, 9°51'18.9"E, 4 August 2011, leg. M. Hirschfeld.

All tadpoles were collected from streams in gallery forest and very degraded forest fragments. The description is mainly based on ZMB 82892 and ZMB 82901. The genotyped tadpoles have been compared with an adult from the Tchabal Mbabo, Cameroon (ZFMK 75632; GenBank MK318894). The uncorrected pairwise p-difference between tadpoles and between tadpoles and the adult ranged from 0–0.2% (0–1 bp).

Description. Long robust tadpole with almost parallel flanks and long, muscular tail (Fig. 15); body bullet-shaped in dorsal view, oval but slightly flattened in lateral view; back with a longitudinal medial depression; snout rounded in dorsal view, more narrowly rounded in lateral view; body length 32.8 ± 1.7% of total length; body height 42.2 ± 4.5% of body length; body width 55.3 ± 5.5% of body length; eyes positioned dorsolaterally, eye diameter 10.8 ± 1.0% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 82.8 ± 5.5% of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base; ventral fin height 79.9 ± 6.8% of dorsal fin height; highest part of tail approximately in the middle of the tail; body height 98.4 ± 9.6% of maximum tail height; tail axis width 46.5 ± 6.9% of body width; tail axis height 71.2 ± 9.9% of maximum tail height; tail tip narrow and pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout, in almost terminal position, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with large rostral gap, short, round papillae restricted to corner of mouth; posterior lip with 2 or 3 rows of about 20–30 uniform, slender, triangular papillae; massive, black and serrated jaws, upper jaw arched with a big medial fang, lower jaw narrowly V-shaped, without visible notch.

The largest specimen at Gosner stage 25, as well as the largest specimen at Gosner stage 36, were the two largest tadpoles in our samples, both reaching about 80 mm total length.

Coloration in preservation. Body light to dark brown, lateral sacs and ventral surfaces lighter, more grayish; fine brown speckling on tail axis, fading from dorsal to ventral parts; fins largely beige transparent, with tiny brown dots along the margin of the last third of dorsal and ventral fin.

Variation. Except the large size range of tadpoles all in Gosner stage 25, tadpoles were very uniform in color-

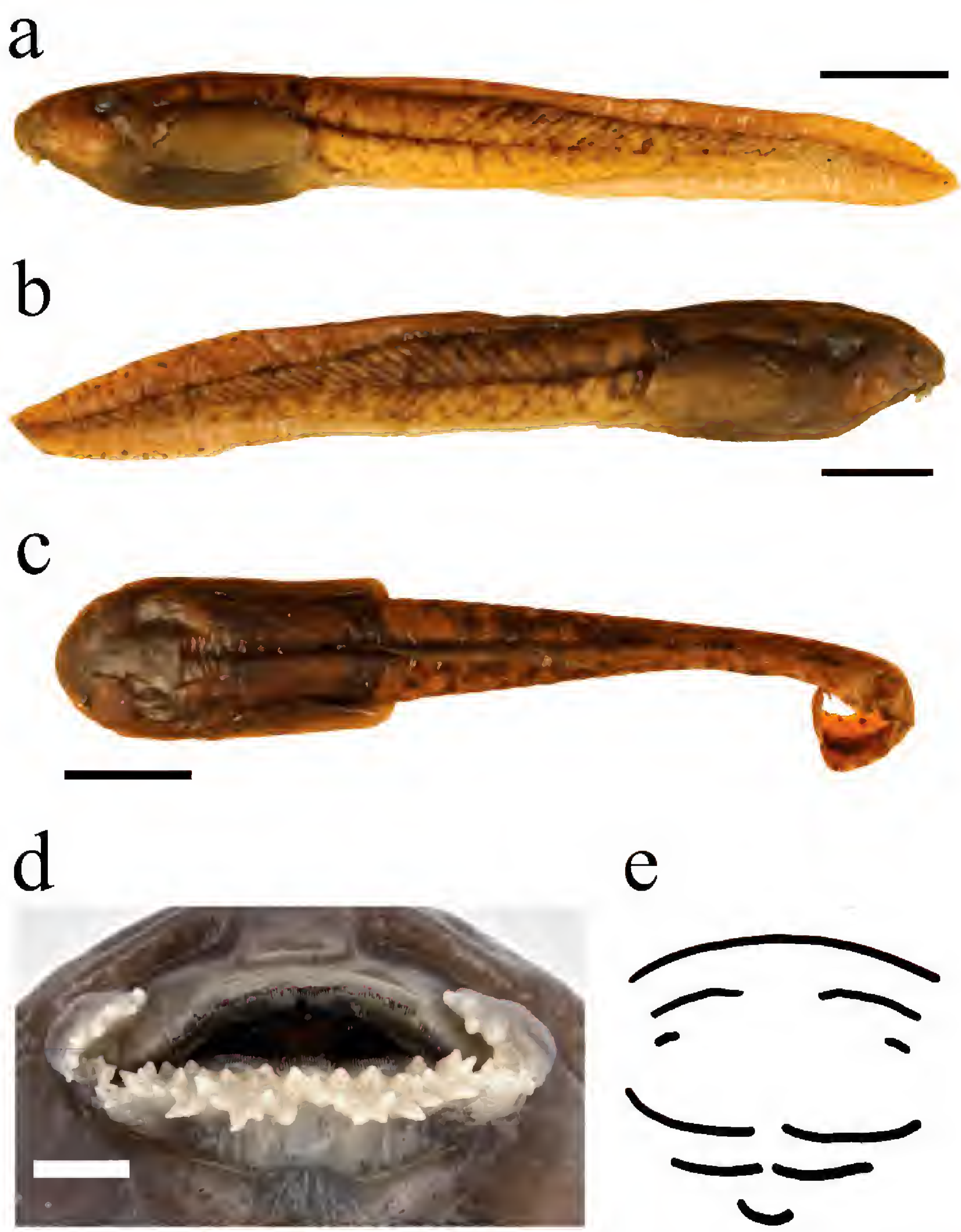

Figure 15. *Astylosternus rheophilus* tadpoles; **a** ZMB 82901A, Gosner stage 26 and **b–d** ZMB 82892, Gosner stage 25; **a–b** lateral, and **c** dorsal view; **d** oral disc; **e** sketch of keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

ation, body and mouth part proportions and characteristics. The tadpole of *A. rheophilus* was already described by Channing et al. (2012). These authors give an additional keratodont formula as 1:2+2/1:1+1:1.

Nyctibates corrugatus Boulenger, 1904

Material examined. ZMB 82109, Gosner stage 25, Cameroon, Mt Kala, near Kala village, 848 m, 3°50'31.86"N, 11°21'4.32"E, 9 November 2015, leg. M.F. Barej, H.C. Liedtke & L.N Gonwouo; ZMB 82112, Gosner stage 25, Cameroon, Ebo Forest, Njuma, 311 m, 4°21'55.68"N, 10°25'18.48"E, 6 October 2011, leg. M. Dahmen; ZMB 82115, Gosner stage 26, Cameroon, Ebo Forest, Njuma, 255 m, 4°20'51.06"N, 10°13'35.04"E, 27 September 2010, leg. M. Hirschfeld & M.-O. Rödel; ZMB 82116, Gosner stage 25, Cameroon, Ebo Forest, Bekop, 825 m, 4°21'55.68"N, 10°25'18.48"E, 10 January 2011, leg. M. Hirschfeld & F. Grözinger; ZMB 88351 (GenBank MK318904), Gosner stage 25, Cameroon, Korup National Park, Esukutan, 422 m, 5°22'24.81"N, 8°59'51.35"E, 20 May 2014, leg. F. Mühlberger).

All tadpoles were collected from small to medium-sized forest streams. The description is mainly based on ZMB 82112 and ZMB 82115. The latter specimen was the bases of the description by Channing et al. (2012). The *N. corrugatus* tadpole was first described by Amiet (1971). The genotyped tadpole has been compared with an adult from the vicinity of Ediensoa, Cameroon (GenBank DQ283361). The two sequences were identical.

Description. Very long and robust, but still slender tadpole with strong, muscular tail (Fig. 16); body oblong

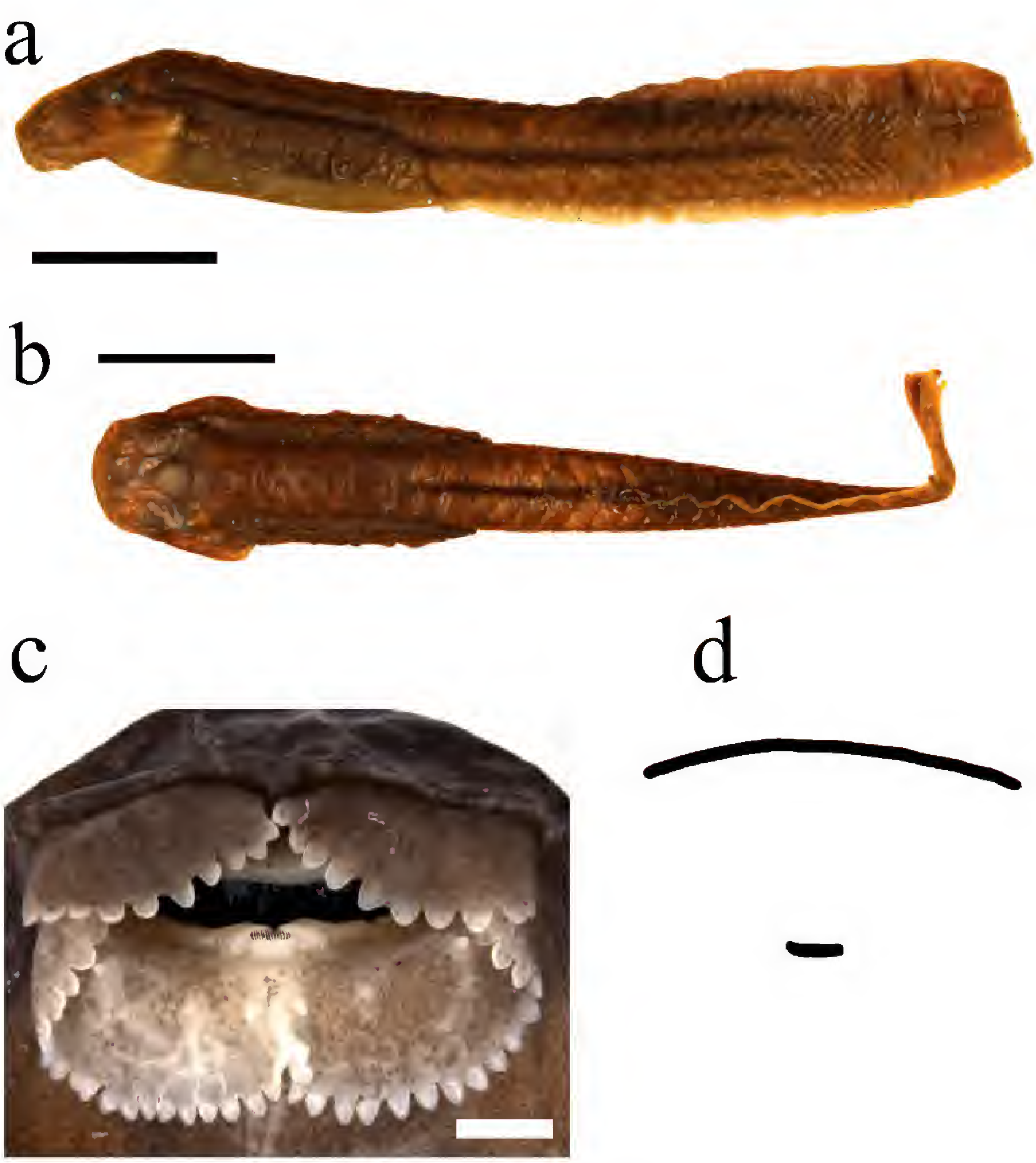

Figure 16. *Nyctibates corrugatus* tadpole (ZMB 82112, Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; the downward bent head (**a**) is a preservation artifact; black bars = 1 cm, white bar = 1 mm.

oval to almost rectangular in dorsal view (Fig. 16b shows some artificial shrinking), flattened and elongated in lateral view, belly region fatter than head; snout rounded in dorsal view, more narrowly rounded in lateral view; body length 38.0 ± 1.3% of total length; body height 29.0 ± 3.5% of body length; body width 39.5 ± 0.7% of body length; eyes positioned dorsolaterally, eye diameter 6.4 ± 0.9% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 83.4 ± 4.9% of interorbital distance; tail fins narrow, ventral fin originating from tail base, dorsal fin originates at about first third of the tail; ventral fin height 76.5 ± 3.3%, than dorsal fin height; highest part of tail in the last third; body height 81.8 ± 8.3% of maximum tail height; tail axis width 53.4 ± 2.9% of body width; tail axis height 62.3 ± 6.8% of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral air sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout and narrower than interorbital distance; labial tooth formula 1/1; anterior labium consists of two semicircular lobes, the edges carrying a row of short round marginal papillae, the gap between the two lobes very small; posterior labium a wide, flat lobe, carrying one row of about 20–30 uniform, short round marginal papillae, a few further, widely spaced small, wart-like papillae are arranged in one transversal row across the labium; heavily serrated, black jaws; upper jaw broadly arched with a medial fang, lower jaw broadly V-shaped without a notch.

The largest specimen (Gosner stage 25) measured 81 mm total length.

Coloration in preservation. Body and tail including fins plain brown in preservation; ventrum brighter and more

Figure 17. *Nyctibates corrugatus* tadpole in life coloration (ZMB 82115, Gosner stage 26), from Ebo forest, southern Cameroon.

grayish; ventral fin brighter and more transparent than dorsal fin (Fig. 16). In life the tadpoles are dark brown to almost black with a blue tinge along the lower parts of flanks, belly and tail axis (Fig. 17). ZMB 82109 shows large areas of little or absent pigmentation, what might be a preservation artifact.

Scotobleps gabonicus Boulenger, 1900

Material examined. ZMB 82118 and ZMB 82118A, both tadpoles Gosner stage 25, Cameroon, Ebo Forest, Ndogbanguengue, 113 m, 4°24'36.54"N, 10°10'10.19"E, 22 September 2012, leg. M. Dahmen; ZMB 88347 (GenBank MK318895), Gosner stage 41, Cameroon, near Korup National Park, Mokango, 5°8'2.26"N, 9°5'17.02"E, 8 May 2014, leg. F. Mühlberger; ZMB 88348 (GenBank MK318896), Gosner stage 25, Cameroon, near Korup National Park, Mokango, 758 m, 5°8'40.46"N, 9°5'6.70"E, 9 May 2014, leg. F. Mühlberger; ZMB 88349 (GenBank MK318897), Gosner stage 39, Cameroon, near Korup National Park, Mokango, 533 m, 5°7'50.1"N, 9°3'46.4"E, 10 May 2014, leg. F. Mühlberger; ZMB 88350 (GenBank MK318898), Gosner stage 25, Cameroon, Korup National Park, Esukatan, 189 m, 5°23'8.54"N, 9°0'36.72"E, 19 May 2014, leg. F. Mühlberger; ZMB 88354 (GenBank MK318899), Gosner stage 25, Cameroon, Korup National Park, Bera, 298 m, 5°21'5.47"N, 8°59'12.27"E, 23 May 2014, leg. F. Mühlberger; ZMB 88355 (GenBank MK318900), Gosner stage 35, ZMB 88356 (GenBank MK318901), Gosner stage 38, Cameroon, near Korup National Park, Ikundukundu, 147 m, 5°2'25.1"N, 8°55'3"E, 1 June 2014, leg. F. Mühlberger; ZMB 88357 (GenBank MK318902), Gosner stage 25, Cameroon, Korup National Park, Ikenge, 292 m, 5°16'30.86"N, 9°6'47.28"E, 13 May 2014, leg. F. Mühlberger.

All tadpoles were caught in small to medium-sized streams and rivers in low- to middle-altitude forests. The description is mainly based on ZMB 88355. The genotyped tadpoles have been compared with an adult from Big Massaka, Cameroon (MHNG 2716.24; GenBank MK318903). The uncorrected pairwise p difference between tadpoles and between tadpoles and the adult ranged from 0–0.4% (0–2 bp).

Description. Long slender tadpole with slim, muscular tail (Fig. 18); body egg-shaped in dorsal view, slightly flattened in lateral view; snout rounded in dorsal view, more narrow-rounded and sloping in lateral view; body length 32.6 ± 1.0% of total length; body height 40.0 ± 5.9% of body length; body width 56.1 ± 3.4% of body length; eyes positioned dorsolaterally, eye diameter 11.7 ± 1.2% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 59.5 ± 10.2% of interorbital distance; tail fins narrow, dorsal and ven-

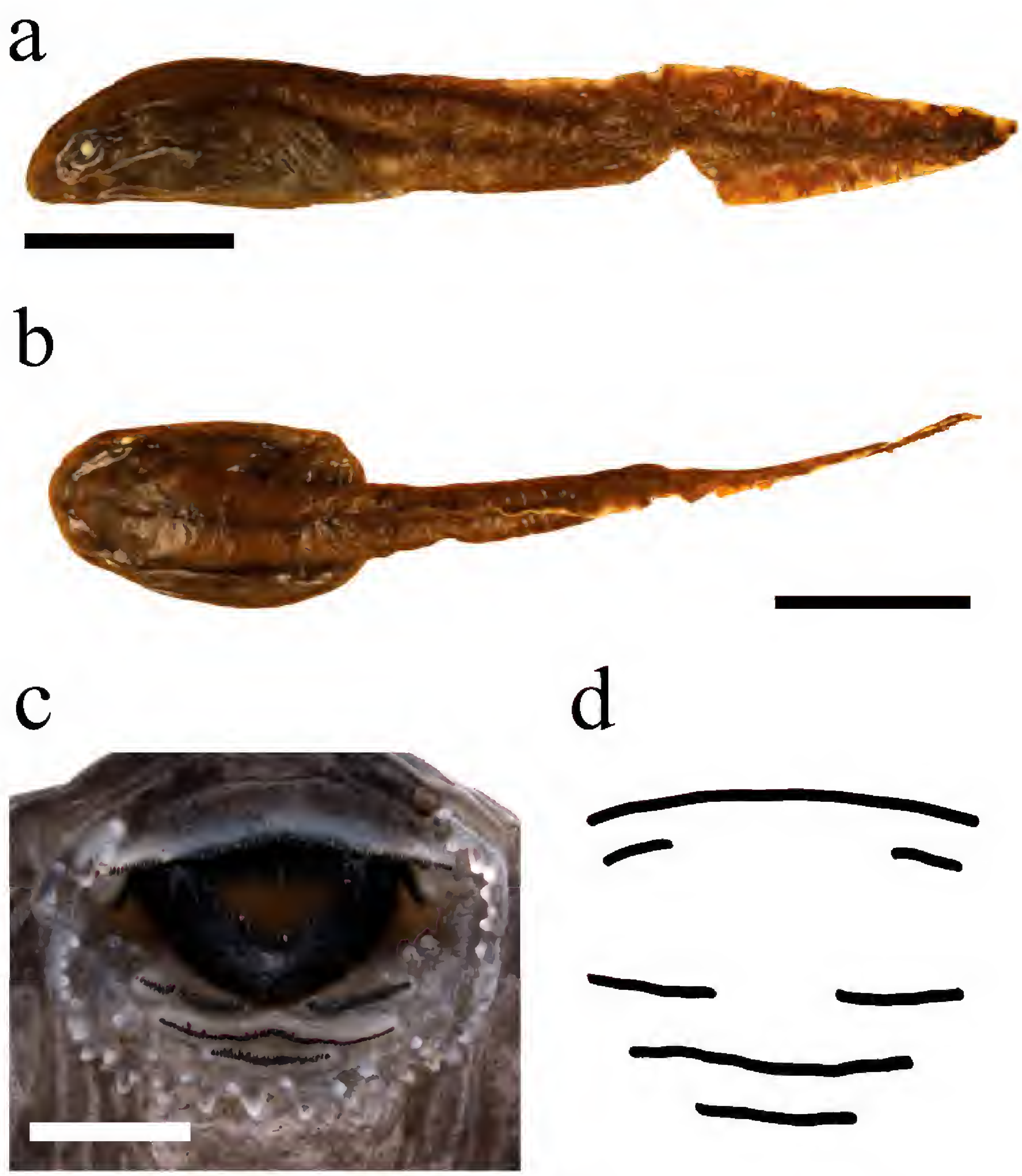

Figure 18. *Scotobleps gabonicus* tadpole (ZMB 88355, Gosner stage 35); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

tral fin originating from tail base, ventral fin height 64.5 ± 5.9%, of dorsal fin height; highest part of tail approximately in the middle of the tail; body height 87.9 ± 11.2% of maximum tail height; tail axis width 41.5 ± 7.2% of body width; tail axis height 68.5 ± 10.1% of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, reaching from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout and smaller than interorbital distance; labial tooth formula 1:2/2:2; anterior lip carries no marginal papillae, posterior lip carries 2 or 3 rows of around 20–30 variable papillae, small lobe on each corner of the mouth (Fig. 18c), large rostral gap, papillae short and triangular (with rounded tip), marginal papillae bigger than those of inner row; jaws massive, black and fully keratinized; both jaws sharply serrated, upper jaw almost rectangular with 2 or 3 enlarged fangs on each side, lower jaw V-shaped without a notch.

The largest tadpole (ZMB 88347, Gosner stage 41) measured 62.2 mm. The tadpoles of Gosner stages 38 and 39 all measured about 60 mm total length.

Coloration in preservation. Body brown, lateral sacs slightly more grayish; tail uniform dark brown at tail base, slightly fading to a fine but dense pattern of lighter brown speckles towards tail tip; fins yellowish brown with a dark reddish brown pattern.

Lateral line-system of the *Astylosternus*, *Nyctibates*, and *Scotobleps* tadpoles

All investigated tadpoles exhibited a similar and complex lateral line-system (LLS), which is usually well developed (Fig. 19). We did not observe any species-specific differences. Some variation occurred on LLSs of the face (number 3 in Fig. 19). However, this varied intra- and

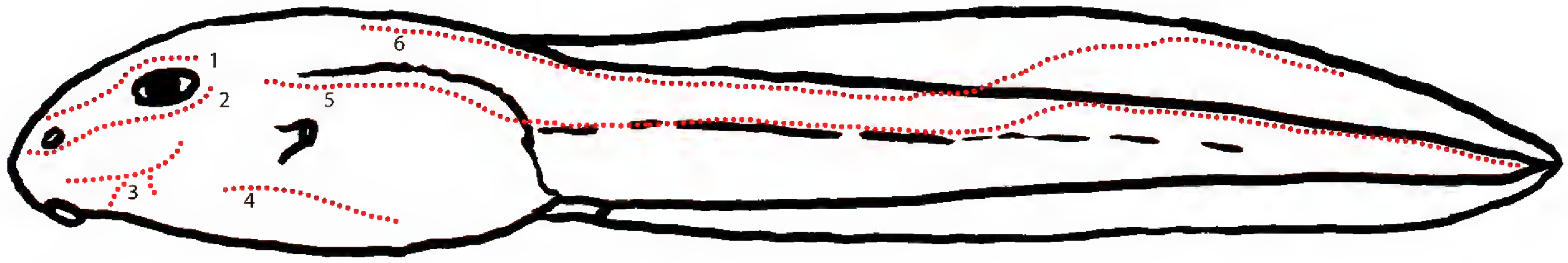

Figure 19. General arrangement of lateral line-system in tadpoles of the genera *Astylosternus*, *Nyctibates* and *Scotobleps*; 1 = supraorbital line, 2 = infraorbital line, 3 = area comprising an angular, an oral, a gular and a jugular line, 4 = lower lateral body line, 5 = middle lateral body line, 6 = upper lateral body line, terminology after Escher (1925).

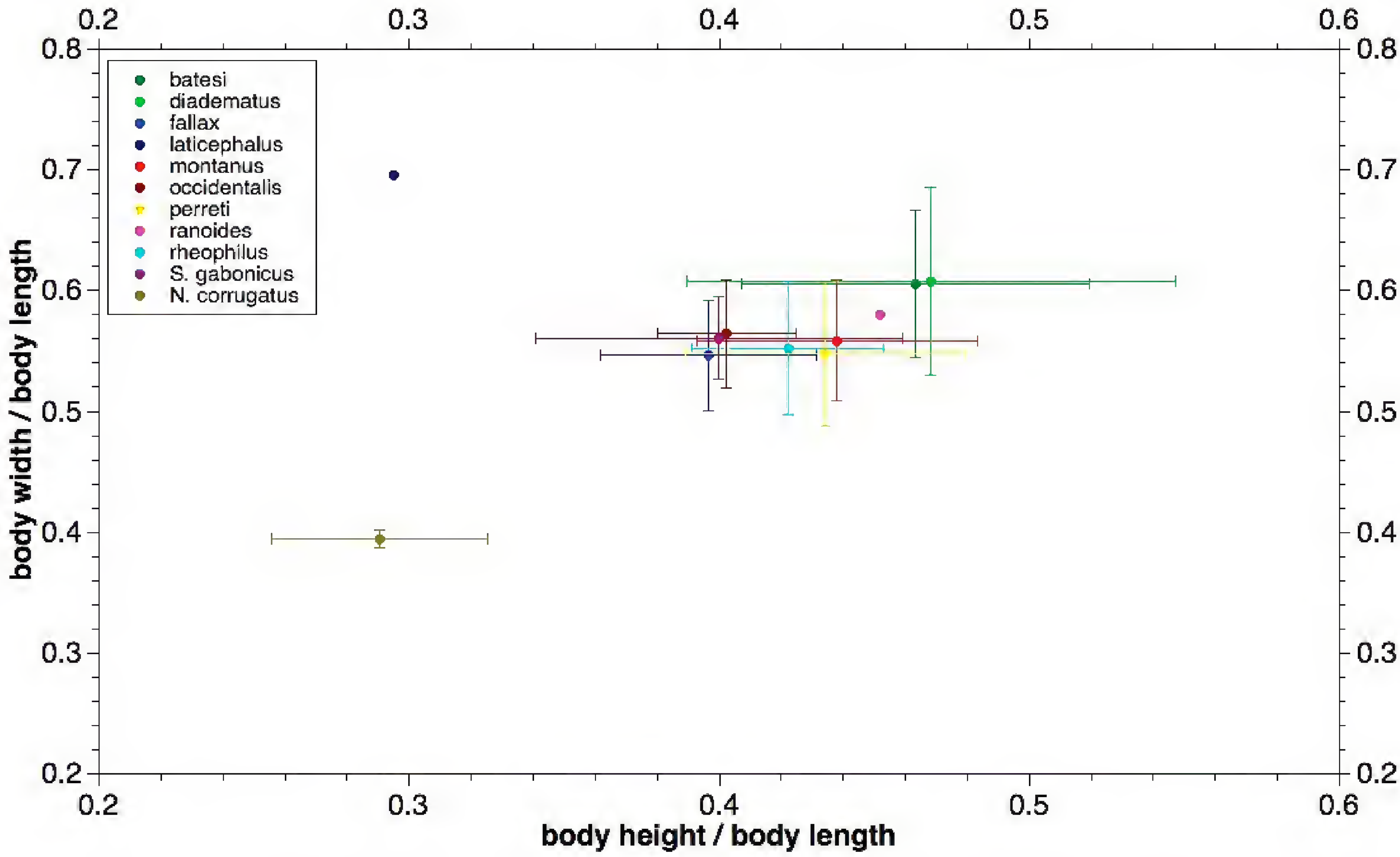

Figure 20. Comparison of two morphological characters (body width and body height) against body length in the tadpole species investigated; *Astylosternus* spp. and *Scotobleps gabonicus* had very similar body shapes; *Nyctibates corrugatus* tadpoles (olive) are much more elongated; the single tadpole of *A. laticephalus* (dark blue dot) had a very flattened body, being proportionally the widest.

interspecifically, and it was not always obvious if the differences were real or due to our difficulty in observing the respective lines. Particularly well visible were the supra- and infraorbital lines, as well as lower, middle and upper lateral body lines (Fig. 19).

Morphological comparison of the *Astylosternus*, *Nyctibates*, and *Scotobleps* tadpoles

Morphological variability between the investigated tadpoles was relatively minor. We compared various indices (ratios) of body measurements against each other and performed PCAs (e.g. Fig. 20) to determine species-specific differences in morphological characters (most results not shown). PCA axes 1–4 accounted for 73% of the cumulative, overall morphological variability of the examined tadpoles. However, there were no significant differences between the species, and it was apparent that only tadpoles of *Nyctibates corrugatus* differed distinctly from all the other species, when comparing body shape (length-corrected width vs height), by having an exceptionally elongated and muscular body. The only other tadpole occupying a unique morphospace was *Astylosternus laticephalus* (Fig. 8). However, measurements were based on only one tadpole in a very advanced stage of development. *Scotobleps gabonicus* seems to have a shorter and rounder head than the other species.

Discussion

The genus *Astylosternus* Werner, 1898 currently comprises 12 species (Amiet 1989; Rödel et al. 2012), which occur in West and western Central Africa, with a small distribution gap in Togo and Benin, the Dahomey-Gap. Most species are found in Cameroon, with many species restricted to small altitudinal zones of mountainous regions in the west of the country. There, they inhabit a variety of forests and varying stream types (Mertens 1938; Amiet 1989; Oates et al. 2004; Plath et al. 2004; Herrmann et al. 2005). In contrast, the widespread *A. batesi* (Boulenger, 1900) and *A. occidentalis* Parker, 1931 prefer humid lowland forests, where their tadpoles are often found in small, shallow, slow flowing creeks (Amiet 1989; Rödel et al. 2012). *Nyctibates corrugatus* predominantly occurs in western Cameroon, but its distribution ranges from the Nigerian Oban Hills in the north to the mainland of Equatorial Guinea in the south (Frétey and Blanc 2000). The preferred tadpole habitats are very fast flowing streams with stony bottoms. Similarly, *Scotobleps gabonicus* is known from southern Nigeria, through Cameroon, south to western Democratic Republic of the Congo (Portik et al. 2017). Tadpoles were all observed in small to medium-sized streams and rivers in low- to middle-altitude forests. Thus, the tadpoles of the species examined here, live in different habitats, ranging from lowland to mountainous forest streams (Fig. 21), and one might expect some adaptive morphological differences as a result.

Herein, we describe for the first time the tadpoles of five *Astylosternus* species, *A. fallax*, *A. laurenti*, *A. montanus*, *A. perreti*, *A. ranoides*, and *Scotobleps gabonicus*. The tadpoles of five additional *Astylosternus* species, *A. batesi, A. diadematus, A. laticephalus, A. occidentalis, A. rheophilus*, and *N. corrugatus* were redescribed, partly based on more specimens (see Channing et al. 2012 and literature cited therein for original descriptions). Based on our investigations, we confirm previous results (e.g. Angel 1930; Lamotte and Zuber-Vogeli 1954; Lamotte 1985; Channing et al. 2012; Rödel et al. 2012) characterizing all *Astylosternus* tadpoles as adapted to torrent currents. They share a long, oval body, slightly flattened in lateral view, with very long muscular tails. The tail fins are narrow, the ventral fin usually is 20–30% narrower than the dorsal fin, and with the tip being mostly pointed. A longitudinal medial depression on the back and large lateral sacs are likewise visible in all specimens. They have massive, serrated jaws, often with a tooth-like medial projection (fang) in the upper jaw. The mouth is always located ventrally but very close to the snout tip. The keratodont formula was 1:2+2/2+2:1 or 1:2+2/1+1:2, and all species have short marginal papillae, which, however, vary in form and length between species. The anterior lip usually has a rostral gap. Our new data mainly agree with previous descriptions, but slight deviations to the literature were noticed in keratodont formulae and coloration (see species accounts). However, both characters usually vary to some extent with developmental stage and are known to be plastic in some species of amphibians (Martin and Pfennig 2011). For instance, Barej et al. (2015) observed an increasing number of keratodonts during ontogenesis. On the other hand, keratodonts may have worn-off over time or get lost during metamorphosis (e.g. see *A. batesi* account). Especially the tiny, last anterior keratodont row (A3 or A4) was sometimes missing. Tadpoles may become darker or distinct patterns fade and blur with development. For instance in *A. perreti* tadpoles pigmentation became denser with advanced developmental stages. Generally coloration in our descriptions may be less distinctive than in life due to preservation. Many tadpoles vouchers, placed directly in ethanol, show slightly wrinkled skin, in contrast to the smooth, bulging bodies of live individuals.

Body proportions of *Astylosternus* were extremely similar. Better characters to distinguish species could be coloration in life (not always available to us) and potentially the shape of labial papillae. For instance, *A. montanus* and *A. rheophilus* had very uniform, triangular papillae. In *A. perreti*, the triangular papillae became larger towards the center of the rows, while papillae of *A. diadematus* had a longish shape. All *Astylosternus* tadpoles (preserved) were more or less brownish. Some species were finely speckled on a lighter base, like *A. diadematus*. Others, like *A. perreti*, had distinct, large, brown marks on the tail or the speckling was dense to almost appearing uniformly brown, as in *A. occidentalis*.

The tadpole of *Scotobleps gabonicus* was similar to *Astylosternus* and only slightly differed in body shape, which was narrower with a shorter and rounder head (e.g. the eyes were closer to the snout). With a total length of around 60 mm, *Scotobleps* tadpoles also seemed to be smaller than those of *Astylosternus* species. The upper jaws of both genera were serrated, but in contrast to *Astylosternus, Scotobleps* upper jaw sheaths carried two to three lateral fangs instead of one medial one.

Tadpoles of *Nyctibates corrugatus*, described previously by Amiet (1971), were also similar to *Astylosternus* but nevertheless easily distinguishable on the basis of their shape and color. Their body is even more elongated, the tail longer, the dorsal fin originates at about one-third of the tail, and the tail tip is broadly rounded; thus, the body form is "eel-shaped" (Channing et al. 2012), and it was in fact not always easy to instantly tell these tadpoles apart from small fish when searching their habitats. They also have different mouth parts, and in particular lips, with conspicuous large, flat lobes. Lastly, the plain bluish-black color distinguishes them from any *Astylosternus* species. Nonetheless, all three genera were very similar morphologically, most likely as a result of convergent adaptation to similar stream environments (Lamotte and Lescure 1988, 1989a, b).

In contrast to the morphological similarity of the herein examined tadpoles, the three genera are markedly different to tadpoles of other arthroleptids. According to Altig and John-

Figure 21. Habitats of *Astylosternus* tadpoles; **a** *A. rheophilus* habitat at Mount Manengouba (5°02'7.56"N, 9°50'46.8"E, 2088 m), Littoral Province, Cameroun; **b** *A. diadematus* habitat at Mount Manengouba (5°04'3.48"N, 9°51'56.22"E, 1459 m), Littoral Province, Cameroun; **c** *A. occidentalis* habitat at Foya Proposed Protected Area; western Liberia (08°02'37.9"N, 010°24'35.1"W; photo: J. Glos); **d** *A. perreti* habitat at Mount Manengouba near Ebonemin (5°00'46.5"N, 9°46'5.82"E, 1372 m), South-West Province, Cameroun; **e** *A. ranoides* habitat at Mount Manengouba (5°00'51.78"N, 9°49'12.12"E, 2114 m), Littoral Province, Cameroun.

ston (1989) arthroleptid genera, except *Leptopelis* (some species with lentic tadpoles) and *Arthroleptis* (endotrophic larvae; Guibé and Lamotte 1958a), have exotrophic, lotic tadpoles with a general shape adapted to fast flowing currents. All have very muscular tails with reduced tail fins and delayed appearance of limbs to withstand the strong currents and reduce flow resistance (many large specimens, but in Gosner stage 25–30; see Appendix 1; compare with Lamotte and Zuber-Vogeli 1954; Doumbia et al. 2018). Despite these similarities, the genera show obvious differences, especially in the mouthparts. Tadpoles of *Leptodactylodon* are very slender and have a funnel mouth with reduced keratodonts (Mapouyat et al. 2014). The huge sucker mouth of *Trichobatrachus,* with narrow jaws but numerous rows of keratodonts, reflects their life history of rasping food from stones in strong currents (Mertens 1938). *Cardioglossa* lack keratodonts and seem to live in less strong currents, but are often well-hidden in sand and detritus, possibly indicated by their long spiracles which may reach the open water although the tadpole is entirely covered with sand (Hirschfeld et al. 2012).

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References

Altig R, Johnston GF (1989) Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. Herpetological Monographs 3: 81–109. https://doi.org/10.2307/1466987

Amiet JL (1971) Le têtard d'*Astylosternus corrugatus* Boulenger (Amphibien Anoure). Annales de la Faculté des Sciences du Cameroun 6: 85–98.

Amiet JL (1978) Les *Astylosternus* du Cameroun (Amphibia, Anura, Astylosterninae). Annales de la Faculté des Sciences de Yaoundé 23–24: 99–227.

Amiet JL (1989) Quelques aspects de la biologie des amphibiens anoures du Cameroun. Année Biologique 28: 73–136.

Angel F (1930) Sur les têtards d'un batracien anoure d'Afrique, de la famille des Ranidés (groupe des Astylosterninés). Bulletin de la Société zoologique de France 55: 219–222.

Barej, MF, Pfalzgraff T, Hirschfeld M, Liedtke HC, Penner J, Gonwouo NL, Dahmen M, Grözinger F, Schmitz A, Rödel MO (2015) The tadpoles of eight West and Central African *Leptopelis* species (Amphibia: Anura: Arthroleptidae). Amphibian and Reptile Conservation 9 (2) [Special Section]: 56–84. [e111]

Blackburn DC (2008) Biogeography and evolution of body size and life history of African frogs: Phylogeny of squeakers (*Arthroleptis*) and long-fingered frogs (*Cardioglossa*) estimated from mitochondrial data. Molecular Phylogenetics and Evolution 49: 806–826. https://doi.org/10.1016/j.ympev.2008.08.015

Boulenger GA (1900) A list of the batrachians and reptiles of the Gaboon (French Congo), with descriptions of new genera and species. Proceedings of the Zoological Society of London 1900: 433–456. [pls 27–32]

Boulenger GA (1904) Descriptions of two new genera of frogs in the family Ranidae from Cameroon. Annals and Magazine of Natural History (Series 7) 13: 261–262. https://doi.org/10.1080/00222930409487067

Channing A (2008) The mud dwelling tadpole of the long-toed tree frog, *Leptopelis xenodactylus* (Arthroleptidae). Herpetological Review 39: 288–290.

Channing A, Rödel MO, Channing J (2012) Tadpoles of Africa – The biology and identification of all known tadpoles in sub-Saharan Africa. Edition Chimaira, Frankfurt/M., 402 pp.

Doumbia J, Sandberger-Loua L, Schulze A, Rödel MO (2018) The tadpoles of all five species of the West African frog family Odontobatrachidae (Amphibia, Anura). Alytes 36: 63–92.

Dubois A (1995) Keratodont formula in anuran tadpoles: proposals for a standardization. Journal of Zoological Systematic and Evolutionary Research 33: I–XV. https://doi.org/10.1111/j.1439-0469.1995.tb00207.x

Ernst R, Nienguesso ABT, Lautenschläger T, Barej MF, Schmitz A, Hölting M (2014) Relicts of a forested past: Southernmost distribution of the hairy frog genus *Trichobatrachus* Boulenger, 1900 (Anura: Arthroleptidae) in the Serra do Pingano region of Angola with comments on its taxonomic status. Zootaxa 3779: 297–300. https://doi.org/10.11646/zootaxa.3779.2.10

Escher K (1925) Das Verhalten der Seitenorgane der Wirbeltiere und ihrer Nerven beim Übergang zum Landleben. Acta Zoologica 6: 307–414. https://doi.org/10.1111/j.1463-6395.1925.tb00269.x

Frétey T, Blanc CP (2000) Liste des Amphibiens d'Afrique centrale. Cameroun, Congo, Gabon, Guinée-Equatoriale, République Centrafricaine, République Démocratique du Congo, São Tomé et Príncipe. Les dossiers de l'ADIE, Série Biodiversité 2: 1–39.

Frost D (2018) Amphibian Species of the World: an Online Reference. Version 6.0. http://research.amnh.org/herpetology/amphibia/index.html [Accessed on: 2019-3-11]

Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183–190.

Guibé J, Lamotte M (1958a) Morphologie et reproduction par développement direct d'un anoure du Mont Nimba, *Arthroleptis crusculum* Angel. Bulletin du Muséum National d'histoire naturelle (2e Série) 30: 125–133.

Guibé J, Lamotte M (1958b) La réserve naturelle intégrale du Mont Nimba. XII. Batraciens (sauf *Arthroleptis, Phrynobatrachus* et *Hyperolius*). Mémoires de l'Institut français d'Afrique noire 53: 241–273.

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT). Nucleic Acids Symposium Series 41: 95–98.

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Herrmann HW, Böhme W, Herrmann PA, Plath M, Schmitz A, Solbach M (2005) African biodiversity hotspots: the amphibians of Mt. Nlonako, Cameroon. Salamandra 41: 61–81.

Hirschfeld M, Barej MF, Gonwouo LN, Rödel MO (2012) Tadpole descriptions of three *Cardioglossa* species from southwestern Cameroon (Amphibia: Anura: Arthroleptidae). Salamandra 48: 147–156.

Lamotte M (1985) Les amphibiens à têtards torrenticoles dans l’Ouest Africain. Notes africaines 187: 88–92.

Lamotte M, Lescure J (1988) Les caractéristiques biométriques du développement et de la métamorphose des têtards rhéophiles d’anoures. Bulletin de la Société zoologique de France 113: 21–30.

Lamotte M, Lescure J (1989a) Les têtards rhéophiles et hygropétriques de l’ancien et du nouveau monde. Annales des Sciences naturelles, Zoologie Série 13 10: 111–122.

Lamotte M, Lescure J (1989b) Les têtards rhéophiles et hygropétriques de l’ancien et du nouveau monde. Annales des Sciences naturelles, Zoologie Série 13 10: 125–144.

Lamotte M, Perret JL (1963) Contribution à l’étude des batraciens de l’Ouest Africain XV. Le développement direct de l’espèce *Arthroleptis poecilonotus* Peters. Bulletin de l’Institut français d’Afrique noire, Série A 25: 277–284.

Lamotte M, Zuber-Vogeli M (1954) Contribution à l’étude des batraciens de l’Ouest Africain III. Le développement larvaires de deux espèces rhéophiles, *Astylosternus diadematus* et *Petropedetes natator*. Bulletin de l’Institut français d’Afrique noire, Série A 16: 1222–1233.

Mapouyat L, Hirschfeld M, Rödel MO, Liedtke HC, Loader SP, Gonwouo LN, Dahmen M, Doherty-Bone T, Barej MF (2014) The tadpoles of nine Cameroonian *Leptodactylodon* species (Amphibia, Anura, Arthroleptidae). Zootaxa 3765: 29–53. https://doi.org/10.11646/zootaxa.3765.1.2

Mertens R (1938) Herpetologische Ergebnisse einer Reise nach Kamerun. Abhandlungen der senckenbergischen naturforschenden Gesellschaft 442: 1–52.

Martin RA, Pfennig DW (2011) Evaluating the targets of selection during character displacement. Evolution 65: 2946–2958. https://doi.org/10.1111/j.1558-5646.2011.01357.x

Oates JF, Bergl RA, Linder JM (2004) Africa’s Gulf of Guinea forests: biodiversity patterns and conservation priorities. Advances in Applied Biodiversity Science No. 6, Conservation International, Washington D.C., 92 pp. http://s3.amazonaws.com/WCSResources/file_20110823_034557_Oates+Africa+Gulf+Guinea+Biodiversity+Patterns+Priorities_fqyVv.pdf

Parker HW (1931) Some new and rare frogs from West Africa. Annals and Magazine of natural History (Series 10) 7: 492–498. https://doi.org/10.1080/00222933108673334

Parker HW (1936) Amphibians from Liberia and the Gold Coast. Zoologische Mededelingen 19: 87–102.

Plath M, Solbach M, Herrmann HW (2004) Anuran habitat selection and temporal partitioning in a montane and sub-montane rainforest on Southwestern Cameroon – first results. Salamandra 40: 239–260.

Portik DM, Leaché AD, Rivera D, Barej MF, Burger M, Hirschfeld M, Rödel MO, Blackburn DC, Fujita MK (2017) Evaluating mechanisms of diversification in a Guineo-Congolian tropical forest frog using demographic model selection. Molecular Ecology 26: 5245–5263. https://doi.org/10.1111/mec.14266

Rödel MO (2000) Herpetofauna of West Africa, Vol. I: Amphibians of the West African savanna. Edition Chimaira, Frankfurt am Main, 332 pp.

Rödel MO, Barej MF, Hillers A, Leaché AD, Kouamé NG, Ofori-Boateng C, Assemian E, Tohé B, Penner J, Hirschfeld M, Doumbia J, Gonwouo LN, Nopper J, Brede C, Fujita MK, Gil M, Segniagbeto GH, Sandberger L (2012) The genus *Astylosternus* in the Upper Guinea rainforests, West Africa, with the description of a new species (Amphibia: Anura: Arthroleptidae). Zootaxa 3245: 1–29. https://doi.org/10.11646/zootaxa.3245.1.1

Schiøtz A (1999) Treefrogs of Africa. Edition Chimaira, Frankfurt am Main, 350 pp.

Schweiger S, Naumann B, Larson JG, Möckel L, Müller H (2017) Direct development in African squeaker frogs (Anura: Arthroleptidae: *Arthroleptis*) reveals a mosaic of derived and plesiomorphic characters. Organisms Diversity and Evolution 17: 693–707. https://doi.org/10.1007/s13127-017-0335-5

Wager VA (1986) Frogs of South Africa, their fascinating life stories. Delta, Craighall, 183 pp.

Werner F (1898) Ueber Reptilien und Batrachier aus Togoland, Kamerun und Tunis aus dem kgl. Museum für Naturkunde in Berlin II. Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien 48: 191–213. [1 plate]

Appendix 1

Measurements (in mm) of the arthroleptid tadpoles described in this study; given are museum accession numbers, Gosner stage (Gosner 1960), and individual measures. For abbreviations of measurements, see Material and methods.

Species	Individual	Gosner	TL	BL	TAL	BH	BW	MTH	TMH	DFH	VFH	TMW	IOD	IND	SP	SSD	ES	SN	EN	ED	ND	MW
A. batesi	ZMB 82865	25	–	25.0	–	10.7	14.2	12.5	9.2	4	2.8	6.56	7.6	5.4	1.1	8.8	5.4	2.2	3.6	2.3	0.7	5
	ZMB 82864	25	–	6.8	–	2.6	3.5	3.4	2.21	1.4	1	1.7	2	1.4	0.2	3.6	1.4	0.6	0.8	0.8	0.25	1.2
	ZMB 82863	25	–	5.3	–	2.7	3.3	–	1.7	–	–	1	1.1	1	–	–	0.5	0.3	0.2	0.5	0.1	0.4
	ZMB 82866	25	–	8.04	–	3.74	4.66	3.8	1.93	1.4	1.1	1.78	2.3	2	0.2	3.7	1.9	0.7	1.2	1	0.25	1.6
	ZMB 82866 A	25	20.7	7.6	13.1	3.3	4.6	3.9	1.8	1.5	1	1.6	2.7	2	0.4	3.8	2.5	0.6	1.5	0.9	0.2	1.3
	ZMB 82866 B	25	25.2	7.9	17.3	4.3	5.6	4.1	1.9	1.7	1.1	2	3.4	2.3	0.5	4.3	2.7	0.9	1.6	1	0.2	1.5
	ZMB 82784	36	–	24.6	–	12	13.92	11.85	9.12	4	3	9	9.2	6.1	1.5	11	7.9	3	5	3	0.8	5.1
A. diadematus	ZMB 82799	25	–	18.71	–	7.5	9.9	8.75	5.67	3.1	2.1	4.38	6.1	4.6	0.7	9.4	4.7	1.8	3.2	2	0.7	3.5
	ZMB 82870	25	–	17.74	–	7.08	9.8	8.61	6.5	2.5	1.8	4.59	5.4	3.9	0.8	7.6	4.2	1.7	2.8	1.9	0.5	3.4
	ZMB 88234	25	52.8	17.3	35.5	9.3	11.6	–	7	2.8	1.8	6.3	6	4.1	1.1	7.8	4.7	1.6	3.2	2.1	0.5	–
	ZMB 88346	36	72.1	23.7	48.4	12.7	16.1	13.3	9.2	4.8	3.2	7.1	9.6	6.5	1.4	10.5	6.5	2	4.8	3	0.7	5.1
A. fallax	ZMB 82868	25	–	14.35	–	5.89	8.92	–	4.29	–	–	2.92	4.35	3.36	0.5	7	3.2	0.9	2.3	1.6	0.6	3
	ZMB 82868 A	25	58.7	21	37.7	8.7	11.9	9	6.6	3.3	2.2	6.5	8.4	6.5	1.4	10.7	7.5	2.8	4.6	2.5	0.6	7.1
	ZMB 82868 B	25	45.2	17.7	27.5	6.3	9.4	7.7	5.5	2.9	1.7	4.9	6.6	4.2	1.2	8.3	5.6	2	3.5	2.1	0.5	3.3
	ZMB 82869	25	74.75	25.44	49.37	10.96	13.42	9.84	6.34	4.3	3.5	5.74	7.8	6.1	1.3	12.3	5.9	1.9	4.1	2.8	1.2	5.5
A. cf. *fallax*	ZMB 82867	25	97.38	30.86	67.01	10.77	14.93	14.9	9.73	5.45	3.99	7.86	9	7.8	1.1	15	7.5	2.4	5.2			
A. laurenti	ZMB 88353	25	51.7	17.7	34	7.4	9.7	9.6	5.9	3.6	2.6	4.6	7	5.4	1.6	8.1	4.8	1.2	3.7			
A. laticephalus	ZMB 75460	39	62.2	22.7	39.5	6.7	15.8	8.6	5.6	2.3	1.9	5.6	9.3	3.2	–	–	5.5	2.1	3.5	2.5	0.5	4.9
A. montanus	ZMB 82875	25	–	22.48	–	10.18	12.57	10.71	7.77	3.7	2.6	6.53	7.2	6.6	1.2	11	5.6	1.9	3.2	2.4	0.7	4.7
	ZMB 82874	25	–	20.19	–	7.92	11.95	8.41	6.38	2.8	2.3	5.4	5.4	5.2	1	9	5	1.8	3.4	2.1	0.6	4.1
	ZMB 82874 A	25	60.4	20.1	40.3	7.6	10	7.4	5	2.4	1.9	5	7	6.5	1.1	9.9	6	1.6	4.3	2.1	0.5	3.6
	ZMB 82871	25	–	14.65	–	6.8	9.36	6.19	5.56	2	1.5	4.62	4.3	3.7	–	6.7	3.7	1.1	2.4	1.5	0.4	3.3
	ZMB 82871 A	28	73.2	23.8	49.4	12.2	12.7	12.8	8.7	4	2.5	8.4	9.1	6.7	1.2	12.2	8.5	2	5.4	2.1	0.9	5
	ZMB 82871 B	25	52.5	18.3	34.2	7.7	9.2	8.3	5.6	3	1.9	4.9	6.1	4.5	1	9	5.2	2	3.2	1.8	0.6	3.4
	ZMB 82872	25	–	11.03	–	4.98	6.9	3.96	2.97	1.6	1.1	2.37	3.4	3	0.4	5.3	2.7	0.9	1.8	1.3	0.4	2.2
	ZMB 82873	25	–	8.79	–	3.81	4.91	3.67	2.35	1.5	1	1.8	2.7	2.2	0.3	4.3	2.1	0.8	1.4	1	0.3	1.6
	ZMB 82873 A	25	34.7	11.4	23.3	5.6	6.5	4.6	2.4	1.9	1.3	2.6	4.5	3.4	0.8	5.2	3.2	0.7	2.6	1.2	0.4	2.1
	ZMB 82876	25	–	21.9	–	8.4	11.1	–	5.8	–	–	5.8	9	5.3	1.2	10	2.3	2.1	5	2.4	0.4	4.1
A. occidentalis	ZMB 77317	25	75.9	25.4	50.5	10.6	15.4	13.3	9	4.1	3.5	7.5	9.6	5.9	1.6	10.8	6.3	1.9	4.5	3	0.6	5.9
	ZMB 77317 A	25	–	24.5	–	9.9	15.2	12	9	4.2	3.3	7.3	9.4	5.9	1.6	10.4	5.5	1.3	4.5	2.4	0.6	5.5
	ZMB 37564	26	80.5	24.3	56.2	9.5	13.8	10	10	3	1.2	9	8.9	5.6	1.7	8.9	6.2	2	4.5	2.5	0.8	5
	ZMB 75368	37	80.5	28.4	52.1	10.6	17	15.1	8	5	3.8	7	9.6	6	1.8	12	6.5	1.7	5.5	3.2	0.7	5.3
	ZMB 75368 A	41	77.5	24	53.5	10.6	13.3	11.5	7	3.9	2.7	6	9.6	5.4	1.8	11.9	6.6	2	4.3	4	0.6	4.7
	ZMB 77440	25	73.6	20.7	52.9	8.6	10.1	9	7	3	2.1	6.3	7.9	5.2	1.4	10.8	7	2.2	4.4	2.3	0.6	4.5
	ZMB 77438	26	–	28.5	–	10.8	14.8	14.4	9.3	5.1	3.9	8.6	10.2	6.4	1.4	13	8.4	2.5	5	3.5	0.8	5.4
	ZMB 77439	25	95.9	27.4	68.5	10.9	15.3	12.4	9.5	4	3.1	8.6	10.2	6.5	1.6	11	6.5	2	5	2.5	0.8	5.3
A. perreti	ZMB 82882	25	–	20.01	–	8.82	11.96	9.2	6.09	2.7	2.4	5.4	6.4	5.7	0.5	10.8	5.3	1.6	3.8	2.2	0.9	4.4
	ZMB 82816	25	–	24.91	–	11.09	13.36	11.09	9.87	3.5	3	8.11	7.9	6.6	0.4	13.2	6.4	1.5	5	2.9	0.5	5.6
	ZMB 82881	25	–	24.27	–	10.1	13.38	10.46	7.67	3.5	3	5.9	7.6	6.9	0.8	13.5	7	2.3	4.7	2.9	1.2	5.6
	ZMB 82881 A	25	58.6	16.9	41.7	8	9.1	7.3	5.3	2.4	2	5.1	6	5.3	1.3	8.2	5.1	1.3	4.2	1.9	0.6	3.9
	ZMB 82880	25	–	26.24	–	10.96	13.09	12.44	8.08	3.5	2.9	6.91	8.2	7.4	0.5	20	7.9	2.2	5.7	2.9	1.2	5.8
	ZMB 82877	25	–	8.22	–	4.02	5.55	3.5	2.56	1	0.7	1.83	3	2.5	0.5	4.9	2	0.6	1.4	1.2	0.4	1.9
	ZMB 82883	25	–	5.31	–	1.94	2.49	2.39	1.78	1.1	0.9	1.36	2.2	2.1	0.3	3.5	1.4	0.6	0.8	0.7	0.2	1
	ZMB 82883 A	25	18.6	5.9	12.7	3	3.1	3	1.8	1.1	0.9	1.2	1.9	1.8	0.4	2.9	1.5	0.5	1.1	0.7	0.2	1
	ZMB 82879	25	–	7.59	–	3.33	4.31	2.84	2.11	1.4	1	1.44	3.3	2.7	0.5	4.9	2.4	0.8	1.6	1.1	0.3	1.9

Species	Individual	Gosner	TL	BL	TAL	BH	BW	MTH	TMH	DFH	VFH	TMW	IOD	IND	SP	SSD	ES	SN	EN	ED	ND	MW
A. perreti	ZMB 82884	27	–	30	–	11	14.3	12.1	9	3.8	3	8.8	10.3	9	(?) 1.5	13.8	9.9	2.4	7.9	3.2	1	5.9
	ZMB 82884 A	28	108.1	35.8	72.3	14.9	20.9	16.2	11.8	4.5	3.1	11.3	13	10.4	3	16.8	11.9	3	9.1	3.6	1	7.8
A. ranoides	ZMB 82823	25	18.2	6.2	–	2.8	3.6	3.4	2.1	1.1	0.9	1.2	1.8	1.5	0.2	2.8	1	0.35	0.7	0.6	0.1	0.9
A. rheophilus	ZMB 82896	25	–	19.47	–	9.09	11.98	8.67	6.15	2.9	2.2	4.95	6.1	5.4	0.9	10.1	5.6	1.6	4	2.3	0.7	4.9
	ZMB 82899	25	–	13.73	–	5.5	7.3	5.96	4.5	1.9	1.4	3.34	4.4	3.8	0.5	7.1	1.7	1.3	2.6	1.6	0.5	3
	ZMB 82895	25	–	18.36	–	6.97	11.67	8.42	5.25	2.8	1.9	4.33	5.5	4.8	0.5	9	4.5	1.3	3.3	2.2	0.6	4.4
	ZMB 82895 A	25	79.8	26.5	53.3	12.5	12.3	11.5	9.2	3.8	2.9	7.1	9.4	6.2	1.6	11.5	7.5	2	5.6	2.5	0.6	5.5
	ZMB 82892	25	–	22.86	–	9.68	13.49	10.81	7.32	3.6	2.5	6.37	7.4	6.5	0.5	10.4	6.6	2.2	4.6	2.4	0.8	5.3
	ZMB 82891	25	–	19.51	–	8.38	11.25	8.79	5.89	2.7	2	5.13	6.1	5.3	0.5	9.5	4.9	1.6	3.5	2.1	0.7	4
	ZMB 82898	25	–	13.68	–	5.48	7.23	5.85	3.93	1.8	1.3	2.92	4.2	3.8	0.4	7.1	3.9	1.3	2.5	1.7	0.5	3.1
	ZMB 82828	25	–	17.24	–	7.37	10.63	7.37	5.1	2.6	1.9	4.3	5.1	4.3	0.4	7.3	4.9	1.7	3.2	1.9	0.6	4
	ZMB 79241	25	–	19.3	–	8.08	11.62	8.16	5.98	3.1	2.2	5.2	6.4	5.2	0.5	10	5.7	1.8	3.9	2.3	0.7	5.5
	ZMB 82894	25	–	19.61	–	7.95	11	8.96	6.4	3	2.2	5.3	6.5	5	0.4	9.7	4.4	1.5	3.1	2.2	0.7	4.2
	ZMB 82897	25	–	18.75	–	7.94	10.14	8	6.14	2.5	2.2	4.44	5.6	4.9	0.6	9.2	5.3	1.9	3.4	2.1	0.7	4.4
	ZMB 82897 A	25	61.5	19.1	42.4	7.6	9.4	8	5.2	2.6	1.8	4.3	6.5	5.4	0.9	9	6.5	1.8	4.5	2	0.6	4
	ZMB 82900	25	–	26.18	–	10.81	13.57	11.1	8.43	4.2	3.1	7.75	8.3	7.1	1	13.8	8.2	2.8	5.4	3	1	5.9
	ZMB 82902	25	–	14.42	–	6.27	8.78	6.26	4.39	2.2	1.5	3.65	4.7	3.9	0.4	7.2	3.9	1.3	2.8	1.7	0.6	3.3
	ZMB 82890	25	–	12.01	–	5.69	7.29	5.65	4.01	1.7	1.3	3.3	4	3.5	0.5	6.3	3.1	1	2.2	1.3	0.4	3.3
	ZMB 82893	25	–	13.65	–	6.55	8.72	5.98	4.28	1.8	1.2	3	4.7	3.5	0.5	6.8	3.7	1.1	2.6	1.2	0.5	2.8
	ZMB 82888	25	–	12.84	–	5.65	7.33	4.26	4.66	1.7	1.4	2.79	3.9	3.4	0.4	6.4	3.4	1.1	2.4	1.5	0.5	3.2
	ZMB 82885	25	–	23.28	–	9.57	12.03	9.78	6.46	3.3	2.6	5.43	7	6.2	0.7	10.7	6.3	1.9	4.4	2.1	0.8	4.9
	ZMB 82886	39	74.2	24	50.2	9.9	12.1	11.4	5.5	4.5	2.7	5.1	8.5	7	2	11.4	8	1.9	6	2.9	0.6	6
	ZMB 82886 A	25	38.8	13.5	25.3	6	8.5	6.5	4	2.1	1.3	3.8	5.5	4.1	0.5	6	4.4	1.1	3.6	1.3	0.4	3.2
	ZMB 82887	36	77	27.5	49.5	10.5	12	10.5	7	3.6	2.7	6.2	9.5	7.5	1.6	13.2	8.7	2.3	6.1	2.6	0.6	5.1
	ZMB 82887 A	36	79.2	25.6	53.6	9.9	12.5	10.6	7	3.2	2.3	6.8	9.4	7.5	2	12.4	8.5	2.1	6	2.5	0.7	5.1
	ZMB 82889	26	–	23.4	–	10.2	12.7	11.1	7.6	3.4	2.5	7.4	8.5	7	1.6	12	8	2.4	5.6	2.5	0.6	5.9
	ZMB 82889 A	26	76.4	23.6	52.8	11.1	12.3	11.5	8.5	4	2.6	7.8	9.5	7.9	1.5	11.5	8.5	2	6.5	2.5	0.5	6.1
	ZMB 82901	27	–	24.1	–	9.4	12.1	8.6	6.5	3.4	2.1	5.6	8.2	6.5	1.1	11	7.4	2.1	5.1	2.4	0.6	4.5
	ZMB 82901 A	26	74.2	23.2	51	9.5	12.3	9	6.5	2.9	2.6	5.9	8.1	6.9	1.1	11	7.9	2.1	5.3	2.5	0.7	5.1
	ZMB 82901 B	25	52.9	17.6	35.3	6.5	9.6	7	5.5	2	1.6	4.4	6.4	4.9	1	8.1	6	1.6	4.3	2	0.5	3.3
N. corrugatus	ZMB 82109	25	81.2	31.6	49.6	8	12.6	10.6	6.8	3	2.3	7.1	8.1	6.4	1.1	10.5	7.8	2.5	5.4	2	0.6	6.5
	ZMB 82112	25	–	22.9	–	6.6	9	8.5	5	3	2.4	5	5.6	5	0.9	9	6.5	2	4.5	1.6	0.5	5.3
	ZMB 82115	26	69.1	25.6	43.5	8.6	10.1	9.1	5.2	2.5	1.8	5.2	7	6	1	10.5	8.5	2.5	5.2	1.9	0.5	6.4
	ZMB 82116	25	–	27.2	–	7.1	10.4	9.5	5.5	3.5	2.7	5.2	6.9	5.9	1.4	11	8.5	3.2	5.3	1.6	0.5	6.6
	ZMB 88351	25	–	21.4	–	6.7	8.6	7.9	5.8	–	–	4.8	5.8	4.5	1.1	8	6	2	3.9	1.1	0.4	4.4
S. gabonicus	ZMB 82118	25	–	6.3	–	1.9	3.5	–	1.2	–	–	1.2	2.3	1.5	0.5	3.5	1.9	0.5	1.2	0.8	0.1	1.1
	ZMB 82118 A	25	20.4	6.7	13.7	2	3.7	3.1	1.4	1	0.6	1.3	2.5	1.8	0.6	3.5	2.2	0.6	1.2	0.6	0.1	1.2
	ZMB 82830	25	–	10.4	–	4.6	5.4	–	3.2	–	–	2.9	3.5	2.4	–	–	2.4	1.3	2	1.2	0.1	2.1
	ZMB 88347	41	62.2	19	43.2	8.3	10.9	8.5	5.9	3.3	2.2	4.1	7.2	2.5	0.9	9	4.3	0.5	2.7	2.4	0.2	3.6
	ZMB 88348	25	37.5	11.8	25.7	4.5	6.6	5.1	3.8	1.9	1.4	3	4.5	2.6	1.1	6.5	3.3	1.1	2.1	1.4	0.2	2
	ZMB 88349	39	57.7	18.7	39	9.2	12.2	9	7	3.3	2.3	4.1	7.5	4.2	1.6	9.8	5.2	1.6	3.5	2	0.2	3.8
	ZMB 88350	25	–	12.9	–	5.3	6.8	–	4	–	–	3.5	5	3.2	0.8	7	4.2	1.6	2.6	1.5	0.2	2.4
	ZMB 88354	25	47.5	15.5	32	5.9	8.6	6.8	4.5	2.7	1.6	3.2	5.8	3.9	0.9	7.6	4	1.2	2.7	1.7	0.2	3
	ZMB 88355	25	48.3	16.1	32.2	6.2	8.9	7.5	5.2	2.9	1.7	3.4	6.4	3.5	0.9	8	4.1	1.2	2.8	1.9	0.2	2.9
	ZMB 88356	38	55.3	18.7	36.6	8.1	10.3	9	6.8	3.2	1.9	5	7	3.8	1.6	9	5.1	1.6	3.6	2.3	0.2	3.5
	ZMB 88357	25	36.6	11.9	24.7	5.2	6.8	5.7	4	1.9	1.3	2.8	4.5	2.7	1	6.7	3.5	1.2	2.4	1.6	0.1	2.4

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Annotated catalogue of the types of Triphoridae (Mollusca, Gastropoda) in the Natural History Museum of the United Kingdom, London

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Abstract

We revise the type specimens of 132 nominal species of worldwide Triphoridae stored in the Natural History Museum of the United Kingdom (NHMUK), London. We provide the species name in its original combination, followed by bibliographic details of the original description, the location of the known type material, the original description (and its translation when in Latin), a diagnosis and curatorial or nomenclatural notes. We illustrated most specimens in the type series in colour and with SEM imaging and we have added the original figure whenever possible. The specimens of *Triphoris alveolatus*, *T. granulatus*, *T. suturalis* and *T. verrucosus*, all A. Adams & Reeve, 1850, *T. pfeifferi* Crosse & Fischer, 1865 and *T. cucullatus* de Folin, 1867, previously considered type material, are not considered here belonging to the type series. Adams & Reeve's taxa should be considered *nomina dubia*. The name *Triphora insularum* is a manuscript name by H.E.J. Biggs who deposited "types" in the NHMUK but refrained from introducing the name due to the lack of apex of the studied material. We selected lectotypes for six species (*T. concors* Hinds, 1843, *T. maxillaris* Hinds, 1843, *T. fuscomaculata* E.A. Smith, 1904, *T. shepstonensis* E.A. Smith, 1906, *T. eupunctata* G.B. Sowerby III, 1907, and *T. rufula* Watson, 1886) to stabilize the nomenclature. Finally, we illustrate original specimens (although not types) of three species described by Turton, whose type material is lost.

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Introduction

Triphoridae is one of the mega-diverse families of marine gastropods (Bouchet et al. 2002). In a single season in Vanuatu, an expedition organized by the Muséum National d'Histoire Naturelle, Paris, collected 259 species and 70% of them were estimated to be new to science (Albano et al. 2011). The study of the material collected during other MNHN expeditions and smaller collections from other sources in the Indo-Pacific province has led to the segregation of ca 670 morphospecies (P.G. Albano and P.A.J. Bakker, unpublished). At the same time, we censused approximately 450 names of Indo-Pacific triphorids which, however, show high redundancy and are strongly biased towards the most characterised species due to colour or other morphological features. Moreover, the family Triphoridae has already shown to host a wealth of cryptic diversity: in the Mediterranean Sea, a single name (*Triphora perversa*) had been used for two centuries before Philippe Bouchet started recognizing what is now known as more than 15 species (Bouchet and Guillemot 1978; Bouchet 1985). Consequently, we felt it mandatory to review thoroughly the type specimens of the already described species to polish taxa redundancy and fix the actual meaning of the introduced names, sometimes not or poorly illustrated. This endeavour started with the revision of the triphorid types in the Museum für Naturkunde in Berlin (Albano and Bakker 2016) and in the Naturhistorisches Museum in Vienna (Albano et al. 2017) and finds here a major step forward revising 132 species preserved in the Natural History Museum of the United Kingdom, London. Our final aim is to set the scene for major taxonomic work on the hundreds of species in the Indo-Pacific province which still await formal description.

Methods

We first compiled a list of type specimens expected at the Natural History Museum based on explicit statements in the original publications. When this information was not available, we looked for the known repositories of authors' collections or information on type material or collection fate in biographic papers. PGA surveyed the collection of recognized types of Triphoridae at the NHMUK in October and December 2015. The general collection had been previously searched by BS during a visit conducted between 7 and 25 February 2000 specifically targeting Indo-Pacific taxa. The present catalogue was updated on December 31st, 2015 and includes all triphorid types encountered in the NHMUK, irrespective of their geographic origin.

The depth of treatment in this work depends on the age of the taxon (a proxy for the accuracy of descriptions and figures) and the amount of type material stored in the Museum or supposed to exist in other institutions. The species described before World War II and whose type material is stored exclusively in NHMUK are treated here in full detail. We give the species name in its original combination, followed by bibliographic details of the original description, the location of the known type material, the original description (and its translation when in Latin) and curatorial or nomenclatural notes. In some cases, the type series contains specimens clearly belonging to different species. Thus, we selected lectotypes to stabilize the nomenclature prioritizing specimens that were illustrated in the original description. Lectotype designation follows the provisions of Article 74 of the International Code of Zoological Nomenclature, 4th Edition. We also provide a diagnosis, focusing on the most significant diagnostic characters as discussed by Marshall (1983) and Albano et al. (2011). We followed a similar approach for old material whose other syntypes have not been located so far or are presumably lost (e.g. Turton). We illustrated most specimens in the type series in colour and with SEM imaging; whenever possible we have added the original figure.

A briefer treatment has been devoted to the species whose type material is known to be stored also in other institutions (e.g. Melvill, Tomlin, Verco). We list the available type material but refrained from selecting any lectotypes even if necessary because material that is more suitable may exist elsewhere. We provide comments where appropriate and fully illustrate the shells.

Species described after World War II were usually well described and illustrated in the original publications (e.g.

Kay, Kosuge, Marshall). Because plates were often in black and white, we illustrate here any type material we found, but do not provide original descriptions nor diagnoses. The Caribbean species described in the 1980s and 1990s (mostly by Rolán and co-authors) were at an even greater level, often with colour and SEM images. We do not treat them in detail, but provide inventory numbers, which were sometimes missing in the original publications.

Any citation to the International Code of Zoological Nomenclature (ICZN 1999) should be considered to its online version, which includes all recent amendments. Although it is already evident that a high degree of synonymy exists among Triphoridae, we refrain here from fully dealing with it, awaiting the study of type material in other museums to provide a single comprehensive work in this respect.

Colour photographs were taken with a Canon EOS 700D with Canon MP-E 65 mm macro lens mounted on a stand, with aperture 5.6, 100 ISO and slightly underexposed (−2/3). Images were taken at different focus levels and stacked with Helicon Focus 5.3. SEM images were taken with a Zeiss LEO 1455 VP without any coating. To avoid damage to specimens, they were not cleaned before imaging. All specimens were measured with a calliper.

Species are listed in the systematic part in alphabetic order by author name. A taxon list in alphabetical order is provided in Table 1.

Abbreviations

coll. collection
AMS Australian Museum, Sydney, Australia
BPBM Bernice P. Bishop Museum, Hawaii, USA
CUMZ Cambridge University, Museum of Zoology, Cambridge, UK
(text-)fig./figs (text-)figure/figures
MCZ Museum of Comparative Zoology, Harvard, USA
MNHN Muséum national d'Histoire naturelle, Paris, France
MNZ Museum of New Zealand, Wellington, NZ
MSIM Museum of Science and Industry, Manchester, UK
NHMUK Natural History Museum of the United Kingdom, London, UK
NMW National Museum of Wales, UK
OUMNH Oxford University Museum of Natural History, Oxford, UK
p page
pl plate
SAM South Australian Museum, Adelaide, Australia
TZM National Science Museum, Tokyo, Japan
USNM United States National Museum, Smithsonian Institution, USA

Taxonomic index

Table 1. List of treated taxa in alphabetic order, with original name, author and date and page and figure in this paper.

Taxon	Author and date	Page	Figure
abruptum, *Cerithium* (*Bittium*)	Watson, 1880	297	113
affinis, *Triphoris*	Pease, 1861	245	72
albicephala, *Metaxia*	Kay, 1979	213	43
albidus, *Triphoris*	A. Adams, 1854	165	2
alboguttata, *Viriola*	Tomlin, 1926	280	99
albovittata var. *mamillata*, *Triphora*	Verco, 1909	291	109
alexandri, *Triphora*	Tomlin, 1931	291	100
alternata, *Triphoris*	Pease, 1861	246	73
alveolatus, *Triphoris*	A. Adams & Reeve, 1850	175	10
angasi, *Triphoris*	Crosse & Fischer, 1865	180	15
apexcrassum, *Cheirodonta*	Rolán & Fernández-Garcés, 1994	255	
apicibulbus, *Triphora*	Turton, 1932	285	102
armillata, *Triphora*	Verco, 1909	287	105
aspera, *Triforis*	Jeffreys, 1885	211	42
asperrimus, *Triphoris* (*Ino*)	Hinds, 1843	184	19
atlantica, *Triforis*	E.A. Smith, 1890	256	80
atratus, *Notosinister*	Kosuge, 1962	219	51
bathyraphe, *Triforis*	E.A. Smith, 1890	256	81
bigemma, *Cerithium* (*Triforis*)	Watson, 1880	297	
bilix, *Triphoris* (*Ino*)	Hinds, 1843	185	20
brunnicephala, *Metaxia*	Kay, 1979	255	44
bubistae, *Marshallora*	Fernández-Garcés & Rolán, 1988	255	
burnupi, *Triphora*	E.A. Smith, 1910	256	82
cana, *Triphora*	Verco, 1909	288	107
cancellatus, *Triphoris* (*Ino*)	Hinds, 1843	185	21
carmelae, *Iniforis*	Rolán & Fernández-Garcés, 1993	255	
carteretensis, *Triphoris* (*Mastonia*)	Hinds, 1843	187	22
castus, *Triphoris* (*Mastonia*)	Hinds, 1843	188	23
cerea, *Trifora*	E.A. Smith, 1906	259	83
chrysolitha, *Triphora*	Kay, 1979	214	5
cingulatus, *Triphoris*	A. Adams, 1854	165	3
cingulifera, *Triphoris*	Pease, 1861	247	74
clavata, *Triphoris*	Pease, 1861	248	75
clemens, *Triphoris* (*Mastonia*)	Hinds, 1843	189	24
coetiviensis, *Triphora* (*Mastonia*)	Melvill, 1909	237	66
collaris, *Triphoris* (*Mastonia*)	Hinds, 1843	192	25
concatenata, *Trifora*	Melvill, 1904	239	67
concors, *Triphoris* (*Ino*)	Hinds, 1843	193	26
conspersus, *Triphoris*	E.A. Smith, 1875 ex A. Adams ms	261	84
convexa, *Trifora*	E.A. Smith, 1904	261	85
corrugatus, *Triphoris* (*Ino*)	Hinds, 1843	194	27

Taxon	Author and date	Page	Figure
cucullatus, *Triphoris*	de Folin, 1867	183	17
decollata, *Cheirodonta*	Rolán & Fernández-Garcés, 1994	255	
dolicha, *Triforis*	Watson, 1880	299	114
earlei, *Triphora*	Kay, 1979	214	46
elegans, *Triphoris* (*Ino*)	Hinds, 1843	194	28
espinosai, *Metaxia*	Rolán & Fernández-Garcés, 1992	255	
eupunctata, *Triphora*	G.B. Sowerby III, 1907	270	92
excelsior, *Triforis* (*Ino*)	Melvill & Standen, 1899	243	70
fallax, *Viriola*	Kay, 1979	215	47
festivus, *Triphoris*	A. Adams, 1854	166	4
flammulata, *Triphoris*	Pease, 1861	251	76
fucata, *Triphoris*	Pease, 1861	251	77
fuscescens, *Trifora*	E.A. Smith, 1904	263	86
fuscoapicata, *Triphora*	G.B. Sowerby III, 1907	273	93
fuscomaculata, *Trifora*	E.A. Smith, 1904	265	87
fuscozonata, *Triphora*	G.B. Sowerby III, 1907	273	94
gigas, *Triphoris* (*Ino*)	Hinds, 1843	196	29
gracilior, *Triforis*	E.A. Smith, 1903	265	88
granicostata, *Inella*	Kosuge, 1962	222	52
granulatus, *Triphoris*	A. Adams & Reeve, 1850	175	11
grayii, *Triphoris* (*Mastonia*)	Hinds, 1843	197	30
gutta, *Marshallora*	Fernández-Garcés & Rolán, 1988	255	
hebes, *Cerithium* (*Triforis*)	Watson, 1880	301	115
hemileuca, *Triphora*	Tomlin, 1931	282	101
hervieri, *Notosinister*	Kosuge, 1962	223	53
hinuhinu, *Iniforis*	Kay, 1979	215	48
hungerfordi, *Triphora*	G.B. Sowerby III, 1914	276	95
idoneus, *Triforis*	Melvill & Standen, 1901	245	71
immaculata, *Iniforis*	Rolán & Fernández-Garcés, 1993	255	
incerta, *Metaxia*	Fernández-Garcés & Rolán, 1988	255	
incisa, *Triphoris*	Pease, 1861	251	78
incolumis, *Triphora*	Melvill, 1918	239	68
inflata, *Cerithium* (*Triforis*)	Watson, 1880	301	
insularum, *Triphora*	Biggs, ms	179	14
interpres, *Triphora*	Melvill, 1918	242	69
isaotakii, *Euthymella*	Kosuge, 1962	223	54
iwaotakii, *Notosinister*	Kosuge, 1963	225	55
kawamurai, *Notosinister*	Kosuge, 1962	226	56
kermadecensis, *Metaxia*	Marshall, 1977	236	65
kurodai, *Isotriphora*	Kosuge, 1962	227	57
labiatus, *Triphoris*	A. Adams, 1854	168	5
laddi, *Triphora*	Kay, 1979	216	49
latilirata, *Triphora*	Verco, 1909	291	108
leucocephala, *Euthymella*	Kosuge, 1963	229	58
levukense, *Cerithium* (*Triforis*)	Watson, 1880	303	116
lilaceocinctus, *Triforis*	E.A. Smith, 1903	267	89
maculosus mcmichaeli, *Cautor* (*Cautor*)	Kosuge, 1962	229	59
mariangelae, *Marshallora*	Fernández-Garcés & Rolán, 1988	255	
maxillaris, *Triphoris* (*Ino*)	Hinds, 1843	198	31
micans, *Triphoris* (*Ino*)	Hinds, 1843	200	32
millepunctatus, *Notosinister*	Kosuge, 1962	229	60
monilifer, *Triphoris* (*Mastonia*)	Hinds, 1843	200	33
nichupte, *Marshallora*	Rolán & Cruz-Abrego, 1995	255	
nigrofuscus, *Triphoris*	A. Adams, 1854	170	6
novapostrema, *Triphora*	Verco, 1910	292	110
osclausum, *Triphora*	Rolán & Fernández-Garcés, 1995	255	
pagodus, *Triphoris* (*Ino*)	Hinds, 1843	201	34
pelorcei, *Iniforis*	Rolán & Fernández-Garcés, 2009	255	
pfeifferi, *Triphoris*	Crosse & Fischer, 1865	180	16
picturatus, *Triforis*	G.B. Sowerby III, 1901	276	96
princeps, *Triphora*	G.B. Sowerby III, 1904	277	97
pseudothomae, *Iniforis*	Rolán & Fernández-Garcés, 1993	255	
pulchellus, *Triphoris*	A. Adams, 1854	170	7
pura, *Triforis*	E.A. Smith, 1903	269	90
retusa, *Triphora*	Turton, 1932	285	103
roseus, *Triphoris* (*Mastonia*)	Hinds, 1843	203	35
ruber, *Triphoris* (*Mastonia*)	Hinds, 1843	203	36
rufanensis, *Triphora*	Turton, 1932	285	104
rufotinctus, *Notosinister*	Kosuge, 1963	230	61
rufula, *Triforis*	Watson, 1886	304	117
scitulus, *Triphoris*	A. Adams, 1854	172	8
sculptus, *Triphoris* (*Ino*)	Hinds, 1843	206	37
shepstonensis, *Trifora*	E.A. Smith, 1906	269	91
smithi, *Triphora*	G.B. Sowerby III, 1904	280	98
spica, *Triphora*	Verco, 1909	293	111
spina, *Triphora*	Verco, 1909	295	112
squalida, *Mastonia*	Kosuge, 1962	231	62
subfenestra, *Inella*	Kosuge, 1962	233	63
suturalis, *Triphoris*	A. Adams & Reeve, 1850	177	12
taenialba, *Isotriphora*	Rolán & Espinosa, 1994	255	
tasmanica var. *lilacina* var. *aureovincta*, *Triphora*	Verco, 1910	288	106
tessellatus, *Notosinister*	Kosuge, 1963	234	64
thaanumi, *Triphora*	Kay, 1979	217	50
tristis, *Triphoris* (*Mastonia*)	Hinds, 1843	206	38
triticea, *Triphoris*	Pease, 1861	251	79
variegatus, *Triphoris*	A. Adams, 1854	173	9
verdensis, *Monophorus*	Fernández-Garcés & Rolán, 1988	255	
verrucosus, *Triphoris*	A. Adams & Reeve, 1850	178	13
vitreus, *Triphoris* (*Sychar*)	Hinds, 1843	206	39
vittatus, *Triphoris* (*Ino*)	Hinds, 1843	208	40
vulpinus, *Triphoris* (*Mastonia*)	Hinds, 1843	208	41

Systematic list of taxa

Species described by A. Adams

Arthur Adams described ten species attributed to Triphoridae. He described nine species on the material of the Cuming collection (A. Adams 1854) which is stored in the NHMUK (Dance 1966). We found the type material of all of them. Although the nineteenth volume of the Proceedings of the Zoological Society of London reports 1851 on the frontispiece, its actual date of publication is 1854 (Sclater 1893). One of the nine species, *Triphoris vestalis* A. Adams, 1854, is a Cerithiopsidae (Rolán and Fernández-Garcés 2008).

The tenth species, *Triforis macandraeae* A. Adams, 1856 is a Newtoniellidae and is not discussed further. In the NHMUK, two worn specimens are present and labelled as "possible type material" but do not bear original labels. Two nicely preserved specimens of *T. macandraeae* with original labels are in the R. MacAndrew collection in the Museum of Zoology of the University of Cambridge (catalogue number I.100200, Fig. 1).

Figure 1. *Triphoris macandraeae* A. Adams, 1856. Syntype CUMZ I.100200. Photo courtesy M. Lowe. Scale bar: 5 mm.

Triphoris albidus A. Adams, 1854

Figure 2

Triphoris albidus Adams 1854: 278, not illustrated.

Type locality. Honduras.

Type material. Syntypes: NHMUK 196563 and 196564: 1 specimen each, Honduras (coll. H. Cuming).

Original description. *T. testâ subulato-pyramidali, albidâ, nitidâ; anfractibus planulatis, subimbricatis, granosoclathratis, granis oblongis, serie granorum inferiore prominulâ, anfractu ultimo basi fulvo; canali brevi, subrecurvo.*

Hab. Honduras (Dyson). Mus. Cuming.

A solid, white, shining, pyramidal species, with oblong granules disposed in three series on each whorl.

Translation of the Latin text. Whitish and clean shell with a pyramidal-subulate shell; flat-sided whorls, subimbricated, clathrated with oblong granules whose inferior series is slightly prominent, base of the last whorl reddish; short anterior siphonal canal slightly curved.

Diagnosis. Syntypes are 9.6 and 8.1 mm high. Shell conical, with rather flat sides. Teleoconch of ca 12 whorls. Three spiral cords are present, the second weaker at the beginning but visible since the early teleoconch. Such cords are large, flat, adorned by elongated and coalescent granules, which become more distinct on the peristome. Base with three additional granulated cords. Apex not present in the type specimens. Colour whitish with brown base.

Remarks. The syntypes lack the apex, but Rolán and Fernández-Garcés (1995) illustrated a morphologically similar specimen with a multispiral protoconch, sculptured by two spiral keels and axial riblets.

Triphoris cingulatus A. Adams, 1854

Figure 3

Triphoris cingulatus Adams 1854: 279, not illustrated.

Type locality. Red Sea.

Type material. Syntypes: NHMUK 196567: 1 specimen, Red Sea (coll. H. Cuming); NHMUK 196568/1–3: 3 specimens, Red Sea (coll. H. Cuming).

Additional material. NHMUK 1878.1.28.452: 1 specimen (coll. H. Adams).

Original description. *T. testâ elongato-pyramidali, cinereâ; anfractibus sexdecim ad octodecim, spiraliter tricingulatis, cingulâ medianâ minore, interstitiis carinarum longitudinaliter valde striates.*

Hab. Red Sea (Rüppell). Mus. Cuming.

An ashy-grey species, with three smooth keels on each whorl, and the interstices strongly striated: somewhat similar to the *T. corrugatus* of Hinds.

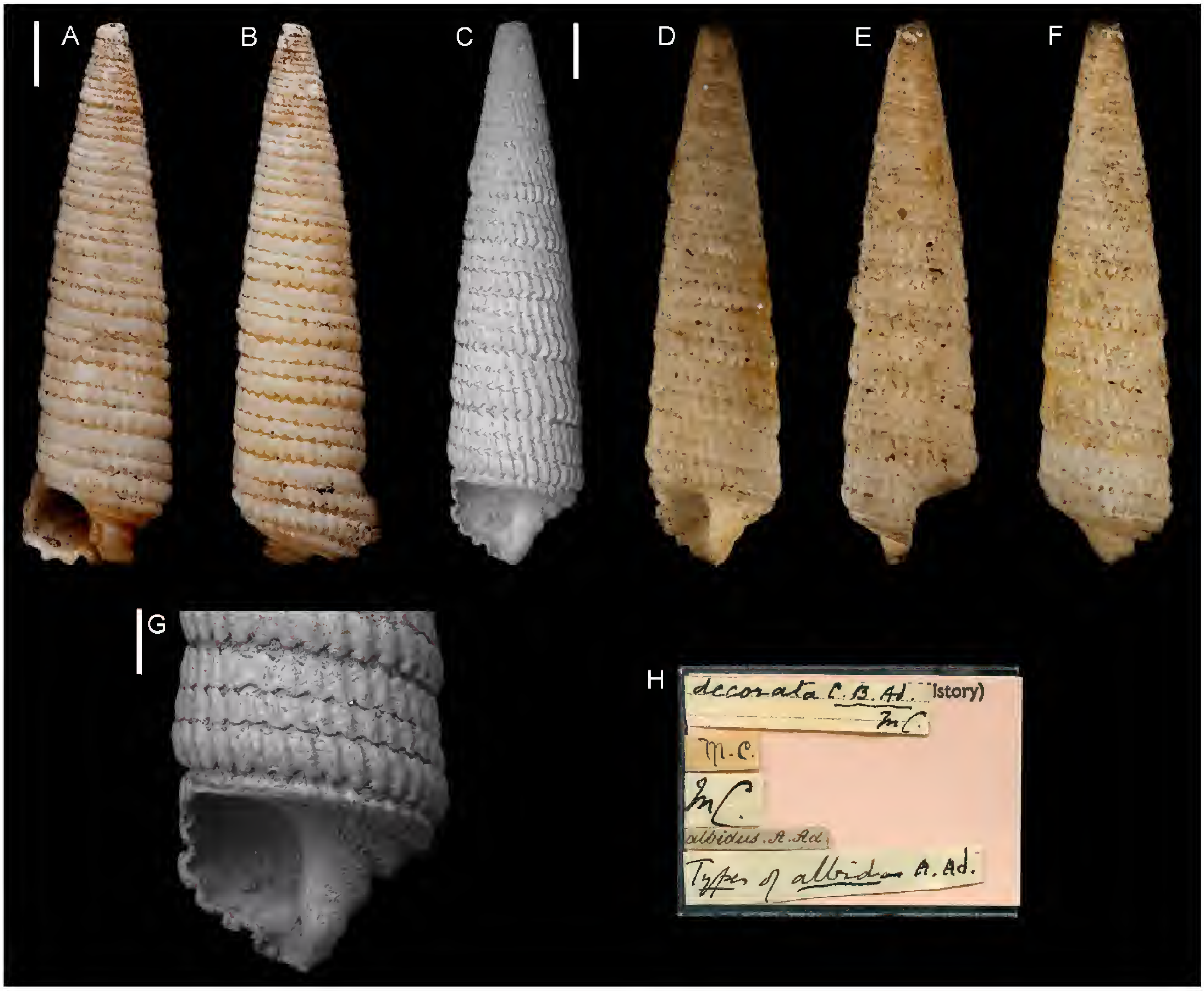

Figure 2. *Triphoris albidus* A. Adams, 1851, Honduras, coll. H. Cuming. **A, B** Syntype NHMUK 196563: front (**A**), side (**B**). **C–G** Syntype NHMUK 196564: front (**C, D**), side (**E**), back (**F**), aperture (**G**). **H** Original labels. Scale bars: **A–F**: 1 mm; **G**: 0.5 mm.

Translation of the Latin text. Elongate-pyramidal shell, ash-gray; sixteen to eighteen whorls with three spiral cords whose intermediate is smaller, interstices among carinas strongly axially striated.

Diagnosis. Syntypes ranging in size from 9.6 to 14.4 mm. A slender conical shell with flat sides. Teleoconch of 15–20 whorls, with two strong smooth spiral cords and a weakly granulated third in between, which appears as a fine thread in the early teleoconch. Fine threads are visible between the cords. No complete peristome is present among the studied material, but the specimen from the H. Adams collection shows additional smooth spiral cords (Fig. 3K). Siphonal canal well developed. The base bears one strong weakly granulated additional spiral cord, followed by a weak thread. Another weak thread runs from the columella on the siphonal canal. The protoconch is present in a single paratype (Fig. 3J); it is poorly preserved but clearly multispiral, possibly with two spiral keels on the lower whorls. Spiral cords greyish, with brown interspaces, protoconch and base.

Remarks. A label accompanying lot NHMUK 1878.1.28.452 specifies that this is not a type specimen "fide Dance, 1965". Indeed, this specimen comes from the H. Adams collection and, thus, is not from the original series of the Cuming collection.

Triphoris festivus A. Adams, 1854

Figure 4

Triphoris festivus Adams 1854: 278, not illustrated.

Type locality. Port Lincoln, Australia.

Type material. Lectotype: NHMUK 196559, designated by Marshall (1983) (coll. H. Cuming). Paralectotype: NHMUK 196560: 1 specimen, Port Lincoln, Australia (coll. H. Cuming).

Original description. *T. testâ pyramidali, basi planâ fuscâ, albidâ, fasciis fuscis interruptis, transversis, ornatâ;*

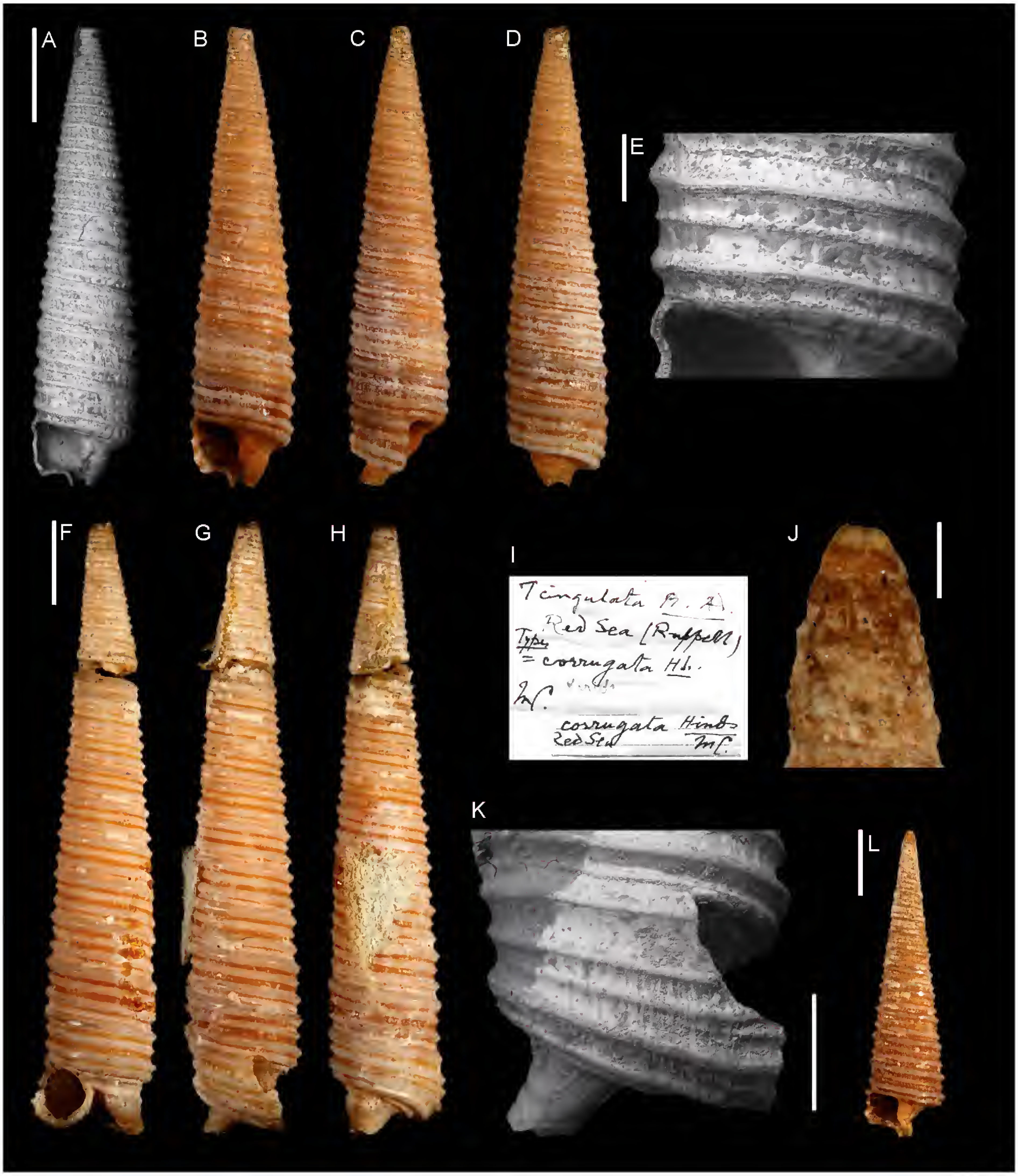

Figure 3. *Triphoris cingulatus* A. Adams, 1854. **A–E** Syntype NHMUK 196567, Red Sea, coll. H. Cuming: front (**A, B**), side (**C**), back (**D**), last whorl (**E**). **F–H, K** Specimen ex coll. H. Adams, NHMUK 1878.1.28.452: front (**F**), side (**G**), back (**H**), peristome (**K**). **I** Original label. **J, L** Syntype NHMUK 196568/1, Red Sea, coll. H. Cuming: protoconch (**J**), front (**L**). Scale bars: **A–D, F–H**: 2 mm; **E**: 0.5 mm; **J**: 0.1 mm; **K, L**: 1 mm.

anfractibus planis, cingulis duabus granorum instructis; interstitiis valde punctatis.

Hab. Port Lincoln. Mus. Cuming.

A small prettily-marked species, with two rows of granules on each whorl, and the interstices deeply punctured.

Translation of the Latin text. Pyramidal shell with a flat dark base, whitish with dark interrupted spiral bands; flat whorls with two rows of granules; interstices deeply punctured.

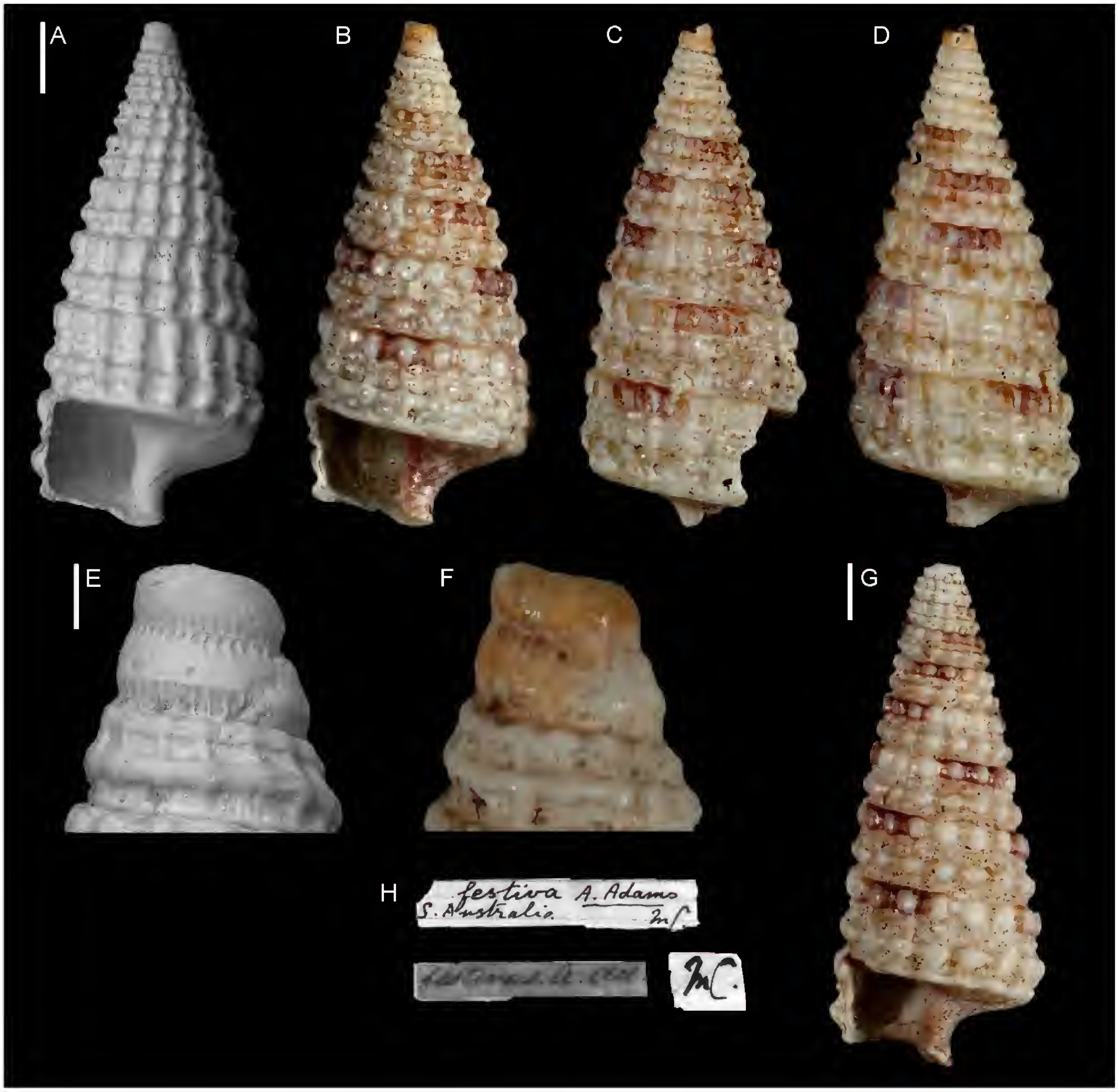

Figure 4. *Triphoris festivus* A. Adams, 1851, Port Lincoln, S. Australia, coll. H. Cuming. **A–F** Lectotype NHMUK 196559: front (**A–B**), side (**C**), back (**D**), protoconch (**E–F**). **G** Paralectotype, NHMUK 196560: front (**G**). **H** Original labels. Scale bars: **A–D**, **G**: 0.5 mm; **E, F**: 0.1 mm.

Diagnosis. Lectotype and paralectotype 3.2 mm and 4.4 mm high, respectively, but both specimens are subadults without a fully developed last whorl. Shell conical with flat sides. Type specimens of eight whorls, an underestimate due to their subadult stage. Each whorl bears two main spiral cords with well-defined tubercles; from the sixth whorl, a fine cord runs between them. Orthocline axial ribs are present and strong. The peristome, the sinuses, the siphonal canal and the base are missing in both type specimens. The lectotype bears the last whorl and half of the protoconch which is clearly multispiral, adorned by two spiral keels and brownish in colour. The teleoconch has a white background. Beginning on the third whorl, brown blotches are present on the first spiral cord.

Remarks. In the same box, a third vial is present with a small worn specimen which is not this species, as already noted by Peter Dance in a handwritten annotation in 1965. The lectotype inventory number 16559 in Marshall (1983) is a mistyping.

Triphoris labiatus A. Adams, 1854

Figure 5

Triphoris labiatus Adams 1854: 279, not illustrated.

Type locality. Sydney, Australia.

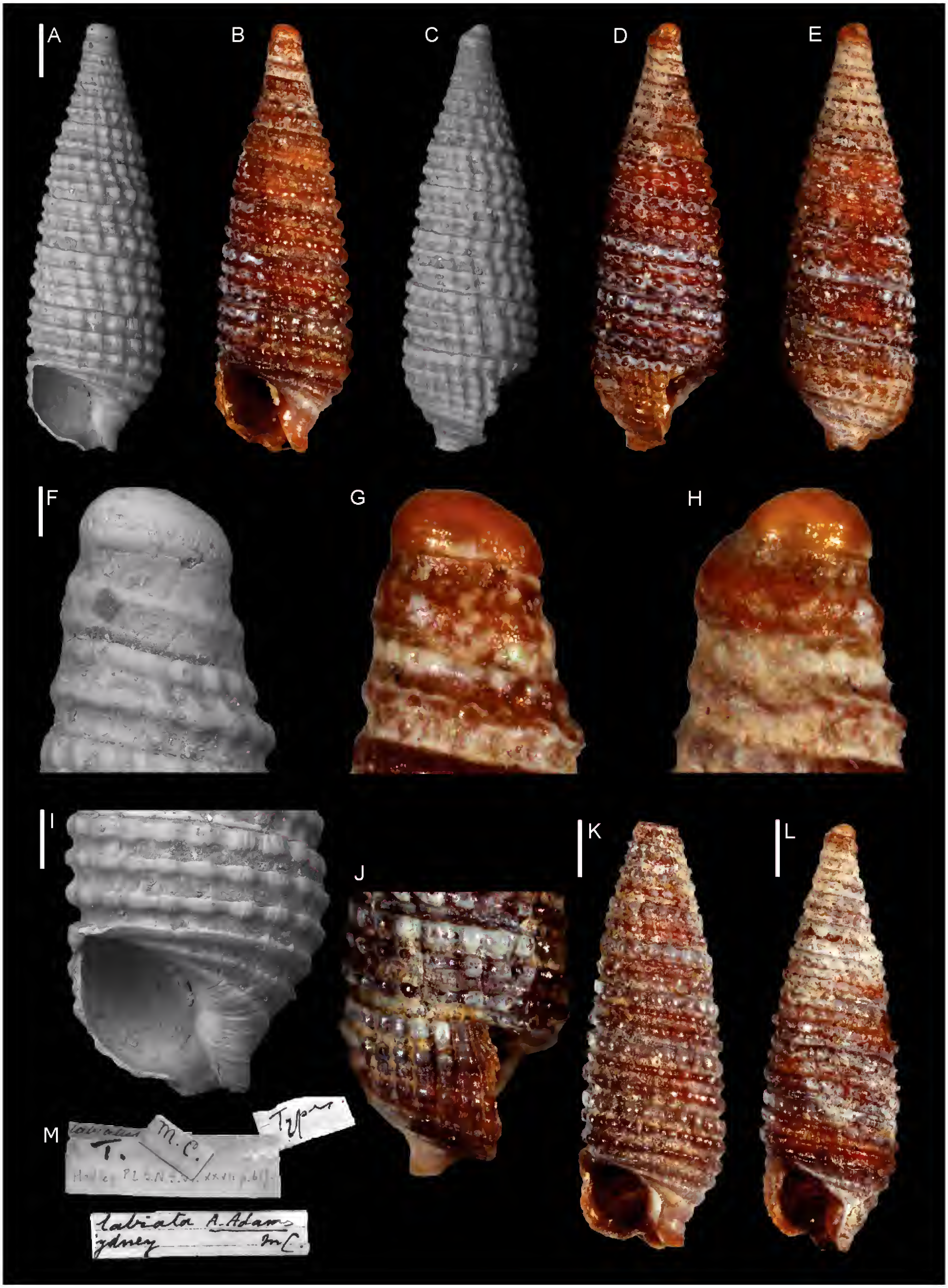

Figure 5. *Triphoris labiatus* A. Adams, 1851, Sydney, Australia, coll. H. Cuming. **A–I** Lectotype NHMUK 196569: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F–H**), aperture (**I**). **J–L** Paralectotypes, NHMUK 196570/1–2: paralectotype 1 peristome (**J**) and front (**K**), paralectotype 2 (**L**). **M** Original labels. Scale bars: **A–E, K–L**: 0.5 mm; **F–H**: 0.1 mm; **I**: 0.3 mm.

Type material. Lectotype: NHMUK 196569, designated by Marshall (1983) (coll. H. Cuming). Paralectotypes: NHMUK 196570/1–2: 2 specimens, Sydney, Australia (coll. H. Cuming).

Original description. *T. testâ subulato-pyramidali, nigro-fuscâ, in medio tumidâ, spirâ apice obtuso; anfractibus 10, planulatis, triseriatim granuloso-carinatis, suturis concavo-impressis; labro reflexo, dilatato, albido; canali brevi, subrecurvo.*

Hab. Sydney, under stones, low water (Mr. Strange). Mus. Cuming.

A small, nearly black shell, with the outer lip dirty white or pale fuscous.

Translation of the Latin text. Subulate-pyramidal shell, nearly black, swollen in the middle, obtuse apex; ten whorls nearly flat with three granulated carinas, suture concave; reflexed, swollen, whitish lip; short anterior slightly bent siphon.

Diagnosis. Lectotype 4 mm high. Cyrtoconoid profile with flat sides. Teleoconch of nine whorls, with three spiral cords; the second cord appears on the third whorl between the other two and is initially faint but becomes as strong as the others on the penultimate whorl. Axial sculpture between the cords weak. Paralectotype A has a complete peristome (Fig. 5J) showing no posterior sinus and additional spiral cords. The base has three weakly sculptured cords. The protoconch is paucispiral, of one whorl and a poorly distinct transition to teleoconch; the protoconchs in the type series are worn, but the lectotype one apparently bears several fine spiral threads. Shell brown, with the tubercles of the first spiral row lighter or grey.

Remarks. The protoconch of the specimen illustrated by Marshall (1983: fig. 32C) has two whorls which bear two strong keels, while the lectotype has a single whorl and fine threads are clearly visible above the suture (Fig. 5F).

Triphoris nigrofuscus A. Adams, 1854

Figure 6

Triphoris nigrofuscus Adams 1854: 278, not illustrated.

Type locality. Sydney, Australia.

Type material. Lectotype: NHMUK 196557, designated by Marshall (1983) (coll. H. Cuming). Paralectotypes: NHMUK 196558: 1 specimen, Sydney, Australia (coll. H. Cuming).

Original description. *T. testâ pyramidali, nigro-fuscâ; anfractibus planis, triseriatim graulatis, granulis aequalibus, confertis, anfractuum suturis impressis, basi convexâ.*

Hab. Sydney, low water, under stones (Mr. Strange).

A black-brown species, with three rows of regular, equal sized granules on each whorl.

Translation of the Latin text. Pyramidal shell, dark brown; flat whorls with three rows of equal sized dense granules, whorls with impressed sutures, convex base.

Diagnosis. Lectotype 6.7 mm high. Shell conical with rather flat whorls. Teleoconch of ten whorls, with three strong spiral cords forming nodules at the intersection with the orthocline axial ribs. Such cords are visible starting on the first whorl. A suprasutural smooth cord is visible in the lower half of the shell. Axial riblets are visible between main ribs on the last whorls. No type specimen bears a complete peristome to allow observation. Siphonal canal short; base with two smooth spiral cords. Paucispiral protoconch of two whorls, bearing two strong spiral keels and equally strong spaced axial ribs. Background teleoconch colour brown, with lighter to pearly grey tubercles. Protoconch brown.

Triphoris pulchellus A. Adams, 1854

Figure 7

Triphoris pulchellus Adams 1854: 278, not illustrated.

Type locality. Not reported.

Type material. Syntypes: NHMUK 196556: 1 specimen, unknown locality (coll. H. Cuming).

Original description. *T. testâ subulato-pyramidali, in medio tumidâ fuscâ, serie moniliformi albo ornatâ; anfractibus convexiusculis, triseriatim granuloso-carinatis; granorum serie inferiore prominulâ, superiore multo minore; aperturâ rotundatâ, constrictâ; canali brevi, recurvo.*

Hab. —? Mus. Cuming.

A handsome brown species with a white series of bead-like granules at the lower part of each whorl.

Translation of the Latin text. Subulate-pyramidal shell, tumid in the middle, brown with a white series of bead-like granules; whorls a little convex, with three rows of granulated carinas; granules of the lower row prominent, those of the upper much less prominent; aperture rounded, contracted, anterior siphonal canal short, bent.

Diagnosis. Syntype 5.8 mm high. Shell conical with flat whorls. Teleoconch of 12 whorls, with three spiral cords forming nodules at the intersection with slightly prosocline axial ribs. The second spiral cord appears at mid-shell height and is very narrow. Between major spiral cords, numerous fine threads are visible. A narrow, smooth, suprasutural cord is visible. Peristome not fully

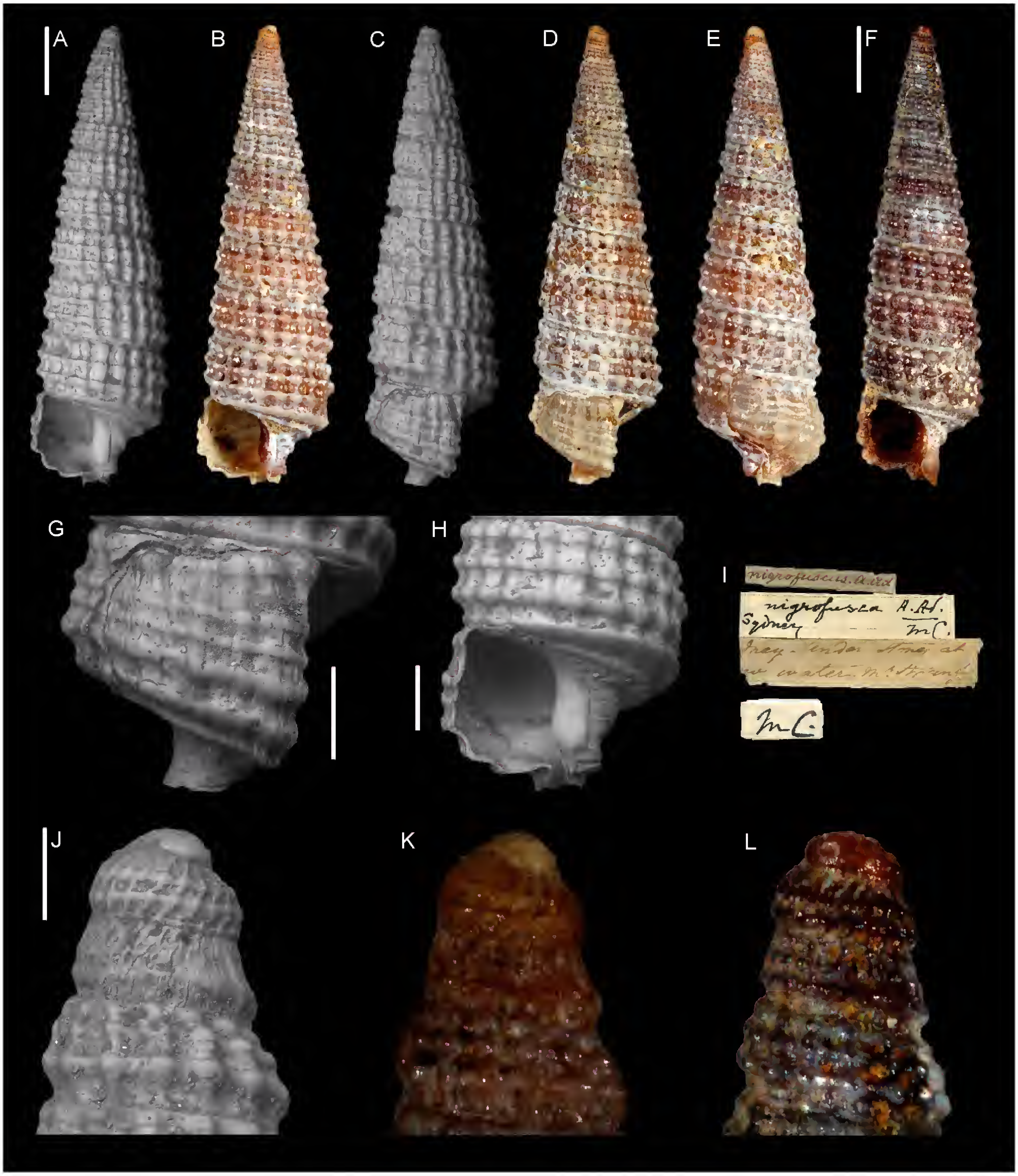

Figure 6. *Triphoris nigrofuscus* A. Adams, 1851, Sydney, Australia, coll. H. Cuming. **A–E, G, H, J, K** Lectotype NHMUK 196557: front (**A, B**), side (**C, D**), back (**E**), peristome (**G**), aperture (**H**), protoconch (**J, K**). **F, L** Paralectotype, NHMUK 196558: front (**F**), protoconch (**L**). **I** Original labels. Scale bars: **A–F**: 1 mm; **G, H**: 0.5 mm; **J–L**: 0.2 mm.

grown on the holotype, but bears at least an additional spiral cord between the second and the third. Siphonal canal short. The base bears two additional smooth spiral cords. Protoconch not present in the holotype, but remains of its last whorl suggest a multispiral protoconch. Teleoconch brown, first teleoconch whorl and spiral cord whitish.

Remarks. It has been considered a Caribbean species and a synonym of *Similiphora intermedia* (C.B. Adams, 1850) by Rolán and Fernández-Garcés (2008). However, the species illustrated as *S. intermedia* by Rolán and Fernández-Garcés (1995) is very different in sculpture and colour. The range of origin of this species remains uncertain.

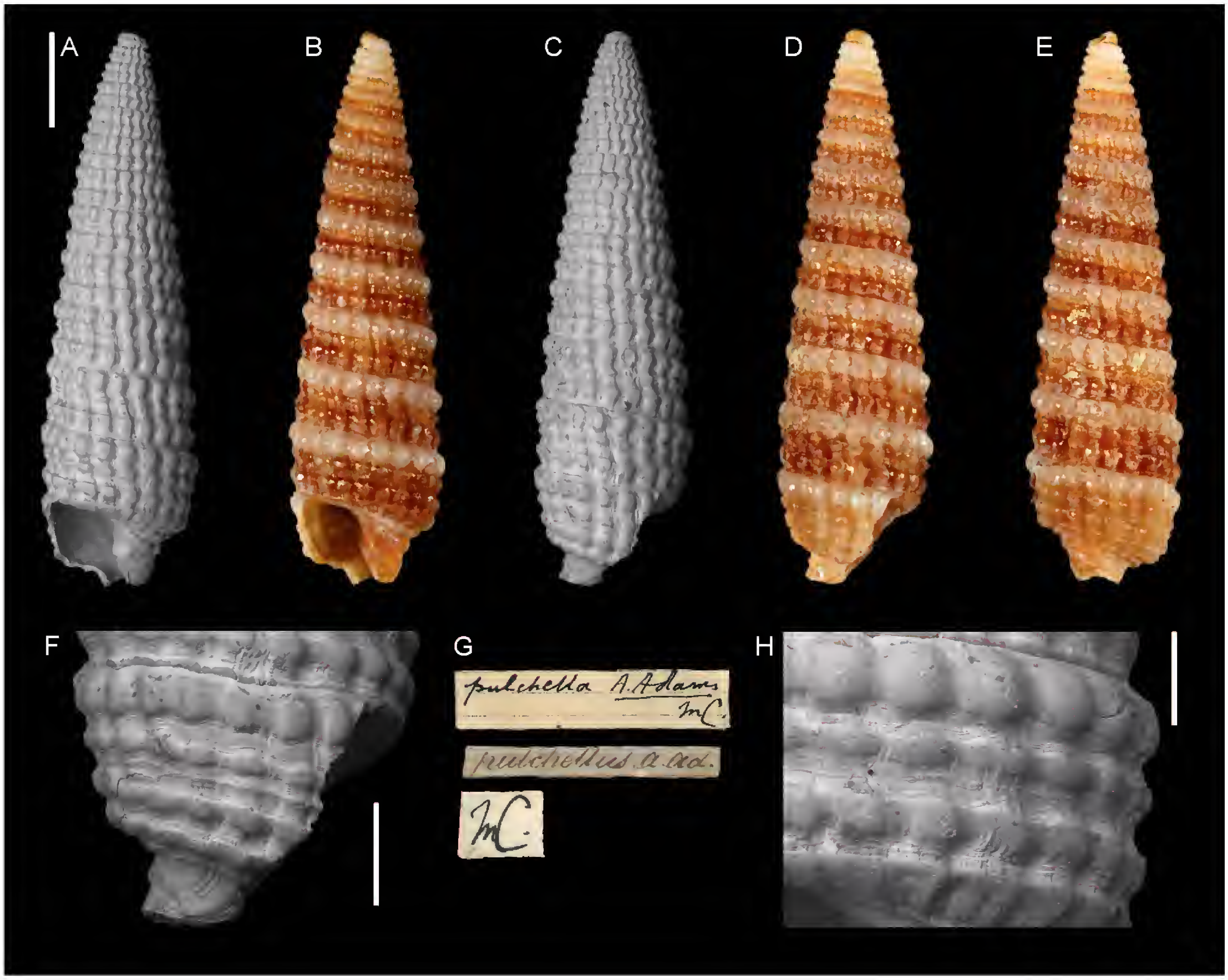

Figure 7. *Triphoris pulchellus* A. Adams, 1851, unknown locality, coll. H. Cuming. **A–F**, **H** Syntype NHMUK 196556: front (**A**, **B**), side (**C**, **D**), back (**E**), peristome (**F**), microsculpture (**H**). **G** Original labels. Scale bars: **A–E**: 1 mm; **F**: 0.5 mm; **H**: 0.3 mm.

Triphoris scitulus A. Adams, 1854

Figure 8

Triphoris scitulus Adams 1854: 278, not illustrated.

Type locality. Port Lincoln, Australia.

Type material. Lectotype: NHMUK 196561, designated by Marshall (1983) (coll. H. Cuming). Paralectotypes: NHMUK 196562/1–2: 2 specimens, Port Lincoln, Australia (coll. H. Cuming).

Original description. *T. testâ subulato-pyramidali, albidâ, nitidâ, subpellucidâ, suturis rufo-tinctis; anfractibus convexiusculis, cingulis tribus nodorum ornatis, cingulâ medianâ majore moniliformi, nodorum interstitiis fuscis, anfractu ultimo basi fusco; canali brevi, aperto.*

Hab. Port Lincoln. Mus. Cuming.

A semipellucid, white and brown species, with the middle row of nodules very prominent.

Translation of the Latin text. Subulate-pyramidal shell, light-coloured, near transparent, reddish sutures; whorls a little convex, with three nodulose spiral cords whose moniliform median is larger, brown interspaces among nodules, the last whorl with brown base; open anterior short siphonal canal.

Diagnosis. Lectotype 4.9 mm high. Shell conical, with flat sides. Teleoconch of 12 whorls with three spiral cords with strong nodules at the intersection with prosocline axial ribs. The second cord appears at mid shell height and is very narrow. The third cord is more prominent than the others and gives the shell a distinct profile. A smooth suprasutural cord is visible, as fine axial threads between the main ribs. Peristome with a shallow posterior sinus and no additional spiral cords. Siphonal canal short. The base has one additional smooth cord. Multispiral protoconch of three whorls; the first with numerous fine granules, whereas the following two are smooth with the exception of a series of elongated supra- and subsutural granules. Teleoconch and protoconch hyaline, with brown base.

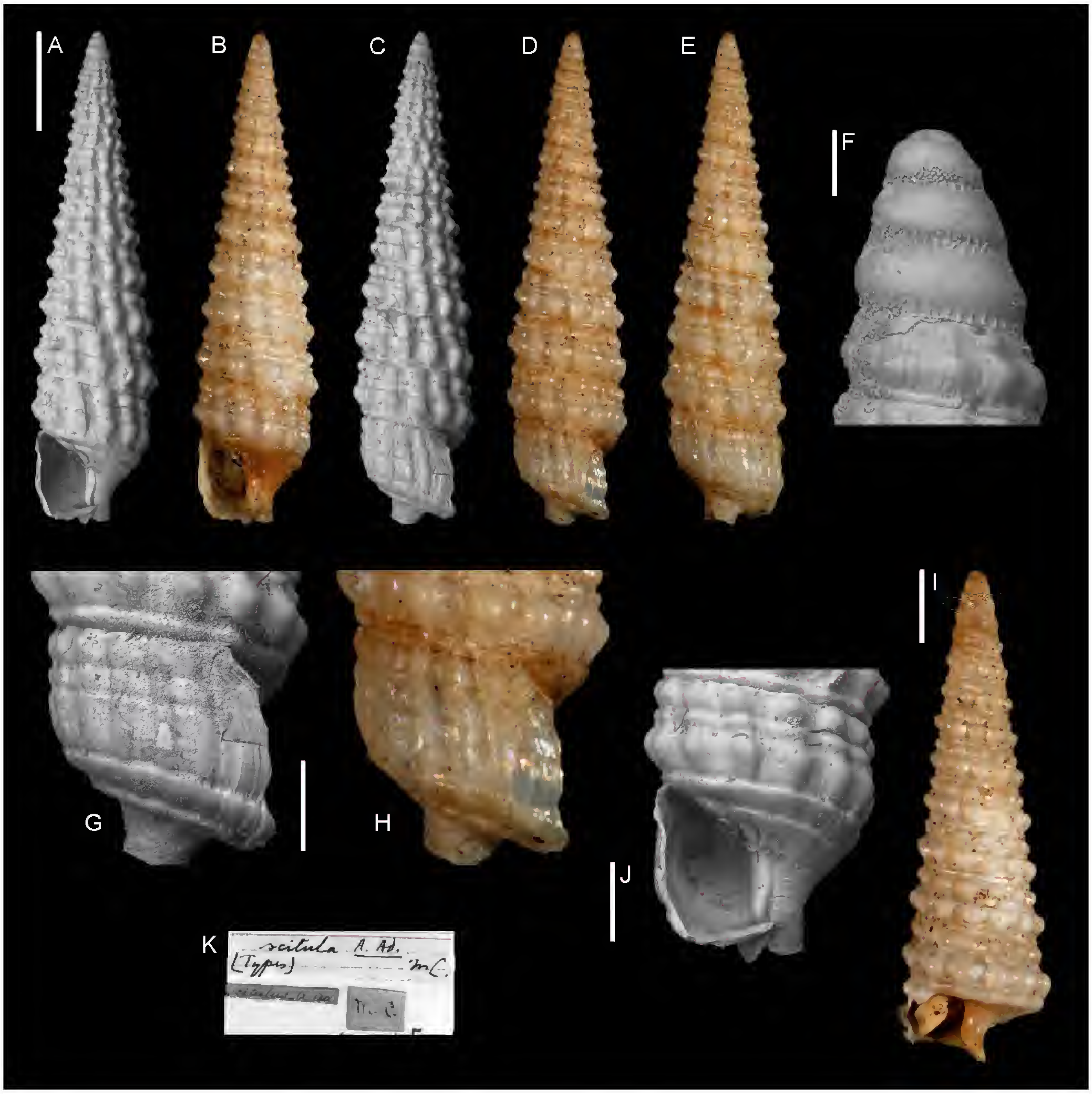

Figure 8. *Triphoris scitulus* A. Adams, 1851, Port Lincoln, S. Australia, coll. H. Cuming. **A–H, J** Lectotype NHMUK 196561: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F**), peristome (**G, H**), aperture (**J**). **I** Paralectotype, NHMUK 196562/1: front (**I**). **K** Original labels. Scale bars: **A–E**: 1 mm; **F**: 0.1 mm; **G–H, J**: 0.4 mm; **I**: 0.5 mm.

Remarks. *Triphoris pfeifferi* Crosse & Fischer, 1865 should be considered a junior synonym (see p. 180) as already suggested by Marshall (1983).

Triphoris variegatus A. Adams, 1854

Figure 9

Triphoris variegatus Adams 1854: 277–278, not illustrated.

Type locality. "St. John's", British Virgin Islands.

Type material. Syntypes: NHMUK 196554: 1 specimen, and NHMUK 196555/1–4: 4 specimens, both St. John's, West Indies, British Virgin Islands (coll. H. Cuming).

Original description. *T. testâ subulato-pyramidali, in medio tumidâ, albâ, maculis triangularibus rufo-fuscis variegatâ; anfractibus planulatis, triseriatim granulates, granis aequalibus, interstitiis punctatis, suturis impressis; canali brevi, apertâ.*

Hab. St. John's. Mus. Cuming.

A large variegated species, somewhat resembling in general appearance *T. ornatus*, Desh.

Translation of the Latin text. Subulate-pyramidal shell, swollen in the middle, white, variegated with triangular dark red spots; flat-sided whorls, three series of equal-sized granules, punctate interstices, impressed sutures; open anterior short siphonal canal

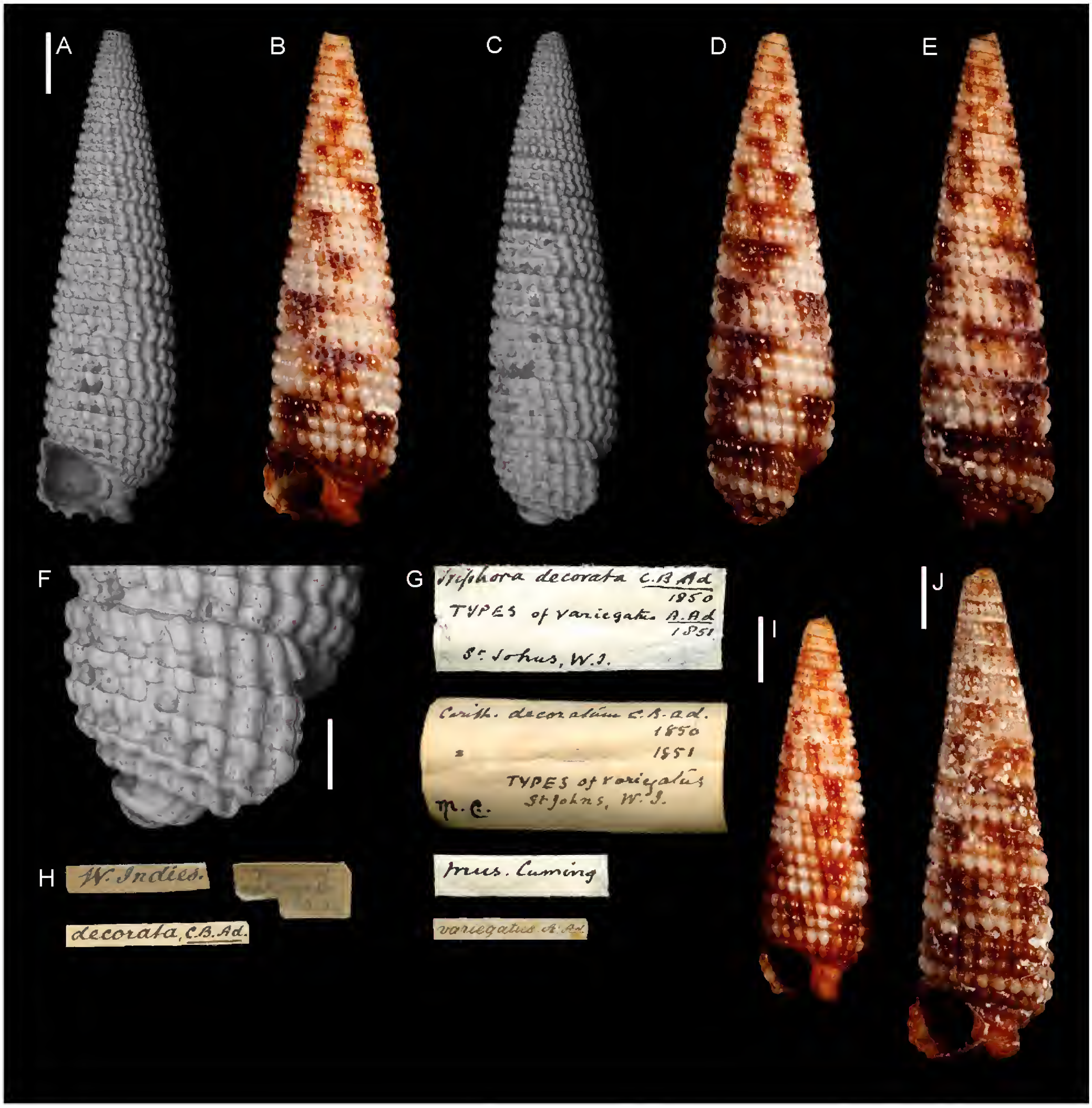

Figure 9. *Triphoris variegatus* A. Adams, 1851, St. John's, West Indies, coll. H. Cuming. **A– F** Syntype NHMUK 196554: front (**A, B**), side (**C, D**), back (**E**), peristome (**F**). **G, H** Original labels. **I, J** Syntypes NHMUK 196555/1–4. Scale bars: **A–E, I, J**: 1 mm; **F**: 0.5 mm.

Diagnosis. Syntype height ranging from 5.9 to 7.9 mm. Shell conical with flat sides. Teleoconch of 12 whorls with three equally strong spiral cords which bear tubercles at the intersection with slightly prosocline axial ribs. The second cord starts at the fifth whorl in the lectotype and is initially narrow. Numerous fine spiral threads are present between the main cords. The peristome bears an initial additional spiral cord between the second and the third, very faint. Siphonal canal short. The base bears three additional granulated cords. Protonch absent in the type series. Teleoconch white with large brown blotches, base brown.

Species described by A. Adams and L.E. Reeve

Arthur Adams and Lovell Reeve (1850) described eight species of Triphoridae based on the material acquired during the voyage of the ship "Samarang". The relevant results were published between 1848 and 1850, but the pages on Triphoridae were published in 1850 (Sherborn 1922; Trew 1992). A ninth species, *Triphoris dextroversus*, is a Cerithiopsidae because of its dextral coiling and sculpture and is indeed the type species of the genus *Seila* A. Adams, 1861.

Edward Belcher was the commander of the "Samarang" and his collection was auctioned in 1877 (Tomlin

1941). The Reverend Lombe-Taylor and Hugh Cuming were among the buyers and both collections eventually ended up in the NHMUK. In its type collection, we found material of *T. alveolatus*, *T. granulatus*, *T. suturalis*, and *T. verrucosus*, although we have serious doubts that any of these specimens are syntypes. No specimens of *T. gemmulatus*, *T. nodiferus*, *T. pyramidalis*, and *T. speciosus* were found in the type collection; the general collection should be further inspected in this respect.

A note of caution must be added for the type localities. The term "China Sea" has been proved to be inaccurate in multiple cases (Carpenter 1857; Hertlein and Strong 1947, 1950; Petit 2007; Herbert 2013) and should be treated with caution for the triphorids as well.

Triphoris alveolatus Adams & Reeve, 1850

Figure 10

Triphoris alveolatus Adams and Reeve 1850: 45, pl. 11, fig. 30a, b.

Type locality. "China Sea".

Type material. Not found, see remarks.

Original description. *Triph. testâ elongato-pyramidali, anfractibus viginti ad quatnor et viginti, planulatis, spiraliter triseriatim liratis, lirarum interstitiis clathratis; intus extusque fuscâ.*

Hab. China Sea.

The whorls of this species are flattened and deeply latticed throughout. The aperture is incomplete.

Translation of the Latin text. Triphorid with an elongated-pyramidal shell of 20 to 24 plain whorls, three latticed spiral rows; brown in colour.

Hab. China Sea

Remarks. The two specimens preserved in the NHMUK (196515 and 196516) and belonging to the Cuming collection cannot be considered syntypes. The original description, as well as the original figure (Fig. 10G), describe a specimen with an incomplete aperture, in contrast to the specimen illustrated in Figure 10A–C. Moreover, the original description refers to a shell with 20 whorls, while both specimens found have 9–12 teleoconch whorls; specimen in Figure 10D has also a large paucispiral protoconch in contrast to the elongated and pointed profile of the original figure which suggests a multispiral protoconch. At present, *T. alveolatus* should be considered a *nomen dubium*.

Triphoris granulatus Adams & Reeve, 1850

Figure 11

Triphoris granulatus Adams and Reeve 1850: 46, pl. 11, fig. 33a, b.

Type locality. "China Sea".

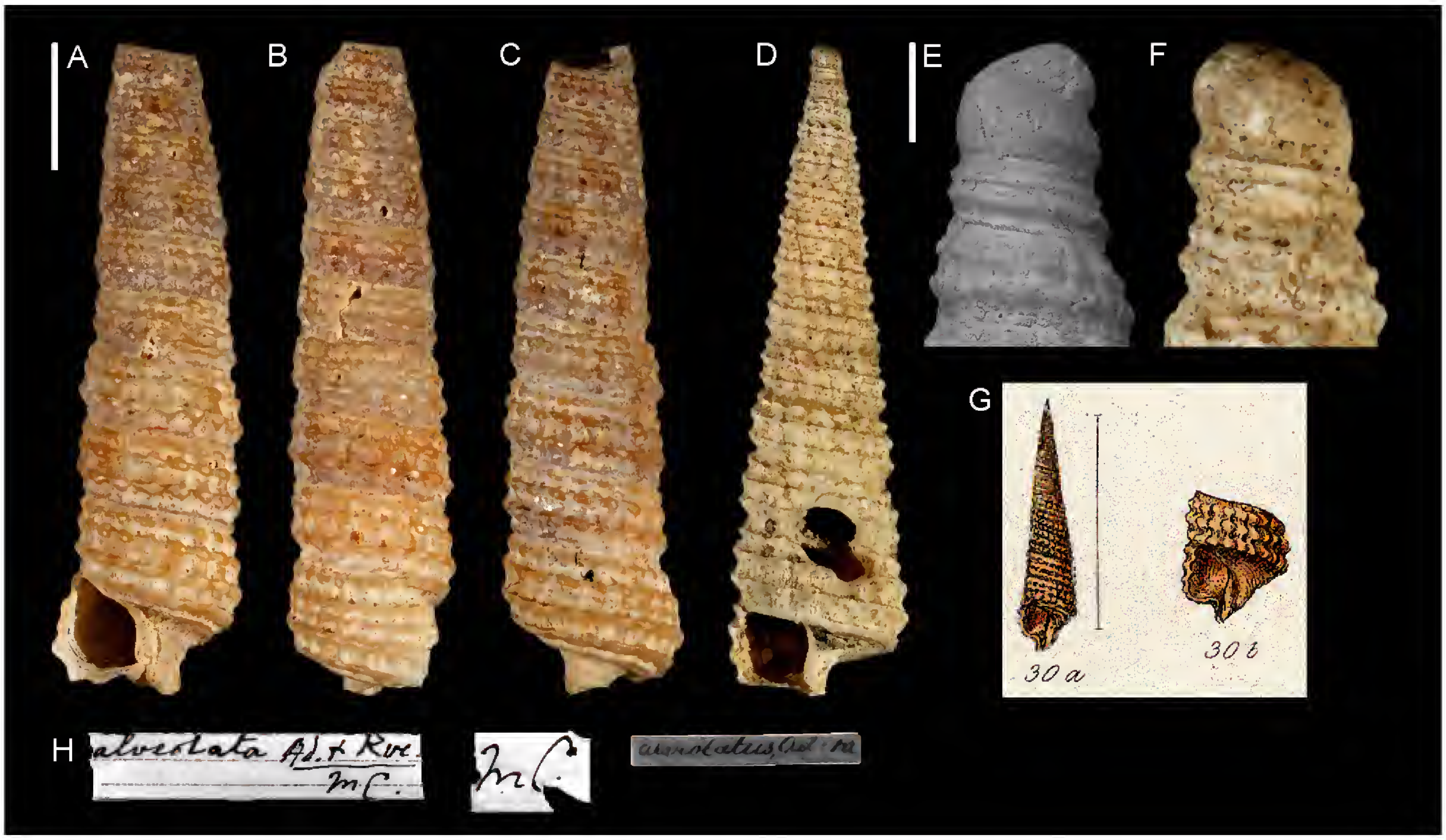

Figure 10. *Triphora* sp. (labelled as *T. alveolatus* Adams & Reeve, 1850). **A–C, H** NHMUK 196515, China Sea, coll. H. Cuming: front (**A**), side (**B**), back (**C**), labels (**H**). **D–F** NHMUK 196516: front (**D**), protoconch (**E, F**). **G** Original figures. Scale bars: **A–D**: 2 mm; **E, F**: 0.3 mm.

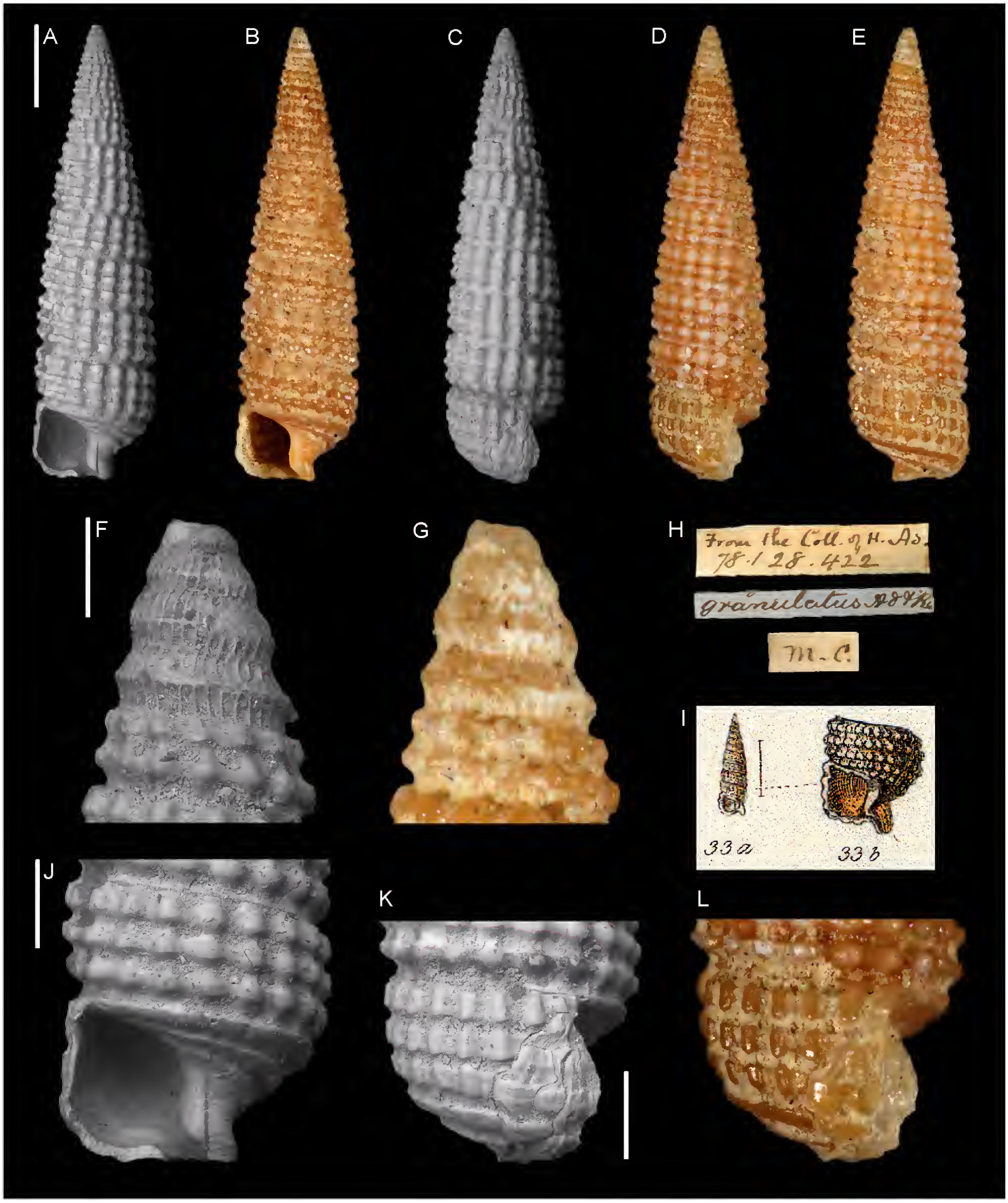

Figure 11. *Triphora* sp. (labelled as *Triphoris granulatus* Adams & Reeve, 1850). **A–H, J–L** NHMUK 1878.1.28.422, China Sea, coll. H. Adams in coll. H. Cuming: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, G**), original labels (**H**), aperture (**J**), peristome (**K, L**). **I** Original figures. Scale bars: **A–E**: 1 mm; **F, G**: 0.2 mm; **J–L**: 0.5 mm.

Type material. Not found, see remarks.

Original description. *Triph. testâ turritâ, medio subcylindraceâ, anfractibus duodecim ad quatuordecim, triseriatim granulatis, granulis regularibus confertis, anfractuum suturis subimpressis; sordidè albâ.*

Hab. China Sea.

Distinguished by its short, cylindrical form, and by the precise arrangement of the granules with which it is sculptured.

Translation of the Latin text. A turreted subcylindrical triphorid with twelve to fourteen triseriated whorls with regular granules and subimpressed sutures; dirty white.

Hab. China Sea

Remarks. We found one specimen from the Cuming collection (NHMUK 1878.1.28.422). Its label specifies that it comes from the collection of H. Adams. This specimen has slightly fewer whorls (11) than stated in the original description (12–14), but has the fourth to sixth spiral cords (clearly visible on the base) completely smooth, while the original figure (Adams and Reeve 1850: pl. 11, fig. 33b) clearly shows that cord four and five bear well-defined granules. Therefore, we doubt that this specimen belongs to the type series and suggest that *T. granulatus* should be considered a *nomen dubium*.

Triphoris suturalis Adams & Reeve, 1850

Figure 12

Triphoris suturalis Adams and Reeve 1850: 45, pl. 11, fig. 29a, b.

Type locality. "China Sea".

Type material. Not found, see remarks.

Original description. *Triph. testâ turritâ, anfractibus duodecim ad tredecim, eximiè triseriatim granuloso-carinulatis, suturis concavo-impressis, laevigatis; pellucido-albâ.*

Hab. China Sea.

The aperture of this delicately grain-keeled species, which is characterized by its hollow sutures, is incomplete.

Translation of the Latin text. Turreted triphorid with twelve to thirteen triseriated whorls well developed with carinated granules, and concave-impressed smooth sutures; clear-white.

Hab. China Sea

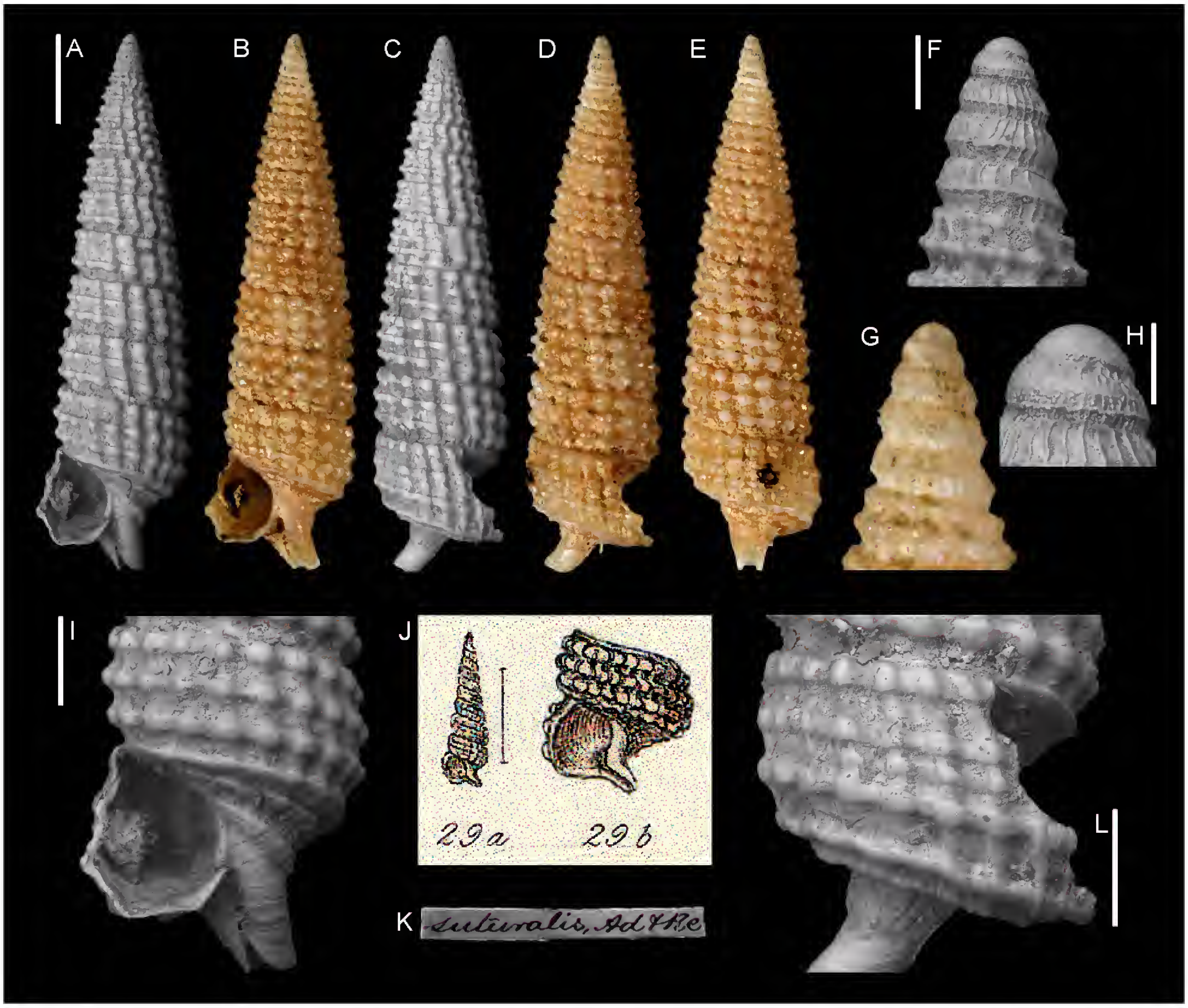

Figure 12. *Triphora* sp. (labelled as *Triphoris suturalis* Adams & Reeve, 1850), China Sea, coll. H. Cuming. **A–I, K, L** NHMUK 196513: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, G**), nucleus (**H**), aperture (**I**), original label (**K**), peristome (**L**). **J** Original figures. Scale bars: **A–E**: 1 mm; **F, G**: 0.2 mm; **H**: 0.1 mm; **I, L**: 0.5 mm.

Remarks. The specimen preserved in the type collection of NHMUK (196513) has 10 whorls instead of the 12 to 13 stated in the original description. Adams and Reeve also highlighted that the studied specimen had an incomplete aperture and particularly hollow sutures. The specimen in NHMUK has an incomplete peristome and impressed sutures, although not unusually hollow for many triphorids. We refrain from considering these specimens as syntypes until further evidence is available. At present, *T. suturalis* should be considered a *nomen dubium*.

Triphoris verrucosus Adams & Reeve, 1850

Figure 13

Triphoris verrucosus Adams and Reeve 1850: 45, pl. 11, fig. 32a, b.

Type locality. "China Sea".

Type material. Not found, see remarks.

Original description. *Triph. testâ gracillimo-subulatâ, anfractibus octodecim ad viginti, granoso-clathratis, granis transversè oblongis; sordidè albâ.*

Hab. China Sea.

A slender species, latticed throughout with transversely oblong granules.

Translation of the Latin text. Very slender subulate triphorid with eighteen to twenty granular-latticed whorls with transversely oblong granules; dirty white.

Hab. China Sea

Remarks. One specimen was found in the type collection of the NHMUK (1878.1.28.483) but we doubt it is a syntype. The original description states that the species has 18 to 20 whorls, while the specimen found has only eight.

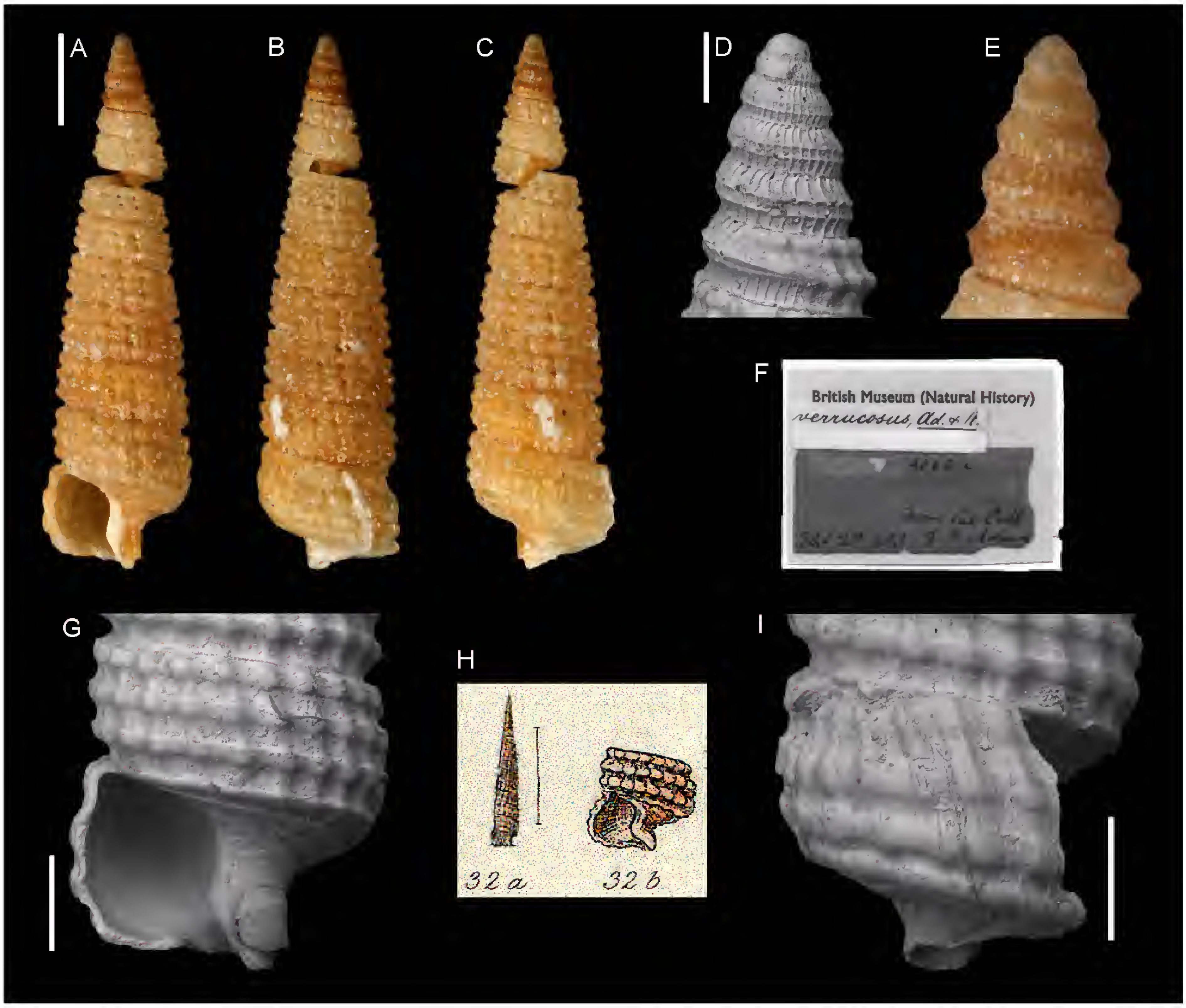

Figure 13. *Triphora* sp. (labelled as *Triphoris verrucosus* Adams & Reeve, 1850), China Sea, coll. H. Adams in coll. H. Cuming. **A–G, I** NHMUK 1878.1.28.483: front (**A**), side (**B**), back (**C**), protoconch (**D, E**), original labels (**F**), aperture (**G**), peristome (**I**). **H** Original figures. Scale bars: **A–C**: 1 mm; **D, E**: 0.2 mm; **G, I**: 0.4 mm.

The original figure shows a slender shell with several whorls, but little more can be inferred because it is poorly detailed. At present, *T. verrucosus* should be considered a *nomen dubium*.

Species described by H.E.J. Biggs

Triphora sp. (*insularum* Biggs, ms)

Figure 14

Triphora sp. Biggs 1973: 362–363, pl. 4, figs 4, 5.

Original locality. NE of Abu Dhabi, United Arab Emirates.

Material examined. NHMUK 1968760–3: 4 specimens (from original locality).

Remarks. Biggs (1973) described and illustrated this species in his work on the Trucial Coast (Persian (Arabian) Gulf) but refrained from naming it because it lacked the apex. We agree that the presence of a complete apex is fundamental for the institution of any triphorid new species due to the important characters it bears as acknowledged by several authors (e.g. Barnard 1963; Marshall 1983; Bouchet and Strong 2010). We thus refrain from redescribing it because we have not been able to locate new suitable material. From the remnants of apexes on the examined material, the species likely bears a multispiral protoconch.

In the NHMUK collection, the specimens studied by Biggs have been located with the manuscript name *insularum*. They are labelled as "holotype" and "paratypes"

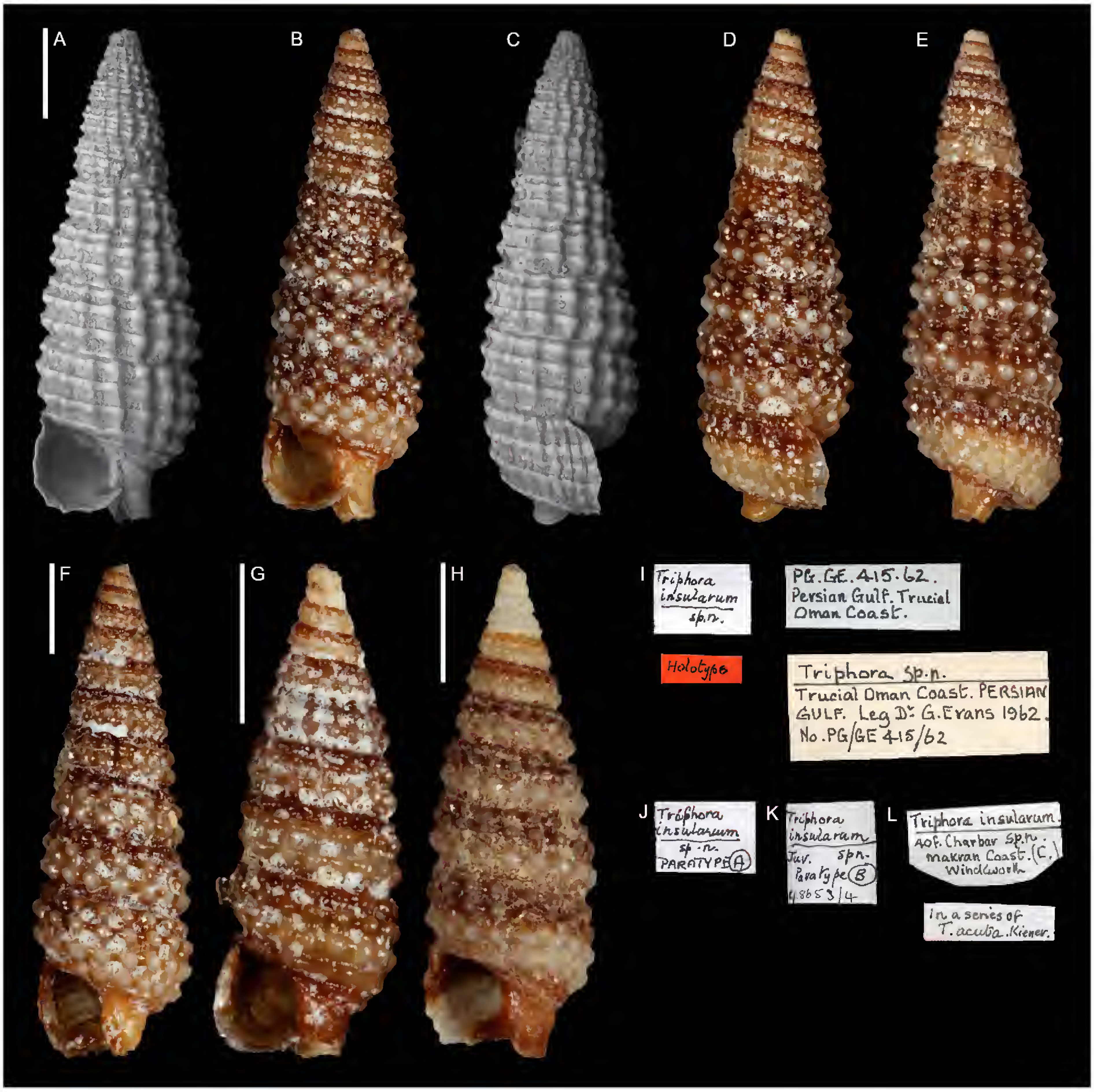

Figure 14. *Triphora* sp. (*insularum* Biggs ms). **A–E** "Holotype", NHMUK 198760, Abu Dhabi, United Arab Emirates: front (**A, B**), side (**C, D**), back (**E**). **F–H** "Paratypes", NHMUK 198761–3: front views of Paratype A (**F**), B (**G**) and C (**H**). **I** Original labels of the "holotype". **J–L** Original labels of "paratypes" A (**J**), B (**K**) and C (**L**). Scale bars: **A–E**, **F–H**: 1 mm.

although, pending a formal introduction of the name, these specimens are not name-bearing types. The label bears the locality “Trucial Oman Coast” and 1962 as collecting year. At the time, the United Arab Emirates had not been founded yet and the coastal emirates were known as Trucial States, a British Protectorate since 1819.

Species described by J. Crosse and P. Fischer

While J. Crosse and P. Fischer’s type material is supposed to be preserved in the collections of the *Journal de Conchyliologie* at the MNHN (Dance 1966), the types of *Triphoris angasi* and *T. pfeifferi* were not found in Paris (Marshall 1983, V. Héros, pers. comm. July 2014). Specimens labelled as types of these two species were found in the NHMUK, likely bequeathed by G.F. Angas among 240 types and 1500 shells (Smith 1906). Indeed, the two species were described on Angas’ material.

Triphoris angasi **Crosse & Fischer, 1865**
Figure 15

Triphoris angasi Crosse and Fischer 1865: 46, pl. 1, figs 12, 13.

Type locality. “St. Vincent” [Gulf St Vincent, South Australia].

Type material. Syntypes: NHMUK 1870.10.26.127, 1 specimen, St. Vincent Gulf, South Australia (coll. G.F. Angas).

Original description. *T. imperforata, sinistrorsa, conico-turrita, subelongata, tenuiuscula, brunnea; apice acuminato; sutura linearis, fere inconspicua; anfr. 15 planiusculi, embryonales 3 laeves, sequentes cingulis 3 granulorum (intermedio paulo minore) spiraliter impressi, ultimus quadricingulatus, transversim zona alba ornatus, basi brunneo-violacea; apertura oblique subquadrato-piriformis, intus brunneo lirata, margine columellari arcuato, externo flexuoso, in vicinio columellae ligulatim ascendente; canali brevi tubuliformi. — Long. 7 millim., diam. maj. 1 millim. 7/19.*

Hab. in sinu “Saint-Vincent” dicto (coll. Angas).

Coquille imperforée, sénestre, de forme conico-turriculée, suballongée, assez mince et de couleur brune; le sommet est acuminé, la suture linéaire et Presque imperceptible. Les tours, au nombre de 15, sont aplatis; les trois premiers sont lisses, les suivants sont ornés transversalement de trois cercles de granulations assez grosses; celui du milieu est un peu plus petit que les autres, et tend même à disparaître dans les tours supérieurs; le dernier tour porte quatre cingulations au lieu de trois, et est orné d’une zone blanche transverse; sa partie basale est d’un brun violâtre. L’ouverture, située un peu obliquement, est plutôt piriforme que quadrangulaire, et marquée de quelques lignes brunes à l’intérieur. Le bord columellaire est arqué, le bord externe est flexueux et vient s’appliquer, en forme de languette, le long de la columelle. Le canal est court et tubuliforme. – La longueur totale de la coquille est de 7 millimètres, son plus grand diameter de 1 7/10.

Cette espèce provident du golfe de Saint-Vincent. Le T. hindsi, *Deshayes (1), est, à notre connaissance, la forme qui s’en rapproche le plus sous le rapport du système de sculpture; mais les granulations sont proportionnellement plus grosses dans le* T. angasi, *qui compte, d’ailleurs, trois tours de spire de plus, et qui se distingue par son ouverture plus large et par la zone blanche de son dernier tour. Nous dédions cette espèce à M. French Angas.*

Translation of the Latin text. Sinistral imperforated shell, turreted-conical, subelongated, rather slender, brown; sharp apex; linear suture more or less inconspicuous; 15 rather flat whorls, three light embryonic, subsequent with three spiral rows of granules (smaller intermediate), four on the last with a white spiral band, base violet-brown; subsquared, pyriform slanting aperture with brown lines inside, arched columellar edge, bending external lip ascending like a strip near the columella; short, tubular anterior siphon. Length 7 mm, major diameter 1 7/19 mm.

Habitat. In the gulf known as “St. Vincent” (coll. Angas).

Diagnosis. Syntype 5.9 mm. Shell conical, with flat sides. Teleoconch of 11 whorls, with three spiral cords with tubercles at the intersection with opisthocline axial ribs. The second cord appears on the fifth whorl as a fine thread and becomes fully grown at mid-shell height. A fourth poorly sculptured cord is sometimes visible suprasuturally. Fine growth striae are visible, especially in the interspaces of cords and ribs. The peristome has a shallow posterior sinus and no additional cords. The siphonal canal is short. The base has two additional almost smooth spiral cords. The protoconch is multispiral, but the upper whorls are missing in the lectotype, impeding the quantification of the number of whorls. The lower three whorls have two spiral keels and axial riblets. Teleoconch brown with lighter tubercles, fourth spiral cord on the last whorl white, base deep brown, apex likely white (although worn in the lectotype).

Remarks. This specimen may not be the one on which Crosse and Fischer based their original description, because it is smaller in size (5.9 vs 7 mm) and with fewer whorls (11 vs 15). However, it matches very well the original description and figure; the label (Fig. 15L) specifies that this is a “type”, from the type locality and collected by G.F. Angas (Crosse and Fischer specified that the new species was based on Angas’ material). Therefore, we consider this specimen as belonging to the type series.

Triphoris pfeifferi **Crosse & Fischer, 1865**
Figure 16

Triphoris pfeifferi Crosse and Fischer 1865: 47, pl. 1, figs 14, 15.

Type locality. “St. Vincent” [Gulf St Vincent, South Australia].

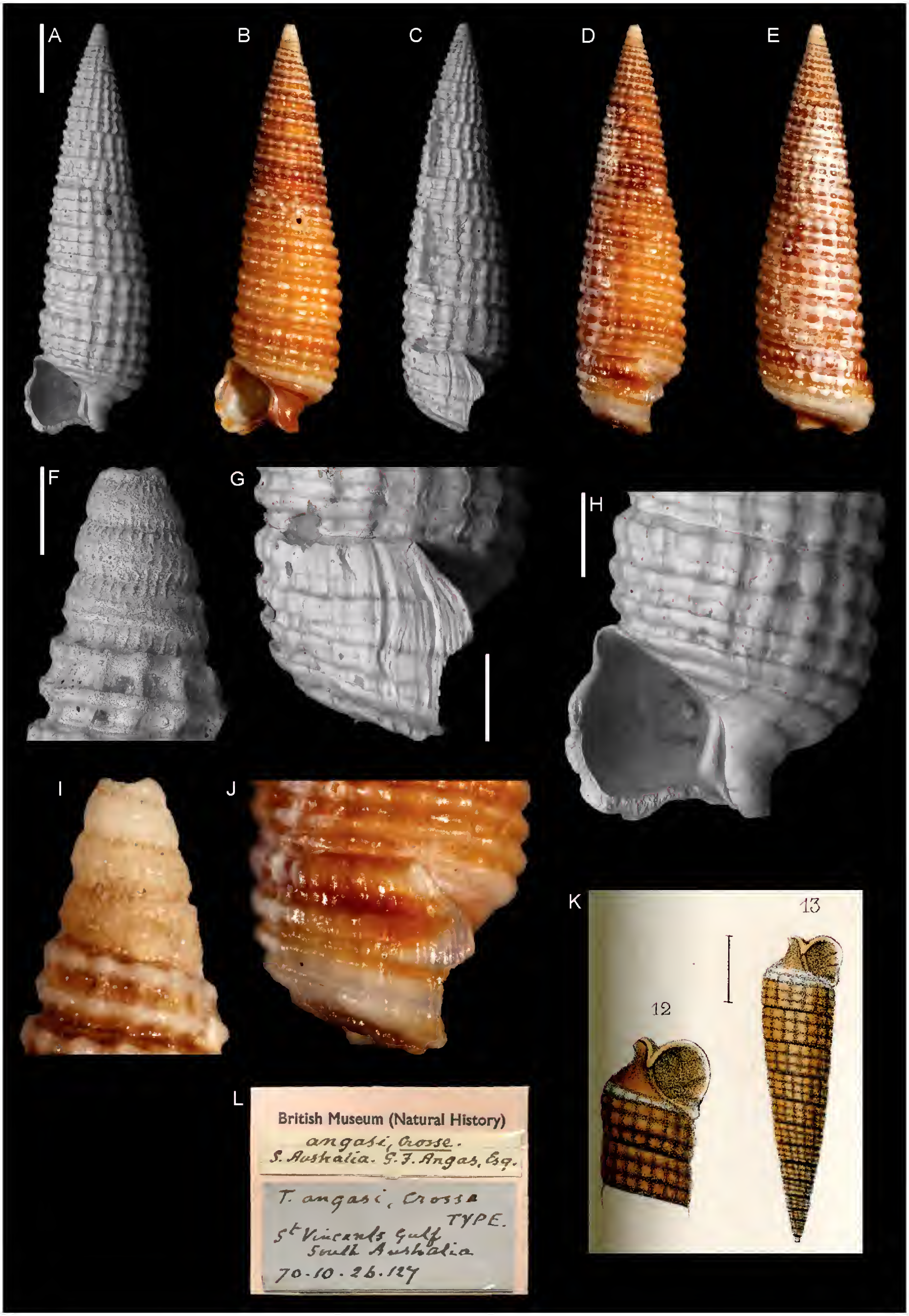

Figure 15. *Triphoris angasi* Crosse & Fischer, 1865, Gulf St Vincent, South Australia, coll. G.F. Angas. **A–J**, **L** Syntype NHMUK 1870.10.26.127: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, I**), peristome (**G, J**), aperture (**H**), original labels (**L**). **K** Original figures. Scale bars: **A–E**: 1 mm; **F, I**: 0.2 mm; **G, H, J**: 0.5 mm.

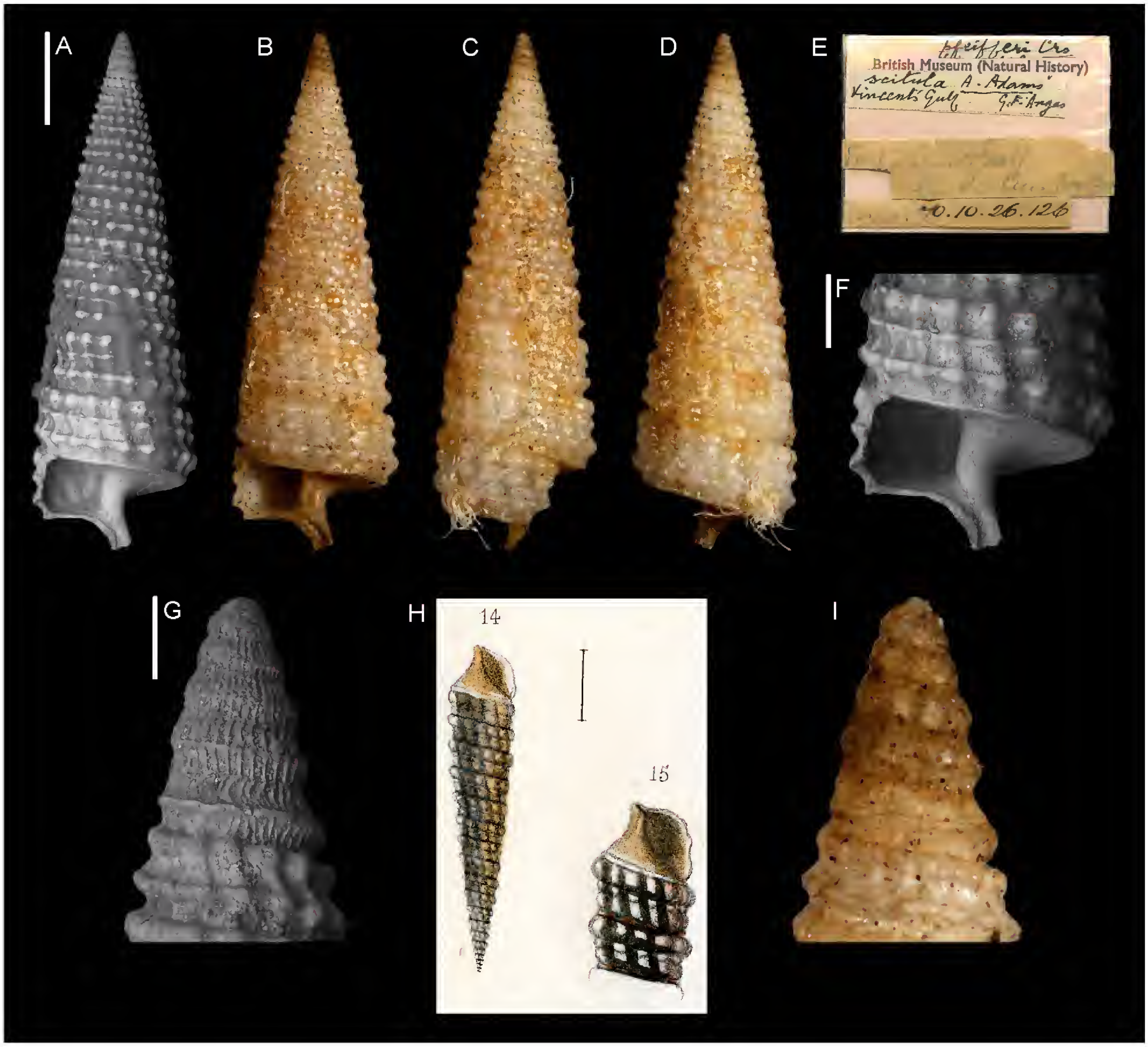

Figure 16. *Triphora* sp. (labelled as *Triphoris pfeifferi* Crosse & Fischer, 1865). **A–G, I** NHMUK 1870.10.26.126, St Vincent Gulf, South Australia, coll. G.F. Angas: front (**A, B**), side (**C**), back (**D**), original labels (**E**), microsculpture (**F**), protoconch (**G, I**). **H** Original figures. Scale bars: **A–D**: 1 mm; **F**: 0.5 mm; **G, I**: 0.2 mm.

Type material. Not found (the specimen NHMUK 1870.10.26.126 labelled as "type" is not this species, see Remarks).

Original description. *T. imperforata, sinistrorsa, turrita, elongata, tenuiuscula, subtranslucida, albida, fusco regulariter maculata; apice acuminato; anfr. 18, lentissime accrescentes, embryonales 3 laeves, caeteri cingulis 3 margaritularum elegantissimis transversim ornate (margaritulis regularibus, nitidis, lacteo-hyalinus), medio compresso, minimo, fere inconspicuo, basali multo majore, prominulo, et, infra cingulum basale, funiculo sat prominulo, fusco et albo articulato; ultimus brevis, basi laeviuscula, violaceabrunnea; apertura oblique subovata, margine columellari subarcuato, externo simplice; canali brevi. — Long. 8, diam. maj. 1 ½ millim.*

Hab. in sinu "St. Vincent" dicto (coll. Angas).

Coquille imperforée, sénestre, allongée, turriculée, assez mince, subtranslucide et blanchâtre avec certaines de ses parties marquées de brun; le sommet est acuminé. Les tours, au nombre de 18, s'accroissent très-lentement; les 3 premiers sont lisses. Le système d'ornementation des autres est des plus élégants: il se compose de trois rangées transverses de petites perles régulières, brillantes et d'un blanc nacré transparent; la rangée médiane est petite, comme écrasée entre les deux autres, et difficile à apercevoir sans le secours d'un fort grossissement; celle qui est le plus près de la base dépasse les autres *de beaucoup en dimension, et présente une forte saillie au-dessous de la rangée basale règne un petit cordonnet saillant, articulé de brun et de blanc, et se confondant avec la suture du tour suivant. Le dernier tour est assez court, sa partie basale est lisse et d'un brun violacé. L'ouverture est obliquement ovale, le bord columellaire subarqué, le bord externe simple et mince, le canal court. – La longueur totale de la coquille est de 8 millimètres, son plus grand diamètre de 1,5.*

L'habitat de cette espèce est le meme que celui de la précédente. L'individu qui nous a été communiqué n'est probablement as complétement adulte, et nous ne pouvons, par conséquent, donner la description de l'ouverture que sous toutes réserves. Néanmoins, son système d'ornementation est si particulier, qu'il sera toujours facile de reconnaître l'espèce, meme sur un fragment.

Notre espèce se rapproche du T. mirificus *de Deshayes, et plus encore du* T. angustissimus *du meme auteur (1). Elle est plus élancée que le premier, n'a pas, comme lui, de troisième ouverture, et compte trois rangs de perles et non deux. Elle est moins allongée que le second, et s'en distinguee par ses tours plus nombreux (18 au lieu de 14), ses trois rangées de tubercules margaritiformes, et son petit funicule saillant régulièrement articulé de blanc et de brun. Nous donnons à cette remarquable espèce le nom de M. Le docteur L. Pfeiffer, don't les éminents travaux sont devenus classiques, en ce qui concerne la nomenclature des Mollusques terrestres.*

Translation of the Latin text. Sinistral imperforated shell, turreted, elongated, rather slender, subtranslucent, whitish with regular brown spots; sharp apex; 18 very slowly growing whorls, three light embryonic, others with three very elegant spiral rows of pearls (regular, glossy, hyaline-milky pearls), the intermediate shrunk, rather inconspicuous, much more developed basally, slightly protruding, and, under the basal row a quite protruding dark white spotted cord; short last whorl, rather slender base, dark violet; subovate slanting aperture, subarched columellar edge, simple external lip; anterior siphon short. — Length 8, major diameter 1½ mm.

Habitat. In the gulf known as "St. Vincent" (coll. Angas).

Remarks. The specimen found and labelled as "type" is remarkably different from the specimen figured by Crosse and Fischer and must not be considered as belonging to the type series. On the basis of the original description and figure, *T. pfeifferi* should be considered a junior synonym of *Triphoris scitulus* A. Adams, 1854 (see p. 172) as already suggested by Marshall (1983).

Species described by L. de Folin

Léopold de Folin (1867) described 58 new species of molluscs in his work on the pearly oysters of Western Panama. Kisch (1960) reported the location of type specimens and highlighted that the type of de Folin's only triphorid, *Triphoris cucullatus*, could not be located. Indeed, we show below that the specimens present in NHMUK and labelled as syntypes are not this species.

Triphoris cucullatus de Folin, 1867

Figure 17

Triphoris cucullatus de Folin 1867: 72, pl. VI, fig. 13.

Type locality. Negritos and Iles aux Perles, Bay of Panama, Panama (de Folin 1867: 9); Iles aux Perles, Panama fide Kisch (1960).

Type material. Not found.

Original description. *Testa elongato-turgidula, apice acuminata, alba, fusco marmorata; anfractibus septedecimis, sutura simplici junctis; prioribus liris duobus spiralibus, margaritis notatis; sequentibus inaequaliter triliratis; ultimo margaritarum seriebus quinis vel sextis ornato, testae ¼ adaequante; apertura subcirculari in canalem brevem, obliquum, clausum, desinente.*
Long. 0,0075. Diam. 0,0019, 0.002.

Très curieuse espèce, allongée, un peu ventrue, très acuminée, de couleur blanche marbrée de brun, se fondant en des nuances légères, quelquefois d'un brun foncé, marbrée par des atténuations de teintes. Cette fort jolie coquille est composée de dix-sept tours de spire qui sont réunis par une suture simple, assez profonde. Le dernier de ces tours équivaut au quart environ de la longueur totale de la coquille. Ils sont ornés, les premiers, de deux cordons, puis de trois, le dernier de cinq et même de six. Sur les tours ornés de trois, le cordon du milieu est plus petit que les deux autres. Ils sont séparés par des sillons assez étroits, et sont divisés par une série de perles arrondies du plus gracieux effet. L'ouverture est presque circulaire et présente un caractère assez singulier. Le bord gauche, simple et crénelé, décrit les trois quarts environ d'un cercle et vient, en passant par dessus la columelle, retomber sur la base de la coquille; en cet endroit il forme un angle très-aigu suivant lequel il se rejette en arrière, suit une autre courbe et produit un canal arrondi fort court qui se trouve ainsi presqu'entièrement recouvert. Le bord droit s'arrondit lui-même en s'inclinant vivement pour rejoindre la base sur laquelle il termine la courbure de l'ouverture.

Translation of the Latin text. Swollen-elongated shell, sharp apex, white, dark marbled; seventeen whorls with a plain suture; earliest with two spiral rows of granules; subsequent with three unequal rows; last with five or six series of granules, as large as ¼ of the shell; subcircular aperture ending in a short, slanting, closed canal.

Length 0.0075. Diam 0.0019, 0.002.

Remarks. The lot NHMUK 1984153 contains two labels stating "De Folin's syntype in coll. Sykes" signed by A. Blake and "*Triphora cucullata* Folin, Panama (Folin coll.)". However, the specimen is very different from what was described by de Folin and from the original figure (Fig. 17G). *T. cucullatus* is described as having 17 whorls while the shell found has seven whorls (although a few may be lacking because the apex is incomplete). In

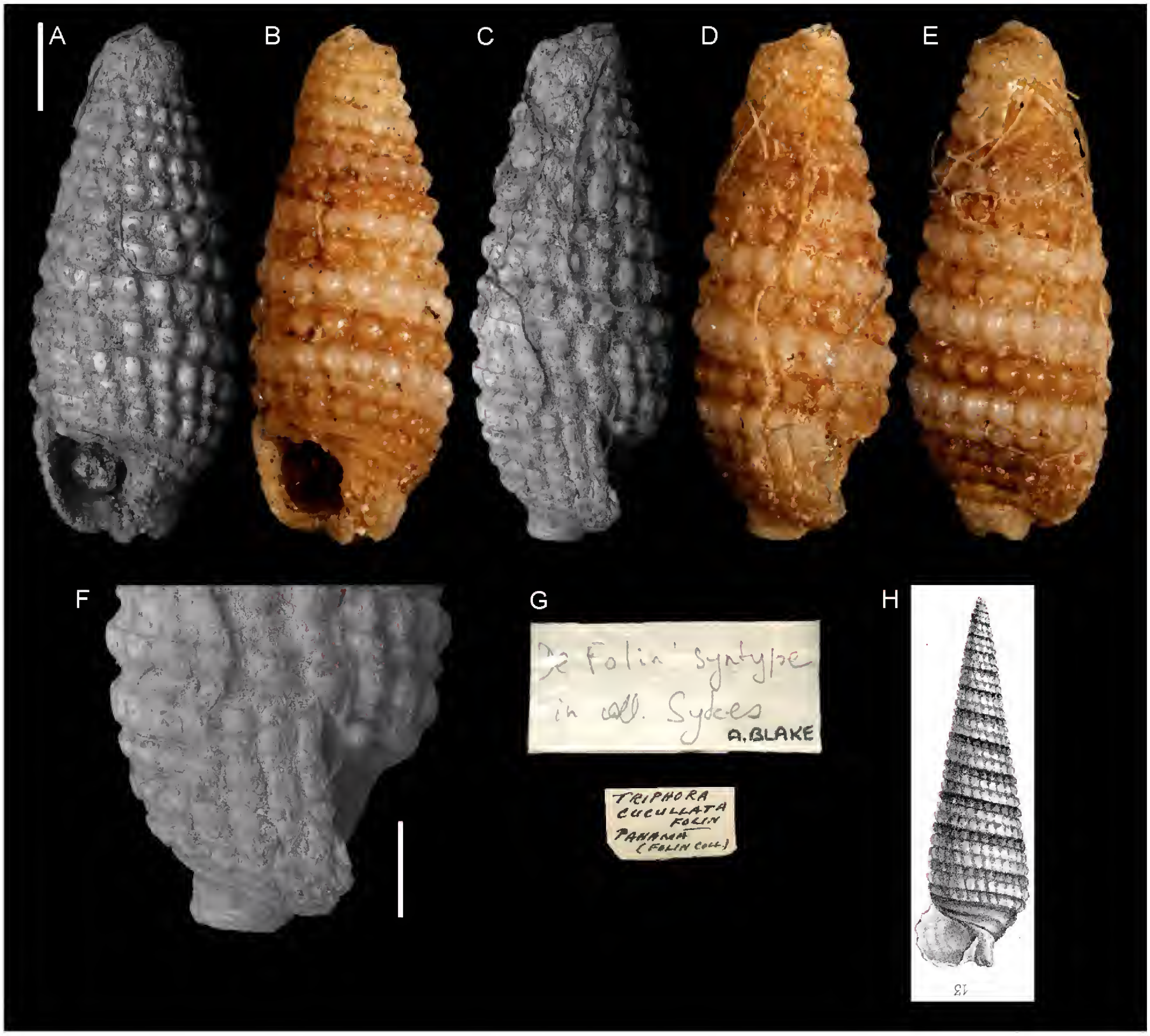

Figure 17. *Triphora* sp. (labelled as *Triphoris cucullatus* de Folin, 1867), Panama, coll. E.R. Sykes. **A–G** NHMUK 1984153: front (**A, B**), side (**C, D**), back (**E**), peristome (**F**), original labels (**G**). **H** Original figure of *T. cucullatus*. Scale bars: **A–E**: 0.5 mm; **F**: 0.3 mm.

addition, the pointed profile is missing, and the original figure shows a colour pattern with a dark first spiral cord on a white background which is the opposite of the one of the shells. Therefore, we do not consider this specimen belonging to the type series.

Species described by R.B. Hinds

Richard B. Hinds described 31 species of Triphoridae from the collections Cuming (Hinds 1843a), Belcher, Gray, and Metcalfe (Hinds 1843b). Those described from the latter (*T. aemulans*, *affinis*, *candidus*, *coelebs*, *concinnus*, *hilaris* and *metcalfei*) were dispersed at auction in the 19th century and the material is not in NHMUK (K. Way, pers. comm.). The type of *T. marmoratus* was also not found. A lot, which apparently was related to this species (NHMUK 20170299) because it came from the "West Indies" and was stored in the Gray collection, is unlikely to belong to *T. marmoratus* because shells are completely white, while Hinds (1843b) described them as brown with white flammulae (Fig. 18).

Hinds stated the length of specimens in "lines" that are equivalent to a tenth of an inch, that is 2.54 mm (Keen 1966).

Triphoris (*Ino*) *asperrimus* Hinds, 1843

Figure 19

Triphoris (*Ino*) *asperrimus* Hinds 1843b: 18, not illustrated. Illustration available in Hinds (1844): 29, pl. 8, fig. 10.

Type locality. New Guinea.

Type material. Holotype: NHMUK 1879.2.26.203, fixed by monotypy (coll. E. Belcher).

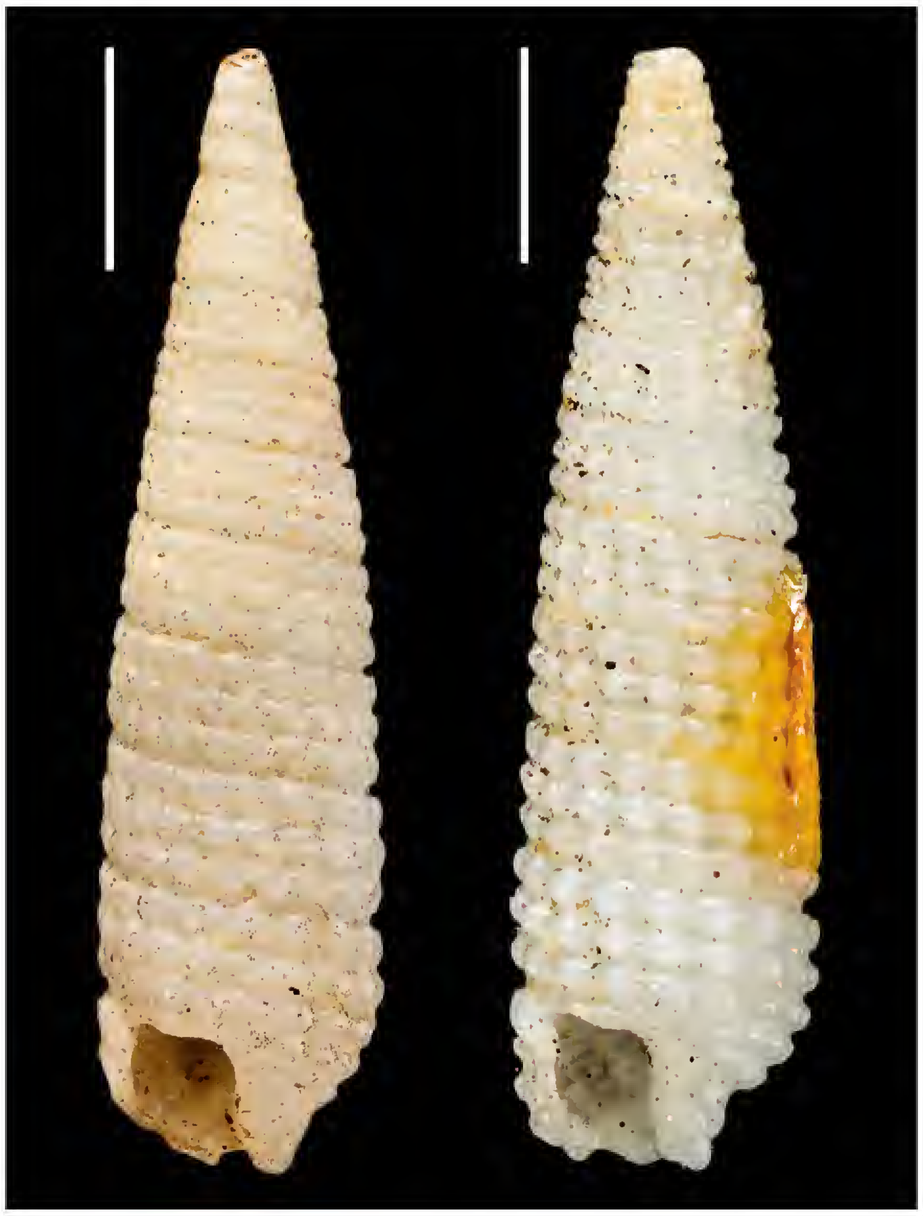

Figure 18. *Triphora* sp., NHMUK 20170299, West Indies, J.E. Gray collection, not *Triphoris marmoratus* Hinds, 1843.

Original description. *Testa gracili attenuata; anfractibus 24–26, superne valde coarctatis, inferne angulatis, serie duplici granulorum; prope suturam granuloso-carinata. Axis 6 lin.*

Geog. New Guinea; dredged from a muddy bottom in 8 fathoms.

The only specimen of this species in the collection has an injured mouth. It is remarkable for its long needle-like shape; and the upper portion of each whorl being strangulated, and the lower angular and with a series of tubercles, the shell has a very rough and jagged appearance.

Translation of the Latin text. Slender shell; 24–26 whorls, very narrow upper portion and angulated lower portion, with two series of tubercles; near the suture a granulated carina. Height 6 lines.

Diagnosis. Holotype 8.5 mm high and bearing 13 whorls, but the specimen lacks several apical whorls. The shell is extremely elongated. Teleoconch whorls have three tuberculated spiral cords, the first is smaller and appears later along the spire; the third is the most prominent. A suprasutural smooth cord is visible in the last whorls. The holotype is a subadult, and thus its peristome, sinuses, and base cannot be described. The apex is missing too. The teleoconch is white.

Triphoris (*Ino*) *bilix* Hinds, 1843

Figure 20

Triphoris (*Ino*) *bilix* Hinds 1843b: 17, not illustrated. Illustration available in Hinds (1844): 28, pl. 8, fig. 5.

Type locality. Straits of Malacca.

Type material. Syntypes: NHMUK 1879.2.26.206: 3 specimens, Straits of Malacca (coll. T. Lombe Taylor).

Original description. *Testa attenuata pallida; anfractibus quindecim tricarinatis; carina inferiore paululum maxima marmorata, media minima; apertura rotundata; sinu laterali patulo. Axis 3 lin.*

Geog. Straits of Malacca; dredged from a muddy bottom in 20 fathoms.

Translation of the Latin text. Slender pale shell; fifteen whorls with three spiral cords; the lower carina is marbled and a little bit more developed, the intermediate is the smallest; mouth rounded; open posterior sinus. Height 3 lines.

Diagnosis. Syntypes ranging in size from 6.7 to 7.5 mm. Teleoconch cyrtoconoid, with flat whorls. Syntype 1 (Fig. 20A–F) teleoconch of 12 whorls, ornamented by three undulated spiral keels; the second being narrower and appearing on the fourth teleoconch whorl. A fourth fine smooth suprasutural cord is visible in the lower part of the shell. Axial prosocline fine growth lines are visible especially on the lower part of the teleoconch. On the last whorl, keels become tuberculated and the profile becomes angulated. The peristome shows an additional tuberculated spiral keel. Siphonal canal quite long. Base flat with an additional smooth spiral cord. Protoconch of six whorls: protoconch I of two apparently smooth whorls, but the preservation of this part of the shell is suboptimal. Protoconch II of four whorls with one spiral keel on the first two, and two on the last two; axial riblets are visible on all four whorls. The protoconch is brown, whereas the teleoconch has a creamy white background colour with orange blotches. The interspaces between the tubercules of the third keel are often orange-brown.

Triphoris (*Ino*) *cancellatus* Hinds, 1843

Figure 21

Triphoris (*Ino*) *cancellatus* Hinds 1843b: 18, not illustrated. Illustration available in Hinds (1844): 28, pl. 8, fig. 6.

Type locality. Straits of Malacca.

Type material. Syntypes: NHMUK 1844.6.7.30: 3 specimens, Straits of Malacca (coll. E. Belcher); NHMUK 1879.2.26.211: 1 specimen (coll. T. Lombe Taylor).

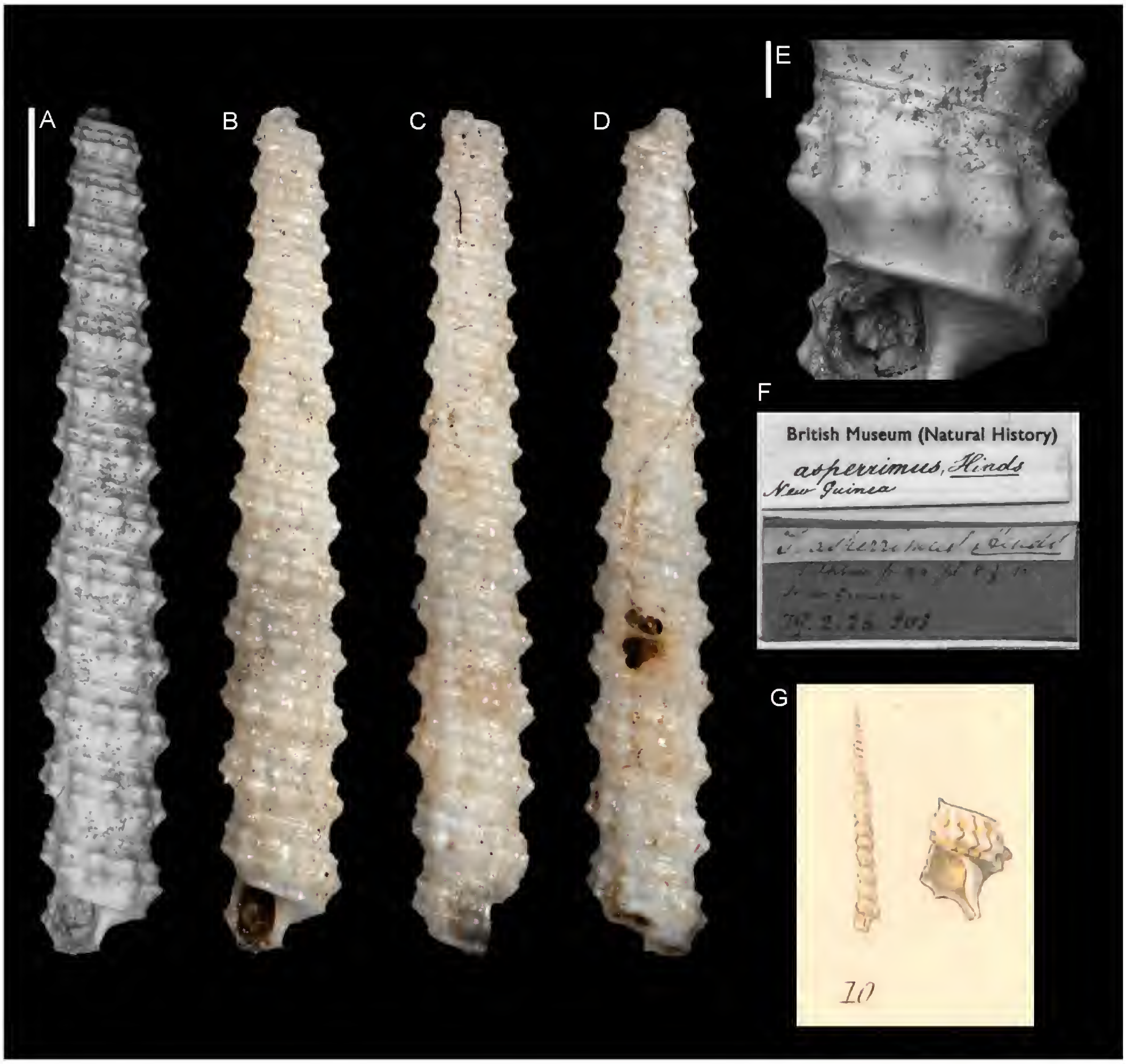

Figure 19. *Triphoris asperrimus* Hinds, 1843, New Guinea, coll. E. Belcher. **A–F** Holotype, NHMUK 1879.2.26.203: front (**A, B**), side (**C**), back (**D**), microsculpture (**E**), original labels (**F**). **G** Figure in Hinds 1844. Scale bar: **A–D**: 1 mm; **E**: 0.2 mm.

Original description. *Testa pallide rufente; anfractibus 15–18 bicarinatis; carinis albo maculatis; inter carinas cancellata lineis albis longitudinalibus intervallis fuscis; sutura sulcata; apertura subquadrata; sinu laterali margine contracta. Axis 4½ lin.*
Geog. Straits of Malacca; in 2 fathoms.

Translation of the Latin text. Pale reddish shell; 15–18 whorls with two spiral cords which bear white spots; a cancellate space with longitudinal white lines and dark intervals occurs between the cords; incised suture; subquadrate aperture; posterior sinus with shrinked edge. Height 4½ lines.

Diagnosis. Syntype 1 (Fig. 21A–G) 8 mm high. Shell cyrtoconoid with 15 teleoconch whorls whose sides are characterized by two prominent smooth spiral cords. In between, a fine tuberculated spiral cord develops; on the first whorls, it appears as a fine thread. Axial riblets are present between the cords. The last whorl has a fourth, weakly tuberculated, spiral cord and the base shows an additional smooth spiral cord. The peristome shows an additional spiral cord between the first and the second and fine spiral threads between main cords. Siphonal canal long. Posterior sinus deep. The protonch is multispiral and composed of six whorls. The first two have numerous rounded tubercles; on the third and fourth, there are axial riblets and an equally strong spiral keel positioned abapically; on the last two whorls, a second strong spiral keel develops apically. The teleoconch orange with white flammulae. The second spiral cord on whorls has white tubercles and deep orange to brown interstices. The protoconch is brown.

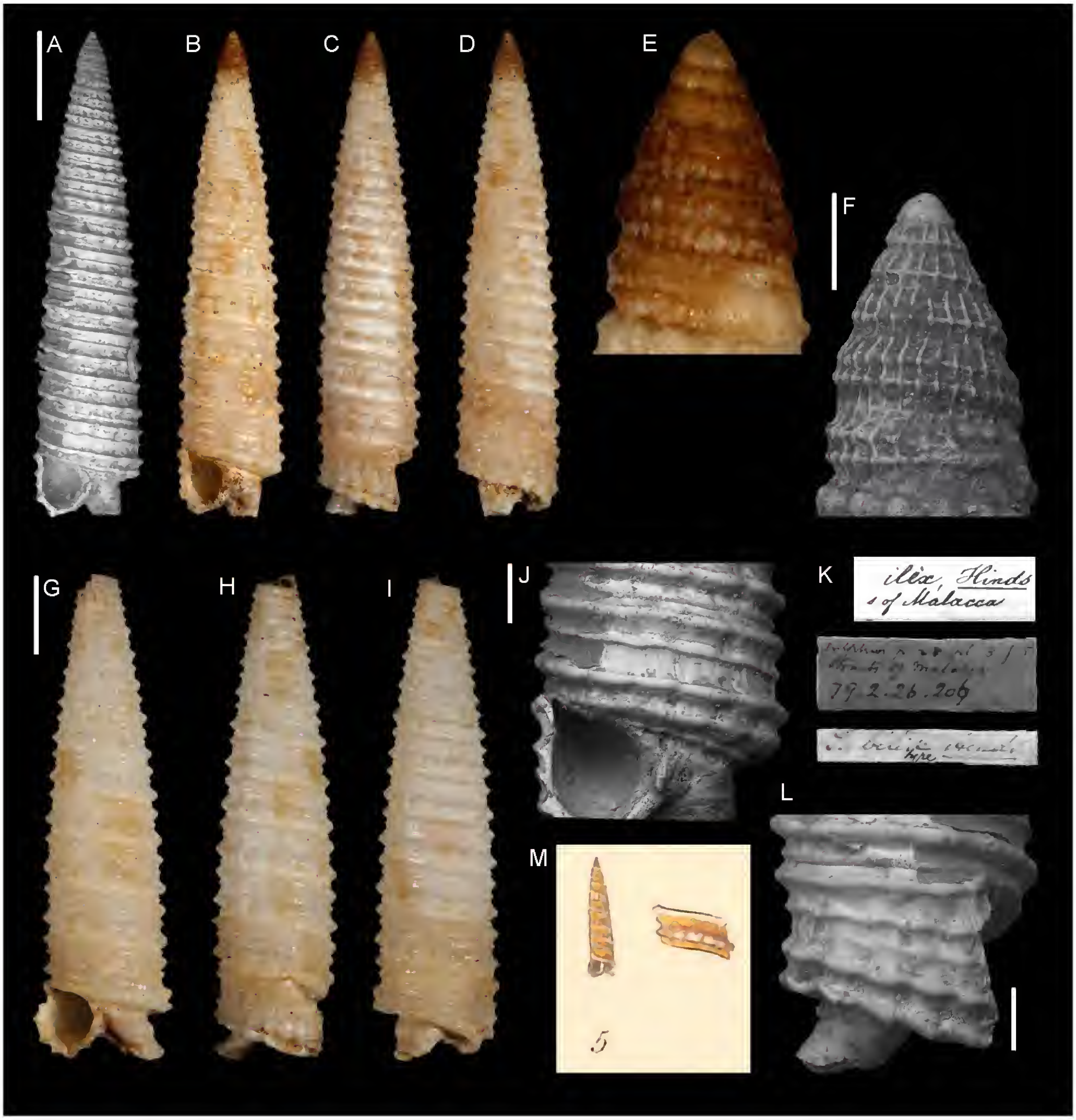

Figure 20. *Triphoris bilix* Hinds, 1843, Straits of Malacca, coll. T. Lombe Taylor. **A–F, J, L** Syntype NHMUK 1879.2.26.206/1: front (**A, B**), side (**C**), back (**D**), protoconch (**E, F**), microsculpture (**J**), peristome (**L**). **G–I** Syntype NHMUK 1879.2.26.206/2: front (**G**), side (**H**), back (**I**). **K** Original labels. **M** Figure in Hinds 1844. Scale bars: **A–D, G–I**: 1 mm; **E, F, J, L**: 0.2 mm.

Triphoris (*Mastonia*) *carteretensis* Hinds, 1843

Figure 22

Triphoris (*Mastonia*) *carteretensis* Hinds 1843b: 20, not illustrated. Illustration available in Hinds (1844): 31, pl. 8, fig. 17.

Type locality. "Port Carteret, New Ireland" [Papua New Guinea].

Type material. Syntypes: NHMUK 1879.2.26.205, 1 specimen, Port Carteret, New Ireland (coll. T. Lombe Taylor).

Original description. *Testa pallida; anfractibus quatuordecim triseriatim granulosis, serie media minima, infra duas superiores sulcatis; apertura subquadrata; sinu laterali patulo. Axis 3 lin.*

Geog. Port Carteret, New Ireland; among fine gravel at low water.

The sulcus, which traverses the whorl transversely, will readily distinguish this species.

Translation of the Latin text. Pale shell, fourteen whorls with three series of granules, the intermediate

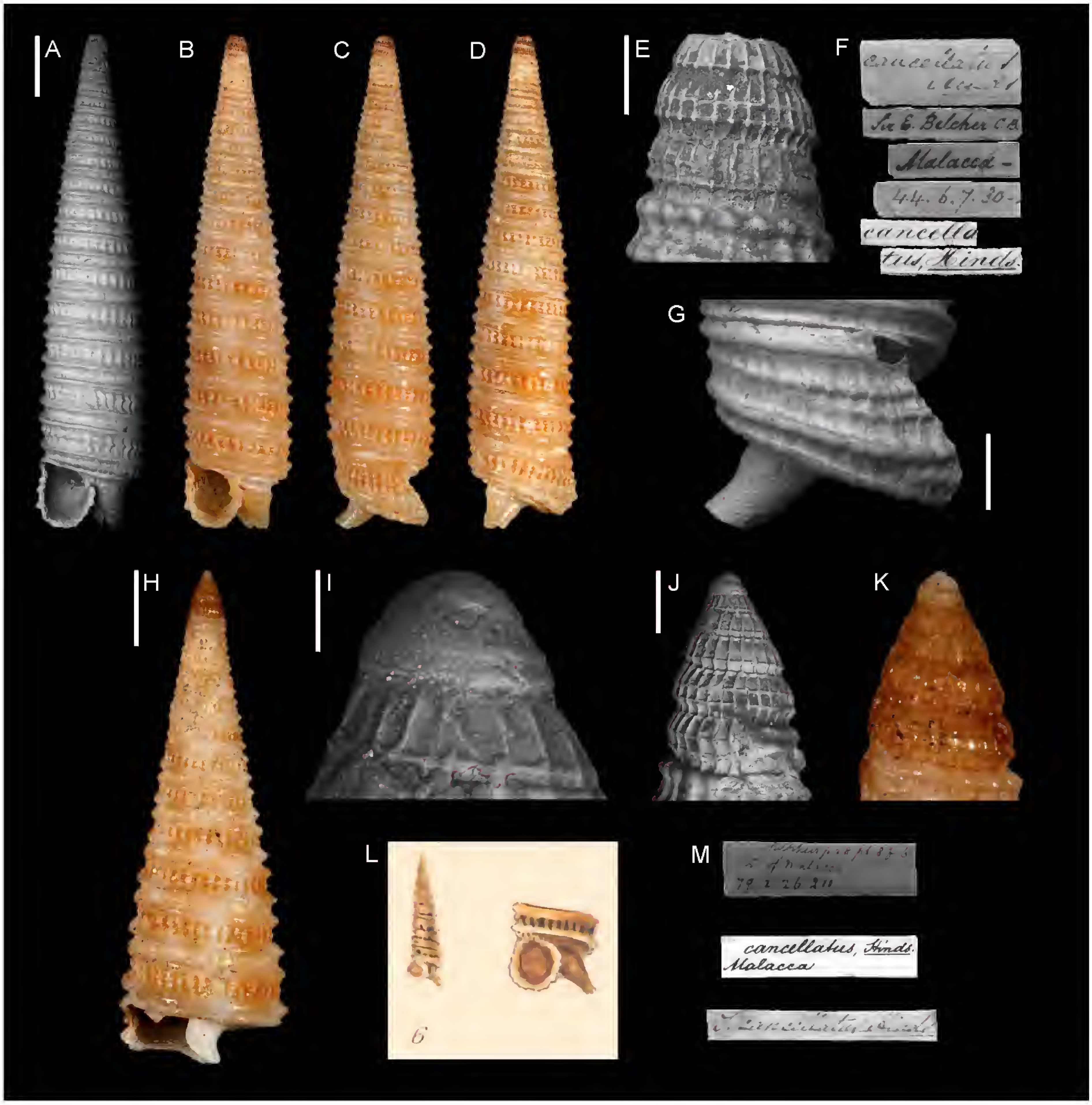

Figure 21. *Triphoris cancellatus* Hinds, 1843. **A–G** Syntype NHMUK 1844.6.7.30/1, Straits of Malacca (coll. E. Belcher): front (**A, B**), side (**C**), back (**D**), protoconch (**E**), original labels (**F**), peristome (**G**). **H–K, M** Syntype NHMUK 1879.2.26.211, Straits of Malacca (coll. T. Lombe Taylor): front (**H**), nucleus (**I**), protoconch (**J, K**), original labels (**M**). **L** Figure in Hinds 1844. Scale bars: **A–D, H**: 1 mm; **E, J, K**: 0.2 mm; **I**: 0.05 mm; **G**: 0.5 mm.

series is the smallest, under the upper ones with two series; subquadrate aperture, open posterior sinus. Height 3 lines.

Diagnosis. Syntype 4.6 mm high. Shell cyrtoconoid with nine whorls with flat sides. Such whorls are ornamented by three spiral cords with tubercles at the intersection with the prosocline axial ribs. The second cord develops at mid-teleoconch and is initially a fine thread. Among the main cords, fine spiral threads are visible. A fourth tuberculated cord is present on the last whorl and the base has one more. The peristome shows additional spiral cords between the main ones. The posterior sinus is shallow, the siphonal canal short. The protoconch is missing. The teleoconch is brown to orange with darker interspaces between the spiral cords.

Triphoris (*Mastonia*) *castus* Hinds, 1843

Figure 23

Triphoris (*Mastonia*) *castus* Hinds 1843b: 20, not illustrated.

Type locality. "St. Vincent's", Caribbean.

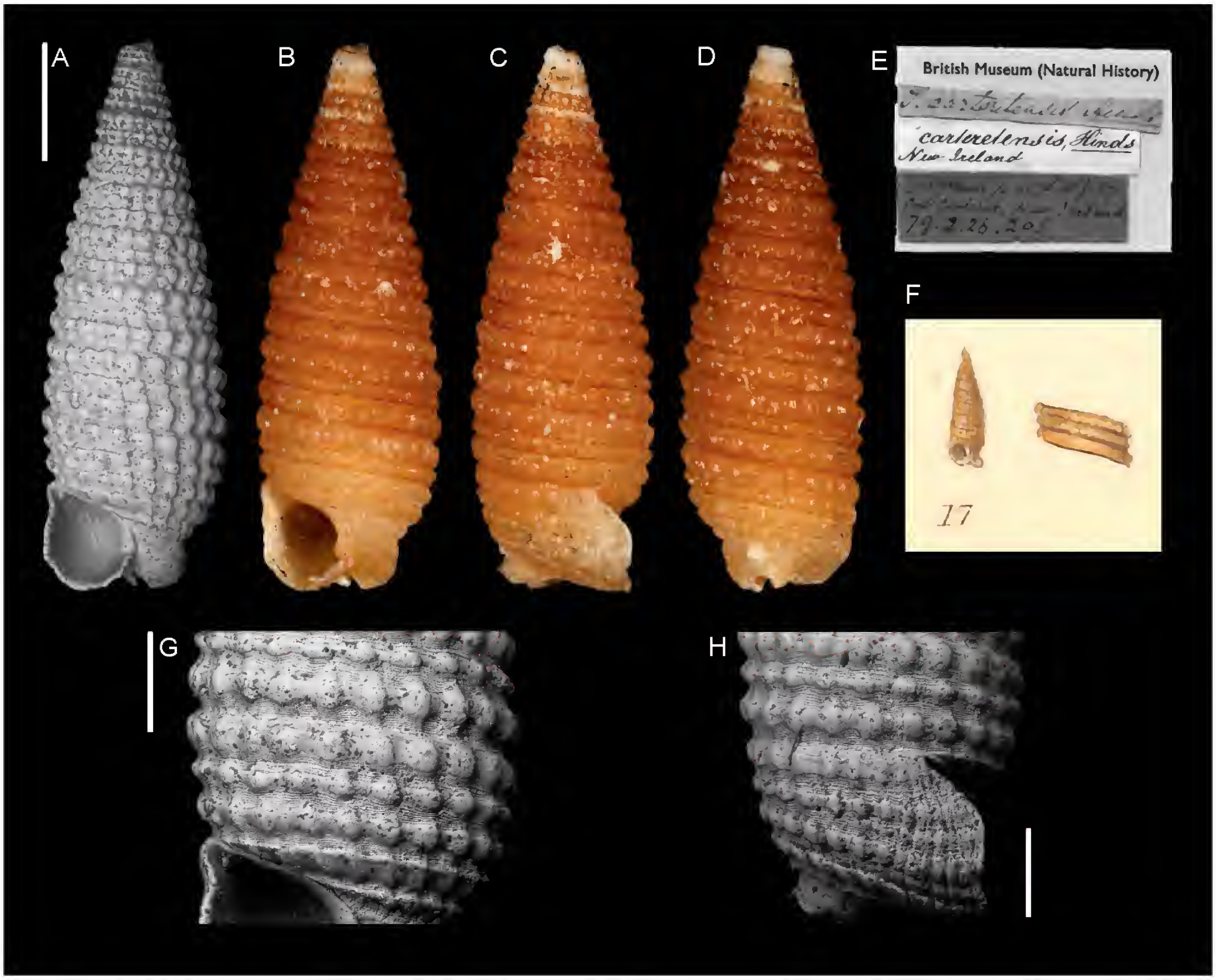

Figure 22. *Triphoris carteretensis* Hinds, 1843, Port Carteret, New Ireland, coll. T. Lombe Taylor. **A–E, G, H** Syntype NHMUK 1879.2.26.205: front (**A, B**), side (**C**), back (**D**), original labes (**E**), microsculpture (**G**), peristome (**H**). **F** Figure in Hinds 1844. Scale bars: **A–D**: 1 mm; **G–H**: 0.5 mm.

Type material. Syntypes: NHMUK 196536: 1 specimen, and NHMUK 196537: 1 specimen, both St Vincent, Caribbean (J.E. Gray coll.).

Original description. *Testa parva; anfractibus duodecim, biseriatim eleganter granosis; serie inferiore parva fusca, superiore maxima margaritacea; apertura rotunda; sinu laterali postico tubiformi. Axis 2 lin.*

Geog. *St. Vincent's, West Indies; Rev. W. J. Guilding. Cab. Gray et Metcalfe.*

Translation of the Latin text. Small shell; twelve whorls with two finely granulated rows; dark smaller lower row, whitish bigger upper one; rounded aperture; lateral sinus posteriorly tubular. Height 2 lines.

Diagnosis. Syntype NHMUK 196536 4.9 mm high. Shell conical, with nine flat whorls bearing two strongly tubercled spiral cords. The base has one additional tubercled spiral cord. Siphonal canal quite long, with two spiral ridges, posterior canal tubular and ca 1 mm more interiorly than the lip. Protoconch paucispiral of 1.5 whorls. Shell white with an orange stripe on the second spiral cord.

Remarks. Rolán and Fernández-Garcés (1993) stated that a lectotype designation was in progress by Moolenbeek and Faber, but the paper was never published (M. Faber, pers. comm., May 2014).

Triphoris (*Mastonia*) *clemens* Hinds, 1843

Figure 24

Triphoris (*Mastonia*) *clemens* Hinds 1843b: 20, not illustrated. Illustration available in Hinds (1844): 30, pl. 8, fig. 16.

Type locality. Straits of Malacca.

Figure 23. *Triphoris castus* Hinds, 1843, St Vincent, Caribbean, J.E. Gray coll. **A–E** Syntype NHMUK 196536: front (**A**), side (**B**), back (**C**), apex (**D**), siphonal canal (**E**). **F–J** Syntype NHMUK 196537: front (**F**), side (**G**), back (**H**), upper teleoconch whorls (**I**) and peristome (**J**). **K** Original labels. Scale bars: **A–C**: 1 mm; **D–J**: 0.5 mm. Images are property of the NHMUK, courtesy of H. Taylor, NHMUK Photographic Unit.

Type material. Syntypes: NHMUK 196540: 1 specimen, Straits of Malacca (H. Cuming coll.).

Original description. *Testa cornea nitenti; anfractibus quindecim triseriatim granulosis; serie media parva ad inferiorem appropinquante; inferiore prominulo-margaritacea; anfractus ultimi granulis parvis; sutura sulcata; apertura rotunda; sinu laterali patulo. Axis 3 lin.*

Geog. Straits of Malacca; from 20 fathoms, mud.

Translation of the Latin text. Bright brown shell; fifteen whorls with three series of granules; the small interme-

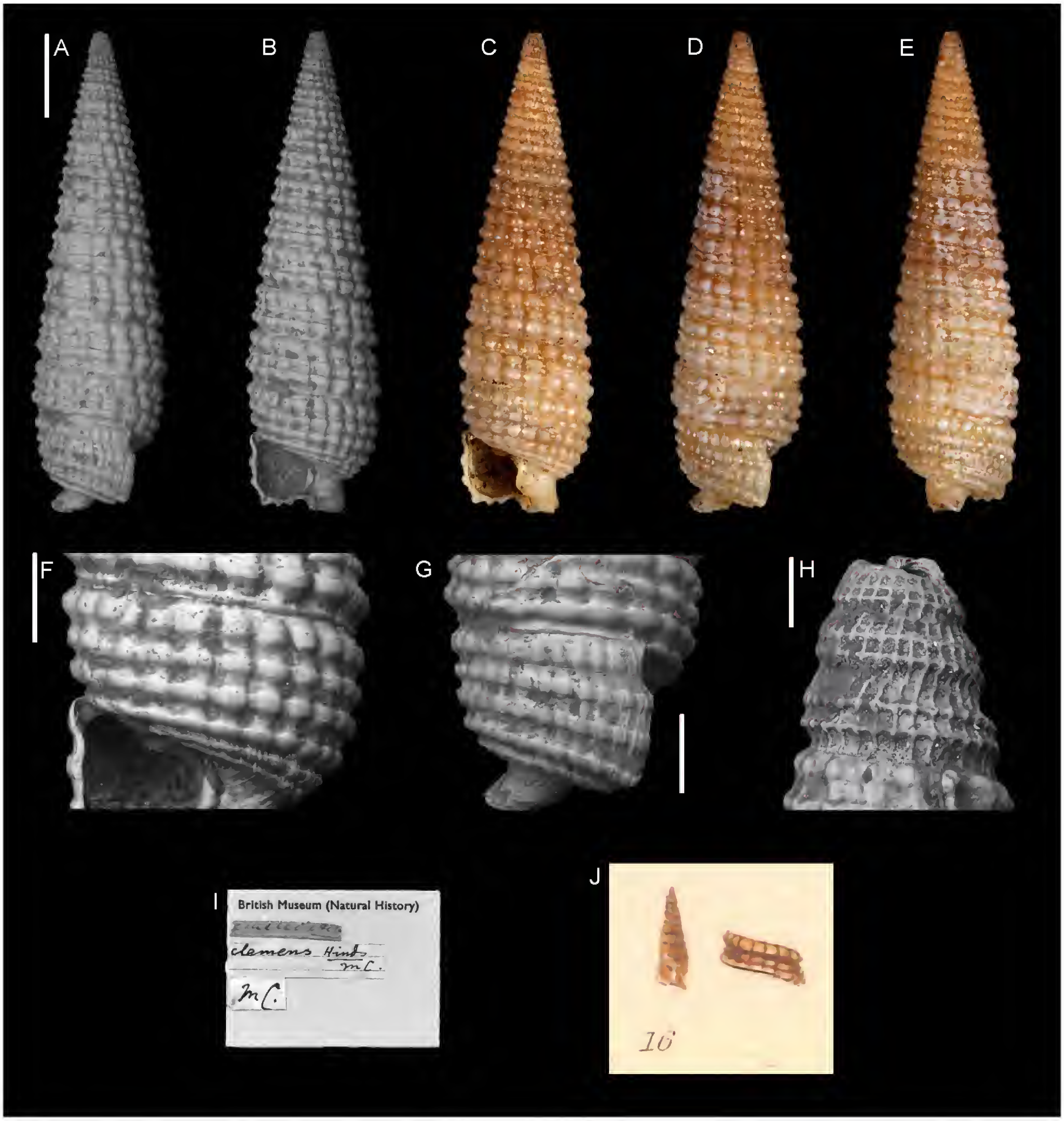

Figure 24. *Triphoris clemens* Hinds, 1843, Straits of Malacca, coll. H. Cuming. **A–I** Syntype NHMUK 196540: front (**B, C**), side (**A, D**), back (**E**), microsculpture (**F**), peristome (**G**), protoconch (**H**), original labels (**I**). **J** Figure in Hinds 1844. Scale bars: **A–E**: 1 mm; **F, G**: 0.5 mm; **H**: 0.1 mm.

diate one closer to the lower which is pearly grey; last whorls with small granules; grooved suture; rounded aperture; open posterior sinus. Height 3 lines.

Diagnosis. Syntype 5.7 mm high. Shell conical with flat sides. The teleoconch has 12 flat whorls ornamented by three spiral cords with large rounded tubercles at the interstices with prosocline axial ribs. The second cord appears on the seventh whorl and is initially very narrow. A fourth suprasutural smooth cord is present which develops into a fully tuberculated cord on the last whorl. The base has two more tuberculated cords. Fine spiral threads are also visible among the main cords. The peristome is incomplete in the holotype hindering its description. Siphonal canal short. In the holotype, the protoconch is incomplete but clearly multispiral. Three whorls are visible and ornamented by two strong spiral keels and several equally strong axial riblets. The teleoconch has a whitish background with pearly tubercles and orange interstices. Protoconch brown.

Triphoris (*Mastonia*) *collaris* Hinds, 1843

Figure 25

Triphoris (*Mastonia*) *collaris* Hinds 1843a: 23, not illustrated.

Type locality. Island of Corregidor, Philippine Islands.

Type material. Syntypes: NHMUK 196518: 1 specimen, Philippines (H. coll. H. Cuming).

Original description. *Tri. (Mastonia) testâ ovatâ, acuminatâ; anfractibus duodecim biseriatim granulosis, serie inferiore paululùm maximâ, margaritaceâ, superiore pallidè fuscâ; anfractu ultimo quadriseriatìm subaequaliter catenato. Axis 4 lin.*

Hab. Island of Corregidor, Philippine Islands.

Found among coarse sand at a depth of six fathoms. Many of these small shells have received an injury which has destroyed the mouth, and the present specimen has not escaped.

Translation of the Latin text. *Triphora* (*Mastonia*) with ovate pointed shell; 12 whorls with two series of granules, the lower a little bit larger, pearly, the upper faintly brown; last whorl with rather equal four cords. Height 4 lines.

Diagnosis. The examined syntype is 6.6 mm high. Shell cyrtoconoid, with flat whorls. The examined specimen lacks the apical part, but it has 11 whorls with two spiral cords ornamented by large tubercles at the intersection with prosocline axial ribs. A third very fine cord is visible below the first one on the last two to three whorls. Among the main cords, numerous finely tuberculated narrow spiral cords can be seen. Peristome and apex missing. Moderately long siphonal canal. The base has two additional, weakly granulated, spiral cords. The teleoconch has the upper spiral cord brown with paler tubercles and the lower spiral cord white. The last whorl has a distinct pattern of white tubercles and brown interspaces.

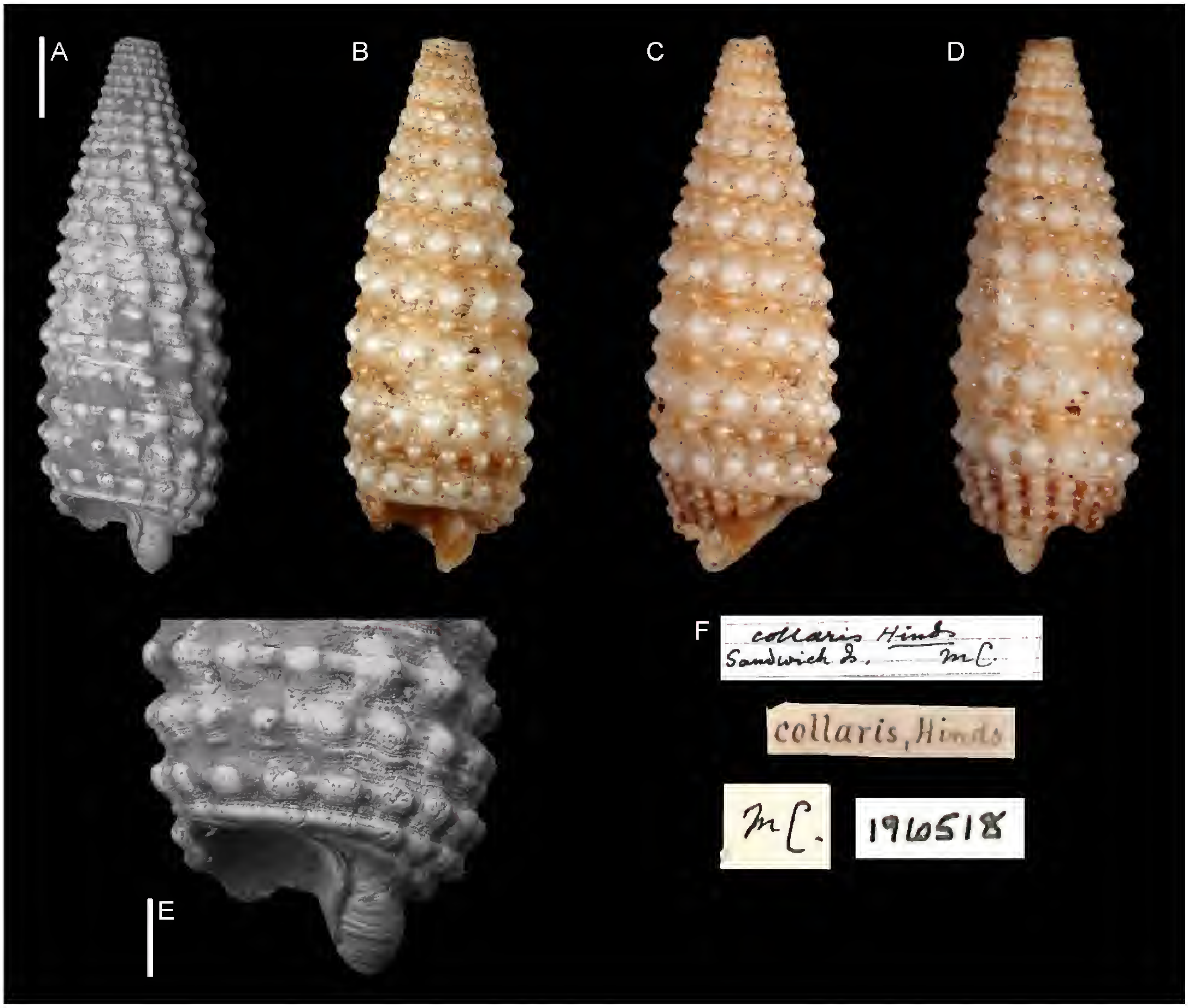

Figure 25. *Triphoris collaris* Hinds, 1843, Baclayon, Bohol Island, Philippines, coll. H. Cuming. **A–F** Syntype NHMUK 196518: front (**A, B**), side (**C**), back (**D**), microsculpture (**E**), original labels (**F**). Scale bars: **A–D**: 1 mm; **E**: 0.5 mm.

Remarks. The *locus typicus* of *T. collaris* is the Island of Corregidor in the Philippines. Although this locality is indicated in modern labels accompanying this lot in the NHMUK, an old label reports "Sandwich I." (Fig. 25F). Hinds stated in the original description the existence of several specimens and we can assume that this specimen is a syntype, although not topotypic. In the same lot, two more specimens were present, but they belong to completely different species, as already annotated by S.P. Dance in 1965.

Triphoris (*Ino*) *concors* Hinds, 1843

Figure 26

Triphoris (*Ino*) *concors* Hinds 1843b: 17, not illustrated. Illustration available in Hinds (1844): 28, pl. 8, fig. 2.

Type locality. Straits of Malacca.

Type material. Lectotype: NHMUK 1844.6.7.27/1, here designated (coll. E. Belcher). Paralectotypes: NHMUK 1844.6.7.27/2: 1 specimen, Straits of Malacca (coll. E. Belcher); NHMUK 1879.2.26.200/1: 1 specimen (broken into two parts), Straits of Malacca (coll. T. Lombe Taylor).

Original description. *Testa cylindracea; anfractibus viginti-duo triseriatim granulosis; serie media paululum minima; sutura lineata; apertura rotundata; sinu laterali tubiformi. Axis 6 lin.*

Geog. Straits of Malacca; in 18 fathoms.

Translation of the Latin text. Cylindrical shell; twenty-two whorls with three rows of granules; the median a little bit smaller; linear suture; rounded aperture; tubiform posterior sinus. Height 6 lines.

Diagnosis. Lectotype 10.4 mm high. Shell cyrtoconoid, with 20 flat-sided whorls with three spiral cords with tu-

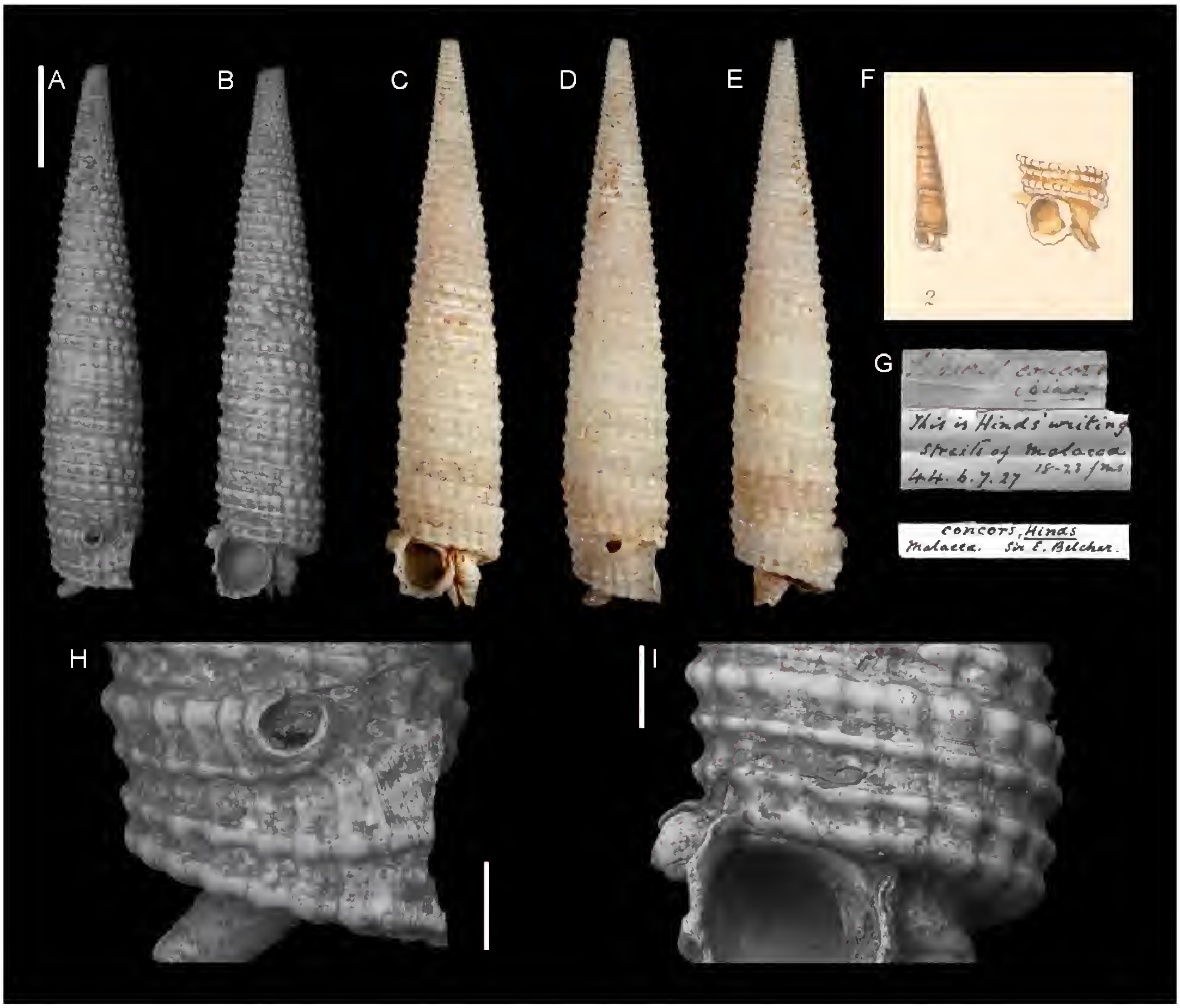

Figure 26. *Triphoris concors* Hinds, 1843, Straits of Malacca, coll. E. Belcher. **A–E, G–I** Lectotype NHMUK 1844.6.7.27/1: front (**B, C**), side (**A, D**), back (**E**), original labels (**G**), peristome (**H**), microsculpture (**I**). **F** Figure in Hinds 1844. Scale bars: **A–E**: 2 mm; **H, I**: 0.5 mm.

bercles. The second row develops later on the spire and on the last whorls a fourth smooth suprasutural cord is visible. Slightly prosocline axial ribs intersect the spiral cords forming the tubercles. Numerous fine spiral striae are visible between the main cords on the lower whorls. Additional spiral cords are visible on the peristome. The posterior sinus is tubular. The base has no additional spiral cords. The protoconch is absent in the type series, but a small remnant suggests it to be brown and multispiral. The teleoconch is dirty white.

Remarks. Lot NHMUK 1879.2.26.200 contains also one subadult specimen that is broader, bears a different sculpture, and thus may not be this species. The lectotype was thus designated to univocally define the morphology of this taxon and stabilize the nomenclature. The lectotype is the best preserved specimen and the only one to bear remnants of the protoconch,

Triphoris (*Ino*) *corrugatus* Hinds, 1843

Figure 27

Triphoris (*Ino*) *corrugatus* Hinds 1843b: 18, not illustrated. Illustration available in Hinds (1844): 29, pl. 8, fig. 7.

Type locality. New Guinea and Straits of Malacca.

Type material. Syntypes: NHMUK 1879.2.26.195: 3 specimens , New Guinea and Straits of Malacca (J. Lombe Taylor coll.); NHMUK 1998167/1–5: 5 specimens, Straits of Malacca (coll. E. Belcher).

Original description. *Testa cornea; anfractibus 17–20 bicarinatis, inter carinas corrugatis, medio carina secondaria; sutura leviter carinata; apertura rotunda; sinu laterali lineari. Axis 6½ lin.*

Geog. New Guinea; dredged from 23 fathoms, among fine gravel. Straits of Malacca; from 18 to 23 fathoms.

Translation of the Latin text. Brown shell; 17–20 bicarinated whorls with corrugated interspaces, smaller median carina; slightly carinated suture; round aperture; linear posterior sinus. Height 6½ lines.

Diagnosis. Adult specimens of the type series range between 11.2 and 14.2 mm. Shell conical and very elongated. The teleoconch has 17 flat sides with three strong smooth spiral cords. The second whorl develops later along the teleoconch and is initially weakly undulated as a result of the intersection with prosocline axial riblets which are well developed in the lectotype. A fourth smooth spiral cord is visible on the last whorls. An additional spiral cord develops between the second and the third and is clearly visible on the peristome. The base has two additional smooth spiral cords. Syntype NHMUK 1879.2.26.195/2 (but see Remarks and Fig. 27A–D) bears a multispiral brown protoconch; the first whorl and half are smooth with numerous rounded tubercles. Three whorls follow with strong axial riblets intersecting one spiral keel in the first and two spiral keels in the following whorls. The original description suggested the species to be brown, but some specimens show darker fletches.

Remarks. Specimens belonging to these lots show variable strength of the prosocline axial ribs between the main cords. Hinds highlighted in the original description the presence of strong axial ribs and likely named the species after it. The significance of this character for species delimitation has still to be understood. Moreover, two colour forms are present in the type series: syntype NHMUK 1879.2.26.195/2 (Fig. 27A–D, H, I) shows a colouration of light spiral cords on a brown background, whereas the syntype NHMUK 1879.2.26.195/1 (Fig. 27F–G) is brown with darker flammulae. Therefore, this syntype may belong to a different species of this complex group.

This name has been used for the first Indo-Pacific triphorid species detected in the Mediterranean Sea, likely introduced through the Suez Canal. Notwithstanding the complexity of the group, the introduced species in the Mediterranean Sea probably best matches *Viriola bayani* Jousseaume, 1884 (Steger et al. 2018).

Triphoris (*Ino*) *elegans* Hinds, 1843

Figure 28

Triphoris (*Ino*) *elegans* Hinds 1843b: 18–19, not illustrated. Illustration available in Hinds (1844): 29, pl. 8, fig. 11.

Type locality. Straits of Malacca.

Type material. Syntypes: NHMUK 1879.2.26.197: 1 specimen, Straits of Malacca (J. Lombe Taylor coll.).

Original description. *Testa alba, fusco marmorata; anfractibus 16–18 quater carinatis; carinis duobus primariis, inferiore maximo; duobus secondariis alternantibus; carinis omnibus maculis albis et fuscis ornatis. Apertura rotundata, sinu laterali patulo. Axis 4½ lin.*

Geog. Straits of Malacca; from 20 fathoms, mud.

Translation of the Latin text. White shell marbled with brown; 16–18 four-keeled whorls; two larger carinae, the greatest in the lower part of the whorl; two smaller carinae alternated; all carinae with white and brown spots. Rounded aperture, open posterior sinus. Height 4½ lines.

Diagnosis. Syntype 8.1 mm high. Shell cyrtoconoid, with flat sides. Teleoconch with 14 whorls bearing four spiral cords which are smooth, with the exception of the third which is undulated. Spiral microsculpture can be observed between the main cords. The peristome and posterior canal are missing in the holotype. The anterior canal is very elongated and bears two strong smooth spiral cords. The last whorl is strongly angulated at the periphery; the base bears an additional undulated strong spiral cord. The apex is missing in the holotype, but remnants of the last protoconch whorl point to a multispiral type. Such last whorl has two spiral keels and axial riblets. The teleoconch has

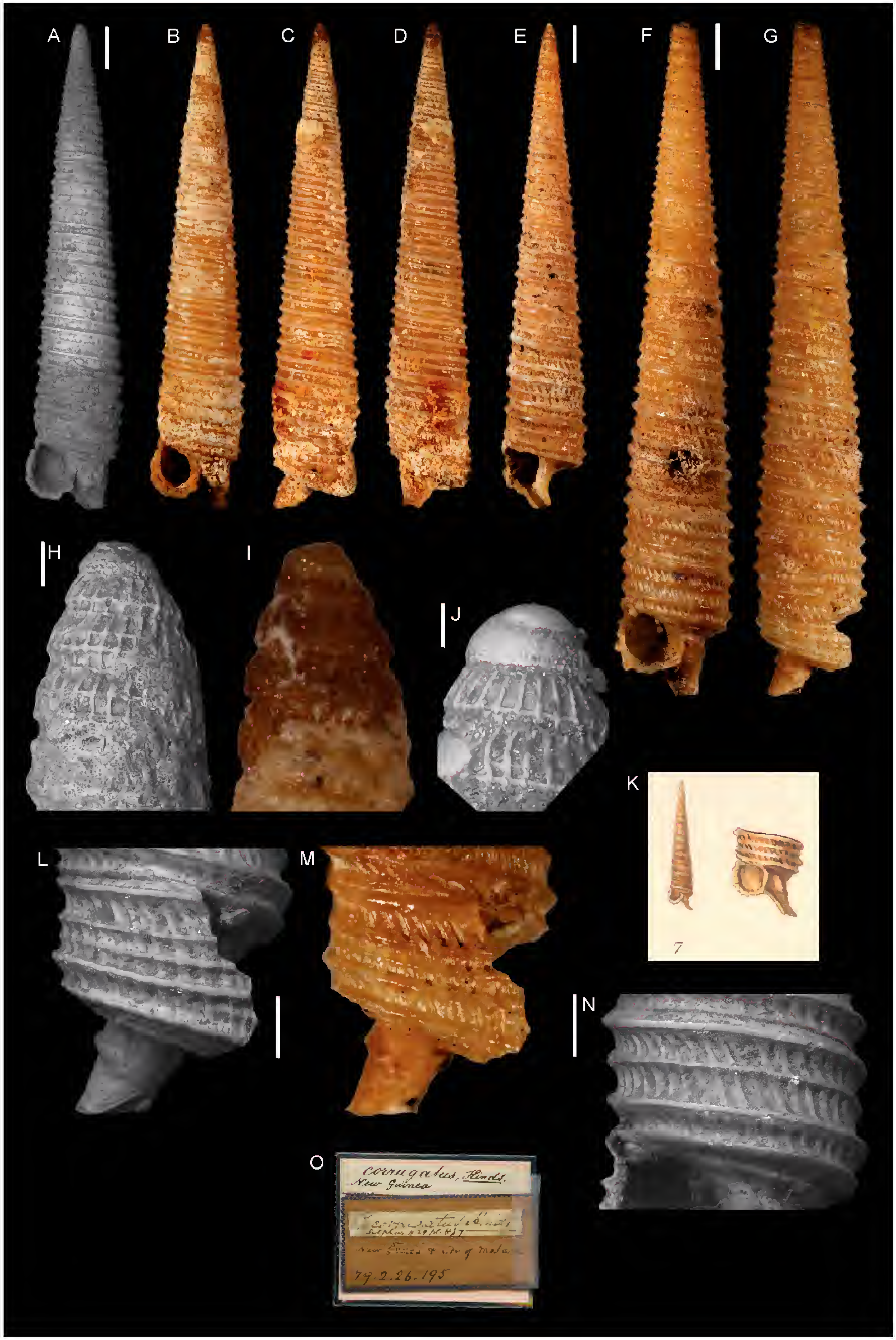

Figure 27. *Triphoris corrugatus* Hinds, 1843. **A–D, H, I** Syntype NHMUK 1879.2.26.195/2, New Guinea and Straits of Malacca (**J**. Lombe-Taylor coll.): front (**A, B**), side (**C**), back (**D**), protoconch (**H, I**). **E, J** Syntype NHMUK 1879.2.26.195/3, New Guinea and Straits of Malacca (**J**. Lombe-Taylor coll.): front (**E**), protoconch (**J**). **F, G, L–N** Syntype NHMUK 1879.2.26.195/1: front (**F**), side (**G**), peristome (**L, M**), microsculpture (**N**), **K** Figure in Hinds 1844. **O** Original labels lot NHMUK 1879.2.26.195. Scale bars: **A–G**: 1 mm; **H, I**: 0.2 mm; **J**: 0.05 mm; **L–N**: 0.5 mm

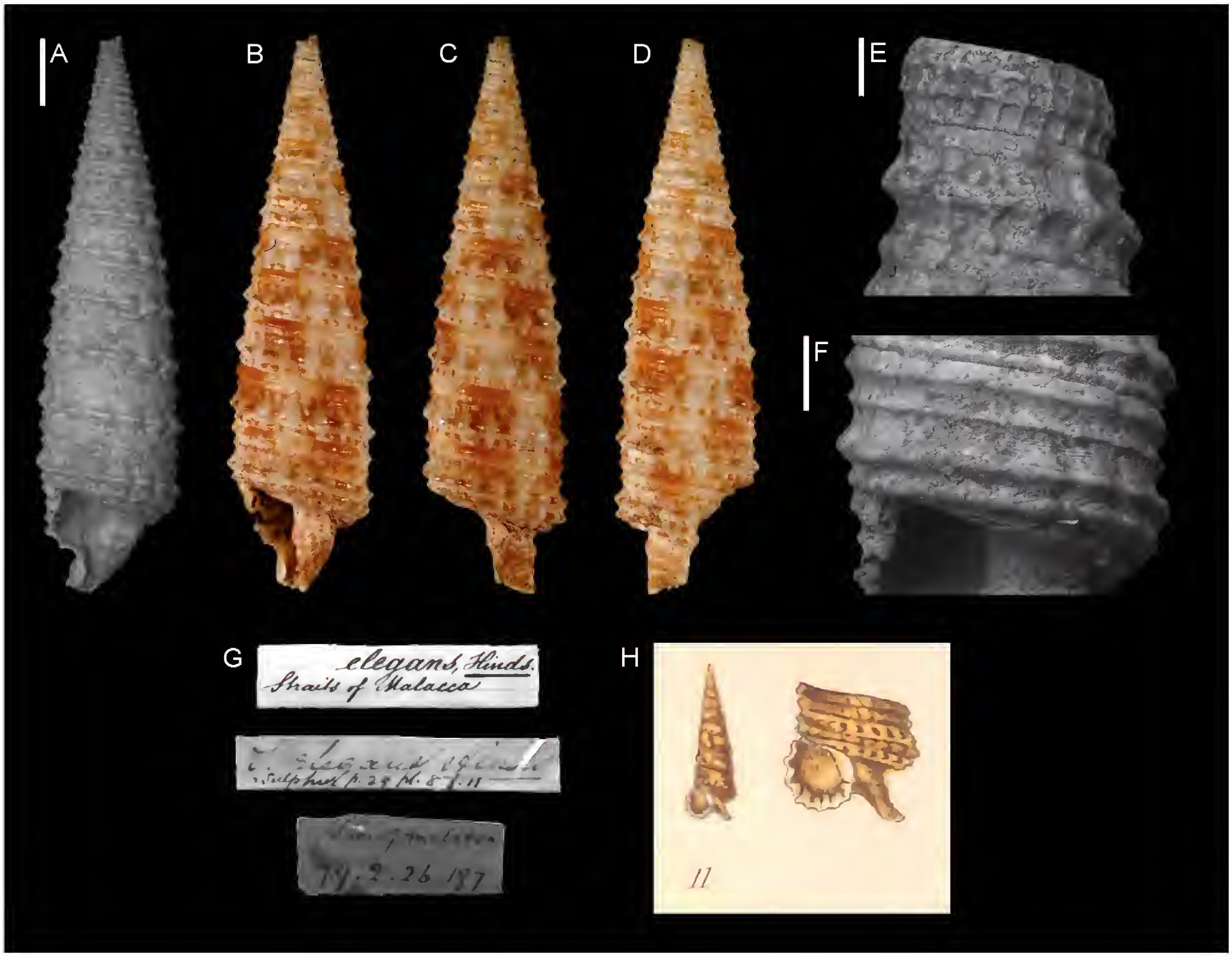

Figure 28. *Triphoris elegans* Hinds, 1843, Straits of Malacca, J. Lombe-Taylor coll. **A–G** Syntype NHMUK 1879.2.26.197: side (**A, B**), front (**C**), back (**D**), protoconch (**E**), microsculpture (**F**), original labels (**G**). **H** Figure in Hinds 1844. Scale bars: **A–D**: 1 mm; **E**: 0.1 mm; **F**: 0.5 mm.

a white background with brown to orange flammulae; the protoconch visible last whorl is brown.

Triphoris (*Ino*) *gigas* Hinds, 1843

Figure 29

Triphoris (*Ino*) *gigas* Hinds 1843b: 17, not illustrated. Illustration available in Hinds (1844): 28, pl. 8, fig. 1.

Type locality. New Guinea.

Type material. Syntypes: NHMUK 1879.2.26.194/1: 1 specimen, New Guinea, (coll. T. Lombe Taylor).

Original description. *Testa valde elongata; anfractibus 25–28 planulatis, quadriseriatim granulosis, inferior paululum maxima ad basin granulorum punctatis. Axis 11 lin.*

Geog. New Guinea; dredged from a muddy bottom at 18 fathoms.

This is the largest species with which I am acquainted. The colour would appear to be brown, but, as the specimens are dead, they cannot be relied on.

Translation of the Latin text. Shell very elongated; 25–28 plain whorls with four rows of granules, the lowest a little bit larger, base dotted by granules. Height 11 lines.

Diagnosis. Syntype broken into two pieces: the abapical and apical ones are 9.5 mm and 3.7 mm, respectively. Shell extremely elongated, cylindrical, with very flat sides. Whorls with four tuberculated spiral cords. The first is initially smooth. The third cord develops later and initially just as a fine thread. Axial ribs prosocline. Apex and base lacking in the available syntype. Syntype background teleoconch colour white, with orange blotches, but likely faded; the original figure shows a deeper brown-orange colour.

Remarks. A "potential" lectotype (NHMUK 196542) had been selected by S. Kosuge in 1965 but then lost while on loan to B. Marshall in 1979. This lectotype designation has never been published and is not deemed valid (as many other "potential" lecto- and paralectotypes of triphorids in NHMUK). A photograph (negative no. 0810) is available (Fig. 29A) and shows a specimen which hardly matches the original description and the figure by Hinds

Figure 29. A *Triphora* sp. (labelled as "potential" lectotype of *Triphoris gigas* Hinds, 1843), NHMUK 196542, New Guinea, coll. H. Cuming. **B, C** *Triphora* sp. (labelled as "potential" lectotype of *Triphoris gigas* Hinds, 1843), NHMUK 196543, New Guinea, coll. H. Cuming: front (**B**), back (**C**). **D, E** *Triphora* sp. (labelled as "potential" paralectotype of *Triphoris gigas* Hinds, 1843), NHMUK 1879.2.26.194/2, New Guinea; coll. T. Lombe Taylor: front (**D**), back (**E**). **F, I, J** *Triphoris gigas* Hinds, 1843, syntype, NHMUK 1879.2.26.194/1, New Guinea; coll. T. Lombe Taylor: apical fragment (**F**), abapical fragment front (**I**) and back (**J**). **H** Figure in Hinds 1844. **I** Original labels lot NHMUK 1879.2.26.194. Scale bars: **A–F, I–J**: 2 mm.

(1844) in the *Zoology of the Sulphur*. In particular, *T. gigas* is characterized by three tuberculated spiral cords of equal size plus a smaller subsutural one, while the lost "potential" lectotype has clearly two main cords and a smaller subsutural one. The lot NHMUK 1879.2.26.194 contains two specimens belonging to two different species. The first specimen (Fig. 29F, I, J) likely belongs to *T. gigas*: it is a juvenile specimen and the third cord is visible between the second and the last as a fine thread (see under *T. princeps* Sowerby III 1904, Figure 97F, the unidentified specimen that is likely a mature *T. gigas*). The second specimen (Fig. 29D, E) has more rounded whorls with two tuberculated spiral cords and strong smooth supra- and subsutural spiral cords which do not appear in *T. gigas*. Lot NHMUK 196543 (Fig. 29B, C) was also labelled as "potential lectotype" but the shell is more conical and an additional spiral cord develops lately between the first and the second, instead of between the second and the third like in *T. gigas*.

Triphoris (*Mastonia*) *grayii* Hinds, 1843

Figure 30

Triphoris (*Mastonia*) *grayii* Hinds 1843b: 19, not illustrated.

Type locality. "The Mediterranean Sea".

Type material. Holotype: NHMUK 1874.9.9.2, fixed by monotypy (J.E. Gray coll.).

Original description. *Testa ovali; anfractibus decem, superioribus biseriatim granulosis moniliferis, duabus inferioribus triseriatim, serie media minima. Axis 4½ lin.*

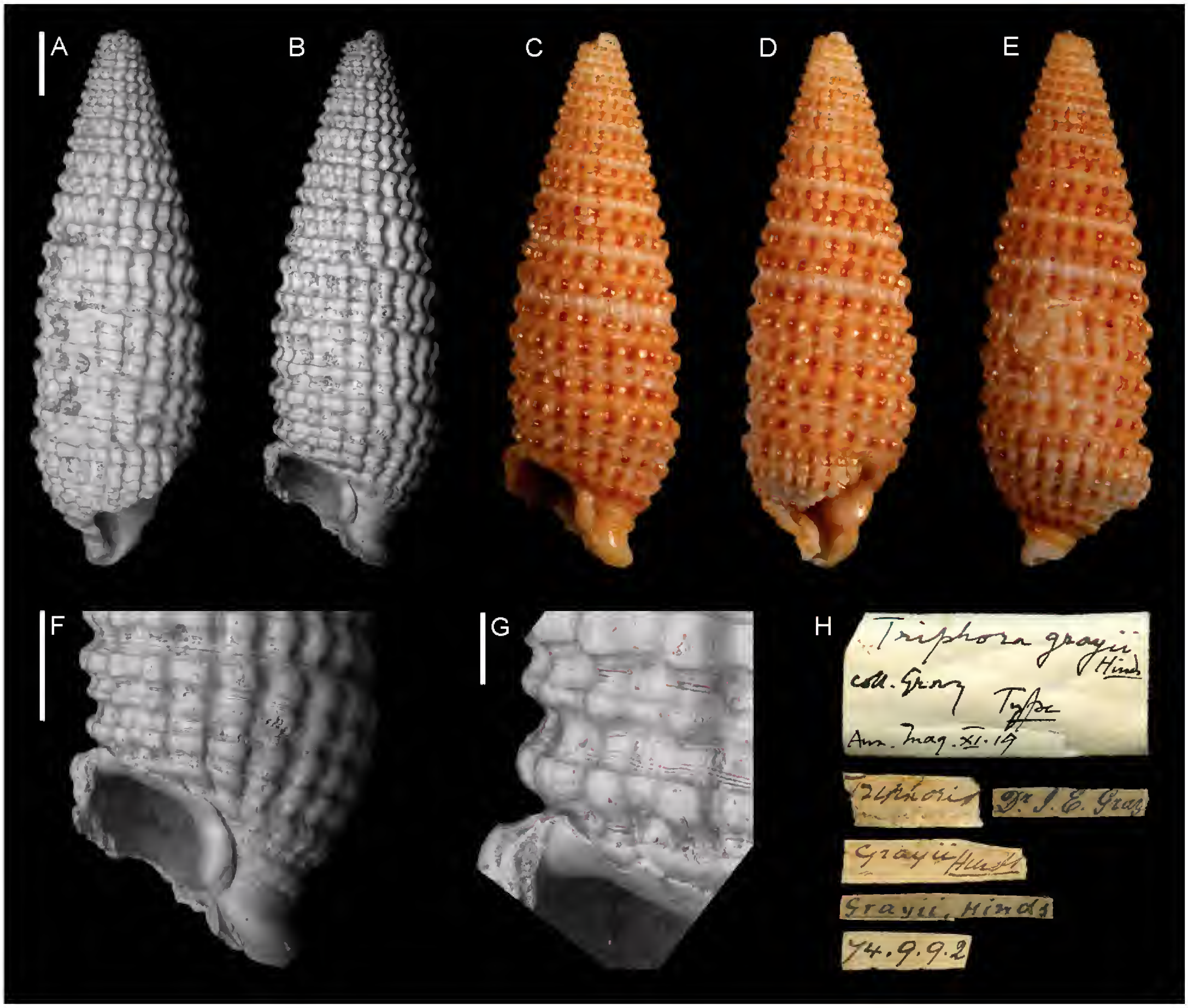

Figure 30. *Triphoris grayii* Hinds, 1843, J.E. Gray coll. **A–H** Holotype, NHMUK 1874.9.9.2: front (**B, C**), side (**A, D**), back (**E**), aperture (**F**), microsculpture (**G**), original labels (**H**). Scale bars: **A–F**: 1 mm; **G**: 0.3 mm.

Geog. The Mediterranean Sea. Cab. Gray.

The single specimen of this very pretty shell has the mouth much injured.

Translation of the Latin text. Oval shell; ten whorls, the upper ones with two rows of granules, the lower ones with three rows, the intermediate the smallest. Height 4½ lines.

Diagnosis. Holotype 8.2 mm high. Shell cyrtoconoid and rather broad. Teleoconch of 10 visible whorls, but likely the very first whorls are missing. Teleoconch whorls have two very strong spiral cords bearing large tubercles at the intersection with orthocline axial ribs. In the second half of the shell, a third finer one develops and a fine smooth suprasutural cord is also visible. Spiral microsculpture is also visible between the main cords. The base has one tuberculated and one smooth additional cords. The peristome is incomplete, but bears an additional spiral cord between the third and the fourth. The siphonal canal is well developed with additional smooth cords. The apex is missing. The teleoconch has a whitish background visible between the main cords which are deep orange in the interspaces and bear creamy tubercles.

Remarks. This has not been recognized as a Mediterranean species (Bouchet 1985). In contrast, it is remarkably similar to the shell identified as *Monophorus* cf. *thiriotae* Bouchet, 1985 illustrated by Rolán (1993, 2001, 2005: 327) from the Canary Islands, the Cape Verde Islands and other localities in West Africa.

Triphoris (*Ino*) *maxillaris* Hinds, 1843

Figure 31

Triphoris (*Ino*) *maxillaris* Hinds 1843b: 18, not illustrated. Illustration available in Hinds (1844): 29, pl. 8, fig. 8.

Type locality. Straits of Malacca.

Type material. Lectotype: NHMUK 1879.2.26.202/1, here designated (J. Lombe Taylor coll.). Paralectotypes:

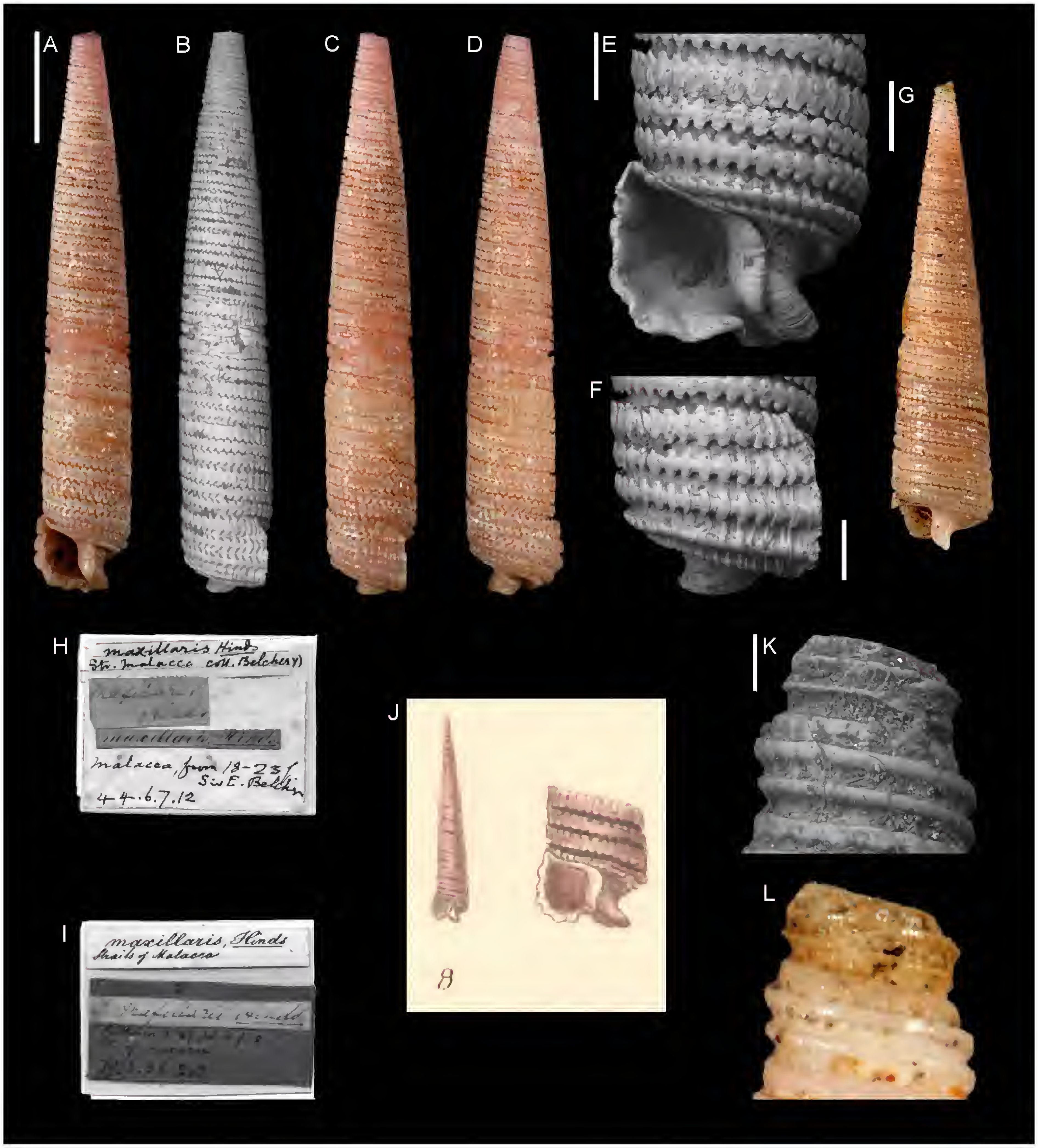

Figure 31. *Triphoris maxillaris* Hinds, 1843. **A–F, H** Paralectotype, NHMUK 1844.6.7.12, Straits of Malacca (coll. E. Belcher): front (**A**), side (**B, C**), back (**D**), aperture (**E**), peristome (**F**), original labels (**H**). **G, I, K, L** Lectotype NHMUK 1879.2.26.202/1, Straits of Malacca (Mrs J. Lombe-Taylor coll.): front (**G**), original labels (**I**), protoconch (**K, L**). **J** Figure in Hinds 1844. Scale bars: **A–D**: 2 mm; **E, F**: 0.5 mm; **G**: 1 mm; **K, L**: 0.1 mm.

NHMUK 1879.2.26.202/2, 1 specimen, Malacca (J. Lombe Taylor coll.); NHMUK 1844.6.7.12, Malacca, 1 specimen (coll. E. Belcher).

Original description. *Testa rosea; anfractibus 16–18, superficie laevigata, bisulcatis; marginibus sulcorum granulatis; sutura sulcata, marginibus granulatis apertura subquadrata, sinu laterali parvo patulo. Axis 5½ lin.* This shell is very remarkably characterized. The surface is perfectly smooth, and of an agreeable rose-colour; but each whorl is divided into three unequal parts by two furrows. The margins of each furrow, and of the depressed line which marks the course of the suture, are provided with a series of horizontal granulations, which look towards each other and do not appear above the surface of the shell, but under a magnifying glass display an appearance which seems to justify the specific name.

Translation of the Latin text. Pink shell; 16–18 whorls with a smooth surface with two grooves whose margins are granulated; deep suture, subquadrate aperture with granulated margin, slightly open posterior sinus. Height 5½ lines.

Diagnosis. The lectotype is a subadult, but the paralectotype is 9.9 mm high. Shell conical and elongated. The lectotype has 17 flat whorls, but the apical part is missing. The three spiral cords have broad flat coalescent tubercles. The base has two more spiral cords with similar tubercles and a depression between the fifth cord and the siphonal canal which is short. The peristome has no additional cords and bears a shallow posterior canal. The protoconch is absent in the types, but remnants of its last whorl suggest a multispiral type. Teleoconch pink, protoconch brown.

Remarks. Specimens with indistinguishable teleoconch sculpture, colour and overall appearance, but with paucispiral protoconch were found in Vanuatu. Consequently, we designated as lectotype of *T. maxillaris* a specimen that, although subadult, retains the last whorl of a typical planktotrophic protoconch (Fig. 31K, L) to unambiguously identify this species.

Triphoris (*Ino*) *micans* Hinds, 1843

Figure 32

Triphoris (*Ino*) *micans* Hinds 1843b: 18, not illustrated. Illustration available in Hinds (1844): 29, pl. 8, fig. 9.

Type locality. New Guinea.

Type material. Syntypes: NHMUK 1844.6.7.10: 1 specimen, and NHMUK 1844.6.7.11: 1 specimen, both New Guinea (coll. E. Belcher); NHMUK 1879.2.26.209, 2 specimens (coll. T. Lombe Taylor).

Original description. *Testa gracili attenuata, fusca; anfractibus 20–22, supra coarctatis, triseriatim granulosis, serie inferiore maxima albida, superiore minima; apertura subquadrata; sinu laterali lineari. Axis 6 lin.*

Geog. New Guinea; dredged from mud in from 5 to 18 fathoms.

Translation of the Latin text. Slender, dark shell; 20–22 whorls, narrow above, with three series of granules, the whitish lower is the greatest, the upper one is the smallest; subquadrate aperture; linear posterior sinus. Height 6 lines.

Diagnosis. Syntypes 12.2–13.3 mm high. Shell conical, narrow and very elongated. Teleoconch of ca 20 whorls with flat sides bearing three spiral cords with large tubercles at the intersection with prosocline axial ribs. The base has two additional almost smooth spiral cords. The last half whorl and peristome bear additional spiral cords between the main ones. Anterior siphonal canal long. The lectotype protonch is incomplete and worn but clearly multispiral and composed of at least four whorls with two strong keels; axial riblets are also likely present. Shell white to creamy-white.

Remarks. The syntypes NHMUK 1844.6.7.10 and 1844.6.7.11 are broken into two fragments.

Triphoris (*Mastonia*) *monilifer* Hinds, 1843

Figure 33

Triphoris (*Mastonia*) *monilifer* Hinds 1843b: 19, not illustrated. Illustration available in Hinds (1844): 30, pl. 8, fig. 14.

Type locality. Straits of Malacca.

Type material. Syntypes: NHMUK 1879.2.26.208: 3 specimens, Straits of Malacca (coll. T. Lombe Taylor); NHMUK 1844.6.7.28–29, 2 specimens, Straits of Malacca (coll. E. Belcher).

Original description. *Testa parva, elegantissime monili; anfractibus decem biseriatim granulosis; granulis seriei inferioris albis intervallis rubris, supremae albis; apertura subquadrata, sinu laterali angusto. Axis 2⅓ lin.*

Geog. Straits of Malacca; in 18 to 23 fathoms, mud. The manner in which the lower series of markings is repeated in the last whorl is very evident in this species, though to be met with in nearly the whole. Thus, the series of beading, which is single on the upper whorls, will here be found to be double on the last.

Translation of the Latin text. Small shell, elegant like a jewel; ten whorls with two series of granules; the lower series with white granules with red interspaces, the upper one white; subquadrate aperture, narrow posterior sinus. Height 2⅓ lines.

Diagnosis. Syntype NHMUK 1879.2.26.208/1 (Fig. 33A–G) 4.4 mm high. Shell conical and rather broad. Teleoconch of nine whorls with two main spiral cords bearing tubercles at the intersection with prosocline axial ribs. A fine third cord develops on the last whorl and numerous fine punctuated spiral striae are present between the main cords. A fourth and fifth smooth spiral cords are visible on the base. The peristome bears a deep posterior sinus and additional spiral cords near the lip. Anterior siphonal canal short. Protoconch multispiral of 5 whorls. The first is apparently smooth, while the others bear a strong spiral keel and axial riblets. Protoconch brown. Teleoconch with a creamy white background and orange interspaces between tubercles.

Triphoris (*Ino*) *pagodus* Hinds, 1843

Figure 34

Triphoris (*Ino*) *pagodus* Hinds 1843a: 22, not illustrated.

Type locality. Baclayon, island of Bohol, Philippines.

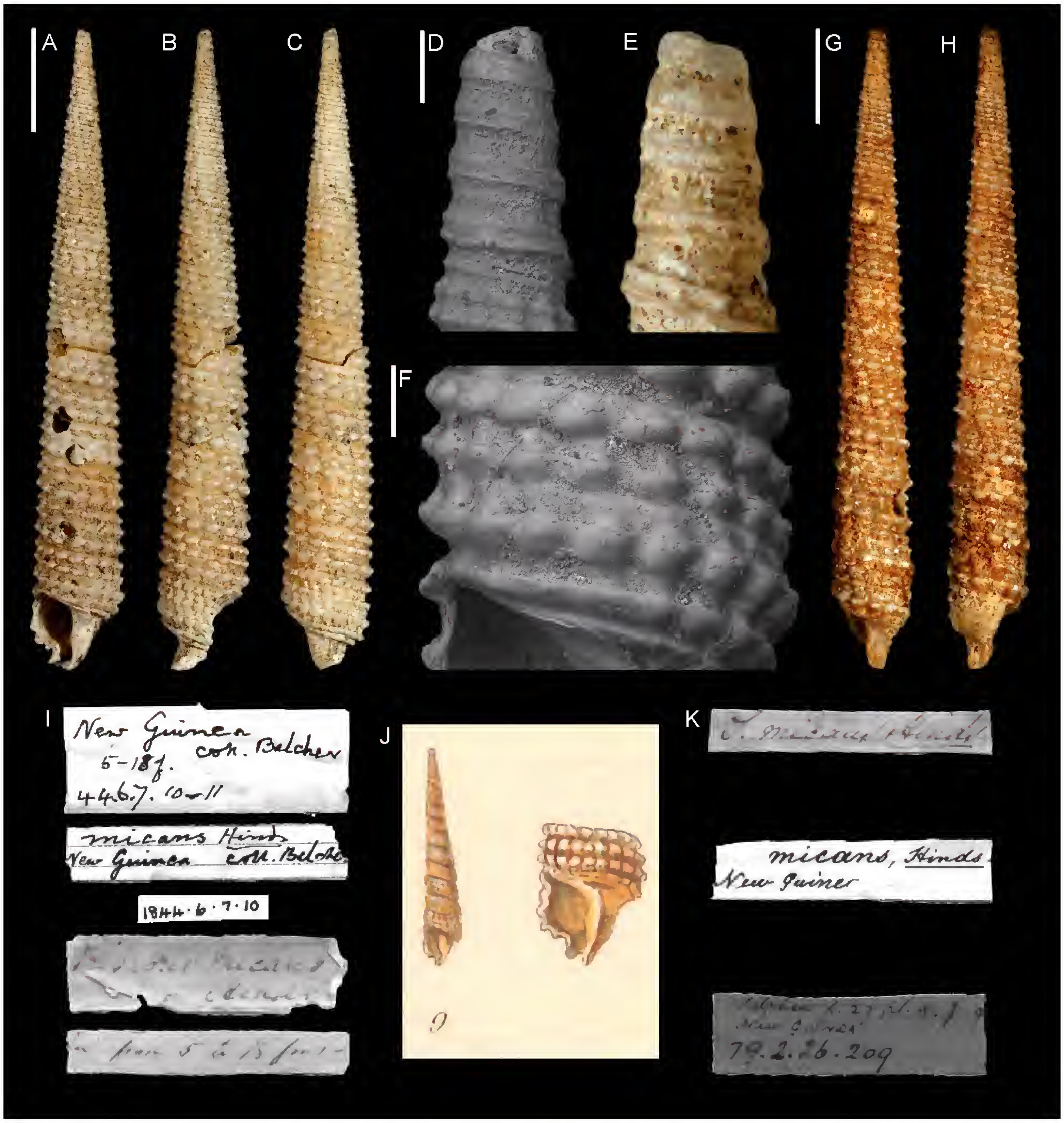

Figure 32. *Triphoris micans* Hinds, 1843. **A–F, I** Syntype NHMUK 1844.6.7.10, New Guinea (coll. E. Belcher): front (**A**), side (**B**), back (**C**), protoconch (**D, E**), microsculpture (**F**), original labels (**I**). **G, H, K** Syntype NHMUK 1879.2.26.209, New Guinea (coll. T. Lombe Taylor): front (**G**), back (**H**), original labels (**K**). **J** Figure in Hinds 1844. Scale bars: **A–C, G, H**: 2 mm; **D, E**: 0.2 mm; **F**: 0.3 mm.

Type material. Holotype: NHMUK 196517, fixed by monotypy (H. coll. H. Cuming).

Original description. *Tri. (Ino) testâ cylindraceâ, elongatâ, acuminatâ, anfractibus 18–20, tricarinatis; carinis inaequalibus, inferiore multo maximâ, duobus superioribus parvis aequalibus; aperturâ quadratâ. Axis 8½ lin.*

The only specimen of this shell is dead and imperfect. It is, however, slightly mottled with brown, being most probably the remains of a uniform colour. It is rendered very distinct from any species hitherto described by the manner of its keeling. A faint elevated line would also appear to traverse the course of the suture.

Hab. Baclayon, island of Bohol, Philippines. Found under stones at low water.

Translation of the Latin text. Cylindrical shell, elongated, acuminate, 18–20 whorls, with three keels of unequal size, the lowest keel by far the largest, the two above equal and smaller; aperture quadrate. Height 8½ lines.

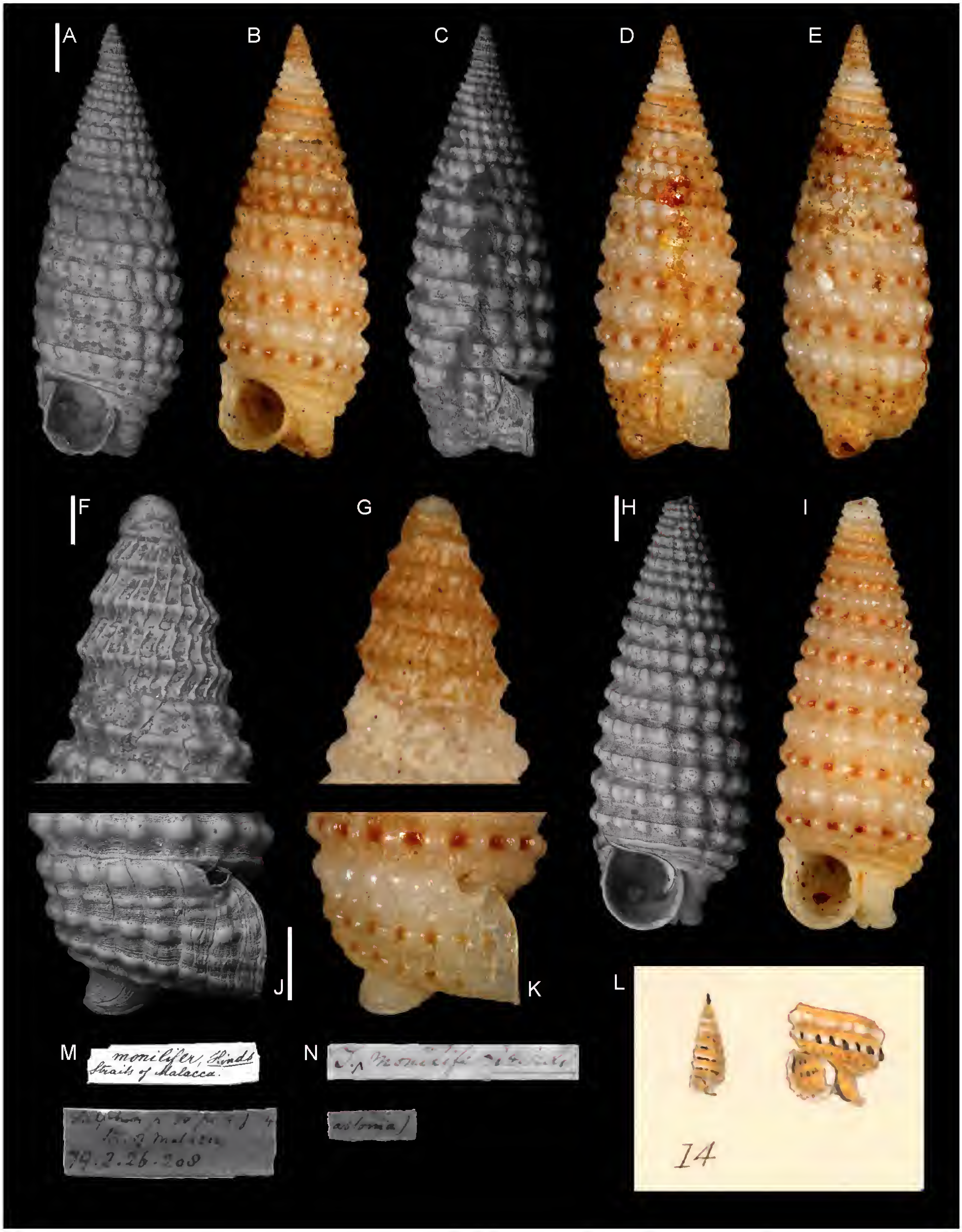

Figure 33. *Triphoris monilifer* Hinds, 1843, Straits of Malacca, coll. T. Lombe Taylor. **A–G** Syntype NHMUK 1879.2.26.208/1: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, G**). **H–K** Syntype NHMUK 1879.2.26.208/2: front (**H, I**), peristome (**J, K**). **L** Figure in Hinds 1844. **M–N** Original labels of lot 1879.2.26.208. Scale bars: **A–E, H–K**: 0.5 mm; **F, G**: 0.1 mm.

Figure 34. *Triphoris pagodus* Hinds, 1843, Baclayon, Bohol Island, Philippines, coll. H. Cuming. **A–D** Holotype, NHMUK 196517: front (**A**), side (**B**), back (**C**), original labels (**D**). Scale bar: **A–C**: 2 mm.

Diagnosis. Holotype 18.9 mm. Shell extremely elongated with flat whorls. It lacks the apical part and a portion of the last whorl. The specimen has 15 whorls, with three spiral keels: the third is very prominent whereas the first two are smaller and of equal size. Between these keels, there are prosocline axial threads. Siphonal canal long, peristome missing in the holotype. The base bears one additional strong keel and a second smaller one. A third faint one runs on the siphonal canal. Apex missing in the holotype. Teleoconch worn, but apparently whitish with brown blotches.

Triphoris (*Mastonia*) *roseus* Hinds, 1843

Figure 35

Triphoris (*Mastonia*) *roseus* Hinds 1843b: 21, not illustrated. Illustration available in Hinds (1844): 31, pl. 8, fig. 19.

Type locality. "Pacific Ocean?"

Type material. Syntypes: NHMUK 1879.2.26.212: 1 specimen, South Pacific Ocean (coll. T. Lombe Taylor).

Original description. *Testa ovali; anfractibus decem biseriatim granulosis, seriebus corneis, medio laevigato roseo serie tertia parva; apertura rotundata. Axis 3½ lin.*

Geog. Pacific Ocean? Cab. Metcalfe.

Translation of the Latin text. Shell oval; 10 whorls with two granulated brownish cords; in the middle, a third small smooth pink cord; rounded aperture. Height 3½ lines.

Diagnosis. Syntype 5.5 mm high. Shell conical with 10 visible flat whorls, but the apical part is missing. Two main spiral cords run on the whorls; a third develops in between, initially as a fine thread and then as a fully-grown cord on the last whorl. Large, subrectangular tubercles are present at the intersection with slightly prosocline axial ribs. The last whorl and the base have three additional weakly tuberculated spiral cords. Very fine microsculpture is visible between the main spiral cords and axial ribs. The peristome has a very shallow posterior sinus and apparently does not bear additional spiral cords. The protoconch is missing in the syntype. Teleoconch light orange with pink to pearly lower spiral cords.

Triphoris (*Mastonia*) *ruber* Hinds, 1843

Figure 36

Triphoris (*Mastonia*) *ruber* Hinds 1843b: 19–20, not illustrated. Illustration available in Hinds (1844): 30, pl. 8, fig. 15.

Type locality. "New Ireland" [Papua New Guinea].

Type material. Syntypes: NHMUK 1844.6.7.22–26: 5 specimens, New Ireland (coll. E. Belcher); NHMUK 1879.2.26.192/1–5: 5 specimens, New Ireland and Straits of Malacca (J. Lombe Taylor coll.).

Original description. *Testa rufa; anfractibus undecim biseriatim granulosis, seriebus subdistantibus suturam obtegentibus; apertura rotundata; sinu laterali margine contracto. Axis 4 lin.*

Geog. New Ireland; numerous among fine gravel at low water. Straits of Malacca; in 20 fathoms.

Its reddish colour and double series of tubercles will readily distinguish this shell. In some of the specimens, a

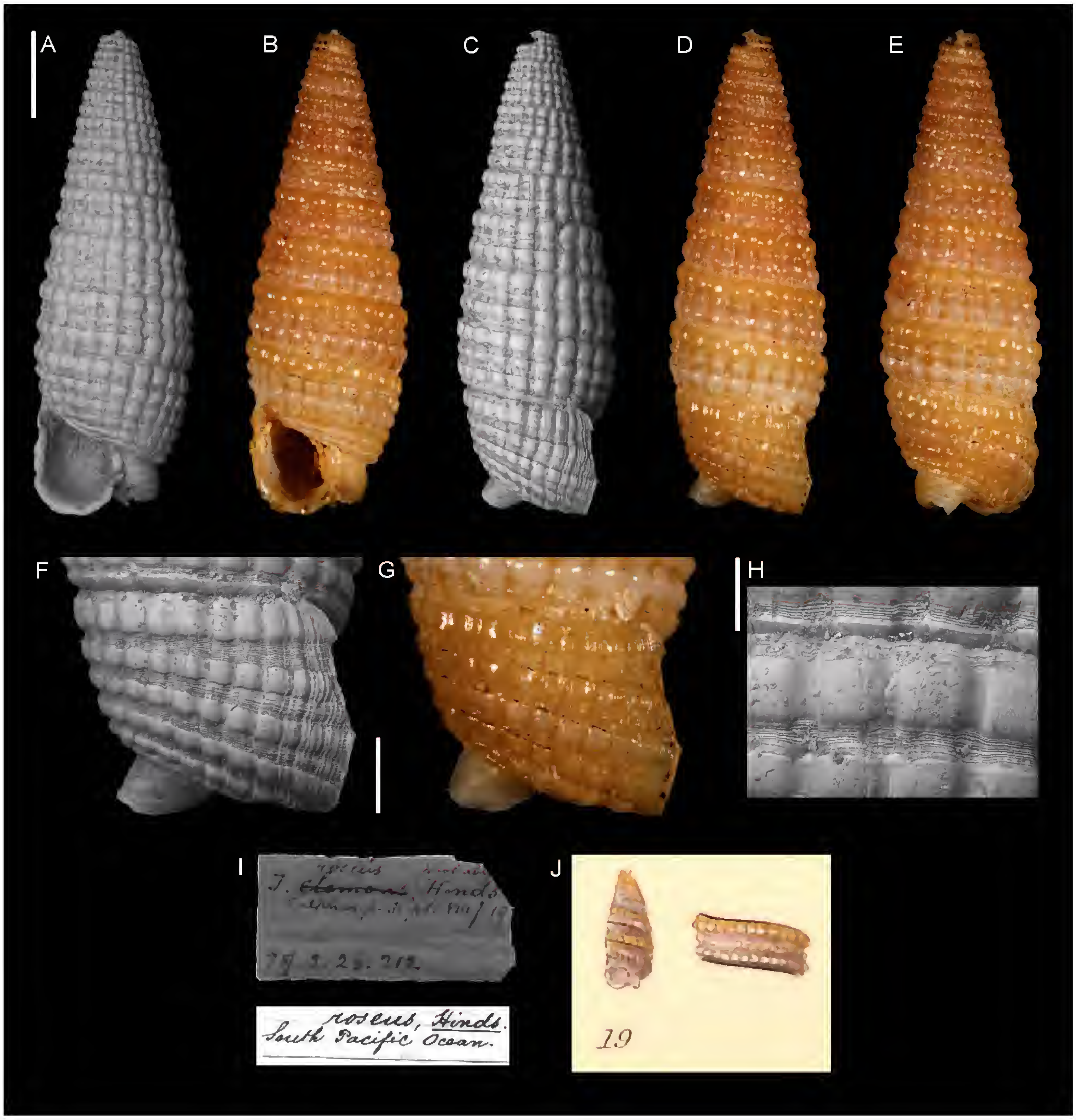

Figure 35. *Triphoris roseus* Hinds, 1843, South Pacific Ocean, coll. T. Lombe Taylor. **A–I** Syntype NHMUK 1879.2.26.212: front (**A, B**), side (**C, D**), back (**E**), peristome (**F, G**), microsculpture (**H**), original labels (**I**). **J** Figure in Hinds 1844. Scale bars: **A–E**: 1 mm; **F, G**: 0.5 mm; **H**: 0.2 mm.

small intermediate series is about to make its appearance on the one or two inferior whorls.

Translation of the Latin text. Shell red; 11 whorls with two granulated threads, lower series covering the suture; aperture rounded; sinus on the peristome with contracted edges. Height 4 lines.

Diagnosis. Syntype NHMUK 1844.6.7.22 (Fig. 36A–H) 5 mm high. Shell conical and broad. Teleoconch of 12 flat whorls bearing two large cords with tubercles at the interstices with opisthocline axial ribs. A third spiral cord is visible on the last whorl as a fine smooth thread just below the first cord. The base bears two additional weakly tuberculated cords. In between the main sculpture, fine numerous finely tuberculated spiral cords are visible. The peristome has a deep posterior sinus and fine additional spiral cords. Siphonal canal short. Protoconch multispiral, of four whorls; the first has spherical tubercles, while the others bear two spiral keels and axial riblets. Teleoconch pink to light violet, with lighter tubercles. Protoconch brown. Operculum horny, rather thin, ovate, multispiral of about 4½ whorls, nucleus a little eccentric, periphery thin and only a little upturned.

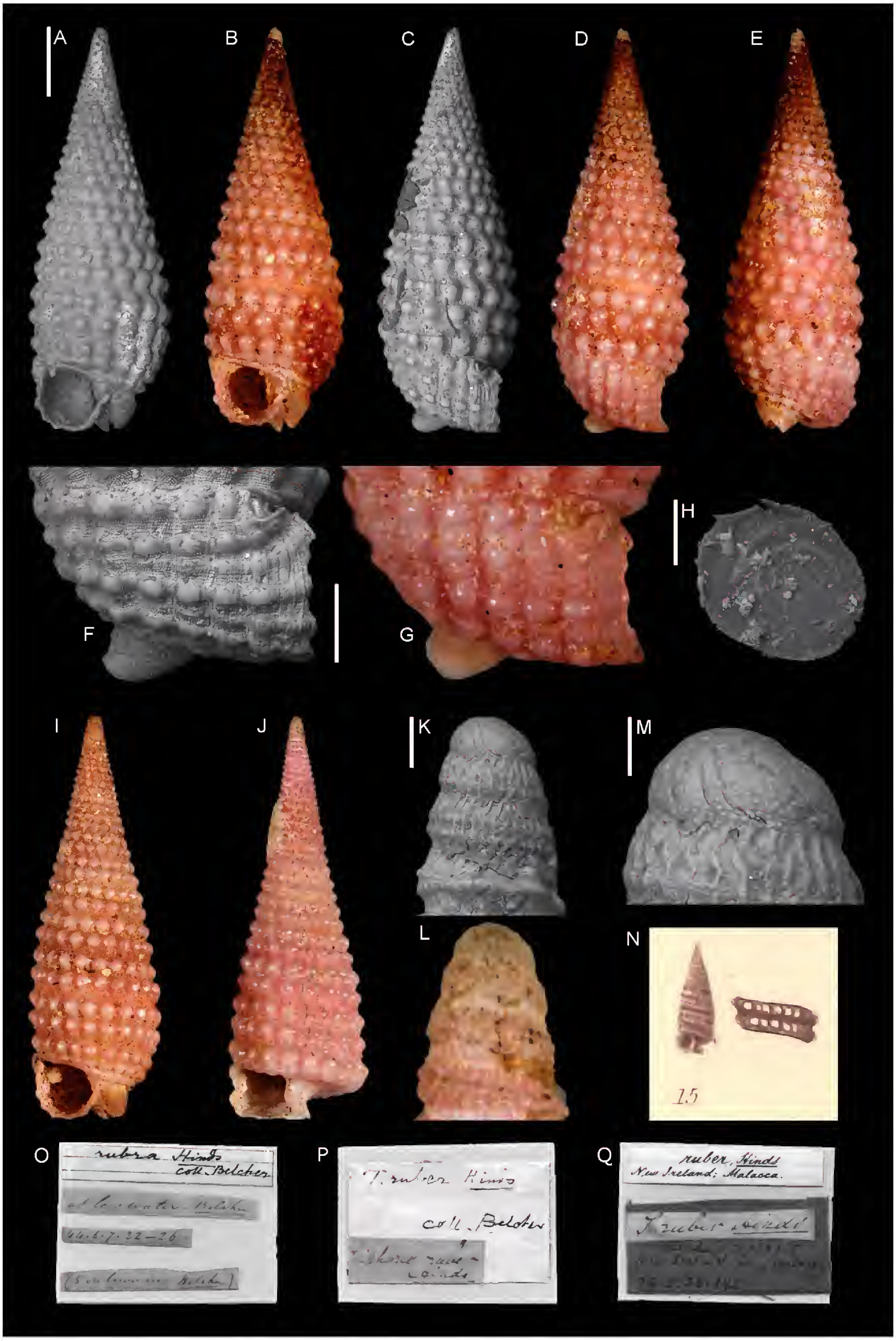

Figure 36. *Triphoris ruber* Hinds, 1843. **A–H** Lectotype NHMUK 1844.6.7.22, New Ireland (coll. E. Belcher): front (**A, B**), side (**C, D**), back (**E**), peristome (**F, G**), operculum (**H**). **I** Paralectotype, NHMUK 1844.6.7.23, New Ireland (coll. E. Belcher): front (**I**). **J–M, Q** Paralectotype, NHMUK 1879.2.26.192, New Ireland and Straits of Malacca (J. Tomble Taylor coll.): front (**J**), protoconch (**K–M**), original labels (**Q**). **N** Figure in Hinds 1844. **O–P** Original labels lot NHMUK 1844.6.7.22–26. Scale bars: **A–E**: 1 mm; **F, G**: 0.5 mm; **H**: 0.3 mm; **K, L**: 0.1 mm; **M**: 0.05 mm.

Triphoris (*Ino*) *sculptus* Hinds, 1843

Figure 37

Triphoris (*Ino*) *sculptus* Hinds 1843b: 17, not illustrated. Illustration available in Hinds (1844): 28, pl. 8, fig. 3.

Type locality. Straits of Malacca.

Type material. Syntypes: NHMUK 1844.6.7.17– 19, 3 specimens, Straits of Malacca (coll. E. Belcher); NHMUK 1855.11.15.20, 1 specimen, no locality (coll. E. Belcher); NHMUK 1879.2.26.201, 1 specimen, Straits of Malacca (J. Lombe-Taylor coll.).

Original description. *Testa pallide rufente; anfractibus 15–18 biseriatim granoso-carinatis, medio laevigatis carina secundaria; prope suturam carinula monilifera; sinu laterali patulo. Axis 4½ lin.*

Geog. Straits of Malacca; in 3 fathoms.

Translation of the Latin text. Shell pale reddish; 15–18 whorls with two granulated-keeled cords, with a smooth interspace with a secondary keel; a thin granulated keel near the suture; open posterior sinus. Height 4½ lines.

Diagnosis. Subadult syntypes ca 9 mm high. Shell conical, with flat whorls bearing two quite thin main spiral cords with large oblong tubercles at the intersection with broad axial ribs. A third very fine spiral cord develops early in the teleoconch but never attains the strength of the other two whereas a fourth smooth cord is visible above the suture. A microsculpture of very fine threads is visible between the main cords. The apex is incomplete, but clearly bears a brown multispiral protoconch whose last two whorls have two strong spiral keels and axial riblets. The teleoconch has a whitish background with orange to brown flammulae.

Remarks. All available syntypes are subadults without a fully developed last whorl and peristome. Specimens NHMUK 1844.6.7.17 (Fig. 37A, B) and NHMUK 1844.6.7.19 (Fig. 37H) are probably those that best fit the figure by Hinds (1844) in terms of sculpture, colour pattern and shell profile. In contrast, NHMUK 1844.6.7.18 (Fig. 37G) has a much more slender profile and resembles *Triphoris bilix* Hinds, 1844 (p. 185), NHMUK 1879.2.26.201 (Fig. 37J) is again more slender and has more numerous tubercles on the third spiral cord, superficially resembling *T. concors* Hinds, 1844 (p. 193), and NHMUK 1855.11.15.20 might be a *sculptus*, but it is too ruined for proper identification.

Triphoris (*Mastonia*) *tristis* Hinds, 1843

Figure 38

Triphoris (*Mastonia*) *tristis* Hinds 1843b: 20, not illustrated.

Type locality. Not reported.

Type material. Syntypes: NHMUK 196538: 1 specimen, and NHMUK 196539: 1 fragment (but likely conspecific), both without locality (J.E. Gray coll.).

Original description. *Testa ovali elongata, ferruginea; anfractibus tridecim biseriatim granulosis; serie superiori paululum maxima et albida; anfractu penultimo serie tertia minima. Axis 3 lin.*

Geog. — ? Cab. Gray.

Translation of the Latin text. Shell oval and elongated, reddish; 13 whorls with two granulated cords; the upper one slightly larger and white; on the penultimate whorl a small third cord appears. Height 3 lines.

Diagnosis. Syntype NHMUK 196538 6.2 mm high. Shell conical, composed of 13 teleoconch flat whorls which bear two main tuberculated spiral cords. A third develops in between on the penultimate whorl as a fine thread but attains full size on the last whorl. The base has two additional weakly tuberculated whorls. The apex is broken in the lectotype, but remnants of the last protoconch whorl suggest a multispiral type. Such last whorl bears a single strong spiral keel and axial riblets. Shell brown, with pearly white tubercles on the first spiral cord.

Triphoris (*Sychar*) *vitreus* Hinds, 1843

Figure 39

Triphoris (*Sychar*) *vitreus* Hinds 1843b: 19, not illustrated. Illustration available in Hinds (1844): 30, pl. 8, fig. 12.

Type locality. Straits of Malacca.

Type material. Syntypes: NHMUK 1879.2.26.210: 1 specimen, Straits of Malacca (J. Lombe Taylor coll.).

Original description. *Testa pellucida; anfractibus quindecim laevigatis rotundatis, lineis duabus elevatis cinctis; apice mamillari; apertura subquadrata; sinu laterali patulo. Axis 4½ lin.*

Geog. Straits of Malacca; dredged from 20 fathoms. One of the elevated lines traverses the whorl about its centre; the other, not at first very apparent, will be found on its lower surface near the suture.

Translation of the Latin text. Transparent shell; 15 rounded whorls, smooth, surrounded by two lines; apex mamillated; aperture subquadrate; open posterior sinus. Height 4½ lines.

Diagnosis. Syntype 8.7 mm high. Conical shell with 12 slightly convex whorls with numerous prosocline growth lines and two deep spiral grooves. Very fine spiral threads are also visible. Base smooth. Peristome with no clear posterior sinus, siphonal canal short. Protoconch paucispiral with one large smooth whorl. Shell colour yellowish-white.

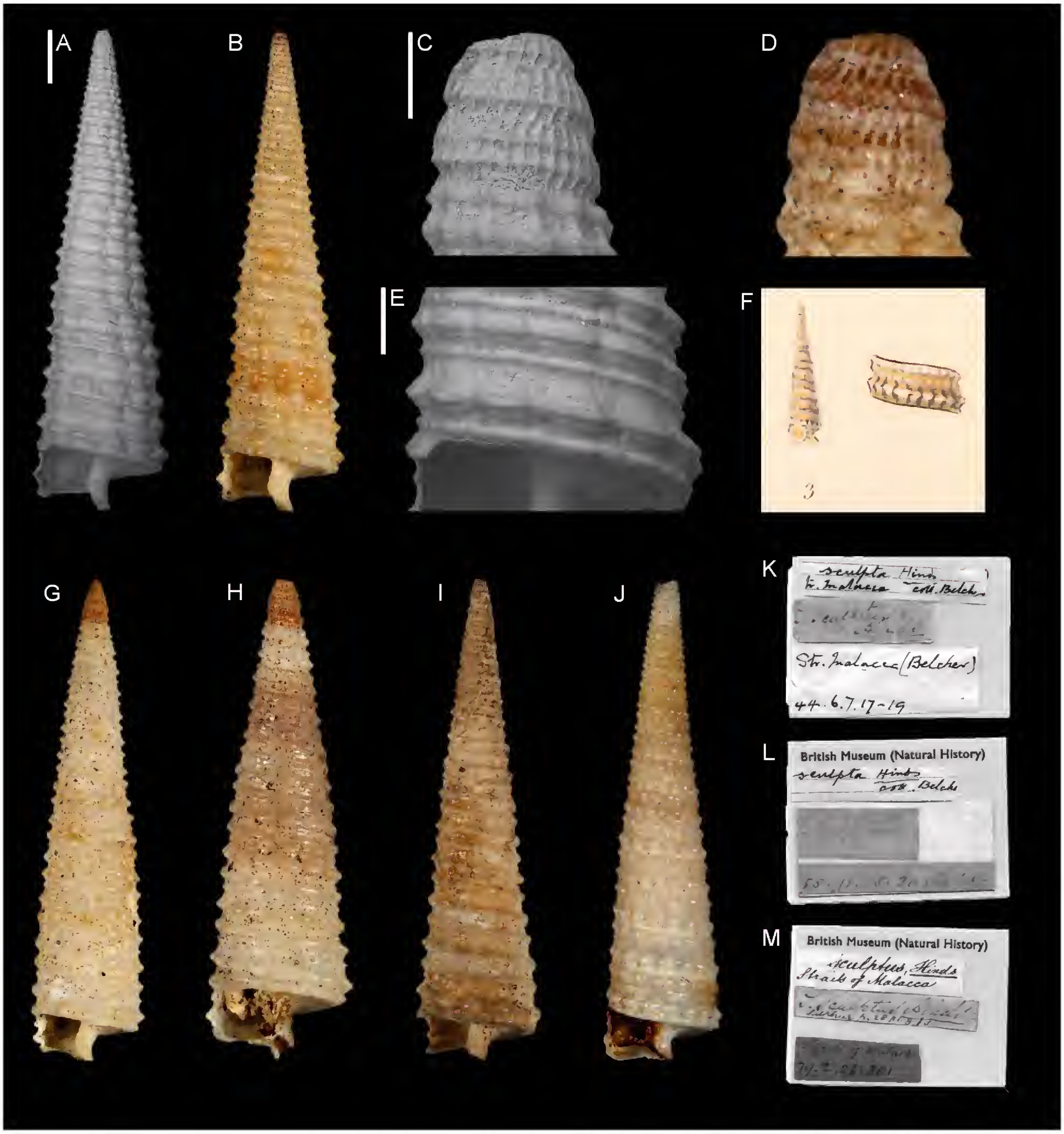

Figure 37. *Triphoris sculptus* Hinds, 1843. **A–E** Syntype NHMUK 1844.6.7.17, Straits of Malacca (coll. E. Belcher): front (**A, B**), protoconch (**C, D**), microsculpture (**E**). **F** Figure in Hinds 1844. **G** Syntype NHMUK 1844.6.7.18, Straits of Malacca (coll. E. Belcher): front. **H** Syntype NHMUK 1844.6.7.19, Straits of Malacca (coll. E. Belcher): front. **I** Syntype NHMUK 1855.11.15.20 (coll. E. Belcher). **J** Syntype NHMUK 1879.2.26.201, Straits of Malacca (J. Lombe-Taylor coll.). **K** Original labels NHMUK 1844.6.7.17–19. **L** Original labels lot NHMUK 1855.11.15.20. **M** Original labels lot NHMUK 1879.2.26.201. Scale bars: **A, B**: 1 mm; **C, D**: 0.2 mm; **E**: 0.5 mm.

Triphoris (*Ino*) *vittatus* Hinds, 1843

Figure 40

Triphoris (*Ino*) *vittatus* Hinds 1843b: 17, not illustrated. Illustration available in Hinds (1844): 28, pl. 8, fig. 4.

Type locality. Straits of Malacca.

Type material. Syntypes: NHMUK 1879.2.26.196: 2 specimens, Straits of Malacca (coll. T. Lombe Taylor); NHMUK 1844.6.7.20, 1 specimen, Straits of Malacca (coll. E. Belcher); NHMUK 1844.6.7.21, 1 specimen, Straits of Malacca (coll. E. Belcher).

Original description. *Testa laevigata, cornea; anfractibus 22–25 transversim leviter sulcatis, medio fusco elegantissime vittatis; apertura subquadrata; sinu laterali obsoleto. Axis 8 lin.*

Geog. Straits of Malacca; in 23 fathoms.

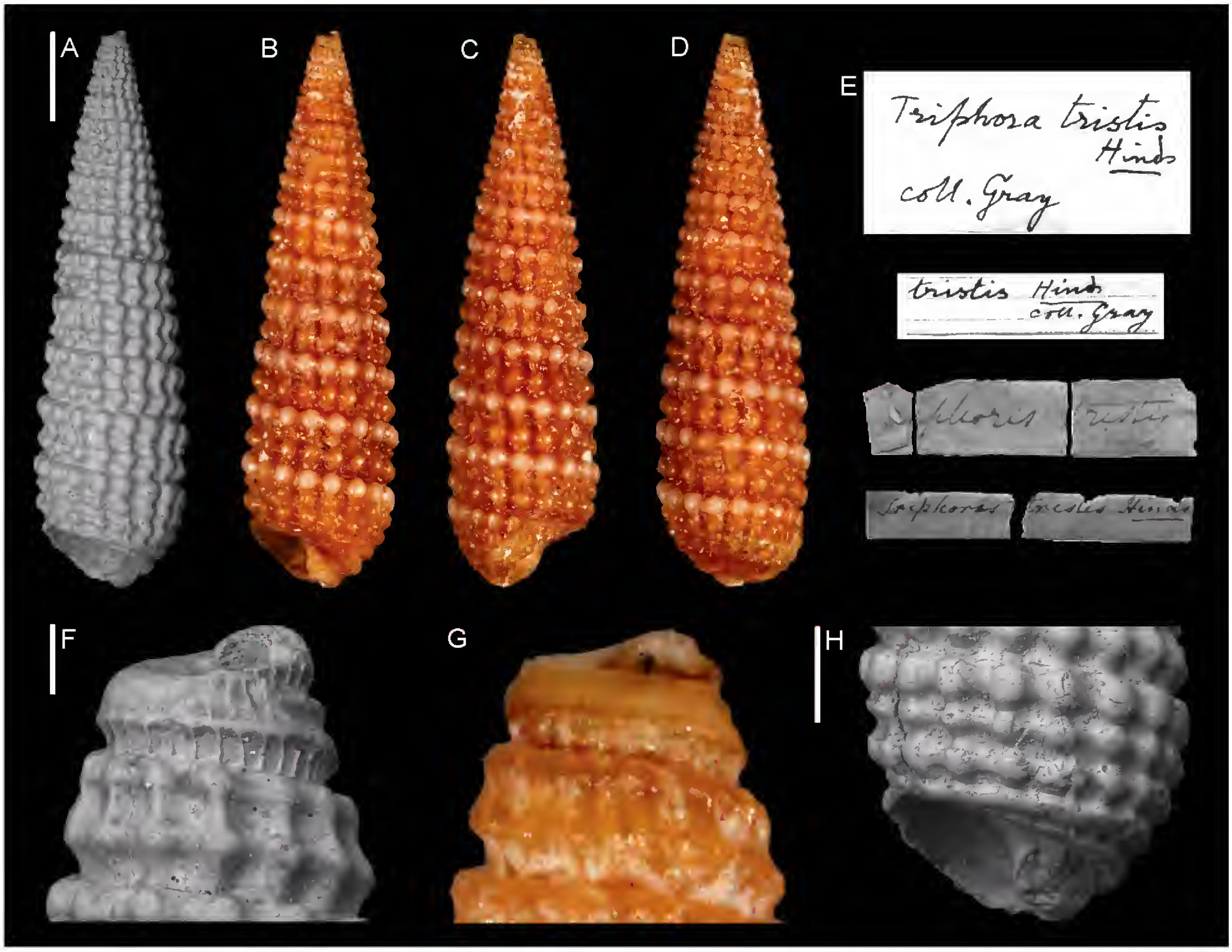

Figure 38. *Triphoris tristis* Hinds, 1843, unknown locality, J.E. Gray coll. **A–H** Syntype NHMUK 196538: front (**A, B**), side (**C**), back (**D**), original labels (**E**), protoconch (**F, G**), aperture (**H**). Scale bars: **A–D**: 1 mm; **F, G**: 0.1 mm; **H**: 0.5 mm.

Translation of the Latin text. Shell smooth, yellowish; 22–25 whorls crossed by faint threads, a graceful median dark band; subquadrate aperture; posterior sinus obsolete. Height 8 lines.

Diagnosis. Syntype NHMUK 1879.2.26.196/1 17.3 mm high. Shell conical and slender, with more than 20 whorls bearing three smooth spiral cords and prosocline growth lines. A suprasutural smooth cord and very fine spiral threads are also visible. Periphery of the last whorl angulated, the base has one smoother spiral cord. Protoconch incomplete and very worn, but apparently multispiral with two spiral keels and axial riblets on the last two whorls. Teleoconch yellowish with an orange band between the second and third spiral cord.

Triphoris (*Mastonia*) *vulpinus* Hinds, 1843

Figure 41

Triphoris (*Mastonia*) *vulpinus* Hinds 1843b: 19, not illustrated. Illustration available in Hinds (1844): 30, pl. 8, fig. 13.

Type locality. New Ireland [Papua New Guinea].

Type material. Syntypes: NHMUK 1879.2.26.199: 1 specimen, New Ireland (coll. T. Lombe Taylor).

Original description. *Testa nigricante; anfractibus quatuordecim tricarinatis; carina inferiore albida; apertura rotundata; sinu laterali subnullo. Axis 3 lin.*

Geog. New Ireland; found, with other small shells, among fine gravel about low-water mark.

Translation of the Latin text. Shell black; 14 whorls with three cords; the lowest cord white; rounded aperture; posterior sinus nearly absent. Height 3 lines.

Diagnosis. Syntype 5.5 mm high. Shell strongly cyrtoconoid, broad. Teleoconch of 11 flat whorls with two main smooth spiral cords. A third develops in between early in the teleoconch. Several fine threads run between the main cords. There are faint prosocline axial ribs which form tubercles on the fourth spiral cord visible on the base which has a fifth smooth cord too. The peristome is incomplete in the lectotype, but like-

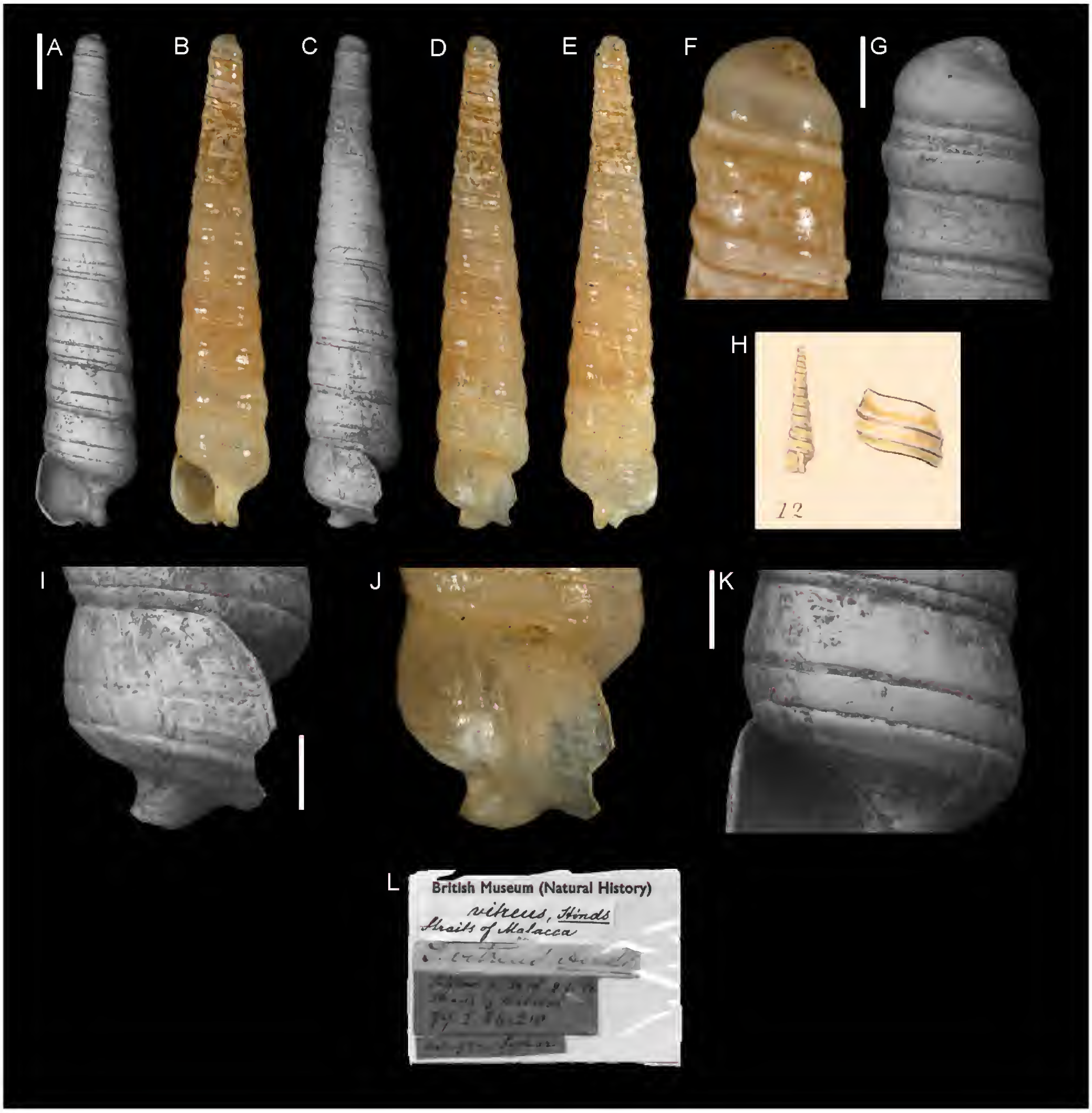

Figure 39. *Triphoris vitreus* Hinds, 1843, Straits of Malacca, J. Lombe Taylor coll. **A–G, I–L** Syntype NHMUK 1879.2.26.210: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, G**), peristome (**I, J**), microsculpture (**K**), original lables (**L**). **H** Figure in Hinds 1844. Scale bars: **A–E**: 1 mm; **F, G**: 0.3 mm; **I–K**: 0.5 mm.

ly bears additional spiral cords. Also, the apex is incomplete, but clearly bears a dark-brown multispiral protoconch whose last two whorls have two strong keels and axial riblets. Teleoconch brown with white to pearly flammulae particularly evident on the abapical spiral cord.

Remarks. Hinds (1843a) introduced the genus *Mastonia* without designating the type species but listing as first species *T. vulpinus*. The type species designation was later done by Jousseaume (1884) who selected *T. ruber* Hinds, 1843. Such designation is valid (ICZN 1999, Article 69.1) because *T. ruber* is an originally included nominal species (ICZN 1999, Article 67.2).

Species described by J.G. Jeffreys

John G. Jeffreys described two species of Triphoridae: *Cerithium perversum* var. *pallescens* Jeffreys, 1867 and *Triphoris aspera* Jeffreys, 1885. The former was reviewed by Bouchet and Guillemot (1978) who selected the lectotype (USNM 62160) (Bouchet 1985 as *Cheirodonta pallescens*). For the former, syntypes have been traced in USNM (87324) and NHMUK (Warén 1980); the latter are here reviewed.

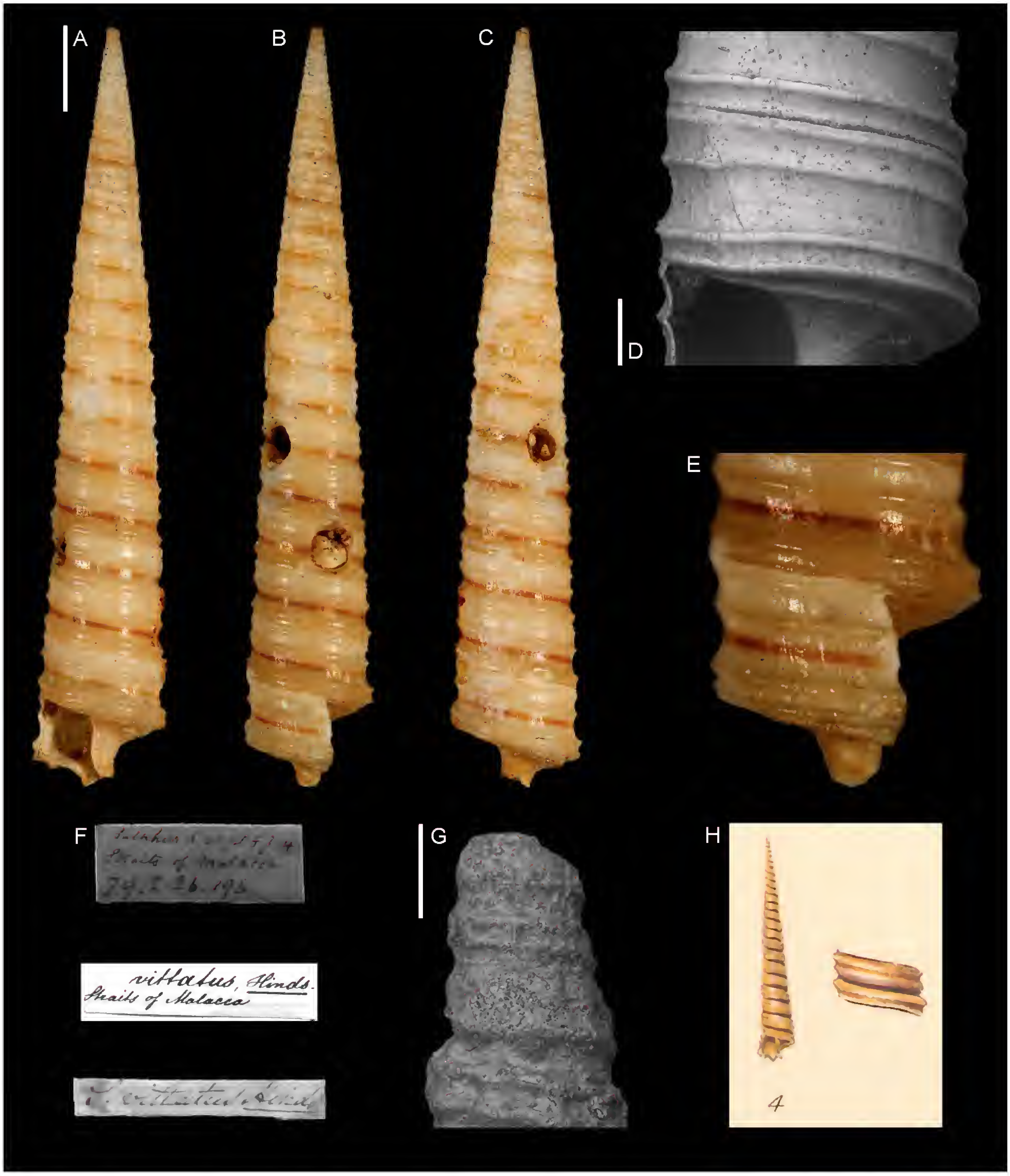

Figure 40. *Triphoris vittatus* Hinds, 1843, Straits of Malacca, coll. T. Lombe Taylor. **A–G** Syntype NHMUK 1879.2.26.196/1: front (**A**), side (**B**), back (**C**), microsculpture (**D**), peristome (**E**), original labels (**F**), protoconch (**G**). **H** Figure in Hinds 1844. Scale bars: **A–C**: 2 mm; **D**: 0.5 mm; **G**: 0.2 mm.

Triforis aspera Jeffreys, 1885

Figure 42

Triforis aspera Jeffreys 1885: 58–59, pl. VI, figs 7, 7a.

Original localities. Porcupine Expedition 1870: off western Portugal, station 16 (994 fathoms, 39°55'N, 9°56'W); off south-western Portugal: station 24 (292 fathoms, 37°19'N, 9°13'W); Gulf of Cádiz: stations 27 (322 fathoms, 36°37'N, 7°33'W), 28 (304 fathoms, 36°29'N, 7°16'W), 28a (286 fathoms, 36°27'N, 6°54'W), 29 (227 fathoms, 36°20'N, 6°47'W) and 30 (386 fathoms, 36°15'N, 6°52'W); the Adventure Bank in the Sicily Channel.

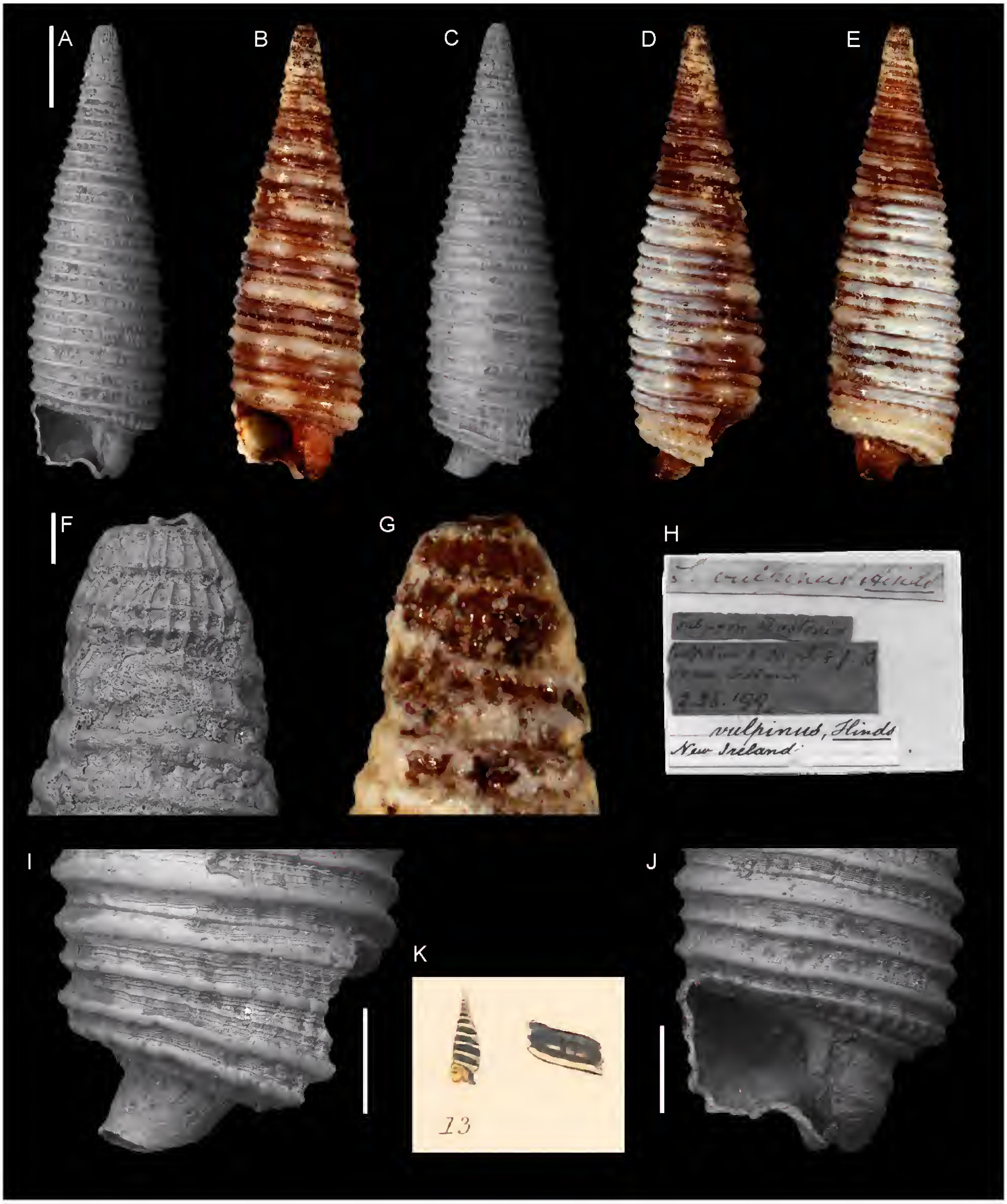

Figure 41. *Triphoris vulpinus* Hinds, 1843, New Ireland, coll. T. Lombe Taylor. **A–J** Syntype NHMUK 1879.2.26.199: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, G**), original labels (**H**), peristome (**I**), aperture (**J**). **K** Figure in Hinds 1844. Scale bars: **A–E**: 1 mm; **F, G**: 0.1 mm; **I, J**: 0.5 mm.

Type material. Syntypes: NHMUK 1885.11.5.2673, 1 specimen, Porcupine Expedition; NHMUK 1885.11.5.2674, 1 fragment, Porcupine Expedition station 16 (fide modern label); NHMUK 1885.11.5.3934–5, 2 fragments, Adventure Bank; NHMUK 1885.11.5.3936, 1 specimen glued on cardboard, Porcupine Expedition, "Coast of Spain" (from original label); NHMUK 1885.11.5.3937–8, 2 specimens (but one is not *T. aspera*, see remarks), Porcupine Expedition, "Atlantic" (from original label); NHMUK 1985008, 32 fragments or juveniles, Porcupine Expedition, Adventure Bank 92 fathoms (fide modern label) (coll. E.R. Sykes). Additional syntypes USNM 87324, not seen.

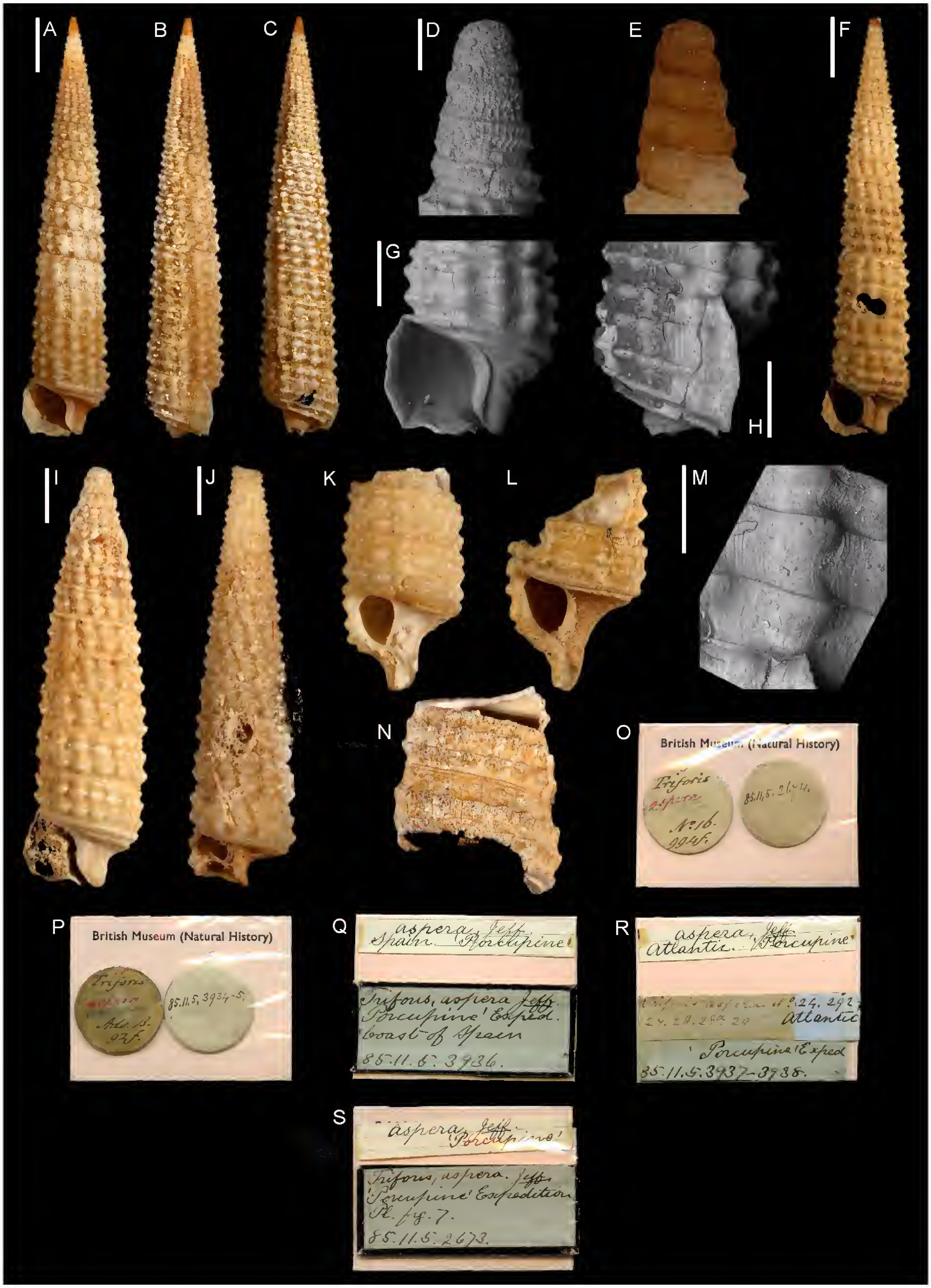

Figure 42. *Triforis aspera* Jeffreys, 1885. **A–E, G, H, M, S** Syntype NHMUK 1885.11.5.2673, Porcupine expedition, unknown locality: front (**A**), side (**B**), back (**C**), protoconch (**D, E**), aperture (**G**), peristome (**H**), microsculpture (**M**), original labels (**S**). **F, Q**: Syntype NHMUK 1885.11.5.3936, Porcupine Expedition, "Coast of Spain". **I, J, R** Syntypes NHMUK 1885.11.5.3937–8, Porcupine Expedition, "Atlantic" (**I** is not *T. aspera*). **K–L, P** Syntypes NHMUK 1885.11.5.3934–5, Adventure Bank, Sicily Channel. **N, O** Syntype NHMUK 1885.11.5.2674, Porcupine expedition station 16. Scale bars: **A–C, F**: 2 mm; **D, E**: 0.2 mm; **G–J**: 1 mm; **M**: 0.5 mm.

Original description. Shell elongated, rather solid, nearly opaque and glossy: *sculpture*, rows or bands of small tubercles (18–20 on the last or bottom row), which arise from the mutual intercrossing of longitudinal and spiral striae; of these rows there are usually three on the last whorl above the periphery, and the same number on several of the succeeding whorls and afterwards two only; each of the apical whorls (3 or 4) is closely striated lengthwise and encircled by two spiral lines; the periphery is defined by a rather strong ridge, a little below which is another ridge, besides a shorter and smaller one at the base; the tubercles which compose the lower two rows are larger and more prominent than those of the uppermost or third row: *colour* pale yellowish, with a faint tinge of brown; apical whorls dark brown: *spire* tapering to a fine point; apex pinched-in and narrower than the rest of the spire: *whorls* 21–22, compressed, gradually enlarging; the last equals only from 1/5 to 1/6 of the shell: *suture* slight, indicated by the uppermost spiral row: *mouth* rhomboidal; and all other characters similar to those of *T. perversa*. L. 0"6, B. 0'15.

Diagnosis. The two adult specimens among the syntypes are 13.7 and 15.1 mm. Shell conical with 18 teleoconch whorls bearing three spiral cords with spiny tubercles at the intersection with orthocline axial ribs. A fourth and a fifth smooth cord are present on the base, and the fourth is already visible on the spire as a suprasutural cord. Numerous fine spiral threads adorn the whorls between the main cords and fine growth lines are also visible. Siphonal canal short. Protoconch multispiral of 4.5 whorls; the last three bearing two strong spiral keels and axial riblets whereas the first are too worn for description. Teleoconch brown with lighter tubercles and whitish first three whorls; protoconch orange-brown.

Remarks. Specimen NHMUK 1885.11.5.2673 (Fig. 42A–C) is likely the one used for the original figure because it is the only adult specimen with complete protoconch known and because of an annotation on the original label. Bouchet and Guillemot (1978) proposed the nomen novum *Triphora brychia* because of omonymy with *Triforis asper* Deshayes, 1864, which is a fossil species from the Paris Basin (Le Renard and Pacaud 1995; Le Renard 1995). Lot NHMUK 1885.11.5.3937–8 contains an adult specimen which is not *T. aspera*, as already noted by Warén (1980): it is broader, with more numerous axial ribs and with the first tubercled spiral cord clearly visible only from mid-teleoconch (Fig. 42I).

Species described by E.A. Kay

Elizabeth A. Kay described nine species of Triphoridae in her monograph on Hawaiian molluscs (1979). With a single exception (*Triphora keiki*), paratypes of all species have been deposited in the NHMUK.

Metaxia albicephala Kay, 1979

Figure 43

Metaxia albicephala Kay 1979: 130, 132, fig. 48L, M.

Type locality. Poipu Beach, Kauai, Hawaiian Islands.

Type material. Holotype: BPBM 9784. Paratypes: NHMUK 1982260, 1 specimen, Keahole Point, Hawaii, Hawaiian Islands. Other paratypes: AMS and USNM (fide Kay 1979; not seen).

Remarks. The specimen in NHMUK may be a different species than the holotype figured by Kay (1979, fig. 48L, M). The holotype has large flat spiral cords (a character also included in the original description) and the interspaces are smaller than the cords. In contrast, the NHMUK specimen has thin spiral cords with ample interspaces. Unfortunately, Kay's illustration of the teleoconch is blurred, and the NHMUK specimen is worn and lacks the apex, which would have offered additional diagnostic characters for observation.

Metaxia brunnicephala Kay, 1979

Figure 44

Metaxia brunnicephala Kay 1979: 132, fig. 48E, F, K.

Type locality. Poipu Beach, Kauai, Hawaiian Islands.

Type material. Holotype: BPBM 9782. Paratypes: NHMUK 1982262, 1 specimen, Keahole Point, Hawaii, Hawaiian Islands. Other paratypes: USNM (fide Kay 1979; not seen).

Triphora chrysolitha Kay, 1979

Figure 45

Triphora chrysolitha Kay 1979: 143–145, fig. 51B, G, H.

Type locality. Makaha, Oahu, Hawaiian Islands.

Type material. Holotype: BPBM 9788. Paratypes: NHMUK 1982275, 5 specimens, Kukuiula, Kauai, Hawaiian Islands. Other paratypes: AMS and USNM (fide Kay 1979; not seen).

Triphora earlei Kay, 1979

Figure 46

Triphora earlei Kay 1979: 145, fig. 52D, E.

Type locality. Kepuhi Point, Oahu, Hawaiian Islands.

Type material. Holotype: BPBM 9794 (not seen, fide Kay 1979). Paratypes: NHMUK 1982255, 4 specimens,

Figure 43. *Metaxia albicephala* Kay, 1979, Poipu Beach, Kavai, Hawaii. **A**, **I** Original figure. **B–H**, **J** Paratype, NHMUK 1982260: front (**B**, **C**), side (**D**, **E**), back (**F**), aperture (**G**), peristome (**H**), protoconch (**I**). **K** Original label. Scale bars: **B–F**: 0.5 mm; **G**, **H**: 0.3 mm; **J**: 0.2 mm.

Makaha, Oahu, Hawaiian Islands. Other paratypes: AMS and USNM (fide Kay 1979; not seen).

Viriola fallax Kay, 1979

Figure 47

Viriola fallax Kay 1979: 140, 142, fig. 50C, G.

Type locality. Milolii, Hawaii.

Type material. Holotype: BPBM 9798 (fide Kay 1979; not seen). Paratypes: NHMUK 1982250, 3 specimens, Kepuhi Point, Oahu, Hawaiian Islands. Other paratypes: USNM (fide Kay 1979; not seen).

Remarks. This is a junior synonym of *Viriola alboguttata* Tomlin (p. 280). These specimens given by Kay to the NHMUK and labelled as paratypes were not listed as such in Kay (1979).

Iniforis hinuhinu Kay, 1979

Figure 48

Iniforis hinuhinu Kay 1979: 134, fig. 48H.

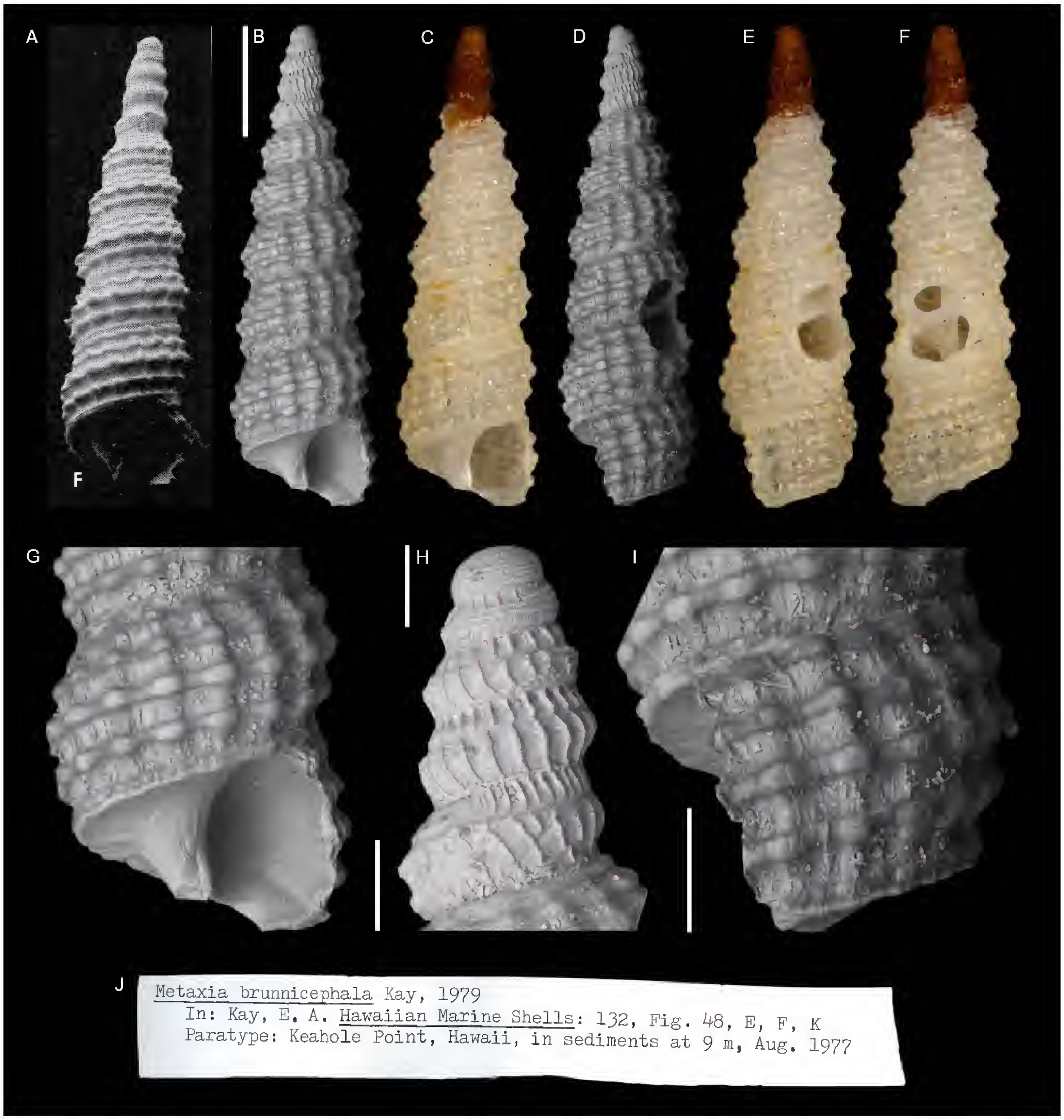

Figure 44. *Metaxia brunnicephala* Kay, 1979, Keahole Point, Hawaii. **A** Original figure. **B–I** Paratype, NHMUK 1982262: front (**B, C**), side (**D, E**), back (**F**), aperture (**G**), protoconch (**H**), peristome (**I**). **J** Original label. Scale bars: **B–F**: 0.5 mm; **G, I**: 0.2 mm; **H**: 0.1 mm.

Type locality. Kepuhi Point, Oahu, Hawaiian Islands.

Type material. Holotype: BPBM 9786 (fide Kay 1979; not seen). Paratypes: NHMUK 1982263, 2 specimens, Kepuhi Point, Oahu, Hawaiian Islands. Other paratypes: AMS and USNM (fide Kay 1979; not seen).

Triphora laddi Kay, 1979

Figure 49

Triphora laddi Kay 1979: 147, fig. 51D–I.

Type locality. off Waikiki, Hawaiian Islands.

Type material. Holotype: BPBM 9800 (fide Kay 1979; not seen). Paratypes: NHMUK 1982273, 3 specimens, Poipu Beach, Kauai, Hawaiian Islands. Other paratypes in USNM (fide Kay 1979; not seen).

Remarks. These specimens given by Kay to the NHMUK and labelled as paratypes were not listed as such in Kay (1979).

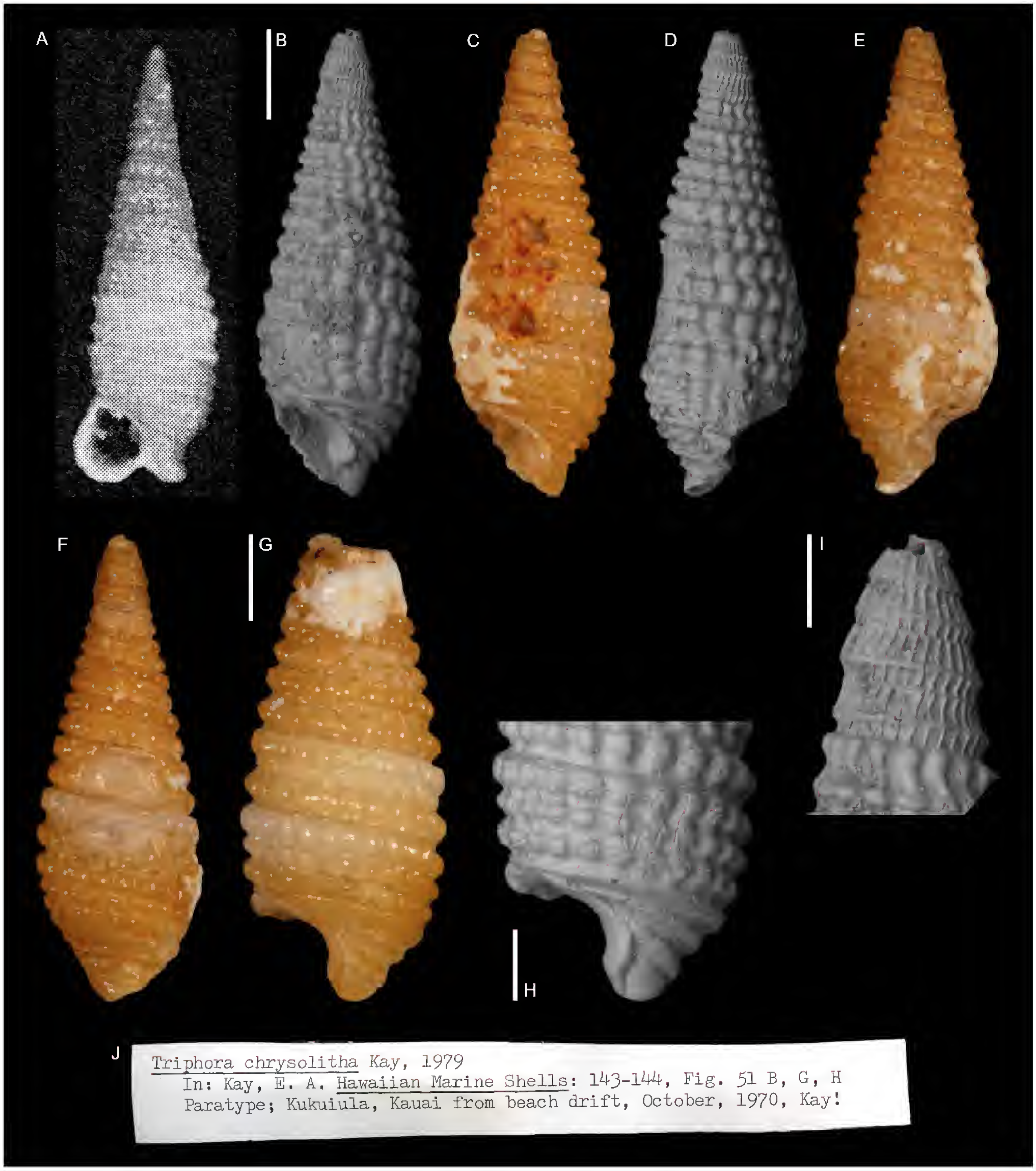

Figure 45. *Triphora chrysolitha* Kay, 1979, Kukuiula, Kauai, Hawaiian Islands. **A** Original figure. **B–F, I** Paratype, NHMUK 1982275/1: front (**B, C**), side (**D, E**), back (**F**), protoconch (**I**). **G, H** Paratype, NHMUK 1982275/2: front (**G**), aperture (**H**). **J** Original label. Scale bars: **B–G**: 0.5 mm; **H**: 0.3 mm; **I**: 0.2 mm.

Triphora thaanumi Kay, 1979

Figure 50

Triphora thaanumi Kay 1979: 149–150, fig. 52A, B.

Type locality. Kahe Point, Oahu, Hawaiian Islands.

Type material. Holotype: BPBM 9796 (fide Kay 1979; not seen). Paratypes: NHMUK 1982252, 1 specimen, Kahe Point, Oahu, Hawaiian Islands; NHMUK 1982281, 1 specimen, Makaha, Oahu, Hawaiian Islands. Additional paratypes in AMS and USNM (fide Kay 1979; not seen).

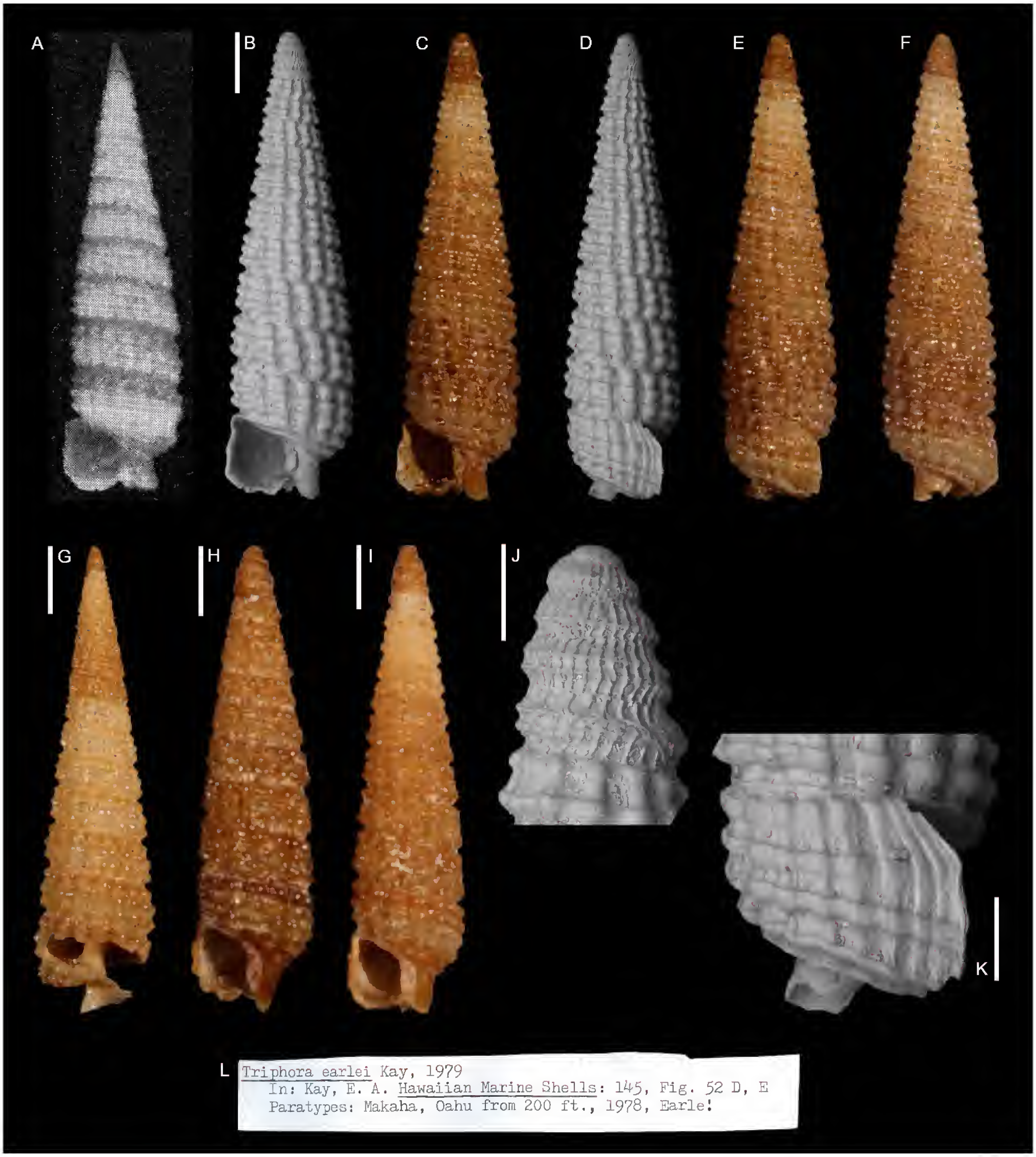

Figure 46. *Triphora earlei* Kay, 1979, Makaha, Oahu, Hawaiian Islands. **A** Original figure. **B–F, J, K** Paratype, NHMUK 1982255/1: front (**B, C**), side (**D, E**), back (**F**), protoconch (**J**), peristome (**K**). **G–I** Paratypes, NHMUK 1982255/2–4: front paratype 2 (**G**), front paratype 3 (**H**), front paratype 4 (**I**). **L** Original label. Scale bars: **B–F, H, I**: 0.5 mm; **G**: 1 mm; **J**: 0.2 mm; **K**: 0.3 mm.

Remarks. The NHMUK labels report two specimens per lot but we found a single specimen per lot only.

Species described by S. Kosuge

Sadao Kosuge was a prolific author who described 47 species of Triphoridae. Most holotypes are in Japanese museums and a few in the USNM. He was usually very accurate in stating the location of type material in his papers. In the NHMUK we found specimens labelled as paratypes of 14 species whose existence he did not report; however, the museum registry confirmed that these specimens were donated by Kosuge himself. We illustrate these shells because the original figures were often in black and white or line drawings. We also add the original descriptions (omitting the type locality and the location of type material which we report in other sections of each spe-

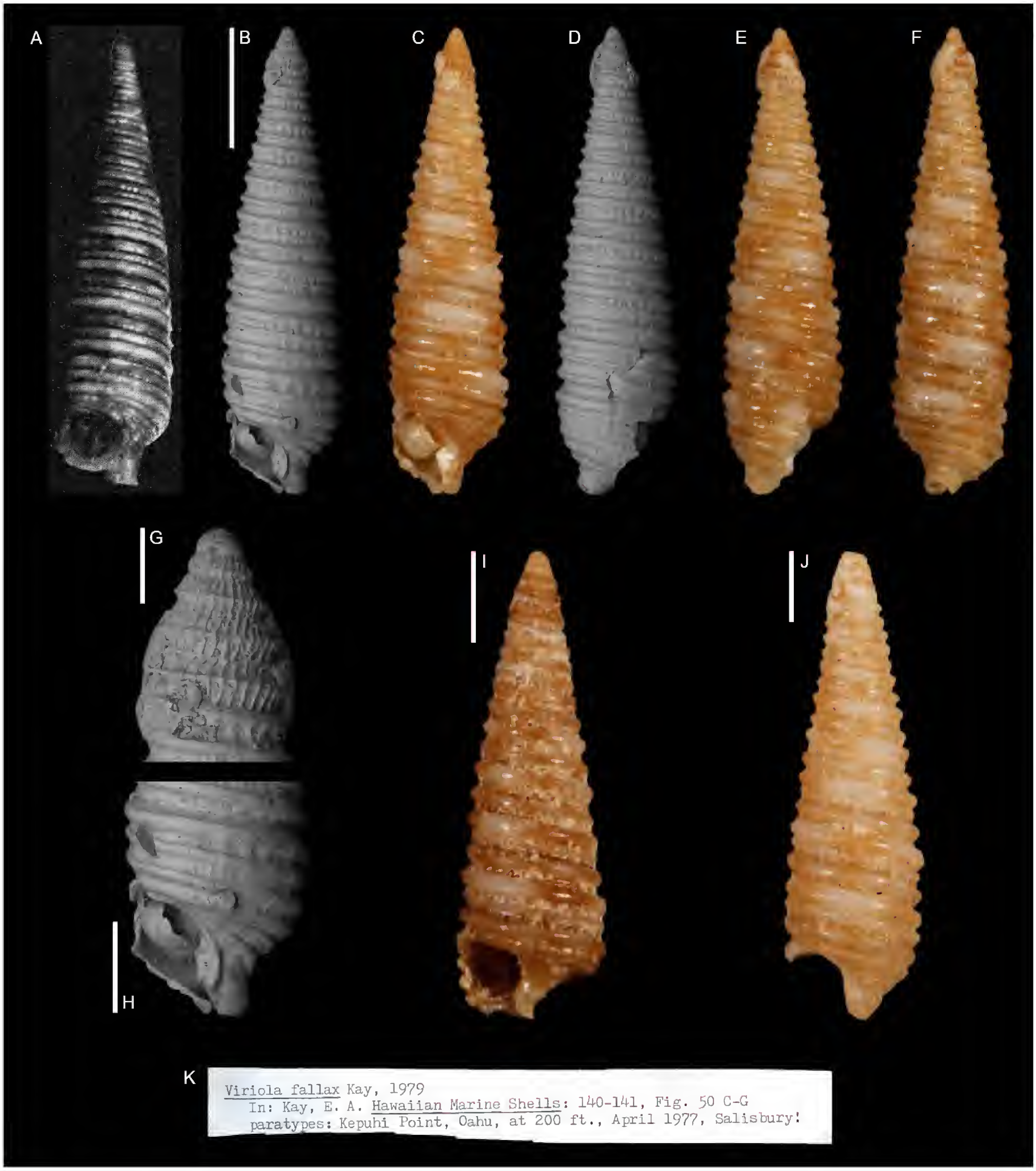

Figure 47. *Viriola fallax* Kay, 1979, Kepuhi Point, Oahu, Hawaii. **A** Original figure. **B–H** Paratype, NHMUK 1982250/1: front (**B**, **C**), side (**D, E**), back (**F**), protoconch (**G**), aperture (**H**). **I** Paratype, NHMUK 1982250/2: front. **J** Paratype, NHMUK 1982250/3: front. **K** Original label. Scale bars: **B–F**: 1 mm; **G**: 0.2 mm; **H–J**: 0.5 mm.

cies' paragraph) because the journals where these species were published were not of wide distribution. However, we do not add diagnoses because Kosuge's descriptions are recent and detailed.

Notosinister atratus Kosuge, 1962

Figure 51

Notosinister atratus Kosuge 1962a: 83, pl. 9, fig. 5, text figs 9, 13.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Figure 48. *Iniforis hinuhinu* Kay, 1979, Kepuhi Point, Oahu, Hawaii. **A** Original figure. **B–E, G–I** Paratype, NHMUK 1982263/1: front (**B**), side (**C, D**), back (**E**), aperture (**G**), peristome (**H**), protoconch (**I**). **F** Paratype, NHMUK 1982263/2: front. **J** Original label. Scale bars: **B–F**: 1 mm; **G, H**: 0.5 mm; **I**: 0.2 mm.

Type material. Holotype: TZM Mo. 13039 (fide Kosuge 1962a, not seen; illustrated in Higo et al. 2001: 51, G1705). Paratype: NHMUK 1966142: 1 specimen, Amami Islands, Japan.

Original description. *Shell small, rather fusiform, inflated, rapidly attenuated to the early whorls, slightly narrowed at the base. Protoconch reddish brown, 2 spiral keels overridden by axial threads. Mature whorls 9 to 10 in number, suture well defined as a shallow groove. Sculpture 3 spiral costae, widely apart from each other and decussated with irregular axial grooves, divided into 26 ill-defined granules, upper row largest, median one faint, and turns to a thread at the antepenultimate whorl and diminished at the earlier whorls. Body whorl has 2 slightly granulated extra-costae, anterior canal slightly recurved, aperture subquadrate. White in colour at the earlier 3 whorls and remainder blackish reddish brown.*

Shell length: 5.5 mm.

Remarks: This species is easily distinguished by its peculiar sculpture and colour patterns from the allied form.

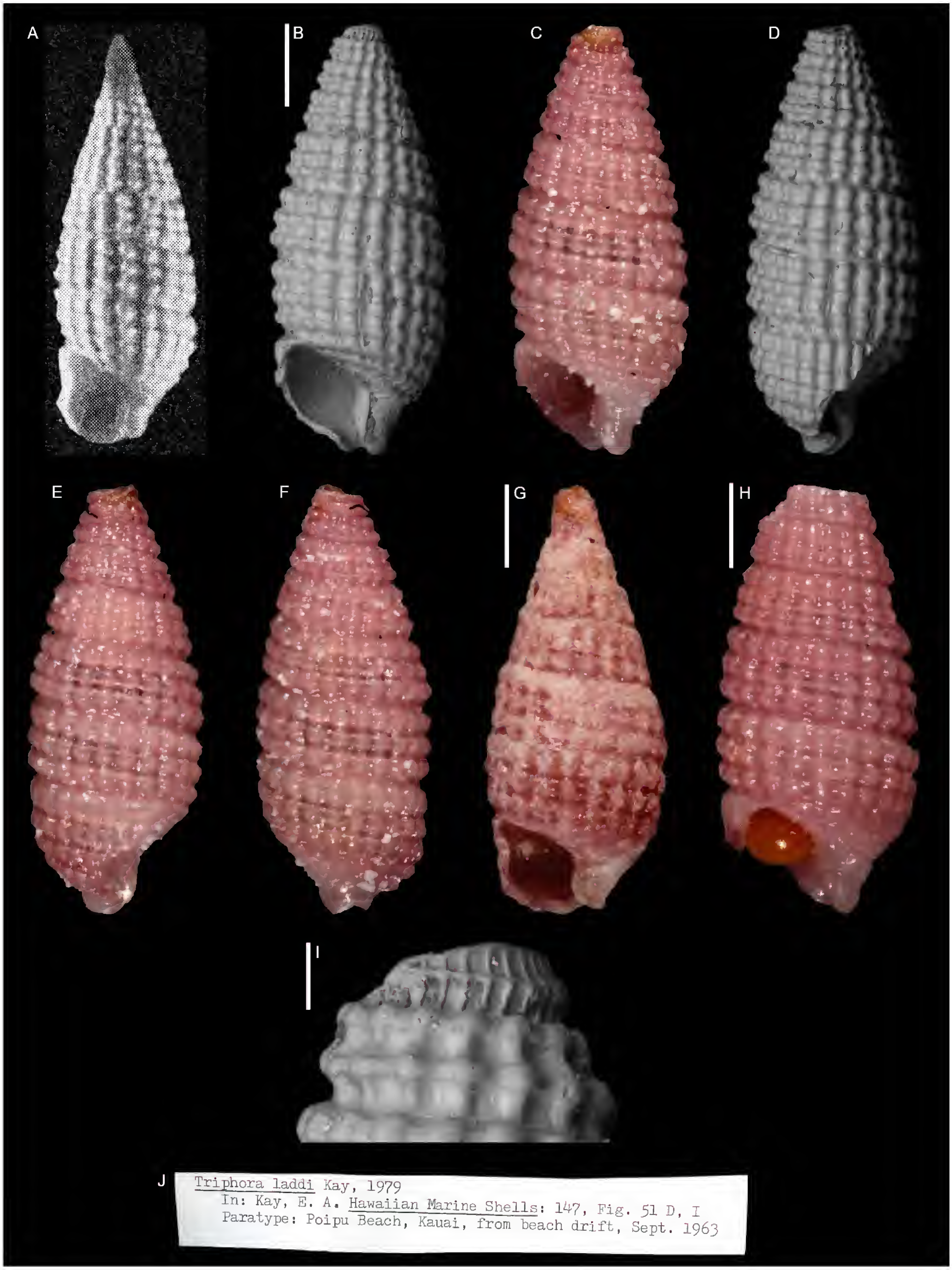

Figure 49. *Triphora laddi* Kay, 1979, Poipu Beach, Kavai, Hawaii. **A** Original figure. **B–F, I** Paratype, NHMUK 1982273/1: front (**B, C**), side (**D, E**), back (**F**), protoconch (**I**). **G, H** Paratypes, NHMUK 1982273/2–3: front views. **J** Original label. Scale bars: **B–H**: 0.5 mm; **I**: 0.1 mm.

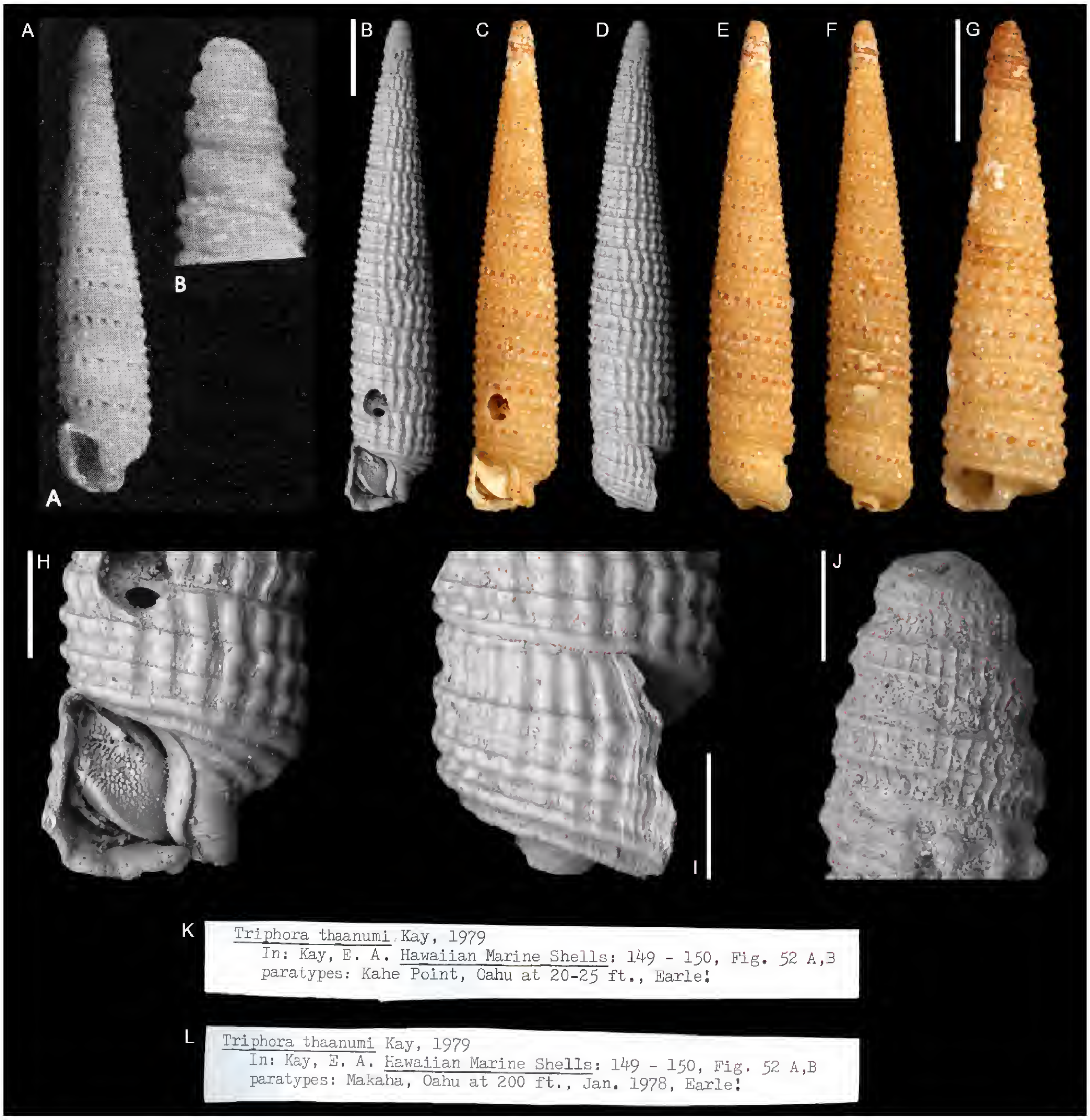

Figure 50. *Triphora thaanumi* Kay, 1979. **A** Original figure. **B–F, H–J, K** Paratype, NHMUK 1982252, Kahe Point, Oahu, Hawaii: front (**B, C**), side (**D, E**), back (**F**), aperture (**H**), peristome (**I**), protoconch (**J**), original label (**K**). **G, L** Paratype, Makaha, Oahu, Hawaii, NHMUK 1982281: front (**G**), original label (**L**). Scale bars: **B–G**: 1 mm; **H**, **I**: 0.5 mm; **J**: 0.2 mm.

Inella granicostata Kosuge, 1962
Figure 52

Inella granicostata Kosuge 1962b: 121, pl. 8, fig. 11, text fig. 7.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 12128 (fide Kosuge 1962b, not seen; illustrated in Higo et al. 2001: 50, G1676). Paratype: NHMUK 1966137: 1 specimen, Amami Islands, Japan.

Original description. *Shell of medium size, conical, rather cylindrical in lower part of spire. Protoconch of 2 whorls, mammillate, suture distinct and grooved. Sculpture of 3 rows of granules, furrows between rows deep. Granules elongate and beset close together, connected by axial threads and spiral keels and appear like somewhat indented costae, 22–24 to a whorl. Upper row slightly larger and blackish brown, lower two light brown and sometimes whitish. 2 extra rows of granules on the body whorl.*

Length: 8.5 mm.

Figure 51. *Notosinister atratus* Kosuge, 1962, Amami Islans, Japan. **A** Original figure. **B–C, E–I** Paratype, NHMUK 1966142: front (**B, C**), peristome (**E**), side (**F, G**), back (**H**), aperture (**I**). **D** NHMUK label. Scale bars: **B, C, F–H**: 1 mm; **E, I**: 0.5 mm.

Remarks: This species is allied to T. angasi *Crosse, though the latter has a white band in lower granules of body whorl and also differs from* T. marmoratus *Pease in details of sculpture of body whorl.*

Notosinister hervieri Kosuge, 1962

Figure 53

Notosinister hervieri Kosuge 1962a: 81, pl. 10, fig. 1, text fig. 15, 18.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 13036 (fide Kosuge 1962a; not seen, illustrated in Higo et al. 2001: 50, G1670). Paratype: NHMUK 1966140: 1 specimen, Amami Islands, Japan.

Original description. *Shell large to medium in size, conical, tapering to the summit, somewhat narrowed at the base. Protoconch of 5 whorls, acuminated conical, with 2 spiral keels overridden by numerous axial threads, brownish red in colour. Mature whorls 16, suture distinct and rather deep, each whorl somewhat inflated and sculptured with 3 equal rows of granules which are connected with fine spiral threads and broad axial columns, median row decreases to a fine thread at its upper 2 or 3 whorls. Granules large, apart by about half of its diameter, 22 to a whorl; on the body whorl, fourth row encircles on the periphery and coloured orange yellow, other 2 faintly*

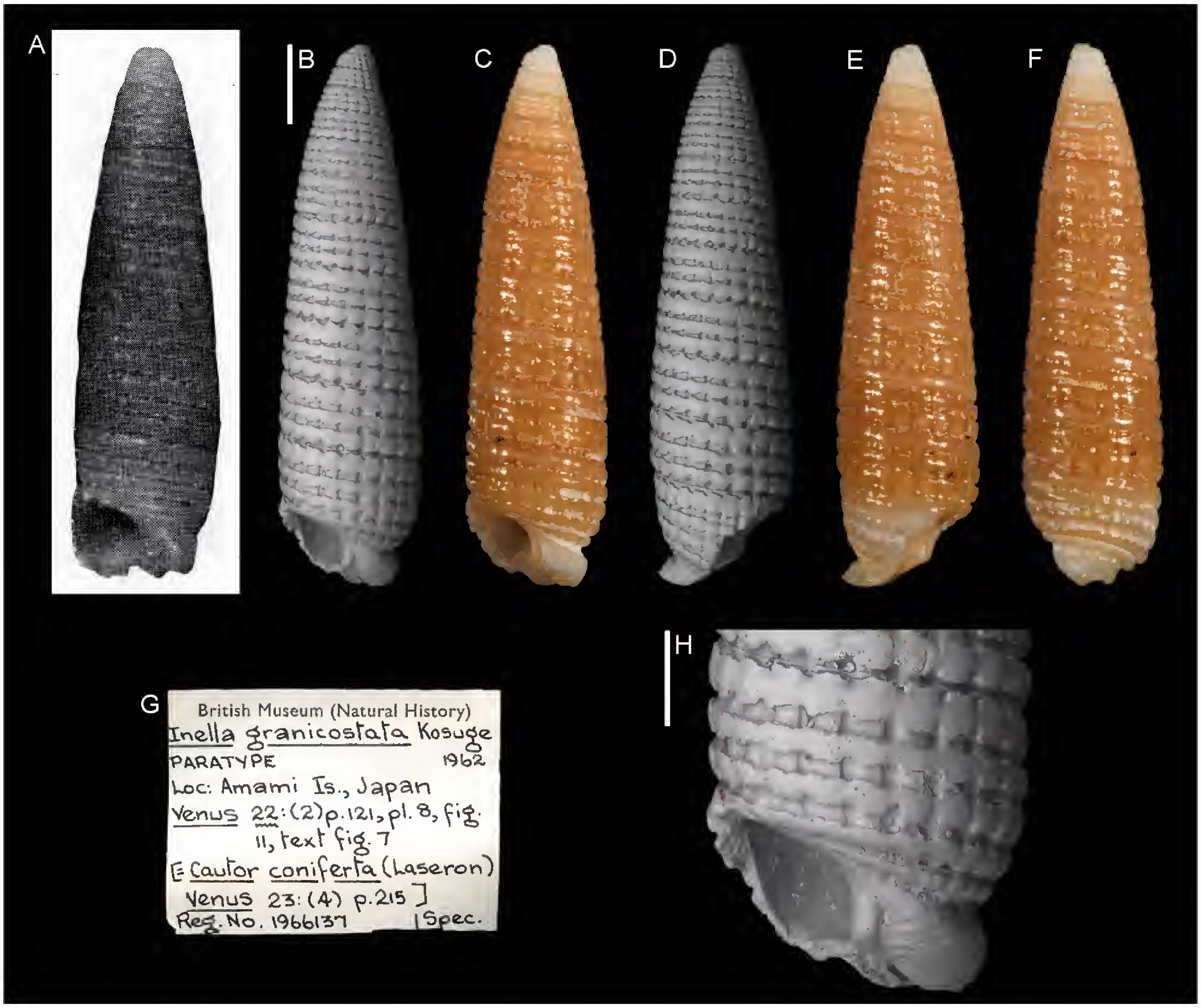

Figure 52. *Inella granicostata* Kosuge, 1962, Amami Islands, Japan. **A** Original figure. **B–F, H** Paratype, NHMUK 1966137: front (**B, C**), side (**D E**), back (**F**), aperture (**H**). **G** NHMUK label. Scale bars: **B–F**: 2 mm; **H**: 0.5 mm.

granulated keels on the rounded base. Aperture subquadrate, anterior canal long and recurved backward. The colouration isdistinctive, upper row orange yellow, others pinkish or lilac brown.

Shell length: 9.7 mm.

Remarks: This species is closely related to T. loyaltyensis *(Hervier) in its sculpture and colour pattern, though differs in having 2 spiral keels on its protoconch in contrast with 1 keel of the latter. This is distributed in Okinawa and Amami Islands, and was formerly treated as* T. loyaltyensis *by Japanese authors.*

Euthymella isaotakii Kosuge, 1962

Figure 54

Euthymella isaotakii Kosuge 1962b: 124, pl. 8, fig. 18, text figs 6, 8.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 12094 (fide Kosuge 1962b; not seen, illustrated in Higo et al. 2001: 50, G1685). Paratype: NHMUK 1966143: 1 specimen, Amami Islands, Japan.

Original description. *Shell of medium size, broad conical and narrowed at the base. Colour very distinctive, protoconch light brown, early 3 whorls white and the next one brown, the remainder olive bistre. Protoconch of 4 whorls, conical with a spiral thread overriden by axial threads. Mature whorls 10, suture distinct but not deep, having a fine supra·sutural thread. Sculpture of 3 rows of granules, strongly connected spirally and axially, and latticed. Granules large and equal·sized, spirally elongate and apart from each other by one third of its diameter, 14 to a whorl. 2 extra rows of granules on the body whorl. Anterior canal tubular.*

Length: 6.8 mm.

Remarks: This species is easily distinguished by its colour dattern, sculpture and shell feature. It is closely related to E. regalis *Jousseaume and* E. pannata *Laseron, though differing in number of rows of granules, shell feature and colour pattern.*

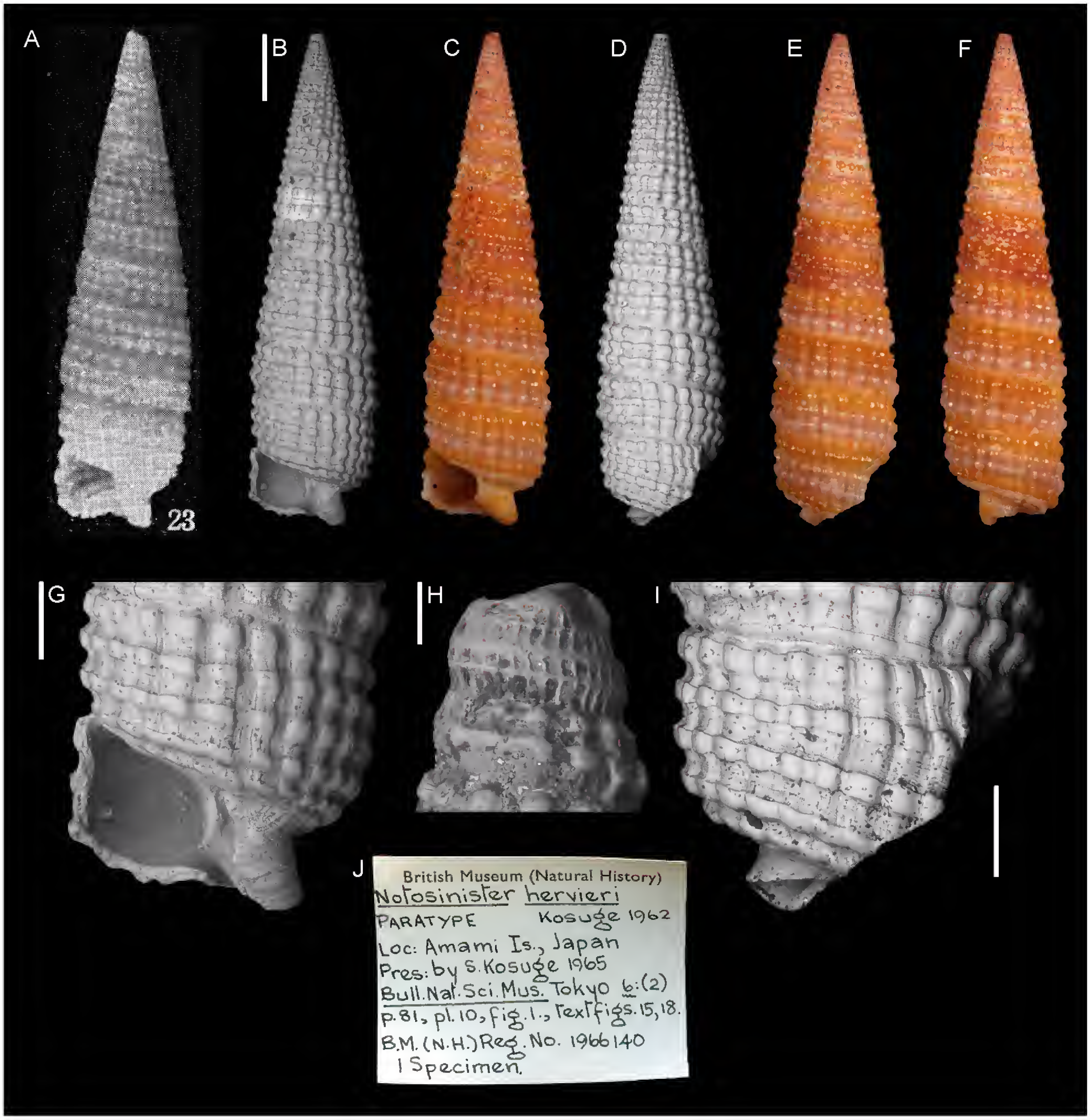

Figure 53. *Notosinister hervieri*, Kosuge, 1962, Amami Islands, Japan. **A** Original figure. **B–I** Paratype, NHMUK 1966140: front (**B, C**), side (**D, E**), back (**F**), aperture (**G**), protoconch (**H**), peristome (**I**). **J** NHMUK label. Scale bars: **B–F**: 1 mm; **G, I**: 0.5 mm; **H**: 0.1 mm.

This species is named in memory of the late Dr. Isao Taki, who was kind enough to guide me in malacology.

Notosinister iwaotakii Kosuge, 1963

Figure 55

Notosinister iwaotakii Kosuge 1963a: 246–247, pl. 16, fig. 27, text figs 3, 10.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 13067 (fide Kosuge 1963a; not seen). Paratype: NHMUK 1966149: 1 specimen, Amami Islands, Japan.

Original description. *Shell rather small, extremely inflated spindle-form, acuminated at the summit and narrowed at the body whorl. Protoconch of 4 whorls, tapering to the summit, bearing 2 spiral keels with crossed fine axial threads. Mature whorls 7, suture narrowly grooved and encircled by a fine supra-sutural thread. Sculpture of 3 rows of granules, each row almost equal-sized even in the early whorls, but median one slightly smaller than the other two; granules large, round, connected by broad axial columns and spiral costae which are finely latticed, forming fine square hollows, apart from each other by about half of its diameter and 18 to a whorl. Body whorl has 2 more rows of granules, viz. fourth row encircles the periphery and smaller than upper 3 rows, filth slender*

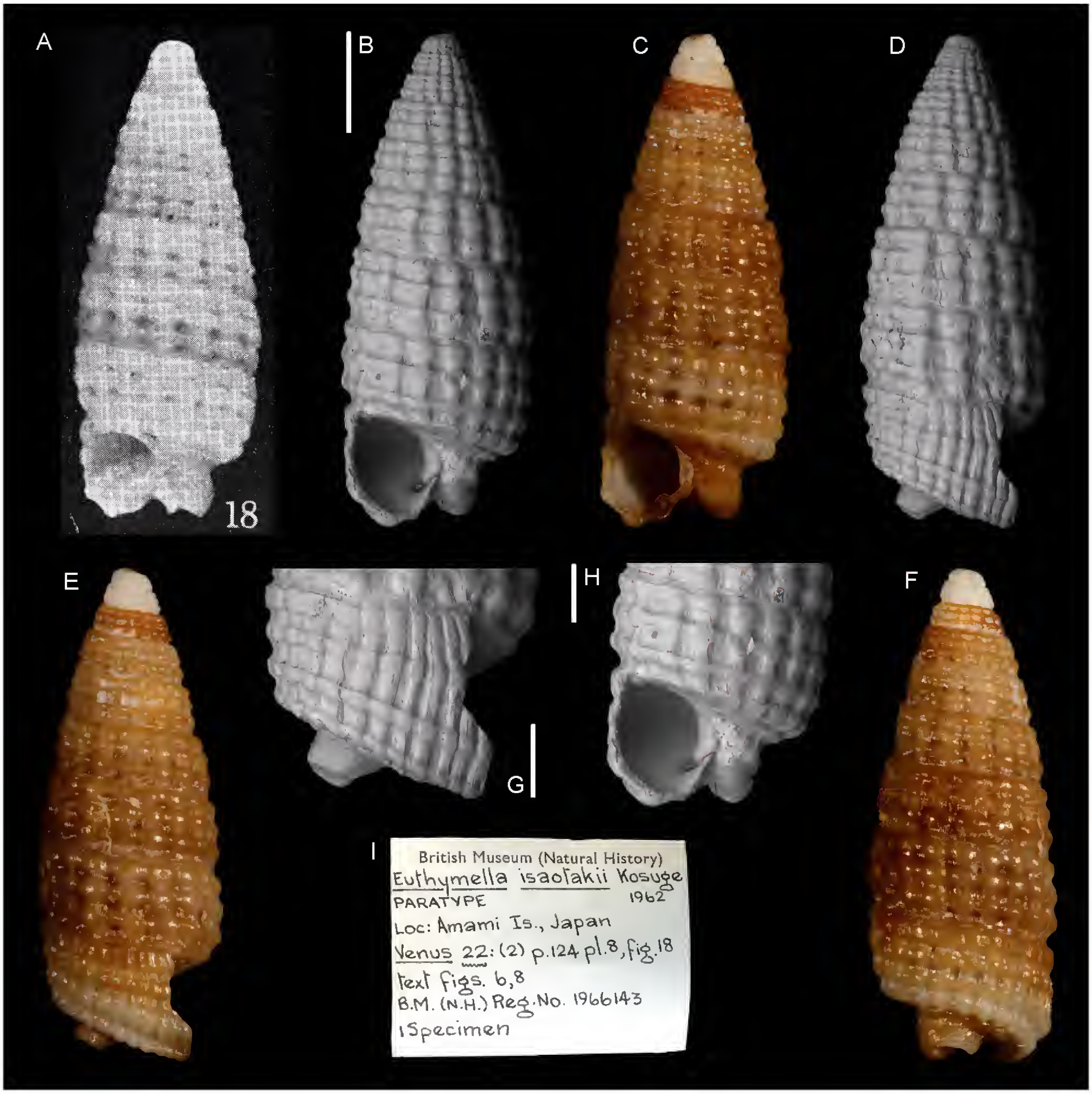

Figure 54. *Euthymella isaotakii* Kosuge, 1962, Amami Islands, Japan. **A** Original figure. **B–H** Paratype, NHMUK 1966143: front (**B, C**), side (**D, E**), back (**F**), peristome (**G**), aperture (**H**). **I** NHMUK label. Scale bars: **B–F**: 1 mm; **G, H**: 0.5 mm.

row on the base. Anterior canal somewhat elongated and recurved backward, posterior canal forming a deep sinus, shell aperture somewhat extended forward. Colouration slate purple, antepenultimate whorl pale or whitish, anterior canal orange yellow.

Shell length: 4.8 mm.

Remarks: This species is distinguished by its inflated spindle-form, sculpture and colouration, and closely related to N. lucidulus *(Hervier), though differs in its shell shape and protoconch which is marked by double spiral keels in contrast to a single keel of the latter species, and also differs from* N. amoena *(Hervier) in its coloration and shell size. This species is dedicated to Prof. Iwao Taki of the Hiroshima University, who is kind enough to read my manuscript with valuable advices.*

Notosinister kawamurai Kosuge, 1962

Figure 56

Notosinister kawamurai Kosuge 1962a: 81, pl. 10, fig. 3, text figs 5, 6.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 13035 (fide Kosuge 1962a; not seen, illustrated in Higo et al. 2001: 50, G1661s). Paratype: NHMUK 1966138: 1 specimen, Amami Islands, Japan.

Original description. *Shell small, conical, tapering to the summit, lower part of spire somewhat cylindrical. Protoconch pale brown, with a single spiral keel and*

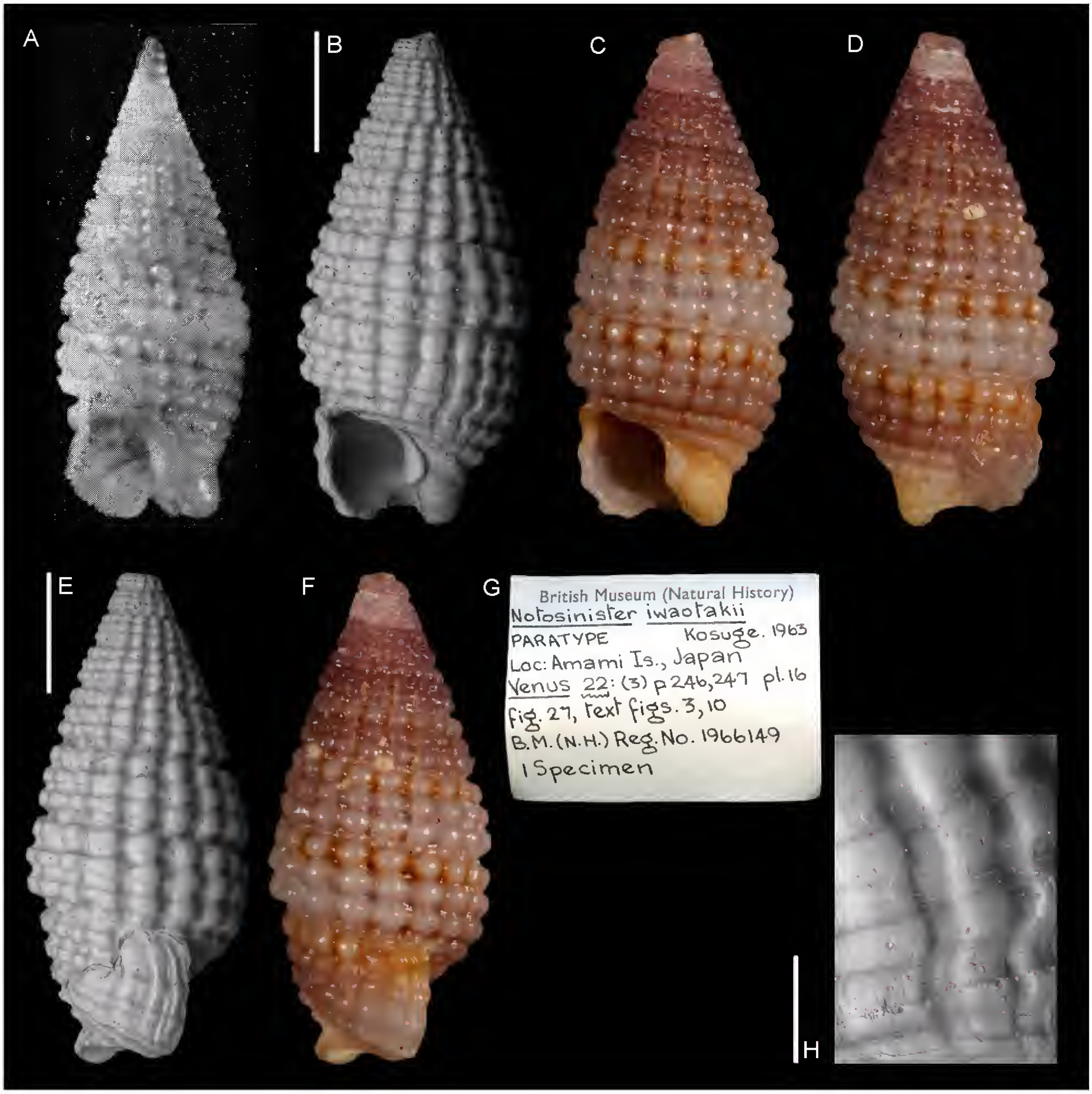

Figure 55. *Notosinister iwaotakii* Kosuge, 1963, Amami Islands, Japan. **A** Original figure. **B–F, H** Paratype, NHMUK 1966149: front (**B, C**), back (**D**), side (**E, F**), microsculpture (**H**). **G** NHMUK label. Scale bars: **B–F**: 1 mm; **H**: 0.3 mm.

crossed axial threads, mature whorls 10 or more, suture well defined with a supra-sutural thread. Sculpture 3 rows of granules, median row rapidly turns to a spiral thread at its earlier whorls. Colour pattern distinctive, upper row of granules and suprasutural thread reddish brown, remainder white, other 2 spiral colour bands on the body whorl. Granules small, somewhat squarish, apart by half of its diameter and 22 to a whorl. Each granule connected with slightly oblique, fine axial columns and faint spiral threads. Fourth row of granules encircles on the periphery of the body whorl and coloured reddish brown, fifth on the base, slightly granulated and also stained reddish brown, and sixth on the anterior canal, smooth. Anterior canal straight.

Shell length: 6.0 mm.

Remarks: This species is closely related to N. sardonyx *(Laseron) and* Cautor albozonatus *(Laseron), though differs from the former in having a distinct sutural groove and a supra-sutural thread, and from the latter in its protoconch and sculpture of body whorl, and also distinguished from* T. regina *Hedley in its colour pattern.*

Isotriphora kurodai Kosuge, 1962

Figure 57

Isotriphora kurodai Kosuge 1962a: 84–85, pl. 10, fig. 7, text figs 11, 19.

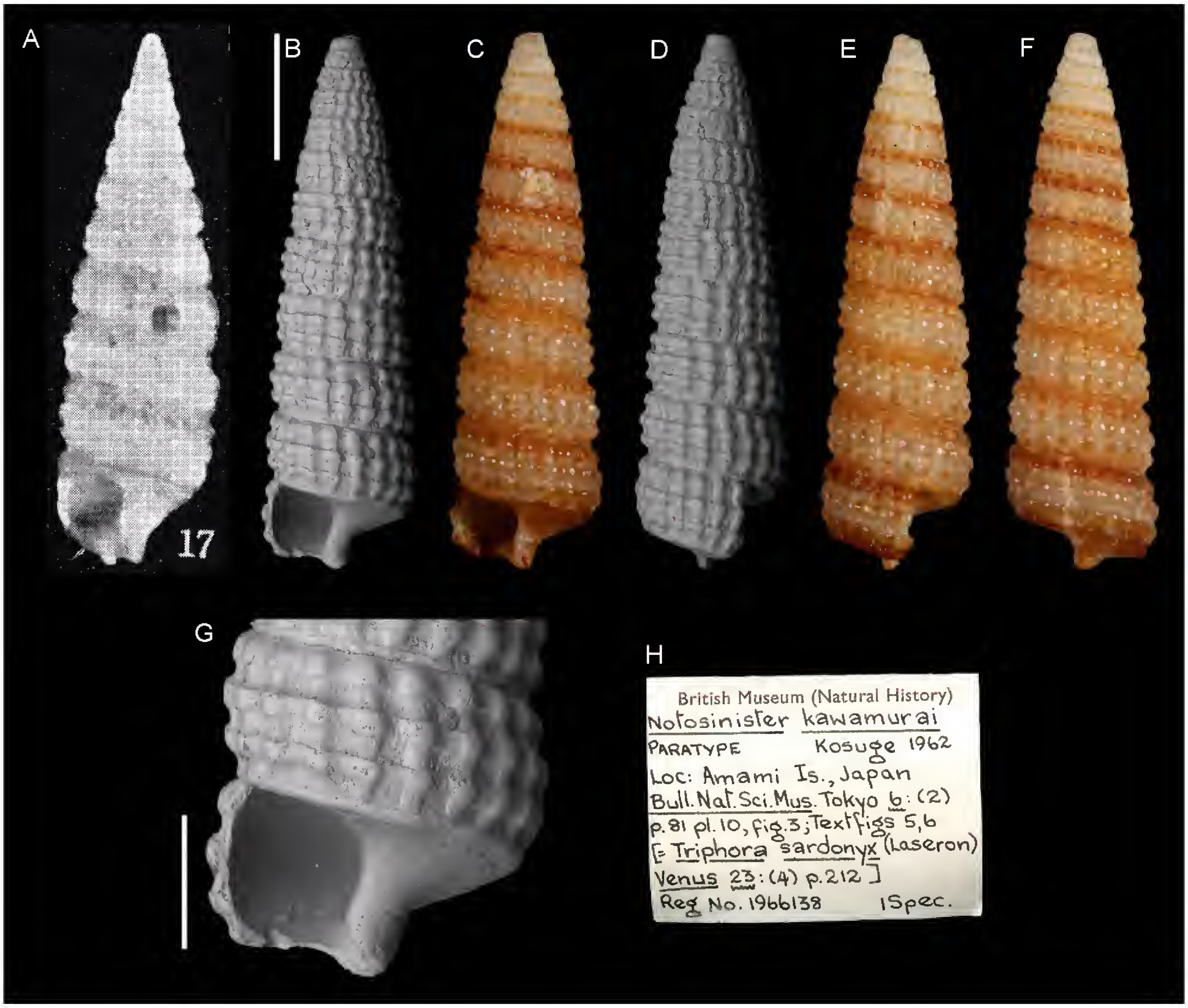

Figure 56. *Notosinister kawamurai* Kosuge, 1962, Amami Islands, Japan. **A** Original figure. **B–G** Paratype, NHMUK 1966138: front (**B, C**), side (**D, E**), back (**F**), aperture (**G**). **H** NHMUK label. Scale bars: **B–F**: 1 mm; **G**: 0.5 mm.

Type locality. Shirahama, Shimoda-machi, Shizuoka Prefecture, Central Japan.

Type material. Holotype: reported in the Dr. T. Kuroda collection (Kosuge 1962a) which is now in the Nishinomiya Shell Museum, Japan (not seen). Paratype: NHMUK 1966151: 1 specimen, Amami Islands, Japan.

Original description. *Shell medium in size, conical, apex blunt, not narrowed at the base, somewhat conoidal rod in shape. Protoconch immersed at the summit, slightly appearing as a tip of the smooth nucleus. Mature whorls 13, with straight side, suture deep and widely channelled. Sculpture 3 rows of granules, each row equal in size at the lower two-third of the spire, median row diminished at the early whorls. Granules connected with both spiral keels and rather broad axial columns which are latticed with spiral keels, apart by about half of its diameter and 22 to a whorl. On the body whorl, there are 3 smooth spiral keels on the periphery and base, anterior canal long and slightly recurved, aperture almost rounded. Colouration reddish brown and light brown in drifted materials.*

Shell length: 7.4 mm.

Remarks: This species is easily recognized by its immersed protoconch, differing from Is. tasmanica *(Ten-Wood) in its protoconch, of which the nucleus is slightly raised up, in contrast to the latter in which protoconch is completely immersed. This feature is taken natural as a generic character, therefore it may be necessary to give this species an appropriate subgeneric name.*

This species is dedicated to Dr. Tokubei Kuroda of the Kyoto University, President of the Malacological Society of Japan, who is kind enough to help in both literature and material.

Figure 57. *Isotriphora kurodai* Kosuge, 1962, Amami Islands, Japan. **A** Original figure. **B–I** Paratype, NHMUK 1966151: front (**B**, **C**), side (**D**, **E**), back (**F**), protoconch (**G**), microsculpture (**H**), aperture (**I**). **J** NHMUK label. Scale bars: **B–F**: 1 mm; **G**: 0.2 mm; **H**: 0.3 mm; **I**: 0.5 mm.

Euthymella leucocephala Kosuge, 1963

Figure 58

Euthymella leucocephala Kosuge 1963b: 260–261, pl. 18, fig. 5, text figs 5, 8.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 13064 (fide Kosuge 1963b; not seen, illustrated in Higo et al. 2001: 51, G1686). Paratype: NHMUK 1966139: 1 specimen, Amami Islands, Japan.

Original description. *Shell medium in size, apex blunt, conical, somewhat inflated at the middle of the spire and slightly narrowed at the body whorl. Protoconch of a single whorl, mammillate and smooth. Mature whorl 9, each whorl convex and widely separated by a rather deep grooved suture, encircled by a fine supra-sutural thread. Sculpture consists of 3 rows of granules, median row somewhat larger than the others at the lower spire, equal in size at the early 2 or 3 whorls and rapidly diminished at its first whorl; each granule spirally elongate and well elevated from the crossing points of broad axial columns and spiral costae which are deeply latticed, aparts* *from each other by about its diameter and 14 to a whorl. On the body whorl, fourth row of granules encircles the periphery, the other 2 slender, smooth, spiral ridges the base and the anterior canal which is short and recurved backward. Protoconch and early 2 whorls white, remainder dark reddish brown.*

Shell length: 6.8 mm.

Remarks: This species is easily distinguished by its protoconch, white apex and spirally elongated granules. It is somewhat related to E. regalis *Jousseaume and* E. isaotakii *Kosuge, though differs in its protoconch, shell shape and colour-pattern, and also differs from* Notosinister atratus *Kosuge in its sculpture and protoconch.*

***Cautor* (*Cautor*) *maculosus mcmichaeli* Kosuge, 1962**

Figure 59

Cautor (*Cautor*) *maculosus mcmichaeli* Kosuge 1962a: 85, pl. 10, fig. 8, text figs 7, 14.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 13042 (fide Kosuge 1962a; not seen, illustrated in Higo et al. 2001: 51, G1745). Paratype: NHMUK 1966150: 1 specimen, Amami Islands, Japan.

Original description. *Shell rather small, conical, lower spire somewhat cylindrical, not narrowed at the base. Protoconch of 3 whorls, apex blunt, second and third whorls have a single spiral keel overridden by axial threads, pure white in colour. Mature whorls 9, suture distinct as a deep groove with a fine supra-sutural thread. Sculpture 3 rows of granules, upper row largest, median one diminished and gradually disappears on the early whorls, each granule almost rounded, connected by axial columns and fine spiral keels, beset close together and 23 to a whorl. On the body whorl, there are other 2 rows of granules and 1 smooth keel on the base, anterior canal broad and slightly recurved, aperture rounded. Irregularly variegated with opaque white, buff and chocolate, usually maculated white and chocolate, base chocolate.*

Shell length: 6 mm.

Remarks: This subspecies is closely related to C. maculosus *(Hedley) in sculpture, colour and the nature of protoconch, though it is much more slender than that species and its whorls are much more squarishly angulated at the base.*

***Notosinister millepunctatus* Kosuge, 1962**

Figure 60

Notosinister millepunctatus Kosuge 1962a: 83, pl. 10, fig. 4, text figs 12, 17.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 13038 (fide Kosuge 1962a; not seen, illustrated in Higo et al. 2001: 51, G1707). Paratype: NHMUK 1966144: 1 specimen, Amami Islands, Japan.

Original description. *Shell medium in size, conical, acuminate at the summit, narrowed at the base. Protoconch turrited conical, 5 whorls with 2 spiral keels overridden by axial threads, dark brown in colour. Mature whorls 13, suture shallow and not distinct. Sculpture 3 rows of granules at the lower part of the spire, median one smaller than the others, and gradually turns to a thread as it ascends the spire and finally disappears at the early whorls. Granules rather large, apart by half of its diameter and 18 or 20 to a whorl, connected both spirally and axially with each other. On the body whorl, fourth row of cranules on the periphery and another spiral keel on the base, anterior canal short and strongly recurved backward. Colouration is white or pale brown with numerous irrerular dark brown spots.*

Shell length: 6.8 mm.

Remarks: This species is closely related to T. dolicha *(Watson) and* T. turricula *(Hervier), though differs in having a protoconch with 2 spiral keels in contrast to 1 keel of the latter two species, and also differs in shell shape.*

***Notosinister rufotinctus* Kosuge, 1963**

Figure 61

Notosinister rufotinctus Kosuge 1963a: 249, pl. 16, fig. 26, text figs 6, 7.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 13065 (fide Kosuge 1963a; not seen, illustrated in Higo et al. 2001: 51, G1719). Paratype: NHMUK 1966146: 1 specimen, Amami Islands, Japan.

Original description. *Shell rather small, somewhat spindle-form, tapering to the summit and narrowed at the base. Protoconch conical, acuminate, of 5 whorls, keeled by a single carina with crossed fine axial threads. Mature whorls 10, suture distinct and grooved in somewhat deep channel. Sculpture consists of 3 rows of granules; middle row slender, about half as large as the other two rows, turns to a thread and disappears at the early 3 or 4 whorls; upper and lower rows large and equal in size. Granules almost round, connected by broad axial columns and spiral keels which are regularly latticed, interspaces between them squarely excavated, apart from each other by about half of its diameter and 21 to a whorl. Body whorl has 5 rows of granules, upper-most row largest, next 2 rows nearly equal in size and about half as large as the upper one, fourth row on the periphery and fifth one*

Figure 58. *Triphora leucocephala* Kosuge, 1963, Amami Islands, Japan. **A–E, G–I** Paratype, NHMUK 1966139: front (**A, B**), side (**C, D**), back (**E**), protoconch (**G, H**), aperture (**I**). **F** Original figure. **J** NHMUK label. Scale bars: **A–E**: 1 mm; **G, H**: 0.2 mm; **I**: 0.5 mm.

on the base more slender than the others. Anterior canal rather short and slightly recurved backward. Colouration olive ochre, tinted among the granules underside of lower spiral keel of each whorl with deep reddish brown and protoconch chocolate.

Shell length: 5.2 mm.

Remarks: This species is distinct by its spindle form and colouration, and somewhat related to Triphora clemens *(Hinds), though differs in its sculpture.*

Mastonia squalida Kosuge, 1962

Figure 62

Mastonia squalida Kosuge 1962b: 126–127, pl. 8, fig. 19, text figs 12, 13.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 12253 (fide Kosuge 1962b; not seen, illustrated in Higo et al. 2001: 51, G1695). Paratype: NHMUK 1966145: 1 specimen, Amami Islands, Japan.

Original description. *Shell of medium size, conical, tapering to the summit and narrowed at the base. Protoconch with 2 spiral keels crossed with many axial threads. Mature whorls 12, suture not clear. 2 rows of granules beset in the upper and lower parts of each whorl, a fine spiral thread encircles upper part of its interstices and shell covered with many fine scale-like*

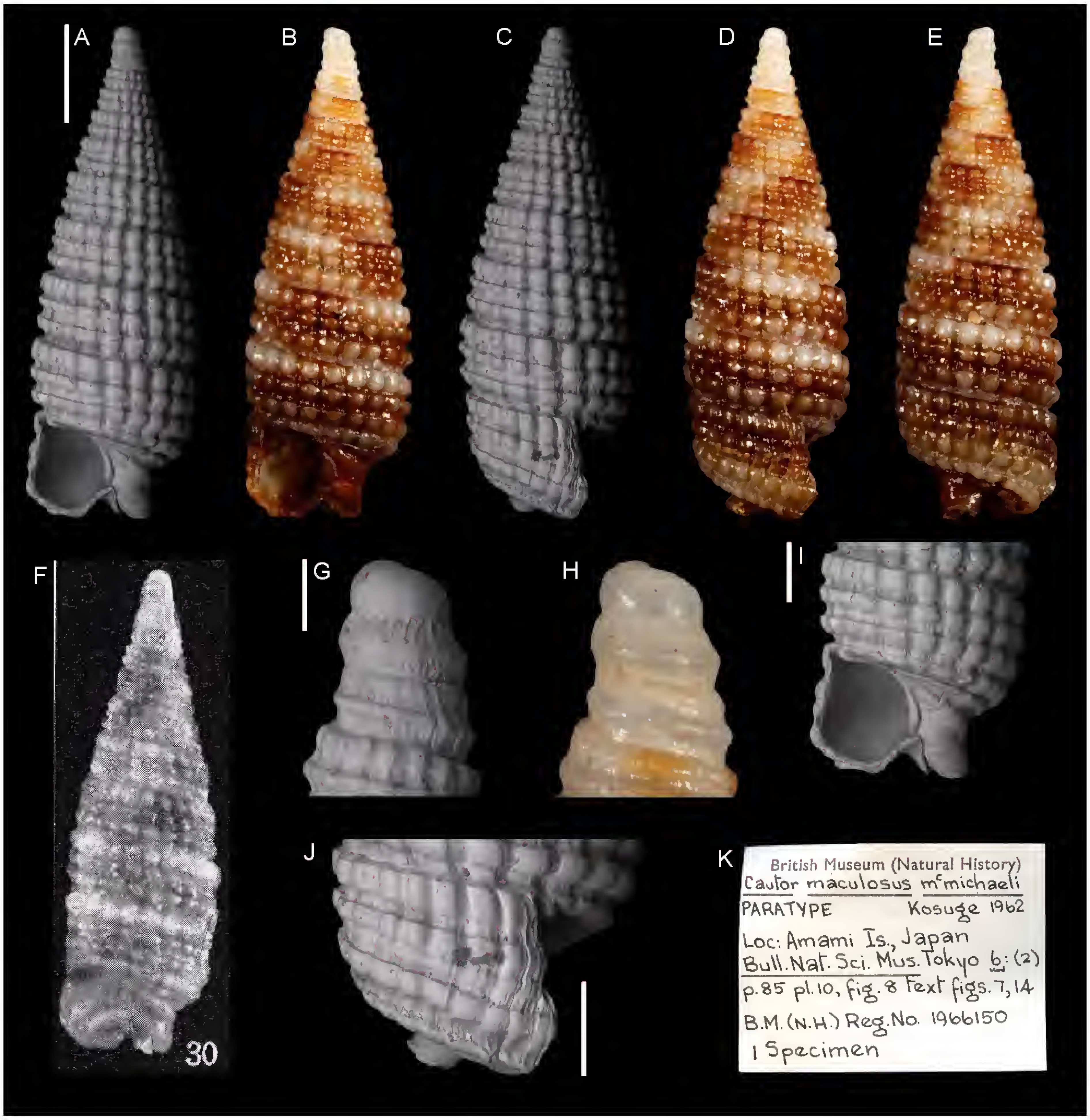

Figure 59. *Notosinister maculosus macmichaeli* Kosuge, 1962, Amami Islands, Japan. **A–E, G–J** Paratype, NHMUK 1966144: front (**A, B**), side (**C, D**), back (**E**), protoconch (**G, H**), aperture (**I**), peristome (**J**). **F** Original figure. **K** NHMUK label. Scale bars: **A–E**: 1 mm; **G, H**: 0.2 mm; **I–J**: 0.5 mm.

sculpture. Granules large and equal-sized, 16 to a whorl. Protoconch brown, early 4–5 whorls white, remainder dull reddish violet.

Shell length: 6.5 mm.

Remarks: This species is allied to M. squamosa *in shell feature and sculpture, though differs from it in colour pattern and also from* T. albogranosa *in shell feature, details of sculpture and colour pattern.*

Inella subfenestra **Kosuge, 1962**

Figure 63

Inella subfenestra Kosuge 1962b: 123, pl. 8, fig. 12, text fig. 1–2.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 12125 (fide Kosuge 1962b; not seen, illustrated in Higo et al. 2001: 51, G1678 as *I. subfenestrata*). Paratype: NHMUK 1966148: 1 specimen, Amami Islands, Japan.

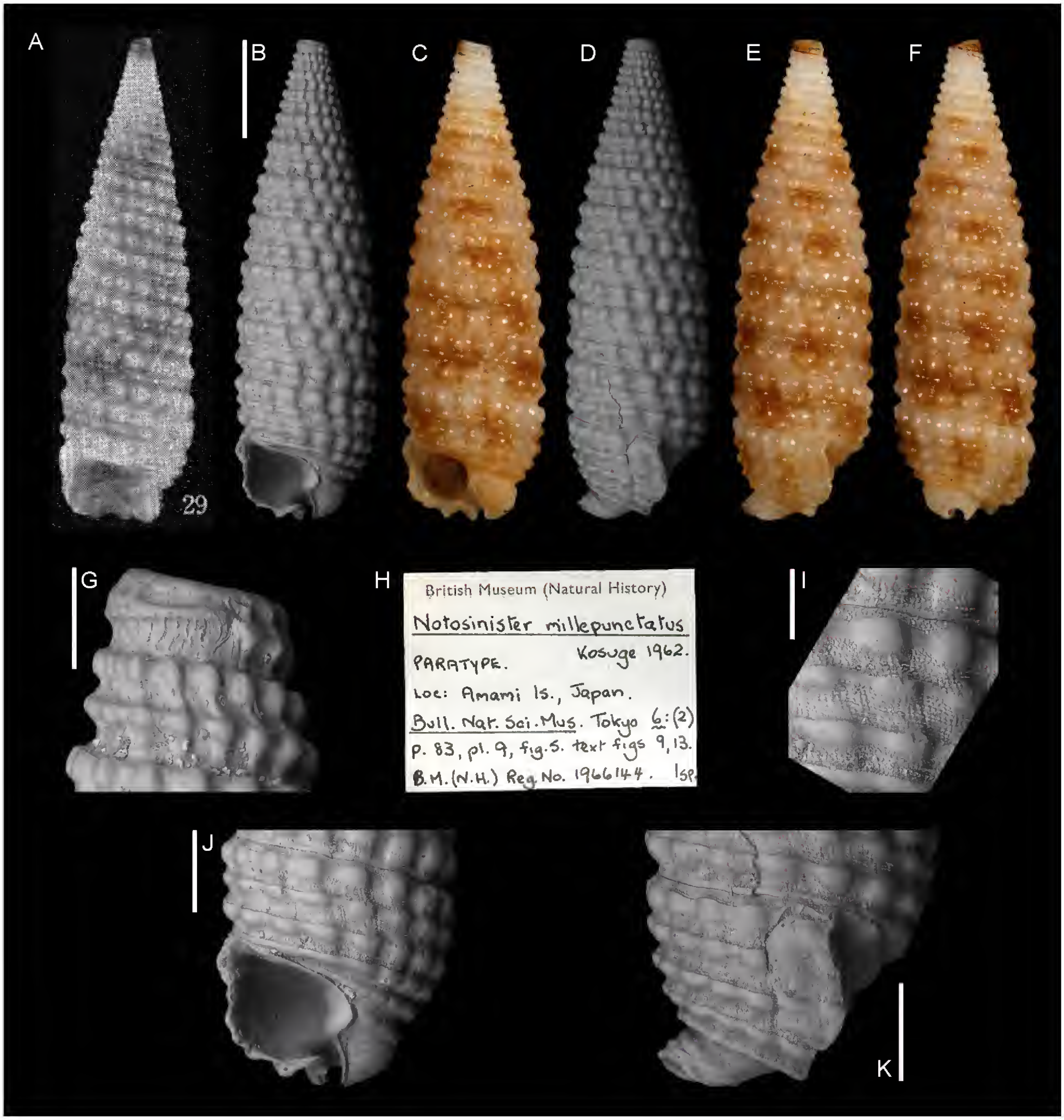

Figure 60. *Notosinister millepunctatus* Kosuge, 1962, Amami Islands, Japan. **A** Original figure. **B–G, I–K** Paratype, NHMUK 1966144: front (**B, C**), side (**D, E**), back (**F**), protoconch (**G**), microsculpture (**I**), aperture (**J**), peristome (**K**). **H** NHMUK label. Scale bars: **B–F**: 1 mm; **G–I**: 0.2 mm; **J, K**: 0.5 mm.

Original description. *Shell large, slender with straight side. Colour of protoconch light brown, remainder purplish pink. Protoconch of 4 whorls, nucleus dome-shaped, each whorl has 2 spiral keels overriden by axial threads.*

Mature whorls 16, suture not clear and has a fine supra-sutural thread. Sculpture of 3 rows of granules, latticed by spiral costae and axial columns, upper row more slender, and nearly equal-sized on the body whorl. Granules spirally elongate, each granule apart from each other by about its diameter and 19 to a whorl. Supra-sutural thread becomes the fourth row of granules on the edge of body whorl and also fifth and sixth slender rows slightly appear on the interstices of main rows at the body whorl, two extra spiral costae at the base of body whorl and faintly granulated. Anterior canal not closed.

Shell length: 9.5 mm.

Remarks: This species is closely related to T. episcopalis *(Hervier) in colour pattern, though in the latter species the median row of granules is diminished on the*

Figure 61. *Notosinister rufotinctus* Kosuge, 1963, Amami Islands, Japan. **A–E, G, I, J** Paratype, NHMUK 1966146: front (**A, B**), side (**C, D**), back (**E**), protoconch (**G**), aperture (**I**), peristome (**J**). **F** Original figure. **H** NHMUK label. Scale bars: **A–E, I, J**: 0.5 mm; **G**: 0.2 mm.

penultimate whorl and gradually turns to spiral thread in contrast with the former's upper row, and somewhat like T. nocturna *Hedley, though this new species differs in sculpture of both protoconch and mature whorls. Also this species is distinguished from* T. xystica *(Jousseaume),* T. verrucosa *and* T. marginata *(Laseron) in details of sculpture and colour pattern.*

Notosinister tessellatus Kosuge, 1963

Figure 64

Notosinister tessellatus Kosuge 1963a: 243 and 245, pl. 16, fig. 28, text fig. 4.

Type locality. Ankyaba, Setouchi-machi, Amami Islands.

Type material. Holotype: TZM Mo. 13070 (fide Kosuge 1963a; not seen, illustrated in Higo et al. 2001: 51, G1723). Paratype: NHMUK 1966147: 1 specimen, Amami Islands, Japan.

Original description. *Shell of medium in size, conical, tapering to the summit, lower part of spire cylindrical. Protoconch with 2 spiral keels and many axial threads. Mature whorls 12, suture distinct as a rather prominent channel. Sculpture consists of 3 rows of granules,*

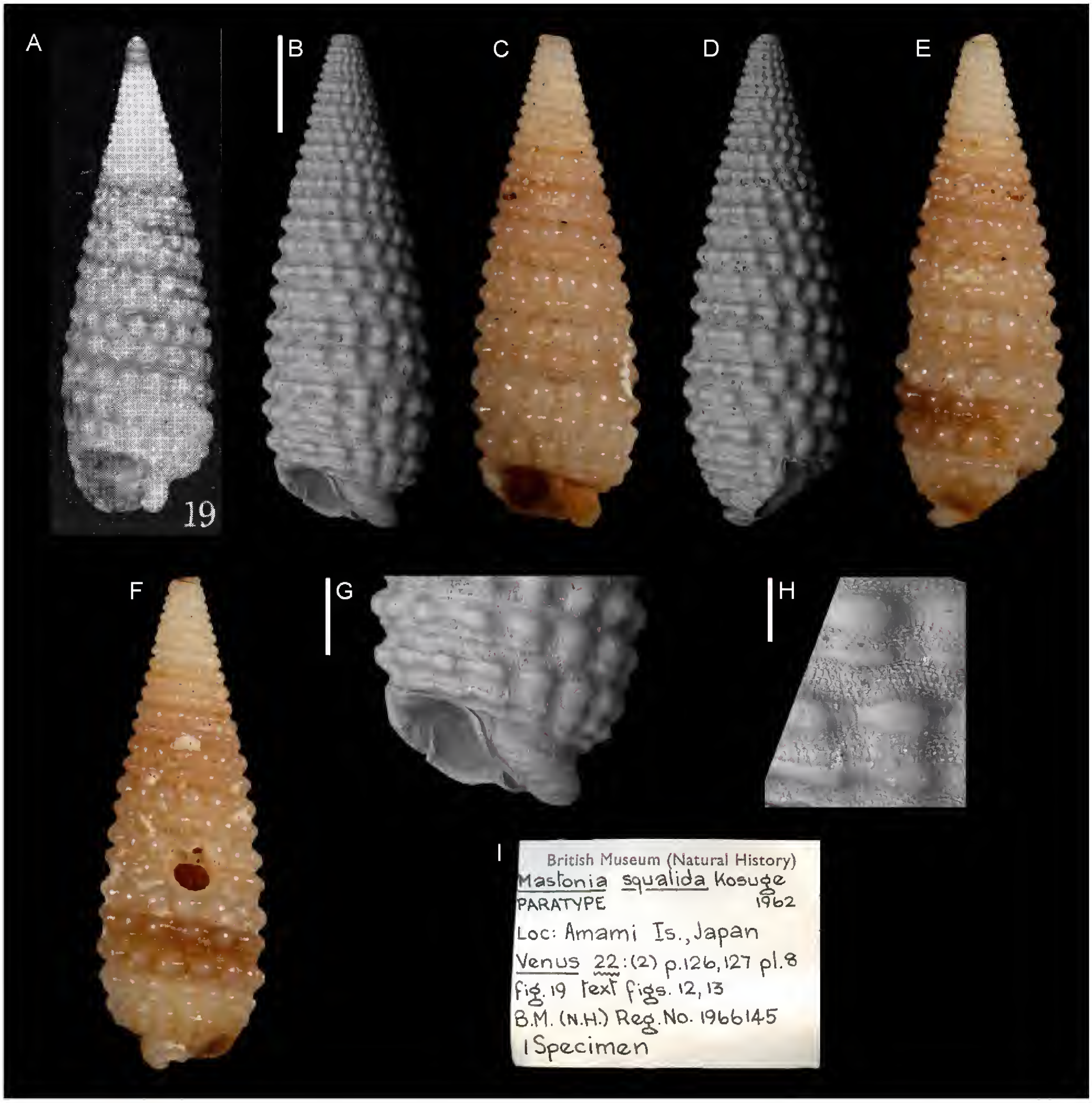

Figure 62. *Mastonia squalida* Kosuge, 1962, Amami Islands, Japan. **A** Original figure. **B–H** Paratype, NHMUK 1966145: front (**B, C**), side (**D, E**), back (**F**), aperture (**G**), microsculpture (**H**). **I** NHMUK label. Scale bars: **B–F**: 1 mm; **G**: 0.5 mm; **H**: 0.2 mm.

upper and lower rows large and equal in size, median row becoming nearly equal to the others on the body whorl and gradually turns to spiral thread as it ascends the spire. Granules small, well rounded, beset close together and 20 to a whorl, connected with oblique axial columns and weak spiral threads. On the body whorl, fourth row of granules encircles the periphery and fifth row the base. Anterior canal strongly recurved backward and encircled by a smooth spiral keel. Colouration of protoconch brown, mature whorl white with squarish brown piltches.

Shell length: 6.5 nun.

Remarks: This species somewhat likes N. quadrimaculatus *(Hervier), though differs in colour pattern and shell shape, and also differs from* Triphora maculosus *Hedley and* Triphora ampulla *Hedley in colour pattern and protoconch, from* Triphora dolicha *(Watson) in its sculpture of protoconch.*

Species described by B.A. Marshall

Bruce A. Marshall described 21 species of Triphoridae, most of them in his seminal work on South Australian species (1983). In the NHMUK, the paratype of a single species is deposited: *Metaxia kermadecensis*.

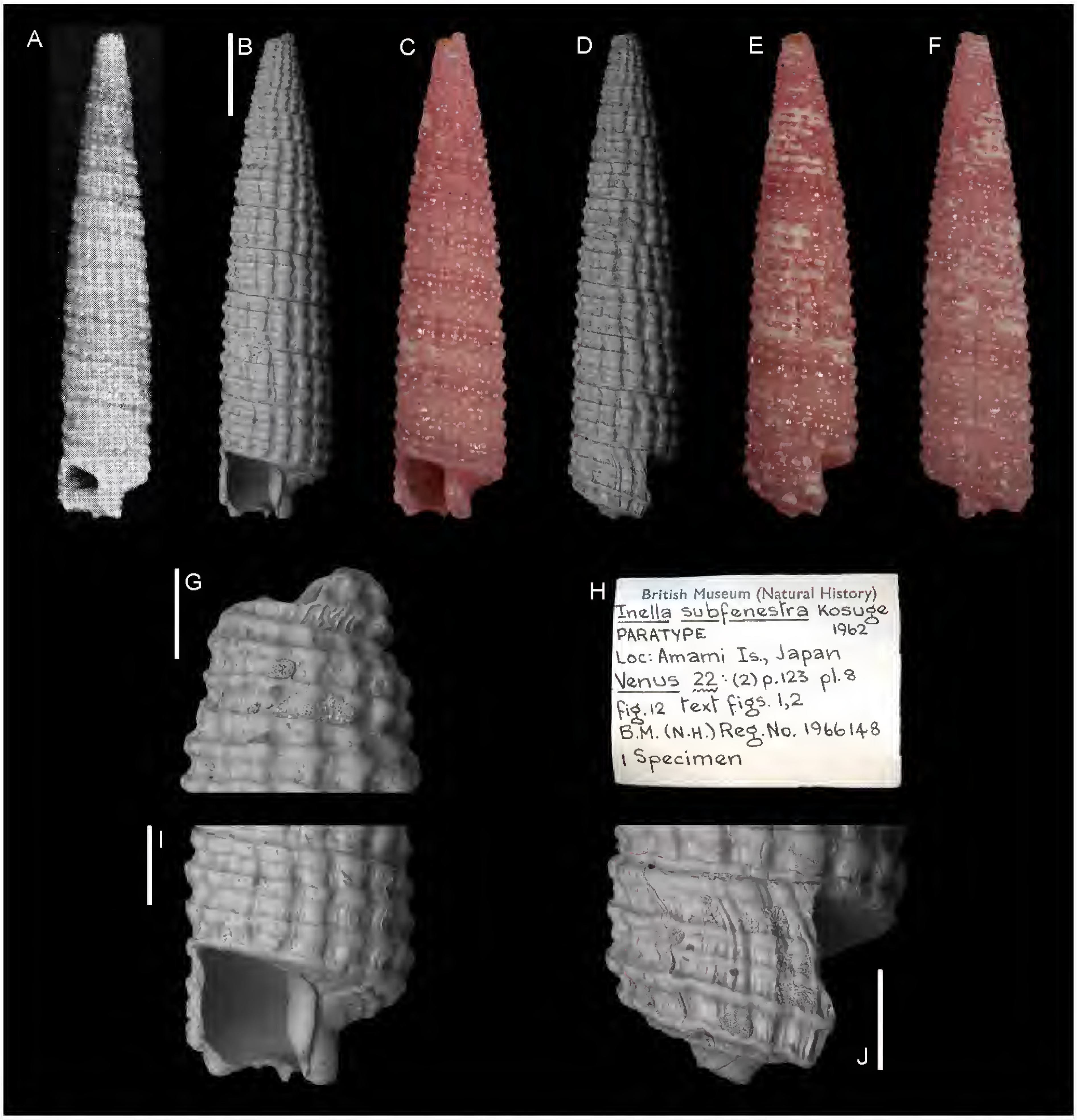

Figure 63. *Inella subfenestra* Kosuge, 1962, Amami Islands, Japan. **A** Original figure. **B–G, I, J** Paratype, NHMUK 1966148: front (**B, C**), side (**D, E**), back (**F**), protoconch (**G**), aperture (**I**), peristome (**J**). **H** NHMUK label. Scale bars: **B–F**: 1 mm; **G**: 0.2 mm; **I, J**: 0.5 mm.

Metaxia kermadecensis Marshall, 1977

Figure 65
Metaxia kermadecensis Marshall 1977: 116–117, figs 2D–F, H.

Type locality. Raoul (Sunday) Island, Kermadec Islands.

Type material. Holotype: MNZ MF 25922 (fide Marshall 1977; not seen). Paratypes: NHMUK 197844: 1 specimen, Sunday Island, Kermadec Islands; additional 19 specimens in AMS and USNM (fide Marshall 1977; not seen).

Species described by J.C. Melvill

James C. Melvill described five species of Triphoridae: *Triphora* (*Mastonia*) *coetiviensis* Melvill, 1909, *T. concatenata* Melvill, 1904, *T. incolumis* Melvill, 1918, *T. interpres* Melvill, 1918 and *T. persica* Melvill, 1918 from various localities. We found in the NHMUK type material of the first four. Syntypes of *T. persica* are in NMW (Trew 1987). Because large sets of syntypes are stored in the NMW, we refrained from selecting lectotypes pending their inspection.

Figure 64. *Notosinister tessellatus* Kosuge, 1963, Amami Islands, Japan. **A** Original figure. **B–H** Paratype, NHMUK 1966147: front (**B, C**), side (**D, E**), back (**F**), aperture (**G**), peristome (**H**). **I** NHMUK label. Scale bars: **B–F**: 1 mm; **G, H**: 0.5 mm.

Triphora (*Mastonia*) *coetiviensis* Melvill, 1909

Figure 66

Triphora (*Mastonia*) *coetiviensis* Melvill 1909: 90, pl. 5, fig. 8.

Type locality. "Coetivy I." (Coëtivy Island, Seychelles).

Type material. Lectotype: NHMUK 1910.3.17.1 (lectotype selection by inference of holotype by Trew (1987)).

Original description. *T. testa mediocri, compacta, solidula, pupoidea, cinereo-brunnea, versus apicem attenuata; anfractibus ad 14, quorum apicales ipsi duo asperi, albo-vitrei, quatuor his proximis duobus ordinibus tuberculatis, caeteris tribus, ultimo quinque spiraliter instructis, tuberculis rotundis, nitidis, albo-cincreis; apertura fere rotunda, labro crenulato, tenui, brunneo tincto, canali breviter rostrato.*

Long. 13, lat. 4 mm.

Loc. Coetivy I.

An ashy-brown little *Triphora*, evenly spirally tubercled throughout with shining small gemmae, of a compact growth, attenuate towards the apex, otherwise robust; on the upper whorls the spiral rows are alternately straw-coloured and grey, the lower whorls, however, are of a uniform dull grey, the orifice being tinged with brown, as is the shortly beaked canal. From figures and descriptions this species must be near *T. funebris* Jouss., from New Caledonia, and *T. intermedia* C.B. Ad., from the Antilles.

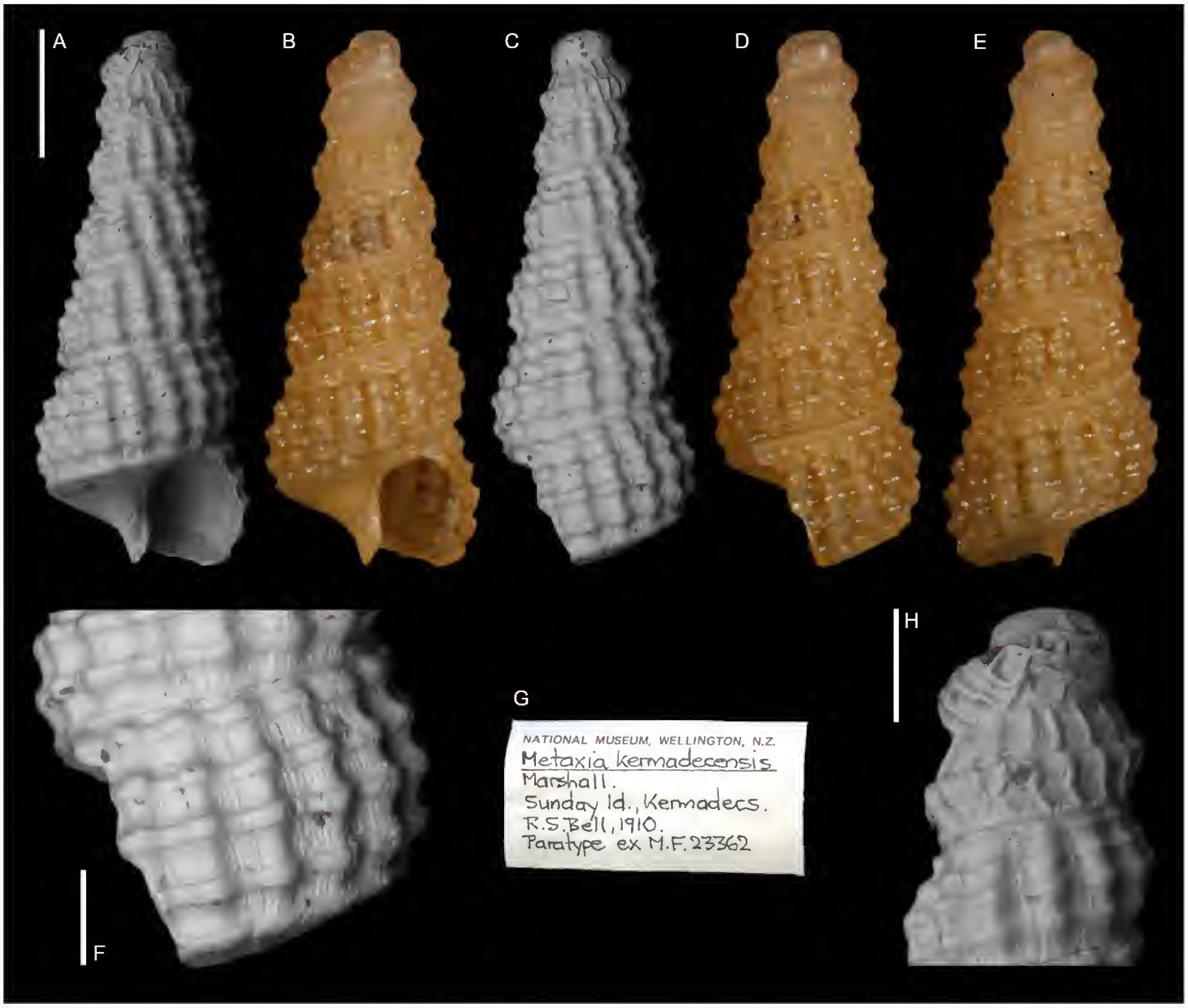

Figure 65. *Metaxia kermadecensis* Marshall, 1977, Sunday Island, Kermadec Islands. **A–F, H** Paratype NHMUK 197844: front (**A, B**), side (**C, D**), back (**E**), peristome (**F**), protoconch (**H**). **G** Original label. Scale bars: **A–E**: 0.5 mm; **F, H**: 0.2 mm.

Translation of the Latin text. Medium-sized shell, compact, rather solid, pupiform, brown-grey, narrowing towards its apex; up to 14 whorls, the two apical ones pointed, translucent white, the next four with two rows of tubercles, others with three rows and the last with five; bright, ash-white, round tubercles; aperture nearly rounded, crenulated brown thin lip, short bent anterior siphon.

Length 13 mm, width 4 mm.

Diagnosis. Lectotype 10.5 mm high. Shell cyrtoconoid, with at least 12 teleoconch flat whorls that bear three spiral cords with tubercles at the intersection with arched axial ribs, a fourth suprasutural smooth cord is visible. The second spiral cord develops later but it is fully developed after one-third of shell height. Fine spiral threads and growth lines are present among the main elements of the sculpture. The peristome bears additional spiral cords and a shallow posterior sinus. Siphonal canal long; on the base, a fifth tuberculated spiral cord is present. Protoconch missing. Teleoconch colour brown, with pearly tubercles and lighter background on the first spiral cord and on the siphonal canal; very first whorls white.

Remarks. Trew (1987) stated that this specimen is the holotype, but Melvill (1909) did not specify how many specimens he studied, nor we have found other evidence that the species was described on a single specimen.

Trifora concatenata Melvill, 1904

Figure 67

Trifora concatenata Melvill 1904: 162, pl. 10, fig. 9.

Type locality. "Gulf of Oman, lat. 24°58'N., long. 56°54'E., 156 fathoms".

Type material. Syntypes: NHMUK 1905.7.14.32–4, 1 specimen (plus 2 belonging to another species, see Re-

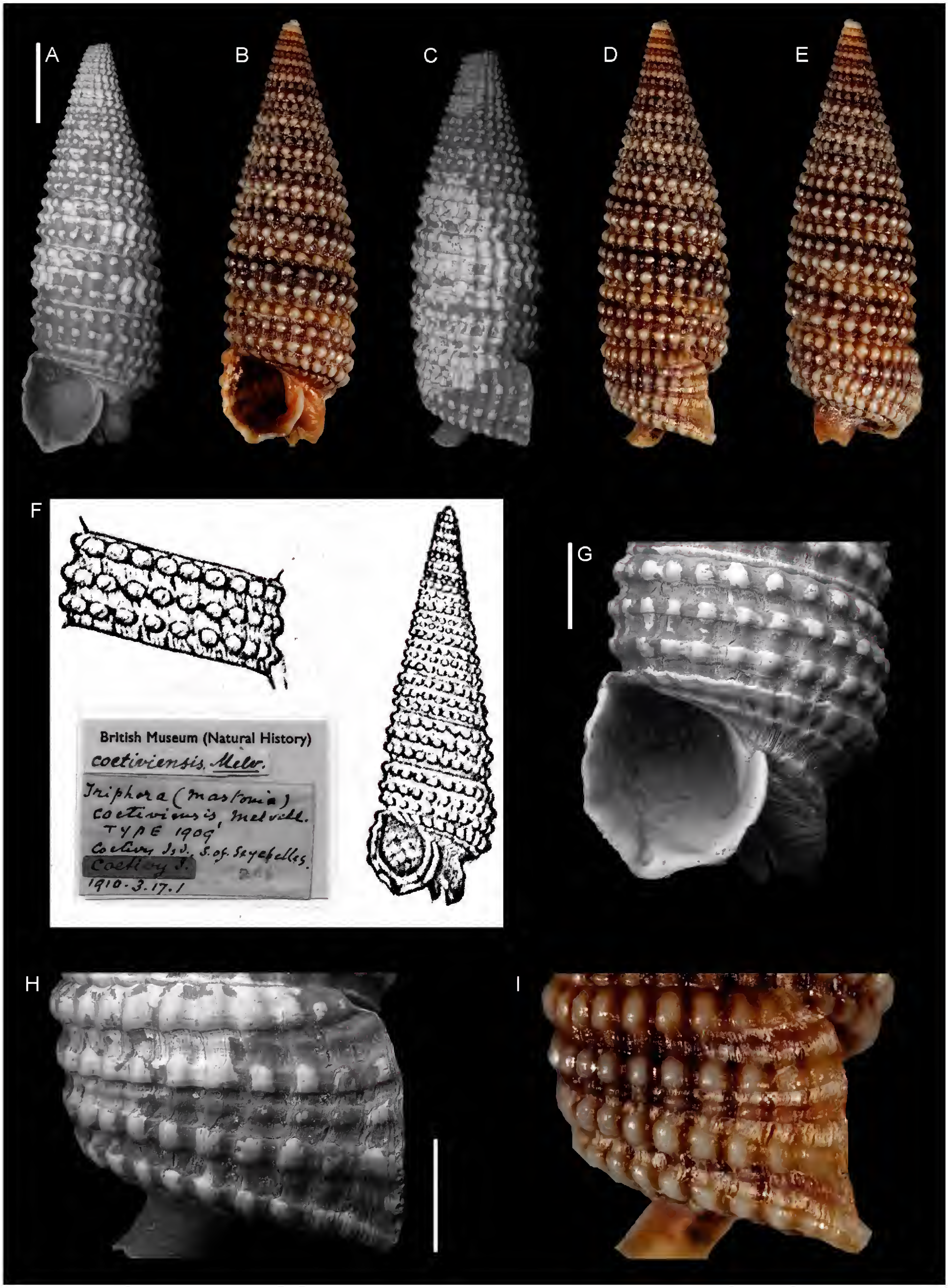

Figure 66. *Triphora coetiviensis* Melvill, 1909, Coëtivy Island, Seychelles. **A–E, G–I** Lectotype NHMUK 1910.3.17.1: front (**A, B**), side (**C, D**), back (**E**), aperture (**G**), peristome (**H, I**). **F** Original figures and labels. Scale bars: **A–E**: 2 mm; **G–I**: 1 mm.

marks), Gulf of Oman. Syntypes: NMW 1955.158.196, 18 specimens, Gulf of Oman (fide Trew 1987; not seen).

Original description. *T. testa pergracili, multum attenuata, albescente, albo-fusca, anfractibus ad 18, quorum apicales 4, ochracei, spiraliter unicarinati, arete et pulcherrime sub lente longitudinaliter lirati, liris sinuosis, caeteris rectis, suturis indistinctis, tribus gemmularum ordinibus concatenatis praeditis, gemmulis rotundis, nitentibus, ultimo anfractu quatuor ordinibus, circa basim angulato, apertura rotundo-ovata, labro simplice, canali brevi. Long. 5, lat. 1 mm., sp. max.*

A small, very gracefully attenuate species, white or whitish-drab, with ochreous apical whorls, these being once keeled spirally, the usual pattern being present on the remaining whorls of three rows of round, shining gemmae – four on the body-whorl, the lowest row being the largest; these spiral rows are more or less concatenate, leaving clear spaces between.

Translation of the Latin text. Very slender thin shell, whitish, white-brown, up to 18 whorls, four unicarinated ochraceus apical ones, with microscopical sinuous lirae then becoming straight, indistinct sutures, three rows of concatenated gemmulae which are round, bright; last whorl with four rows, angulated near the base, rounded-ovate aperture, simple lip, short anterior siphon. The largest specimen is 5 mm long, 1 mm wide.

Diagnosis. Syntype 5.6 mm high. Extremely slender shell with 14 flat teleoconch whorls bearing three spiral cords with tubercles at the intersection with prosocline axial ribs. The first spiral cord is smaller. The peristome is incomplete in the syntype, the siphonal canal appears short. On the base, three additional smooth cords are present. Protoconch incomplete, but clearly multispiral with the last three whorls bearing two spiral keels and axial riblets. Shell whitish.

Remarks. Lot NHMUK 1905.7.14.32–4 contains three shells belonging to two species. One shell clearly resembles the specimen figured by Melvill (1904) (NHMUK 1905.7.14.32, Fig. 67B–F), while the other two can be readily distinguished by one instead of two spiral keels on the protoconch (Fig. 67J) and the second spiral cord on the teleoconch appearing later than the other two (Fig. 67H, I); in the true *T. concatenata* all three spiral cords are present since the first teleoconch whorl. According to Trew (1987), the specimen shown in Figure 67B is the syntype figured by Melvill (1904). Therefore, upon inspection of the syntypes in NMW, it may be selected as lectotype.

Triphora incolumis Melvill, 1918

Figure 68

Triphora incolumis Melvill 1918: 149, pl. 4, fig. 18.

Type locality. Persian Gulf: Fao Cable (Fao was a small village at the confluence of Tigris and Euphrates).

Type material. Syntypes: NHMUK 1921.1.28.18–20, 3 specimens, Persian Gulf. Syntypes: NMW 1955.158.207, 13 specimens, Persian Gulf (fide Trew 1987; not seen).

Original description. *T. testa cylindrico-fusiformi, pallide straminea, solidula; anfractibus 16–17, quorum apicales 5 pulchre et minute longitudinaliter striati, paullum decussati, apice ipso laevi, deplanato, caeteris ad suturas profunde impressis, lateribus paullulum convexis, quatuor supernis bi-, his proximis triseriatis, ordinibus nodulato-gemmatis decoratis, ultimo anfractu serie quarta praedito, gemmis interdum versus basin evanidis, circa basin tribus liris succinctis; apertura quadrata, peristomate tenui, canali brevi, paullum recurvo.*

Long. 10, lat. 3 mm.

Hab. Persian Gulf; Fao Cable, and along the north coast; not rare.

A fine species, of pronounced character. Cylindro-fusiform in shape, with channelled sutures, whorls (including the five nuclear, three of which are very finely striate) 16–17 in number, the lower whorls all ornamented with three equal spiral regular rows of gemmae, shining, round, large proportionately; the body-whorl possessing four, the lowest of them sometimes has the gemmae partly evanescent, the base being encircled with spiral plain ridges. Aperture somewhat squarrose, peristome thin, canal shortly recurved, pronounced. It may be compared with *T. rufula*, Watson, a somewhat smaller species * [footnote refers to: 'Challenger' Exp. xv. p. 566, pi, xlii. fig. 2] (long. 7.5 mm.) from Wednesday Island, Torres Straits. This is much of the same sculpture, with channelled suture, the shell being of a ruddy yellow tint throughout. It differs from *T. idonea*, M. & St., not only in the channelled sutures and greater breadth of contour, but in the mouth being more contracted. We have seen a live albino form from Fao; in this the fourth row of noduled gemmae at the periphery of the basal whorl is extremley distinct and perfect.

Translation of the Latin text. Rather solid, pale yellow cylindro-fusiform shell; 16–17 whorls, the five apical ones with faint nice longitudinal striae, slightly decussated, the apex is delicate, rather flat; next whorls with deep sutures, a little convex; four apical whorls with two spiral cords, the next with three series of nodose gemmules, four in the last whorl with vanishing gemmules near the base which bears three smooth spiral cords; quadrate aperture, thin peristome, lightly recurved short anterior siphon.

Length 10, width 3 mm.

Diagnosis. Syntypes between 7.5 and 8.4 mm high. Shell conical with 12 whorls bearing three spiral cords with tubercles at the intersection with orthocline axial ribs. The second spiral cord appears on the sixth whorl and becomes quickly as strong as the others. A smooth suprasutural cord is also visible. Growth lines are present. The peristome bears additional, although short, spiral cords and a shallow posterior sinus. The siphonal canal is short. On the base, the fourth cord is tuberculated and

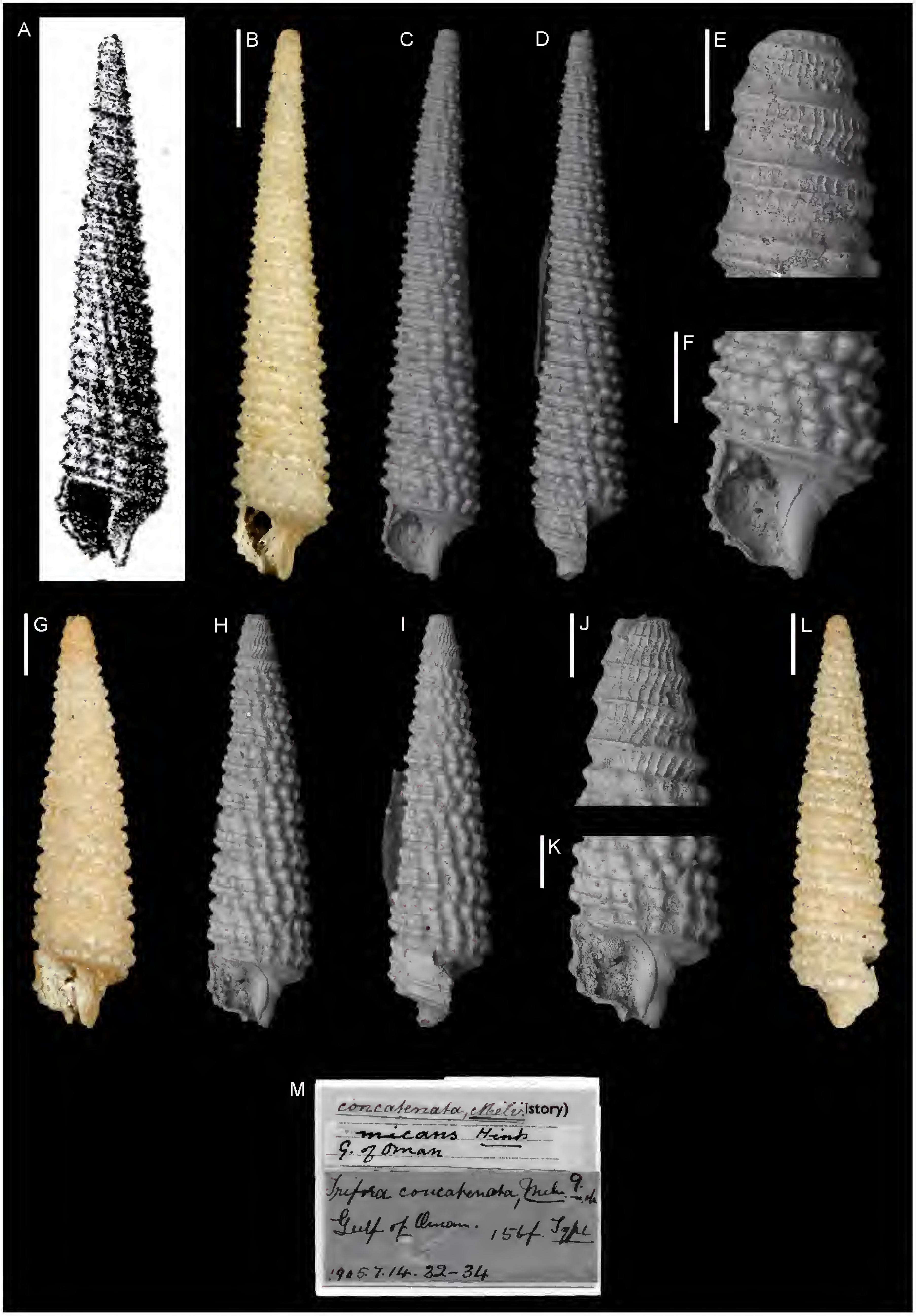

Figure 67. *Trifora concatenata* Melvill, 1904. **A** Original figure. **B–F** Syntype NHMUK 1905.7.14.32: front (**B, C**), side (**D**), protoconch (**E**), aperture (**F**). **G–K** *Triphora* sp. (not *concatenata*), NHMUK 1905.7.14.33, Gulf of Oman: front (**G–H**), side (**I**), protoconch (**J**), aperture (**K**). **L** *Triphora* sp. (not *concatenata*), NHMUK 1905.7.14.34, Gulf of Oman: side. **M** Original labels. Scale bars: **B–D**: 1 mm; **F–I, L**: 0.5 mm; **E, J**: 0.2 mm; **K**: 0.3 mm.

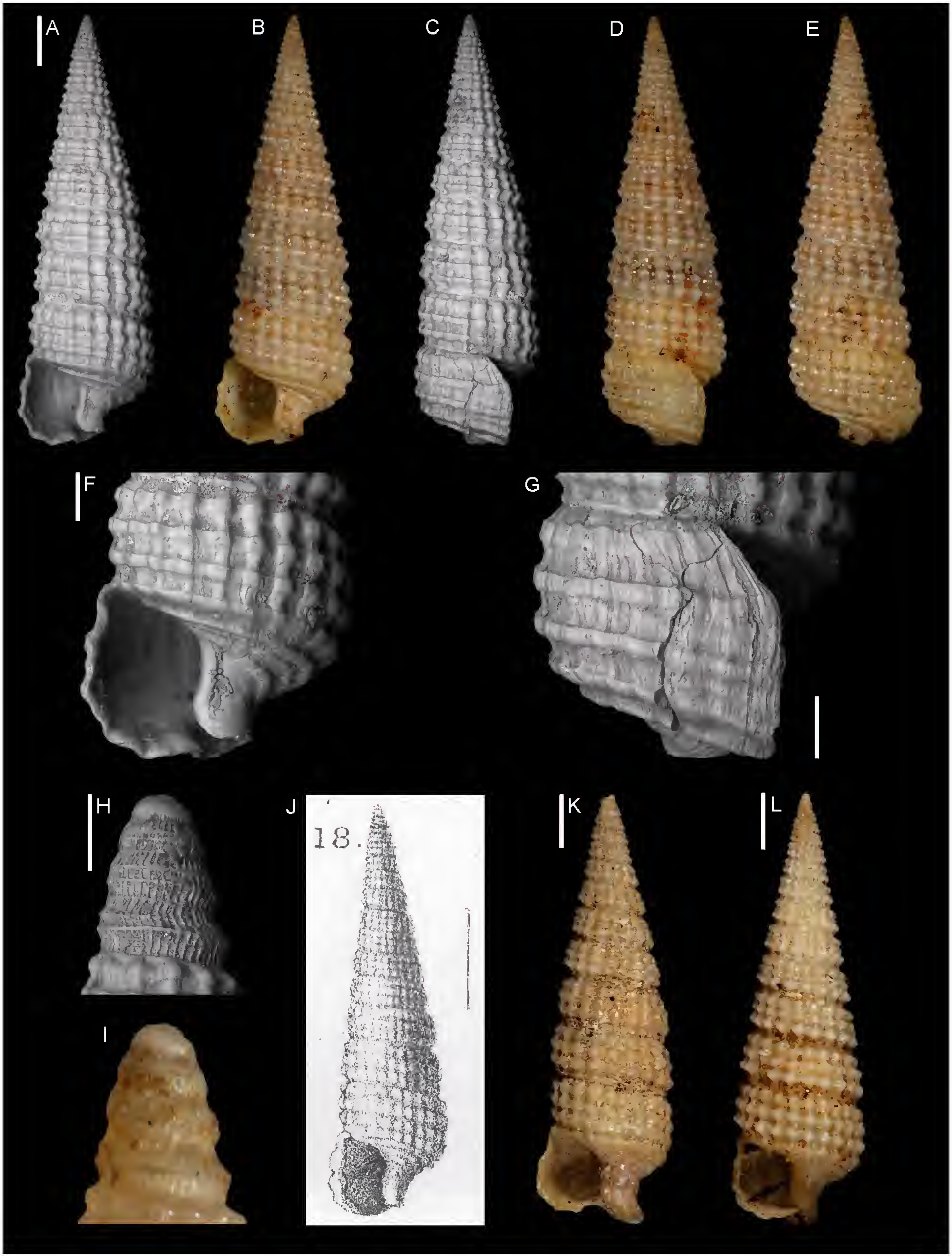

Figure 68. *Triphora incolumis* Melvill, 1918, Persian Gulf, Fao Cable. **A–I** Syntype NHMUK 1921.1.28.18: front (**A, B**), side (**C, D**), back (**E**), aperture (**F**), peristome (**G**), protoconch (**H, I**). **J** Original figure. **K, L** Syntypes NHMUK 1921.1.28.19–20: front views. Scale bars: **A–E, K, L**: 1 mm; **F–G**: 0.5 mm; **H, I**: 0.2 mm.

three more smooth cords are visible. The multispiral protoconch has four whorls: the first has abapically short axial riblets but it is too worn to be properly described, the other three have two spiral keels and axial riblets. Shell dirty white, with lighter tubercles.

Remarks. According to Trew (1987), lot NHMUK 1921.1.28.18–20 contains the specimens figured by Melvill (1918). Therefore, upon inspection of the syntypes in NMW, a lectotype may be selected.

Triphora interpres Melvill, 1918

Figure 69

Triphora interpres Melvill 1918: 150, pl. 5, fig. 23.

Type locality. “Persian Gulf, Mussandam, 55 fms” (Musandam, Oman).

Type material. Syntypes: NHMUK 1921.1.28.26, 1 specimen, Musandam, Oman. Syntypes: NMW 1955.158.208, 4 specimens, Musandam, Oman (fide Trew 1987; not seen).

Original description. *T. testa elegantula attenuato-fusiformi, gracili, cinerea; anfractibus ad 20, quorum 5 apicales, apice ipso pallide fusco, laevi, his proximis pulchre cancellatis, ochraceo-fuscis, caeteris leniter et anguste ad suturas impressis, lateribus fere rectis, tribus spiralium gemmularum ordinibus arcte et regulariter praeditis, ordine medio minorum, superficie hic illic castaneo-tessellato, ultimo circa basin bilirato; apertura parva, semicirculari, canali conspicuo, brevi, recurvo.*

Long. 11, lat. 2.25 mm. (sp. max.).

Hab. Persian Gulf, Mussandam, 55 fathoms.

A rare species, very gracefully attenuate, many (20 or more) whorled, the apical being five in number, ochreous-brown and finely cancellate in young specimens, but soon getting worn, the remainder slightly impressed suturally, with three spiral bands of gemmuled nodules, those on either side of the sutures being the largest and most pronounced, the median row smaller; the body-whorl has but three gemmuled rows in all the examples we have examined, the fourth row, at the periphery, being a simple ridge. The colour is ashy-white, flecked with pale chestnut dashed over the whorls at certain intervals. Mouth small proportionately, semicircular; peristome thin, canal short, recurved.

Translation of the Latin text. Graceful light fusiform shell, slender, ash-grey; up to 20 whorls, of which 5 belong to the apex which is pale brown, smooth; the next whorls are finely cancellate and ochraceous brown; the others nearly straight, impressed at the sutures, with three spiral cords of regular gemmulated nodules, the middle one smaller; surface with brown spots, last whorl with two cords around the base; small semicircular aperture, remarkable, short bent anterior siphonal canal.

The largest specimen is 11 mm high, 2.25 mm wide.

Diagnosis. The studied syntype is 4 mm high. Shell conical, with nine teleoconch flat whorls with two main spiral cords with tubercles at the intersection with slightly prosocline axial ribs. A third fine thread appears around half teleoconch height between the two main cords and becomes a fully developed tuberculated cord only on the last whorl. A very fine smooth suprasutural cord is also visible and becomes a fully developed tuberculated cord on the last whorl too. The peristome is regrown after breakage in the syntype but the posterior sinus appears shallow. The siphonal canal is short. The base bears a fifth smooth cord. The protoconch is incomplete in the syntype but clearly multispiral. The last three whorls bear two main spiral keels and axial riblets. The teleoconch has a white background with orange-brown blotches. Siphonal canal and protoconch brown.

Remarks. There is a major discrepancy in size between this syntype (4 mm) and what stated in the original description (11 mm). Only the study of other syntypes will clarify the real identity of this taxon, because there are several species with this colour pattern which can be easily mixed together.

Species described by J.C. Melvill and R. Standen

James C. Melvill and Robert Standen described two species of Triphoridae: *T. excelsior* Melvill & Standen, 1899 and *T. idoneus* Melvill & Standen, 1901. Types of both species are present in the NHMUK. Because additional syntypes are present in the NMW and MSIM (Trew 1987), we refrain from selecting any lectotypes pending their inspection.

Triforis (*Ino*) *excelsior* Melvill & Standen, 1899

Figure 70

Triforis (*Ino*) *excelsior* Melvill and Standen 1899: 166, pl. 10, fig. 5.

Type locality. Torres Strait.

Type material. Syntypes: NHMUK 1899.2.23.18, 1 specimen, Torres Strait. Syntypes: NMW 1955.158.204, 1 specimen, Torres Strait and MSIM, 4 specimens, Torres Strait (fide Trew 1987; not seen).

Original description. *T. testa producta, multum attenuata, angusta, brunnea, hic illic rufo-maculata; anfractibus quinque- vel sex-et-viginti, tornatis, apud suturas elevatis, transversim arcte tricarinatis, laevibus; carina infra, juxta suturas, minore, duabus alteris magis conspicuis, interstitiâ interveniente planata, ultimo anfractu quadricarinato, carina bina ad peripheriam addita; apertura rotunda, parva, canali breviter recurvirostri, in uno specimine pone aperturam ipsam clausa. Long. 30, lat. 5 (sp. maj.) mm.*

Four or five, mostly imperfect, examples. The form is much acuminate and attenuate, narrow; colour light brown, here and there indistinctly flecked with rufous

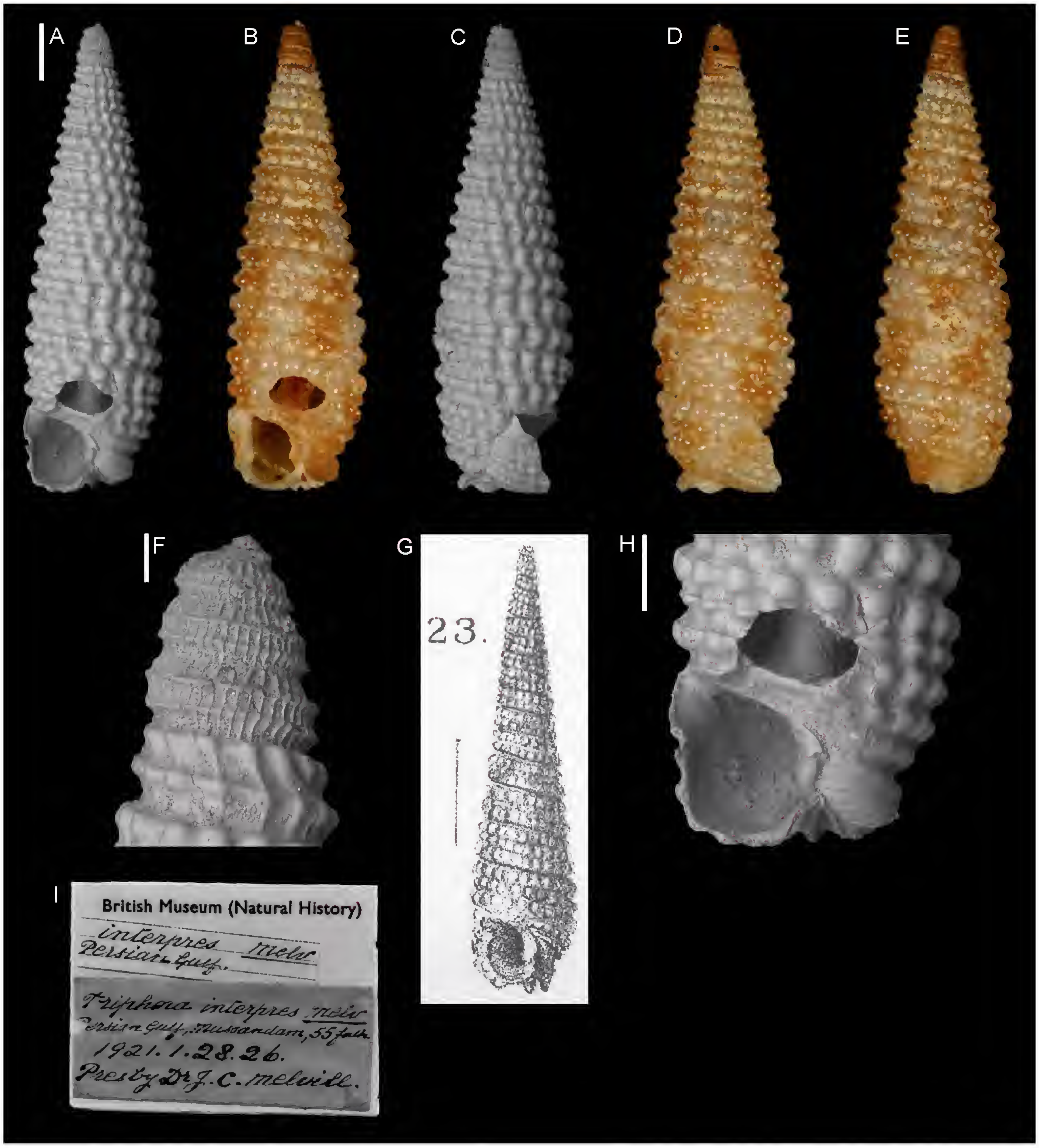

Figure 69. *Triphora interpres* Melvill, 1918, Musandam, Oman. **A–F, H** Syntype NHMUK 1921.1.28.26: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F**), aperture (**H**). **G** Original figure. **I** Original label. Scale bars: **A–E**: 0.5 mm; **F**: 0.1 mm; **H**: 0.3 mm.

spotting; whorls 25 or 26, tornate, smooth, elevated at the sutures, closely thrice-keeled transversely, the keel just below the sutures is smaller and less conspicuous than the two lower, the last whorl is four-keeled, there being two on the periphery; the aperture is roundish, small; in one (the most perfect) specimen the recurved and beaked canal is closed with shelly matter behind the aperture.

The only species to which, in size, this very conspicuous *Triforis* could be referred is *T. gigas*, Hinds, also occurring in the same localities. The sculpture, as seen by the above description, is however totally different, being smooth, with no interstitial pitting or gemmuled ribs of any kind. Owing to no one specimen being in a state of absolute perfection, we have been compelled to estimate the number of whorls and the dimensions generally with

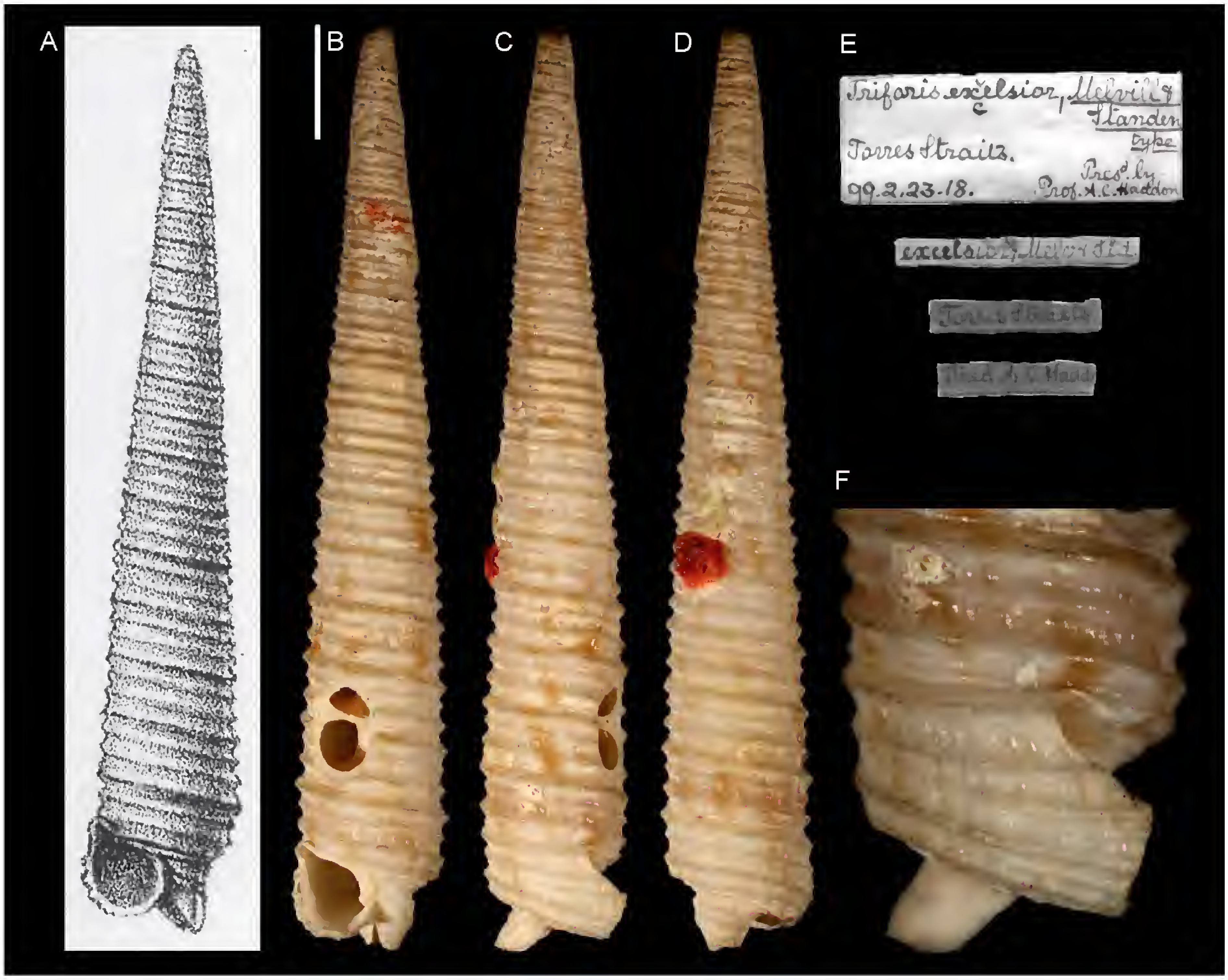

Figure 70. *Triforis excelsior* Melvill & Standen, 1899, NHMUK 1899.2.23.18, Torres Strait. **A** Original figure. **B–D, F** Syntype: front (**B**), side (**C**), back (**D**), peristome (**F**). **E** Original labels. Scale bar: **B–D**: 3 mm.

the aid of two or more examples, each complete in some one particular.

Translation of the Latin text. Much acuminate and slender narrow shell, brown in colour with reddish spots; twenty-five or twenty-six elegant whorls, elevated at the sutures, with three spiral keels; the keel just below the suture is smaller and less conspicuous than the other two, interspaces flat; the last whorl is four-keeled, a double keel is present at the periphery; the aperture is roundish, small; the bent and beaked anterior siphonal canal in one specimen is closed with shelly matter behind the aperture. The largest specimen is 30 mm high and 5 mm wide.

Diagnosis. Syntype 24 mm high. Shell narrowly pyramidal, very slender with 22 whorls bearing three smooth spiral cords, the second being smaller than the others. A fourth smooth suprasutural spiral cord is visible. Between the main cords, there are prosocline axial riblets. The peristome is a bit broken in the syntype, but clearly bears additional spiral cords. Base with a fifth smooth spira cord. Siphonal canal long. Apex missing. Teleoconch whitish with few small brown blotches.

Triforis idoneus Melvill & Standen, 1901

Figure 71

Triforis idoneus Melvill and Standen 1901: 376, pl. 22, fig. 17.

Type locality. Linjah Anchorage (Iran).

Type material. Syntypes: NHMUK 1901.12.9.219, 1 specimen, Linjah, Iran.

Original description. *T. testa anguste fusiformi, solida, calcareo-alba; anfractibus forsan quatuordecim, quorum apicales ...?, caeteris (undecim) omnino regulariter spiraliter triseriatis, cancellatis, suturaliter impressis, ad juncturas nodulifero-gemmatis, nodulis regularibus, rectis, ultimo anfractu serie quarta praedito; apertura ovata; columella crassa; canali brevi, paullulum recurvo.*

Long. 10, *lat*. 2.50 mm.

Hab. Linjah Anchorage, 5 fathoms.

This *Triforis*, distinguished by its uniform chalky whiteness and regular rows of gemmuled cancellations, coarse, uniform, three-ranked on all the upper whorls, four on the body-whorl, is of a graceful shape and fairly sized. It is unfortunate that all the specimens we have examined are without the apical whorls.

Translation of the Latin text. Narrow fusiform shell, solid, chalky white; probably fourteen whorls, apical …?, others (eleven) with three regular spiral cords, cancellated and impressed sutures, noduliferous in their junction, straight regular nodules, last whorl with four rows; ovate aperture; thick columella; slightly recurved short anterior siphonal canal.

Height 10 mm, width 2.50 mm.

Diagnosis. Syntype 10.4 mm high. Shell conical, with 13 whorls bearing three spiral cords with tubercles at the intersection with orthocline axial ribs. The second cord appears later on the teleoconch and attains full size only on the penultimate whorl. A thin smooth suprasutural spiral cord is also visible and attains full size on the base which has a fifth smooth spiral cord too. The peristome is missing, the siphonal canal appears moderately long. The protoconch is missing. The shell is whitish to yellowish but is very worn and colours may have faded away.

Remarks. The original description refers to several specimens found, of which only this one has been located so far. The study of more syntypes would be precious to unambiguously identify this species: Melvill and Standen described "three-ranked on all the upper whorls", but the syntype has the second spiral cord developing later along the teleoconch.

Species described by W.H. Pease

William H. Pease described 25 species of Triphoridae. He often sent shells to Hugh Cuming in London for identification; as a consequence of this correspondence, the types of eight species from the Hawaiian Islands are stored in the NHMUK (Kay 1965): *T. affinis*, *alternata*, *cingulifera*, *clavata*, *flammulata*, *fucata*, *incisa*, and *triticea*, all Pease, 1861. The types of most of the other species are stored in the MCZ (Johnson 1994), but those of two species, *T. cylindricus* and *punctatus*, have not been located so far. The species here treated were described in volume 28 (1860) of the Proceedings of the Zoological Society of London but the actual year of publication is 1861 (Duncan 1937; Dickinson 2005). Pease rarely specified the number of specimens studied to describe the new species. Therefore, it is not straightforward to establish the status of "holotype" as done by Kay (1965), when apparently a single specimen has been located so far.

Triphoris affinis Pease, 1861

Figure 72

Triphoris affinis Pease 1861: 434, not illustrated.

Type locality. "Sandwich Islands" (Hawaiian Islands).

Type material. Lectotype: NHMUK 1962808 (coll. H. Cuming) (lectotype selection by inference of holotype by Kay (1965)).

Original description. Shell elongately turreted, shining; whorls composed of three regular-sized rows of granules; canal short, tubular. Colour reddish brown.

Diagnosis. Lectotype 6.4 mm high. Shell conical with flat whorls. Teleoconch of 13 whorls with three tubercled spiral cords of which the first is weaker on the very first whorls. A very fine smooth suprasutural cord is also visible on the lower whorls. Almost orthocline axial ribs intersect the spiral cords to form the tubercles. Fine growth striae are visible in the interspaces. The last whorl has a fourth spiral cord between the second and the third. The peristome is broken. The siphonal canal is very short. The base has three smooth additional spiral cords. The holotype protoconch is clearly multispiral with at least three whorls, but it is apically very worn and thus it is difficult to precisely quantify the number of whorls. The last two are ornamented by two spiral keels and axial riblets. The shell is brown.

Remarks. This name is preoccupied by *T. affinis* Hinds, 1843. Therefore, Jousseaume (1884) introduced a new name, *Mastonia peasi*.

Triphoris alternata Pease, 1861

Figure 73

Triphoris alternata Pease 1861: 434, not illustrated.

Type locality. "Sandwich Islands" (Hawaiian Islands).

Type material. Lectotype: NHMUK 1962816, designated by Kay (1965) (coll. H. Cuming). Paralectotypes: NHMUK 1962817, 2 specimens (see Remarks), Hawaiian Islands (coll. H. Cuming).

Original description. Shell turreted; whorls composed of three regular-sized rows of granules, the middle one of dark reddish brown, the remaining two of a waxy-yellow colour; base longitudinally striated; canal closed, tubular.

Diagnosis. Lectotype 6.2 mm high. Shell slightly cyrtoconoid, with very flat whorls. Teleoconch of ten whorls with three spiral cords bearing tubercles at the intersection with slightly prosocline axial ribs. The second cord develops later on the fifth whorl. Very fine growth lines are visible all along the shell. Peristome partly broken in

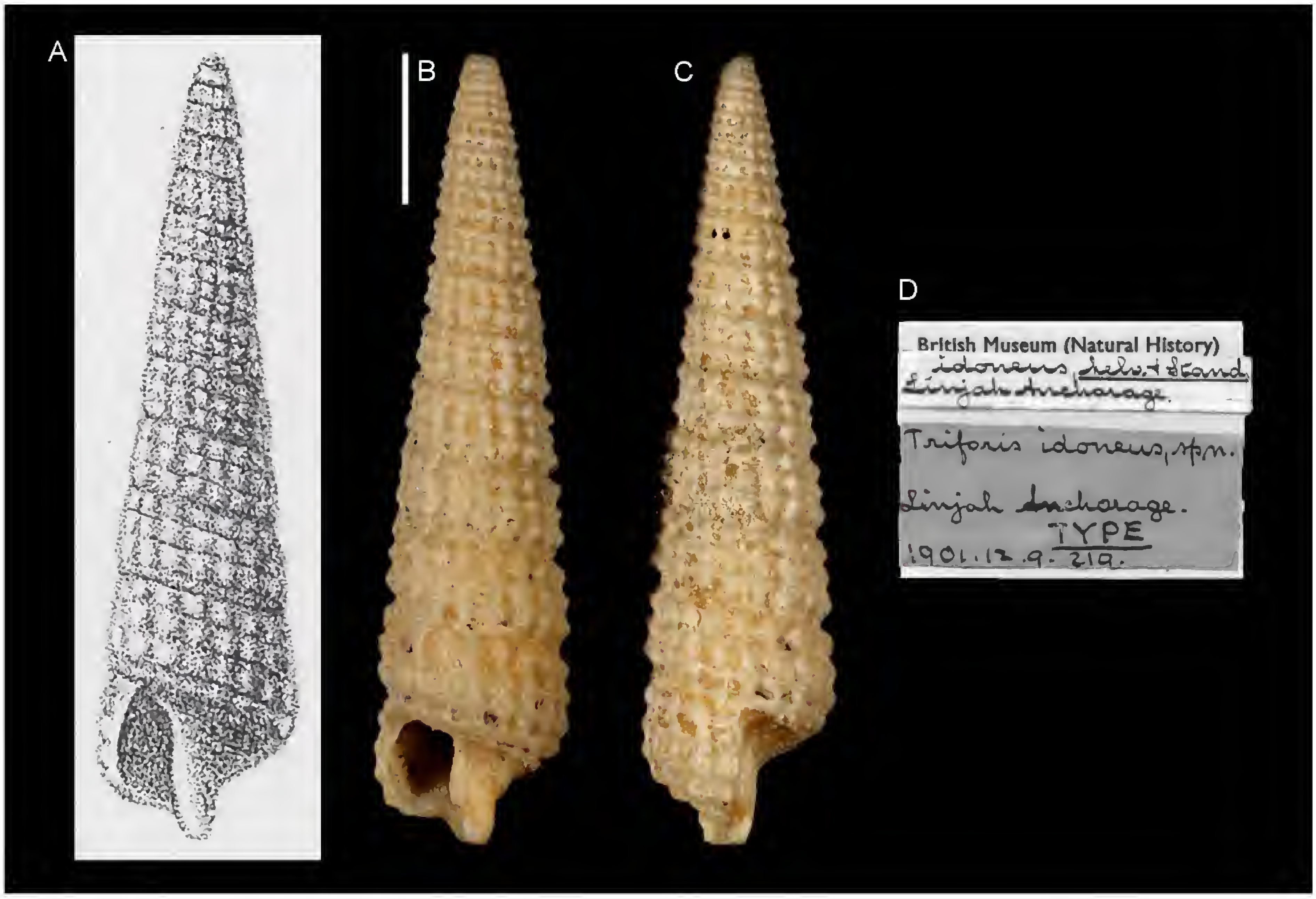

Figure 71. *Triforis idoneus* Melvill & Standen, 1901, Linjah, Iran. **A** Original figure. **B, C** Syntype NHMUK 1901.12.9.219: front (**B**), side (**C**). **D** Original labels. Scale bar: **B, C**: 2 mm.

the type specimens, but it apparently bears at least one additional spiral cord between the second and the third. Siphonal canal short. The base has a fourth weakly tubercled spiral cord and two more smooth ones. The apex is missing in the type series. The teleoconch has the first spiral cord very light brown, the second and the third brown and the interspace in between dark brown. The last whorl is very light brown with three distinct dark brown spiral stripes.

Remarks. Lot NHMUK 1962817 contains two specimens. Both were listed as paralectotypes by Kay (1965), but they actually represent two species. The second (Fig. 73K) can be easily distinguished from *T. alternata* by its colour pattern (the first spiral cord and not the second is dark brown), the more numerous axial ribs and smaller tubercles. *Triphoris alternata* is a junior homonym of *T. alternatus* C.B. Adams, 1852 (ICZN 1999, Article 57). Therefore, Pease (1868) introduced *Triphoris bicolor* Pease, 1868 as a replacement name. A specimen with this name labelled as "holotype" is reported for the MCZ (50057). Jousseaume (1884) also later introduced *Mastonia harperi* to replace *T. alternata*.

Triphoris cingulifera Pease, 1861

Figure 74

Triphoris cingulifera Pease 1861: 434, not illustrated.

Type locality. "Sandwich Islands" (Hawaiian Islands).

Type material. Lectotype: NHMUK 1962812, designated by Kay (1965) (coll. H. Cuming). Paralectotypes: NHMUK 1962813, 4 specimens (see Remarks), Hawaiian Islands (coll. H. Cuming); MCZ 50056, 4 specimens, Hawaiian Islands; MCZ 50076, 1 specimen, Hawaiian Islands (see Remarks); MCZ 73737, 25 specimens, Hawaiian Islands.

Original description. Shell subulate; whorls about ten, ornamented by a row of granules at both margins, interstices concavely rounded, with a raised stria at the upper side, last whorl with three granulose ribs; canal short and tubular. Colour waxy-yellow, lower row of granules and ribs on last whorl purplish-red.

Diagnosis. Lectotype 5.6 mm high. Shell cyrtoconoid with flat whorls. Teleoconch of nine whorls bearing three spiral cords. The second develops later and remains much thin-

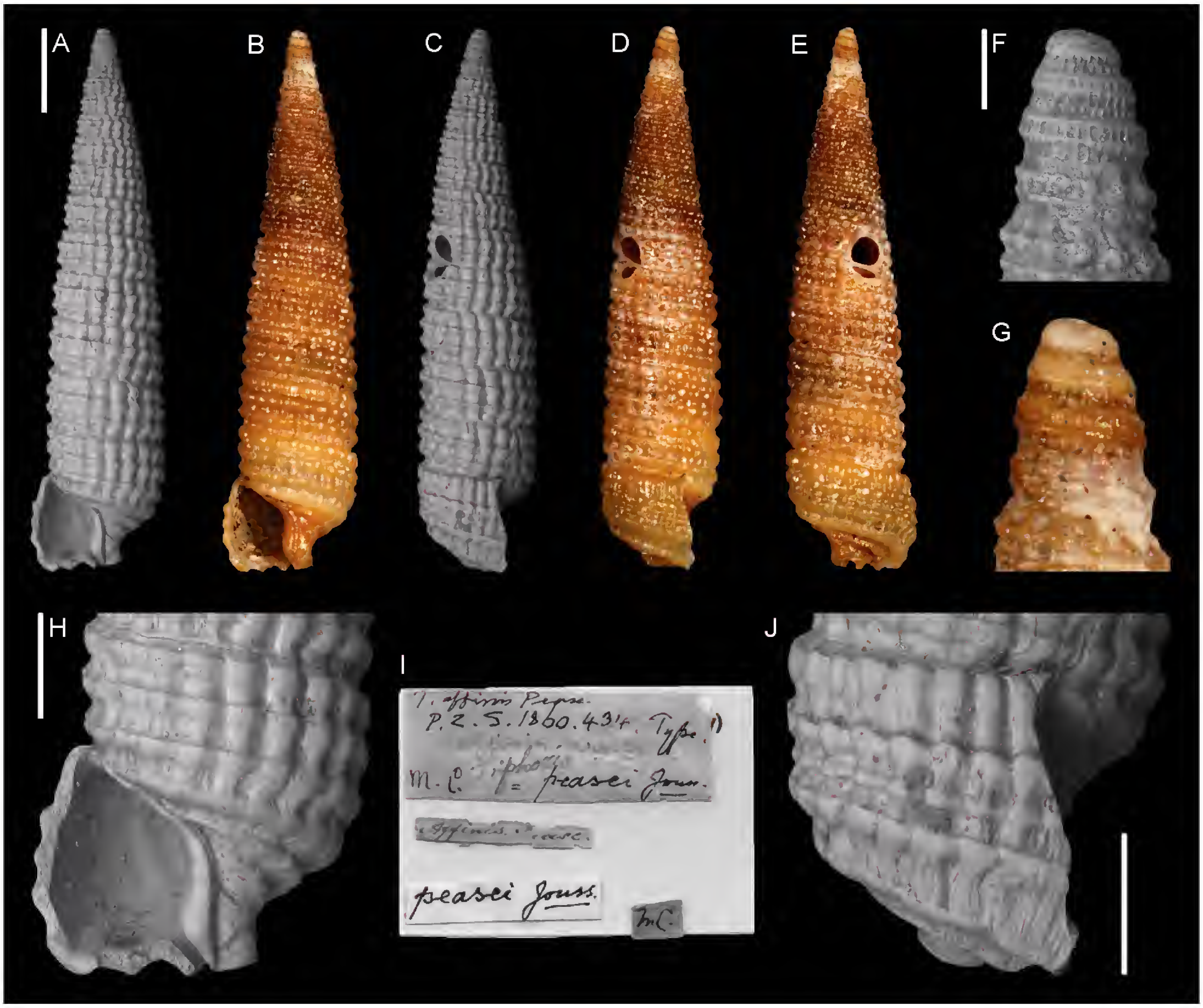

Figure 72. *Triphoris affinis* Pease, 1861, Hawaiian Islands, coll. H. Cuming. **A–H, J** Lectotype NHMUK 1962808: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, G**), aperture (**H**), peristome (**J**). **I** Original labels. Scale bars: **A–E**: 1 mm; **F, G**: 0.2 mm; **H, J**: 0.5 mm.

ner than the others all along the teleoconch. These cords bear tubercles and the intersections with the prosocline axial ribs. Growth lines are visible, especially between the ribs. The peristome bears numerous additional spiral cords and a deep posterior sinus. Siphonal canal relatively long. The base has a fourth tubercled spiral cord and two smoother ones. The apex is missing in the lectotype. The teleoconch background colour is yellowish-brown, the third, fourth and fifth spiral cord are dark brown.

Remarks. MCZ 50056 is erroneously identified as the holotype in the MCZ ledger and in the online catalogue. Pease (1861) did not specify on how many specimens he based his description, but the multiple specimens in the H. Cuming collection suggest that he had more than one on which he based the description. Thus, the "holotype" remark in the MCZ ledger has no support and Kay's (1965) lectotype designation should be regarded as valid. Kay (1965) listed seven paratypes in lot 1962813, but only four are currently present (as also noted by Kathie Way in 1983 on labels accompanying the shells).

Triphoris clavata Pease, 1861

Figure 75

Triphoris clavata Pease 1861: 434, not illustrated.

Type locality. "Sandwich Islands" (Hawaiian Islands).

Type material. Lectotype: NHMUK 1962814, designated by Kay (1965) (coll. H. Cuming). Paralectotype: NHMUK 1962815, 1 specimen, Hawaiian Islands (coll. H. Cuming).

Original description. Shell elongate subulate; whorls fifteen to eighteen, bordered on each side by a row of granules, interstices concavely rounded, finely striated

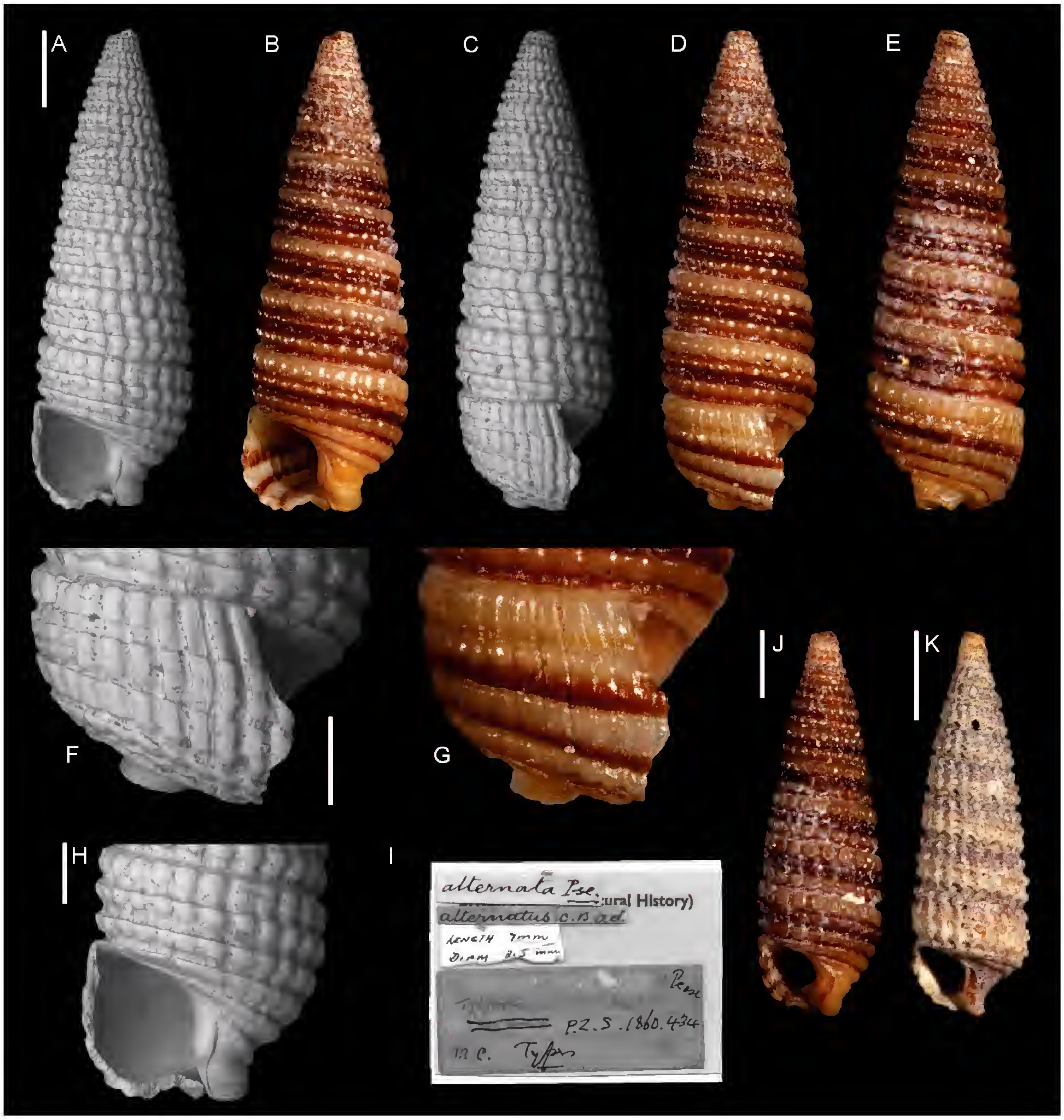

Figure 73. *Triphoris alternata* Pease, 1861. **A–H** Lectotype NHMUK 1962816, Hawaiian Islands (coll. H. Cuming): front (**A, B**), side (**C, D**), back (**E**), peristome (**F, G**), aperture (**H**). **I** Original labels. **J** Paralectotype, NHMUK 1962817, Hawaiian Islands (coll. H. Cuming): front. **K** *Triphora* sp., NHMUK 1962817, Hawaiian Islands (coll. H. Cuming): front. Scale bars: **A–E, J, K**: 1 mm; **F–H**: 0.5 mm.

spirally, and bordered against the upper row of granules by a light ridge, obsoletely granulose; canal slightly recurved. Colour white or yellowish, interstices between the granules of a purplish or reddish brown, and spotted irregularly with the same.

Diagnosis. Lectotype 7.3 mm high. Shell weakly cyrtoconoid with flat whorls. Apical whorls broken off. The remaining eight whorls bear two strong spiral cords and a weaker one in second position which develops around mid-shell height. The cords bear tubercles at the interstices with prosocline axial ribs. A fine smooth suprasutural cord is also visible. Numerous very fine spiral cords are present in the interspaces of the main cords. The peristome is partly broken but likely bears weak additional spiral cords. The posterior siphonal sinus is deep and roundish. Siphonal canal rather long. The base has two additional tubercled spiral cords. The protoconch is missing. The shell has a whitish background colour with an orange-brown spiral band between the two main spiral cords with occasional darker blotches.

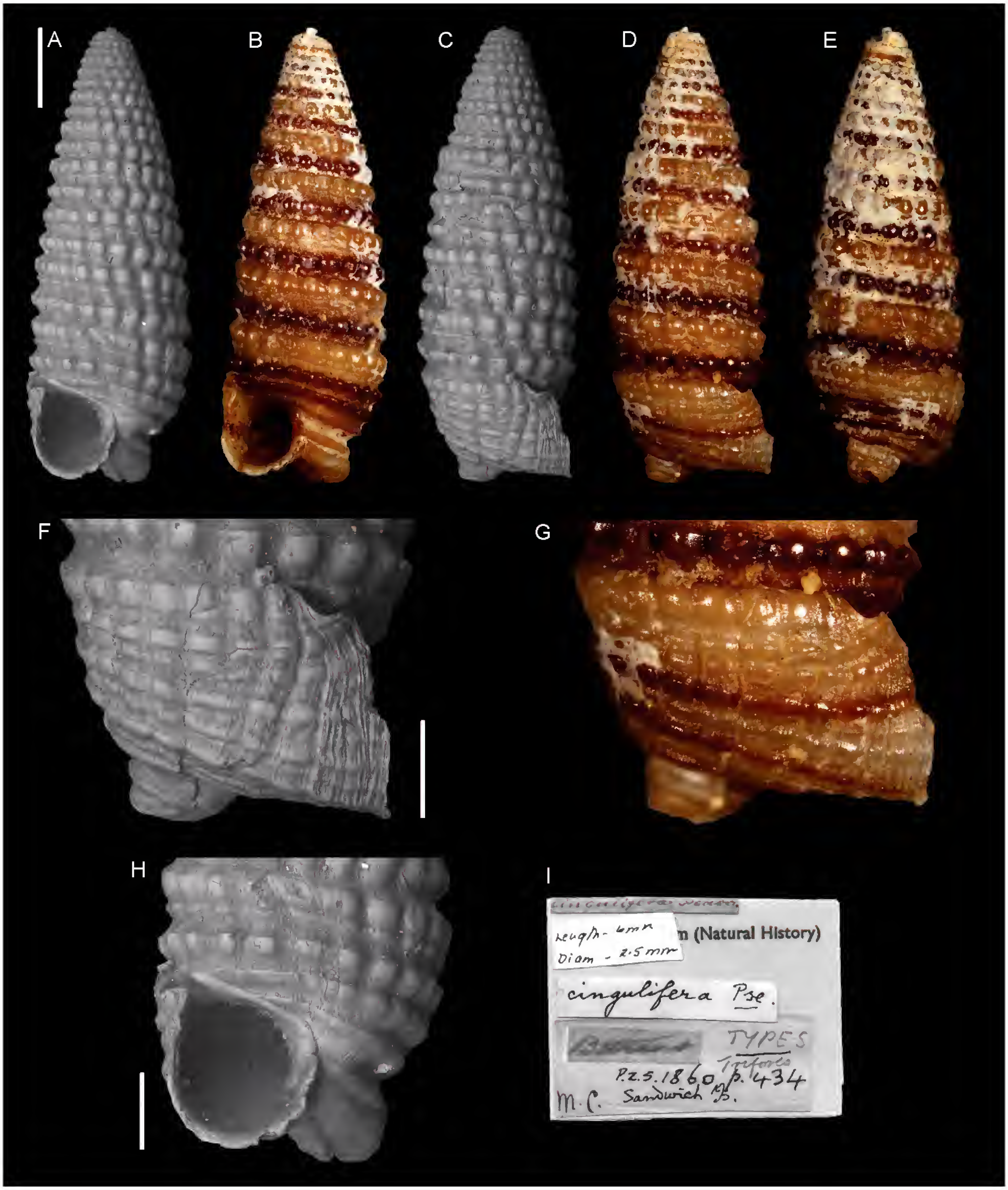

Figure 74. *Triphoris cingulifera* Pease, 1861, Hawaiian Islands, coll. H. Cuming. **A–H** Lectotype NHMUK 1962812: front (**A, B**), side (**C, D**), back (**E**), peristome (**F, G**), aperture (**H**). **I** Original labels. Scale bars: **A–E**: 1 mm; **F–H**: 0.5 mm.

Triphoris flammulata Pease, 1861

Figure 76

Triphoris flammulata Pease 1861: 434, not illustrated.

Type locality. "Sandwich Islands" (Hawaiian Islands).

Type material. Lectotype: NHMUK 1961175, designated by Kay (1965) (coll. H. Cuming). Paralectotypes: NHMUK 1961176, 3 specimens (see Remarks), Hawaiian Islands (coll. H. Cuming).

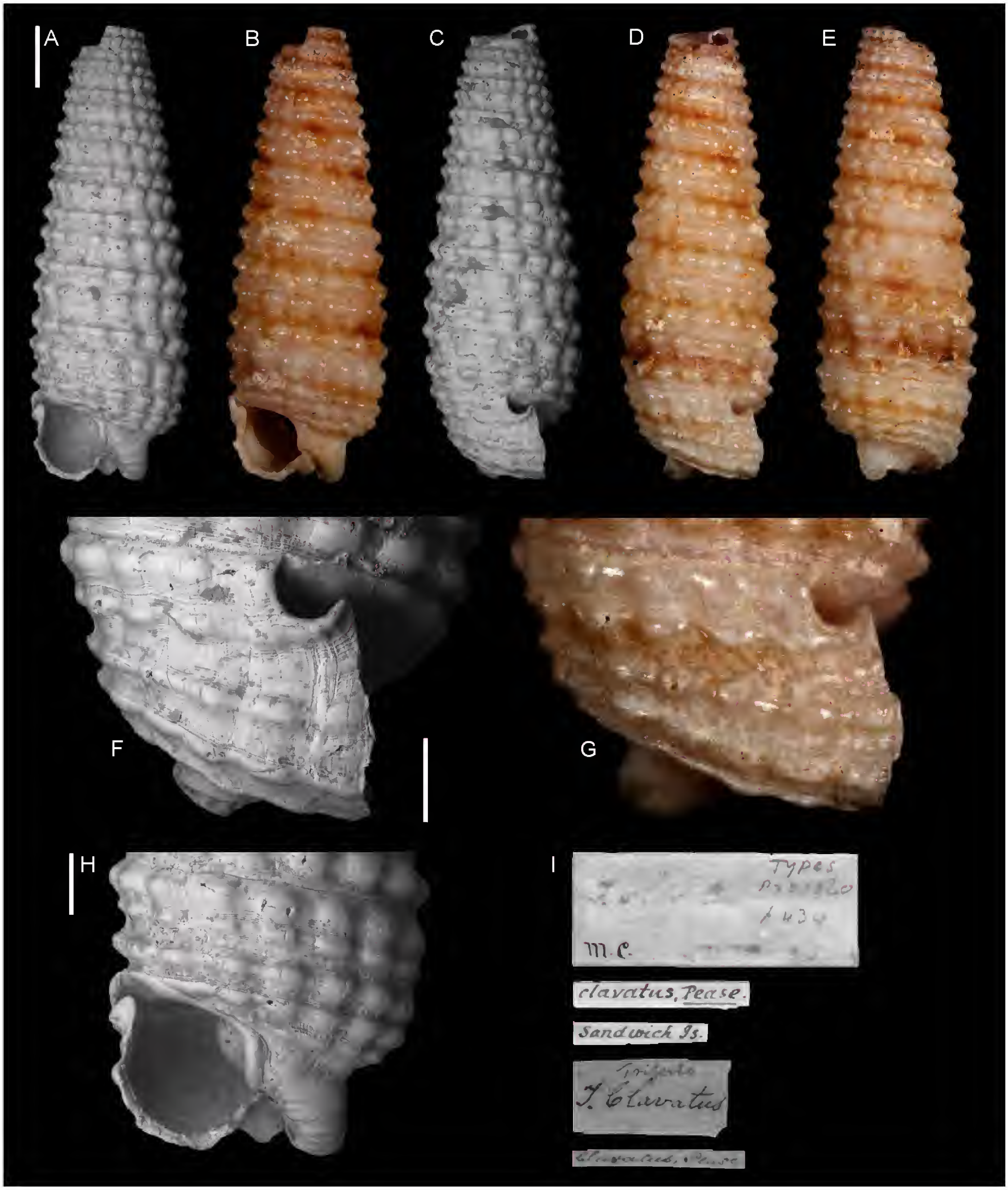

Figure 75. *Triphoris clavata* Pease, 1861, Hawaiian Islands, coll. H. Cuming. **A–H** Lectotype NHMUK 1962814: front (**A, B**), side (**C, D**), back (**E**), peristome (**F, G**), aperture (**H**). **I** Original labels. Scale bars: **A–E**: 1 mm; **F–H**: 0.5 mm.

Original description. Shell elongately pyramidal; whorls twelve to fourteen, spirally carinately ribbed, ribs three, central one much the smallest, a rib of same size at the sutures; canal tubular, enclosed. Colour white, marked with spots and longitudinal flammules of light yellowish-brown.

Diagnosis. Lectotype 13.5 mm high. Shell conical with flat whorls. Apical part of the lectotype broken off, the visible teleoconch has 14 whorls with three very weakly tubercles to smooth spiral cords. The second cord develops near mid-shell height and remains small until the last whorl. A fine smooth suprasutural cord is slightly visible.

Growth lines are visible in the interspaces. The peristome shows a posterior sinus and additional spiral cords. The base has three more weakly tubercled spiral cords. Protoconch missing. Teleoconch background colour white with brown flammulae, siphonal canal brown.

Remarks. Kay (1965) reported four paralectotypes in lot NHMUK 1961176, but only three are now present. A 9 mm specimen that was measured by Kay is missing, as also noted by Kathie Way in 1983 on labels accompanying the lot.

Triphoris fucata Pease, 1861

Figure 77

Triphoris fucata Pease 1861: 433–434, not illustrated.

Type locality. "Sandwich Islands" (Hawaiian Islands).

Type material. Lectotype: NHMUK 1961171, designated by Kay (1965) (coll. H. Cuming). Paralectotypes: NHMUK 1961172, 1 specimen (see Remarks), Hawaiian Islands (coll. H. Cuming), MCZ 73736, 1 specimen, Hawaiian Islands.

Original description. Shell elongate subulate; whorls sixteen to eighteen, with three granulose ribs and one much smaller at the suture; base subplanulate; canal short and recurved. Colour white, spotted irregularly with brown.

Diagnosis. Lectotype 9.5 mm high. Very elongated shell with flat whorls. Apical part broken off. The 17 visible teleoconch whorls have three spiral cords with tubercles and the intersections with slightly prosocline axial ribs. The second spiral cord appears later on the fourth teleoconch whorl. A suprasutural smooth cord is also clearly visible as well as numerous very fine spiral threads between the main cords. The posterior sinus is tubular and prominent. The peristome has additional spiral cords. The siphonal canal is long. The profile of the last whorl at the base is very angulated. The base has no additional cords after the fourth tubercled cord. Protoconch missing. Teleoconch background colour whitish with orange-brown blotches in the first shell half.

Remarks. Lot NHMUK 1961172 contains two fragments, probably belonging to the single specimen reported by Kay (1965). This species is very similar to *T. concors* Hinds, 1843 (page 193). The lack of protoconchs impedes a final decision on the synonymy between these two entities.

Triphoris incisa Pease, 1861

Figure 78

Triphoris incisa Pease 1861: 434, not illustrated.

Type locality. "Sandwich Islands" (Hawaiian Islands).

Type material. Lectotype: NHMUK 1961151, designated by Kay (1965) (coll. H. Cuming). Paralectotypes: NHMUK 1961152, 5 specimens, Hawaiian Islands (coll. H. Cuming), MCZ 73738, 12 specimens, Hawaiian Islands.

Original description. Shell subulate; whorls encircled by three prominent smooth and regular ribs, interstices deep and very finely striated longitudinally, irregularly spotted and marbled with yellowish-white, brown, and purple of various shades.

Diagnosis. Lectotype 15.7 mm high. Shell slightly cyrtoconoid with flat whorls. Apical part broken off but the visible teleoconch (likely almost complete) has 15 whorls with three smooth spiral cords. The second develops later in the first whorls. The very first whorls have distinct tubercles on the cords. A smooth suprasutural cord is also clearly visible as well as growth lines between the cords. The peristome has additional spiral cords and a rather deep posterior sinus. The siphonal canal is long. The base has a fourth, fifth, sixth (narrow) and seventh spiral cord of which the fourth and the fifth are slightly tubercled, the others are smooth. Protoconch missing. Teleoconch brown, with the exception of the very first three whorls which are whitish to yellowish. The third spiral cord is usually lighter in colour. Small white blotches are randomly present on cords.

Triphoris triticea Pease, 1861

Figure 79

Triphoris triticea Pease 1861: 433, not illustrated.

Type locality. "Sandwich Islands" (Hawaiian Islands).

Type material. Lectotype: NHMUK 1962807 (coll. H. Cuming) (lectotype selection by inference of holotype by Kay (1965)).

Original description. Shell minute, fusiformly ovate, ornamented throughout by spiral rows of regular-sized granules; aperture oval and in a line with the axis of the shell, lip slightly recurved and thickened (plicate on the inner side?); canal posterior, enclosed, tubular. Colour dark purplish-red, granules dusky white.

Diagnosis. Holotype 2.7 mm high. Shell cyrtoconoid, rather broad with flat whorls. The apex is broken off but the teleoconch (likely complete) has seven whorls with two spiral cords with large tubercles at the intersections with slightly opisthocline axial ribs. Growth lines are occasionally visible. The peristome has a deep posterior sinus and an additional tubercled spiral cord developing in second position on the last half of the last whorl. The siphonal canal is very short. The base has three additional tubercled spiral cords. The protoconch is missing. Teleoconch background colour dark brown, except the first two-three whorls which are yellowish. Tubercles progressively lighter along the shell until becoming pearl-grey on

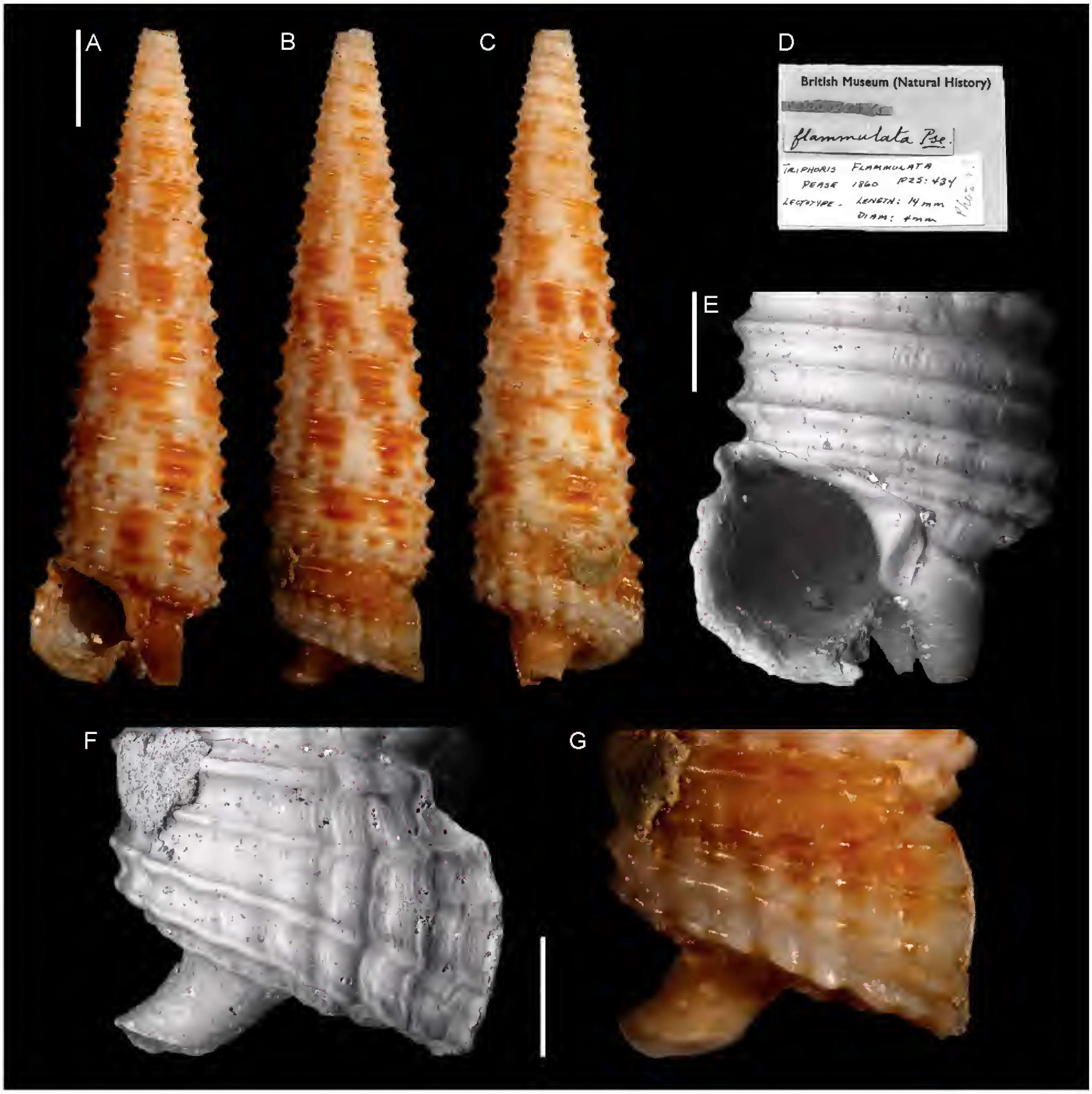

Figure 76. *Triphoris flammulata* Pease, 1861, Hawaiian Islands, coll. H. Cuming. **A–C, E–G** Lectotype NHMUK 1961175: front (**A**), side (**B**), back (**C**), aperture (**E**), peristome (**F, G**). **D** Original labels. Scale bars: **A–C**: 2 mm; **E–G**: 1 mm.

the last whorl. Interspaces usually darker except on the last whorl whose first spiral cord is entirely white.

Species described by E. Rolán and co-authors

Types of 15 species described by Emilio Rolán and his co-authors Cruz-Abrego, Espinosa, Fernandes, Fernández-Garcés are stored in the NHMUK (Fernández-Garcés and Rolán 1988; Rolán and Fernández-Garcés 1992, 1993, 1994, 1995, 2009; Rolán and Espinosa 1994; Rolán and Cruz-Abrego 1995) and listed in Table 2.

Species described by E.A. Smith

Edgar A. Smith described 14 species of Triphoridae. The types of *Triforis excellens* E.A. Smith, 1903 and *T. recta* E.A. Smith, 1890 have not yet been found in the NHMUK. Because Smith spent his whole career curating the Mollusca collection at the Museum and did not own a private collection, the types of the species he described are thought to be mostly in the NHMUK (Trew 1993). Still, pending any statement by Smith in his works on the number of specimens he examined, we consider them syntypes and select lectotypes when appropriate.

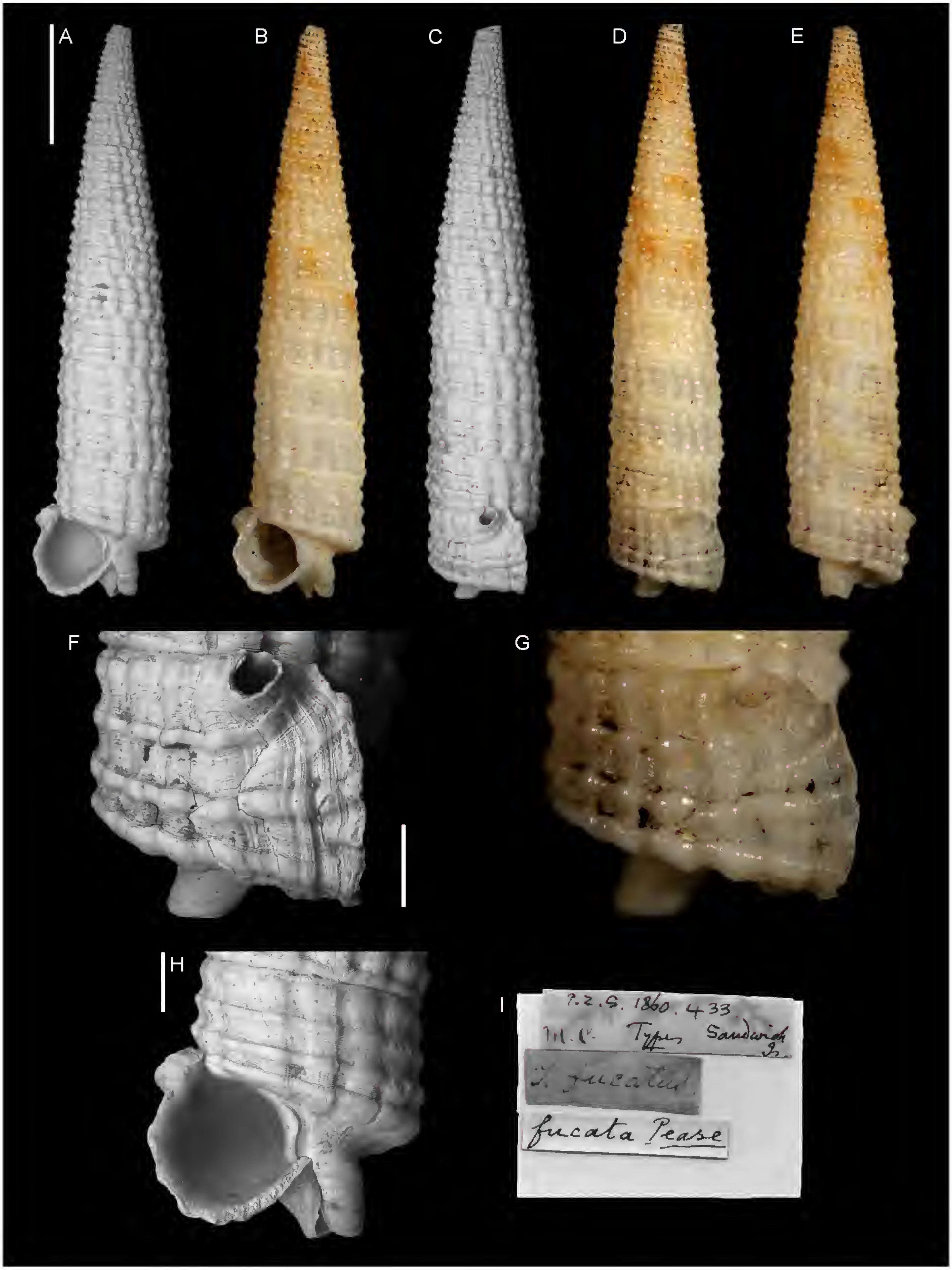

Figure 77. *Triphoris fucata* Pease, 1861, Hawaiian Islands, coll. H. Cuming. **A–H** Lectotype NHMUK 1961171: front (**A, B**), side (**C, D**), back (**E**), peristome (**F, G**), aperture (**H**). **I** Original labels. Scale bars: **A–E**: 2 mm; **F–H**: 0.5 mm

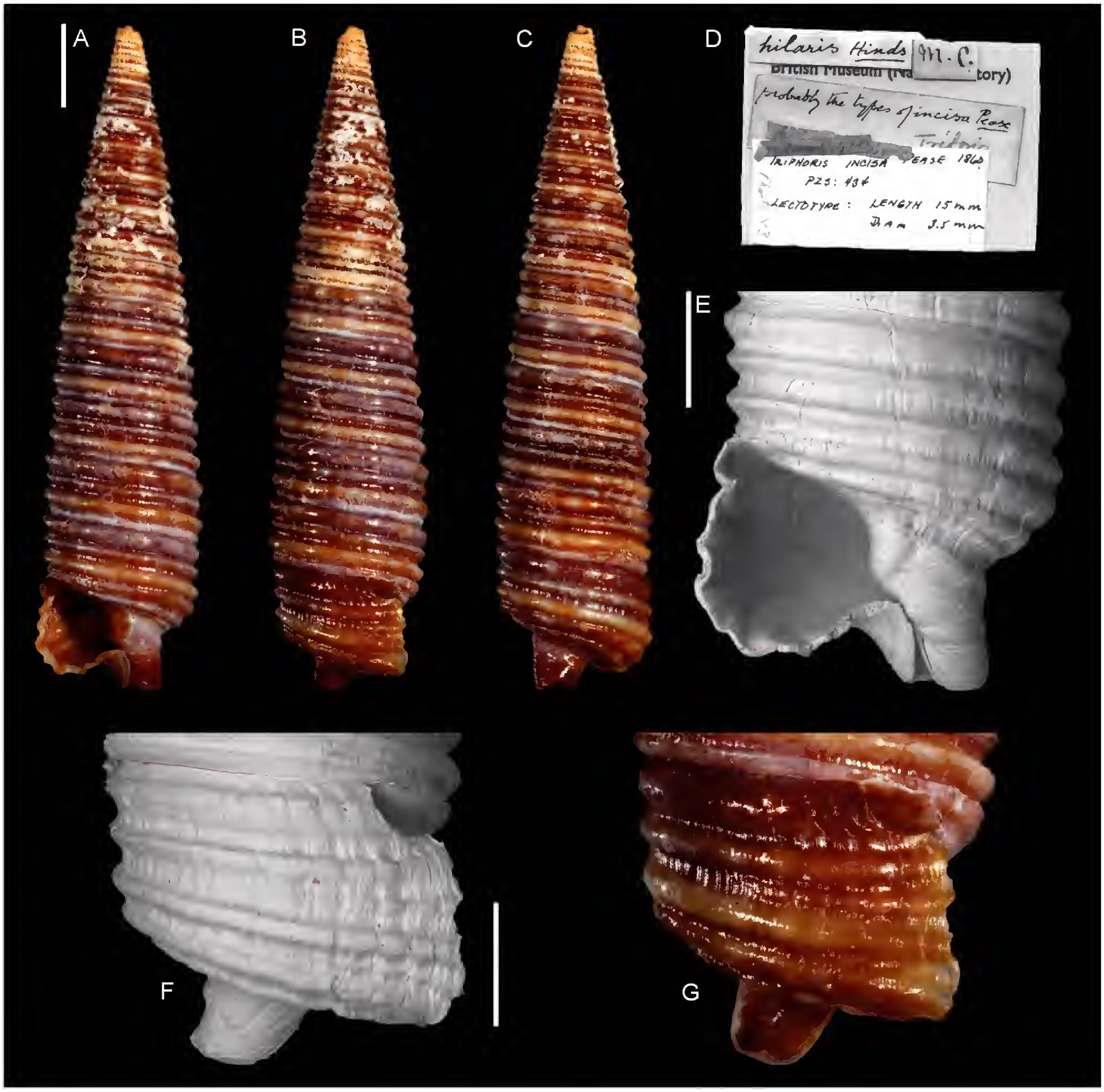

Figure 78. *Triphoris incisa* Pease, 1861, Hawaiian Islands, coll. H. Cuming. **A–C, E–G** Lectotype NHMUK 1961151: front (**A**), side (**B**), back (**C**), aperture (**E**), peristome (**F, G**). **D** Original labels. Scale bars: **A–C**: 2 mm; **E–G**: 1 mm.

Triforis atlantica E.A. Smith, 1890

Figure 80

Triforis atlantica Smith 1890: 292, pl. 21, fig. 26.

Type locality. Saint Helena.

Type material. Lectotype: NHMUK 1889.10.1.1374, designated by Rolán and Fernández-Garcés 2008). Paralectotypes: NHMUK 1889.10.1.1375–93, 18 specimens (two gold coated).

Original description. *Testa haud perelongata, alba, livido-fusco inferne zonata; anfractus 13, anguste turriti, supremi minute cancellati, cateri plani, granulorum seriebus duobus vel tribus cincti, ultimus seriebus quinque, infima minus tuberculata, ornatus; cauda brevis, carina valida instructa, fuscescens; apertura obliqua, ovata, superne canaliculata; peristoma superne leviter incisum, inferne columellae callo crasso junctum.*

Longit. 6 millim., diam. 2

The outlines of this species are a little convex. Only the penultimate and antepenultimate whorls have three distinct rows of granules, and of those the central one is the smallest. The granules of the lowermost series, or rather the interstices between them, are brown and the uppermost series is white.

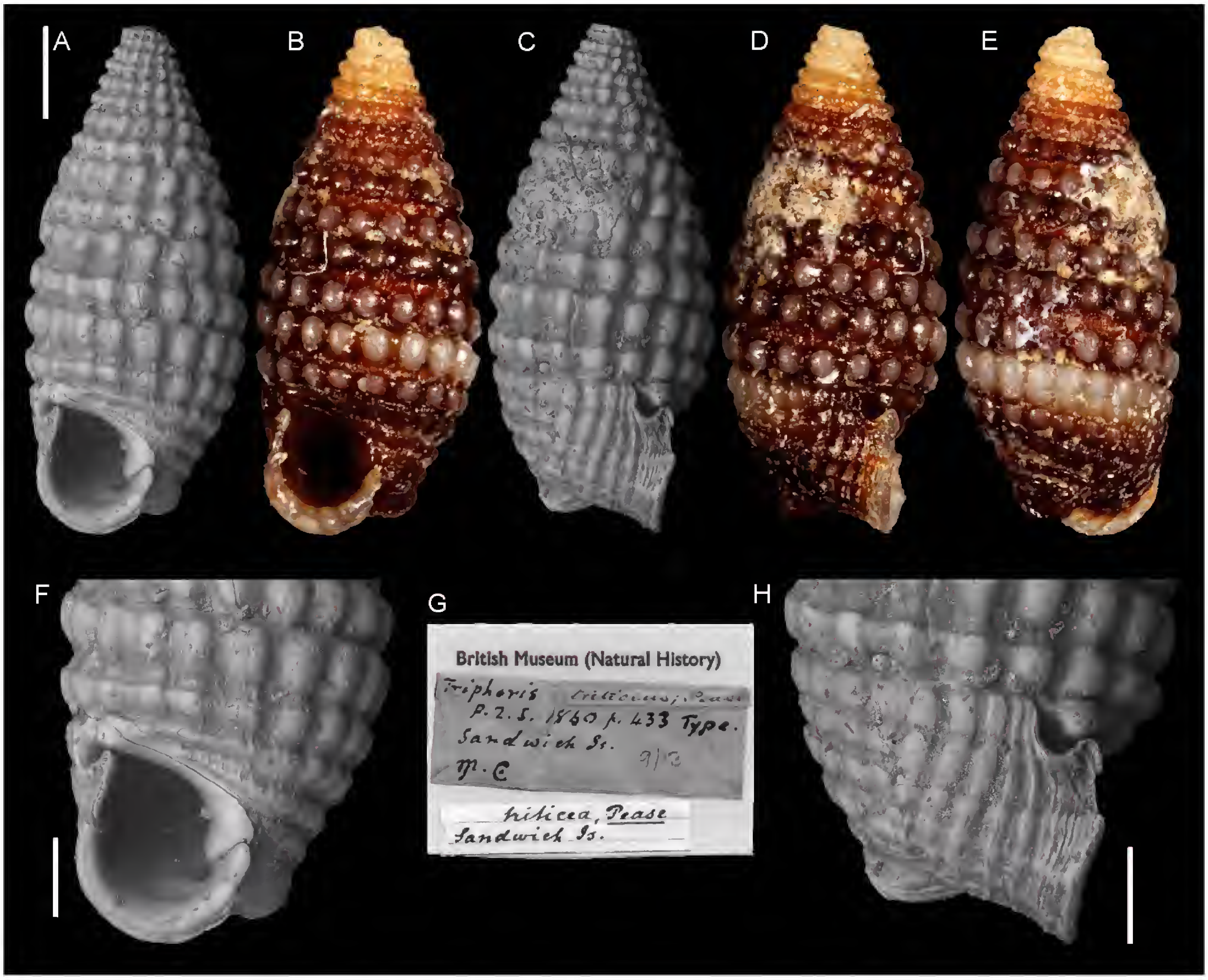

Figure 79. *Triphoris triticea* Pease, 1861, Hawaiian Islands, coll. H. Cuming. **A–F, H** Lectotype NHMUK 1962807: front (**A, B**), side (**C, D**), back (**E**), aperture (**F**), peristome (**H**). **G** Original labels. Scale bars: **A–E**: 0.5 mm; **F, H**: 0.3 mm.

Table 2. List of species described by Rolán and his co-authors Cruz-Abrego, Espinosa, Fernandes, and Fernández-Garcés whose type material is present in the NHMUK at the date of December 31, 2015, in alphabetic order by species name.

Species	Type locality	Inventory number	Number of paratypes
Cheirodonta apexcrassum Rolán & Fernández-Garcés, 1994	Jibacoa, in North of Cuba	1993061	1
Marshallora bubistae Fernández-Garcés & Rolán, 1988	Boavista Is., Cape Verde Archipelago	1988079	2
Iniforis carmelae Rolán & Fernández-Garcés, 1993	Cienfuegos Bay, Cuba	1992134	1
Cheirodonta decollata Rolán & Fernández-Garcés, 1994	Marianao Beach, La Habana, Cuba	1993062	2
Metaxia espinosai Rolán & Fernández-Garcés, 1992	Faro de los Colorados, Cienfuegos Bay, Cuba	1992093	1
Marshallora gutta Fernández-Garcés & Rolán, 1988	Boavista Is., Cape Verde Archipelago	1988081	2
Metaxia incerta Fernández-Garcés & Rolán, 1988	Sal Is., Cape Verde Archipelago	1988077	2
Iniforis immaculata Rolán & Fernández-Garcés, 1993	Cienfuegos Bay, Cuba	1992135	1
Marshallora mariangelae Fernández-Garcés & Rolán, 1988	Boavista Is., Cape Verde Archipelago	1988080	2
Marshallora nichupte Rolán & Cruz-Abrego, 1995	Bojórquez- Nichupté Lagoons, Cancún, Quintana Roo, México	1996045	2
Triphora osclausum Rolán & Fernández-Garcés, 1995	Jibacoa, in North of Cuba	1996051	1
Iniforis pelorcei Rolán & Fernández-Garcés, 2009	Caribbean, Saint Lucia, north of Grenadines Is.	20090255	1
Iniforis pseudothomae Rolán & Fernández-Garcés, 1993	Cienfuegos Bay, Cuba	1992133	1
Isotriphora taenialba Rolán & Espinosa, 1994	Cienfuegos Bay, Cuba	1993060	2
Monophorus verdensis Fernández-Garcés & Rolán, 1988	Boavista Is., Cape Verde Archipelago	1988078	2

Translation of the Latin text. Not very elongated shell, white, inferiorly with a dark brown zone; 13 whorls narrowly turreted, the uppermost minutely cancellated, the other flat with two or three rows of granules, five on the last with the lowest sligtly tuberculated; anterior siphon short, with a strong brownish carina; oblique aperture, ovate, canaliculated above; slightly incised peristome in its upper part, joined below with the large columellar callus.

Height 6 mm, diameter 2 mm.

Diagnosis. Lectotype 4.5 mm high. Shell conical, with flat sides. Teleoconch of nine whorls (but apex missing) with two main spiral cords with tubercles at the intersection with prosocline axial ribs; a third cord develops in between at mid-shell height and attains full size only on the last whorl. Peristome broken and regrown in the lectotype; siphonal canal short. Base with two additional weakly tubercled cords and a smooth third. Protoconch absent in the lectotype, but reported to be multispiral (Rolán and Fernández-Garcés 2008). The first teleoconch whorls are white; the following with a white first and brown second spiral cord (with lighter tubercles). Base brown.

Remarks. Rolán and Fernández-Garcés (2008) erroneously reported the inventory numbers as 1889.10.1.1874–93.

Triforis bathyraphe E.A. Smith, 1890

Figure 81

Triforis bathyraphe Smith 1890: 292, pl. 24, fig. 4.

Type locality. Saint Helena.

Type material. Syntypes: NHMUK 1889.10.1.1413: 1 specimen, Saint Helena.

Original description. *Testa haud perelongata, albida vel pallide fusca; anfractus 11, convexiusculi, sutura profunda sejuncti, liris spiralibus tribus subaequalibus, lirisque longitudinalibus circiter 26 granose cancellati; anfr. ultimus liris sexcinctus; apertura rotunde ovata; labrum tenue, superne ad suturam anguste sinuatum, inferne columellae junctum; cauda brevis, leviter recurva. Longit. 5 ¾ millim., diam. 2.*

This species is peculiar on account of the deep suture and the distinct cancellation of the surface. The whorls, too, are convex, so that the central row of granules are most prominent. It is a much stouter shell than *T. recta* and has a different aperture.

Translation of the Latin text. Not very elongated shell, white or pale dark; 11 slightly convex whorls, separated by a deep suture, with three almost equal spiral cords and about 26 longitudinal tuberculated cancellate lirae; last whorl with six rows; roundish ovate aperture; thin lip with a posterior sinus at the suture, joined with columella on the underside; short slightly recurved anterior siphon.

Height 5¾ mm, diameter 2 mm.

Diagnosis. Syntype 5 mm high. Shell conical with seven slightly convex whorls. The teleoconch with three spiral cords with tubercles at the intersection with almost orthocline axial ribs. A fourth suprasutural smooth cord is visible on the lower whorls. Peristome with no additional spiral cords and an indented posterior canal. Siphonal canal of moderate length. The fourth spiral cord becomes tuberculated on the base which bears two additional weakly tubercled cords. Protoconch apparently paucispiral of two whorls but too worn to observe the sculpture. Shell yellowish.

Triphora burnupi E.A. Smith, 1910

Figure 82

Triphora burnupi Smith 1910: 196, pl. 7, fig. 8.

Type locality. Durban, Natal, South Africa.

Type material. Syntypes: NHMUK 1911.8.30.10: 1 specimen, Durban, South Africa.

Original description. *Testa parva, angusta, subulata, albida circa medium anfractuum linea saturate fusca cincta, et inter gemmules supra liras spirales dilute fusco notata; anfractus 17, superiores quatuor fusci, longitudinaliter tenuiter lirati, tertius et quartus circa medium liris spiralibus duo cincti, quintus ad octavus seriebus gemmarum duabus (serie infima majori) instructi, caeteri liris quatuor inaequalibus ornati, lira infra lineam fuscam distincte gemmata; anfr. ultimus ad peripheriam gemmato-carinatus, infra concavus, lira unica instructus; apertura rotunde piriformis; canalis obliquus, recurvus, praeter extremitatem clausus.*

Longit. 7, diam. 1.5 mm.

Hab.—Durban (H. Burnup).

Of the four lirae upon the later whorls, that below the brown line is the most conspicuous and most distinctly gemmate. The lira or thread above the brown line is the most slender and faintly gemmate, and the lira above that is the least gemmate of all, and exhibits here and there only very faint traces of the light brown dotting which occurs between the gemmules on the other lirae.

Translation of the Latin text. Small, narrow, subulate shell, white with a dark brown line in the middle of the whorls, and marked with light brown between the gemmules on the spiral rows; 17 whorls, upper four brown, slightly lyrate longitudinally, the third and the fourth with two median spiral rows, from the fifth to the eighth two series of gemmules (the lower the greater), other decorated by four unequal lirae, lira under the brown line clearly gemmate; last whorl gemmate-carinated at the periphery, concave at its underside, with only one lira; round pyriform aperture; anterior siphon slanting, curved, closed at its end.

Height 7 mm, diameter 1.5 mm.

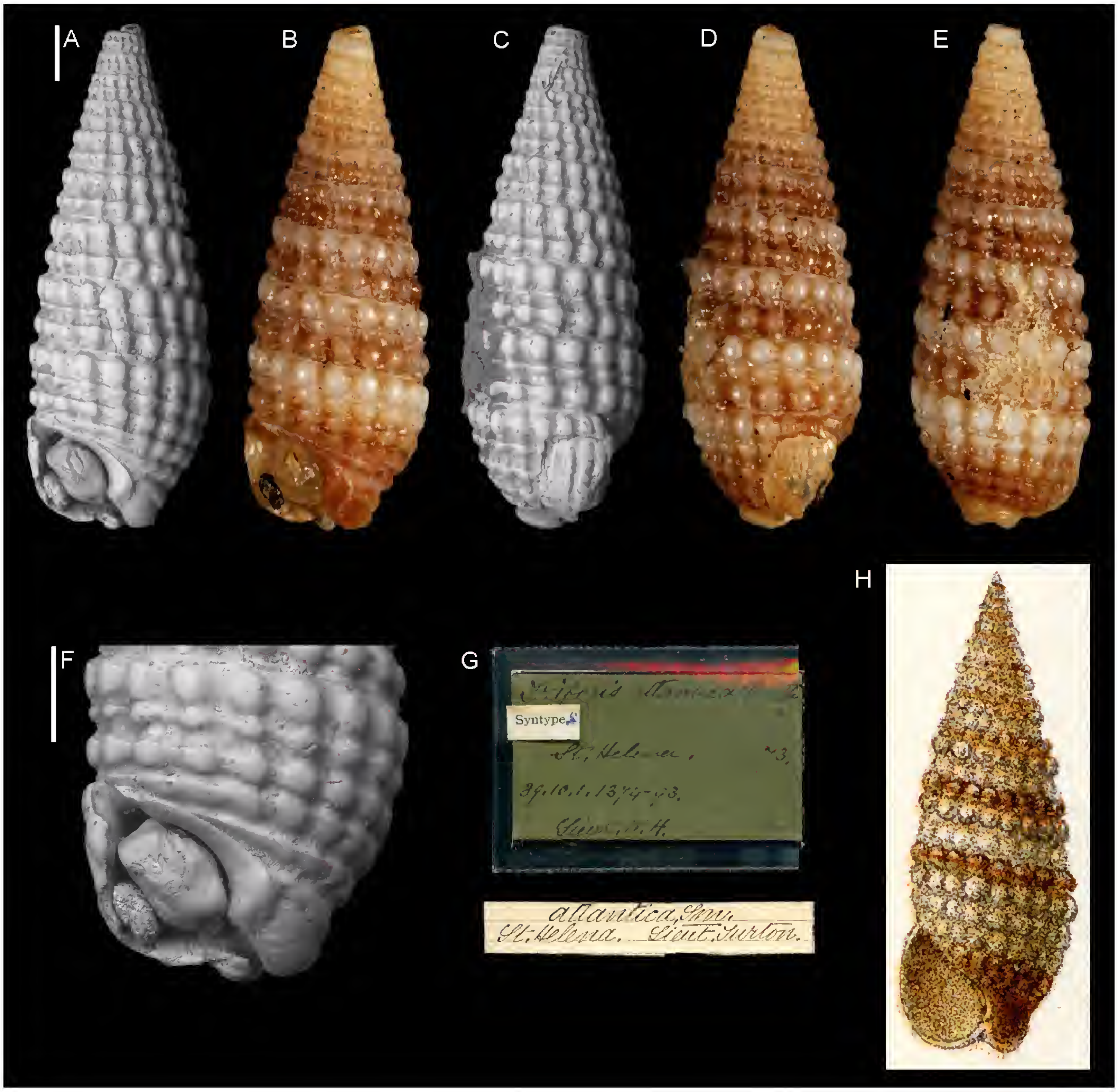

Figure 80. *Triphoris atlantica* E.A. Smith, 1890, Saint Helena. **A–F** Lectotype NHMUK 1889.10.1.1374: front (**A, B**), side (**C, D**), back (**E**), aperture (**F**). **G** Original labels. **H** Original figure. Scale bar: **A–F**: 0.5 mm.

Diagnosis. Syntype height 6.5 mm. Shell conical with flat sides. Teleoconch of 12 whorls bearing three main narrow and faintly tubercled spiral cords; a fourth is visible suprasuturally. The first four whorls bear better defined tubercles. Peristome with a quite deep slit-like posterior sinus and additional spiral cords appearing close to the lip. Base angular with a thick smooth spiral cord at the periphery. Siphonal canal long. Protoconch multispiral of probably four whorls but the apical part is worn in the syntype. The last three whorls bear axial riblets; a spiral keel is present on the third last whorl and two on the other whorls. Background colour pinkish-white with a brown mid-whorl band; protoconch brown.

Trifora cerea E.A. Smith, 1906

Figure 83

Trifora cerea E.A. Smith 1906: 43, pl. 7, figs 11, 11a.

Type locality. Port Shepstone, Natal, South Africa.

Type material. Syntypes: NHMUK 1906.6.23.13: 1 specimen, South Africa.

Original description. *Testa subulata, flavescens, nitida; anfractus 14 (?), convexi, costis spiralibus tuberculatis quatuor cincti, duobus medianis caeteris majoribus, inter costas oblique costulati, ultimus costis sex instructus, duobus inferioribus vix tuberculatis; columella supra arcuata, callo albo crassiusculo induta; canalis brevis,*

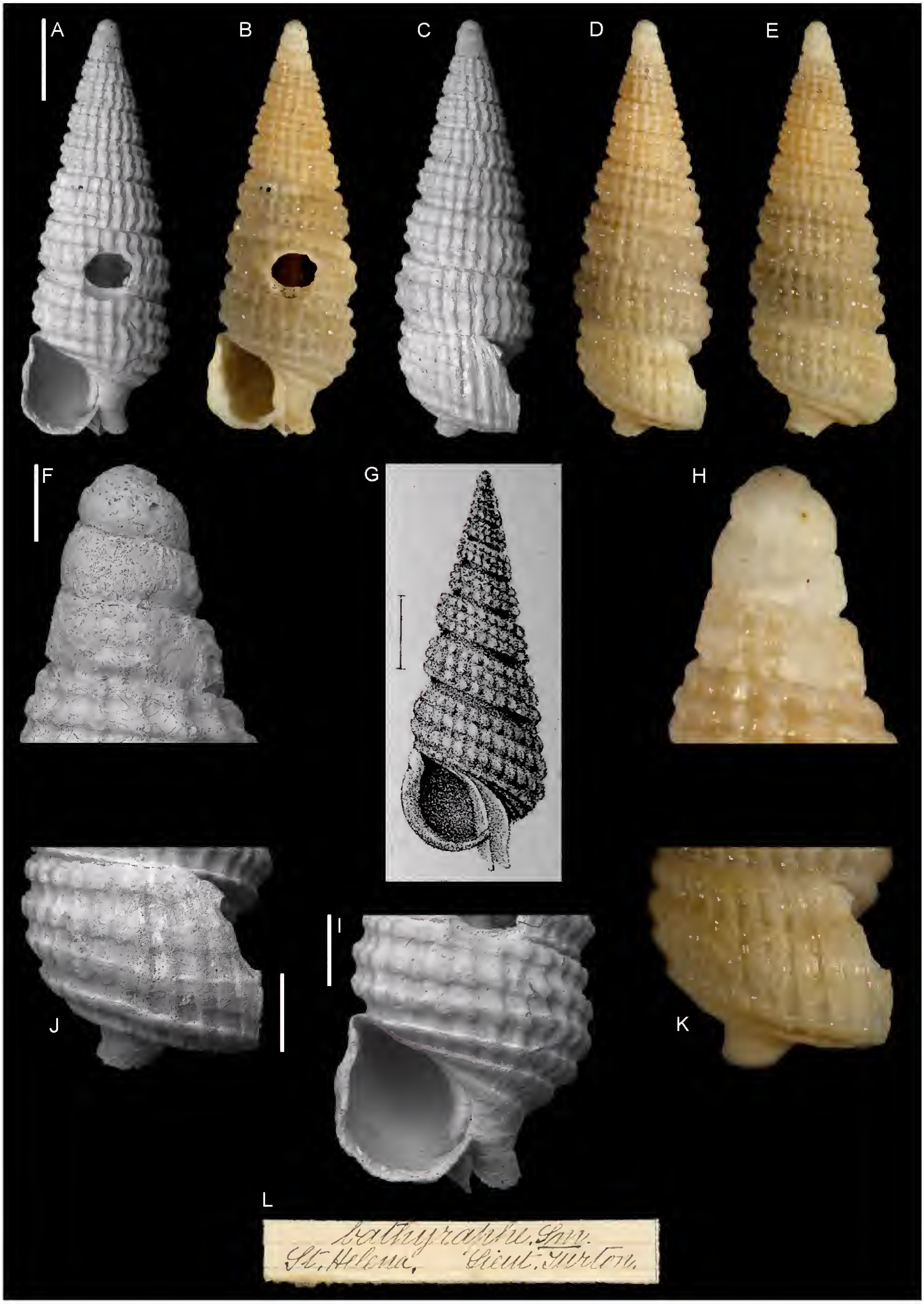

Figure 81. *Triphoris bathyraphe* E.A. Smith, 1890, Saint Helena. **A–F, H–K** Syntype NHMUK 1889.10.1.1413: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, H**), aperture (**I**), peristome (**J, K**). **G** Original figure. **L** Original label. Scale bars: **A–E**: 1 mm; **F, H**: 0.2 mm; **I–K**: 0.5 mm.

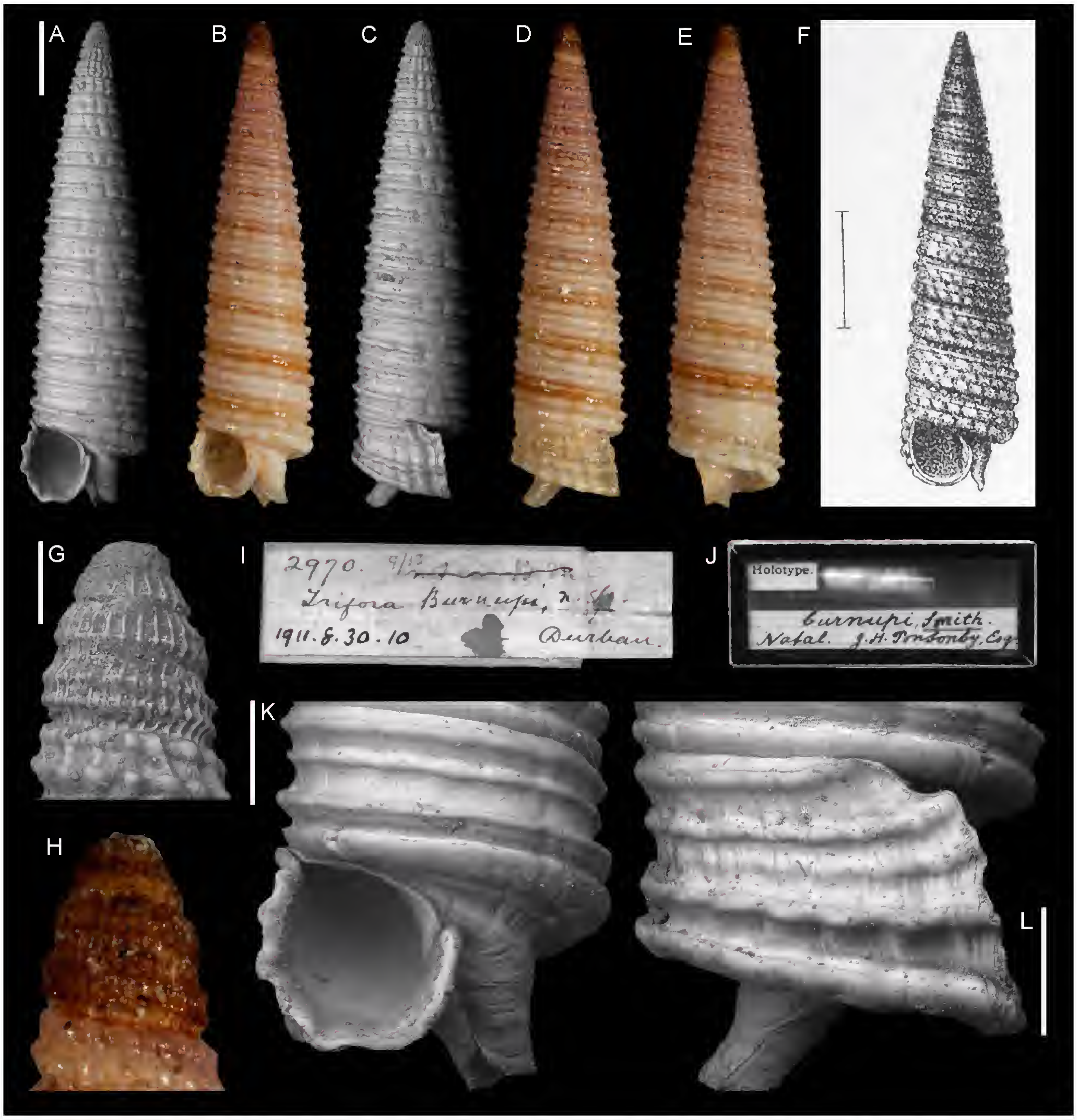

Figure 82. *Trifora burnupi* E.A. Smith, 1910, Durban, South Africa. **A–E, G, H, K, L** Syntype NHMUK 1911.8.30.10: front (**A, B**), side (**C, D**), back (**E**), protoconch (**G, H**), aperture (**K**), peristome (**L**). **F** Original figure. **I, J** Original labels. Scale bars: **A–E**: 1 mm; **G, H**: 0.2 mm; **K, L**: 0.5 mm.

obliquus, recurvus, haud clausus; labrum subpatulum, extremitatibus costarum leviter dentatum.

Longit. 10.5 mm., diam. 2.25. Apertura 1.25 longa.

Hab. —Port Shepstone (Burnup).

Of a uniform yellow wax colour, ornamented with four rows of granules on each whorl, the lowest row being the smallest, and the two central series rather more prominent than the uppermost row.

Translation of the Latin text. Subulate shell, yellowish, bright; 14 (?) whorls, convex, encircled by four tuberculated spiral cords, the greater two in the middle, costulated obliquely between cords; last with six cords, the two lower ones barely tuberculated; columella arched above, covered by a rather large callus; short anterior siphon, slanting, curved, not closed; extended lip, slightly dentate at the end of the cords.

Height, 10.5 mm, diameter 2.25. Aperture length 1.25 mm.

Diagnosis. Syntype 7.1 mm high (but apical part missing). Shell conical with slightly convex sides. Teleoconch

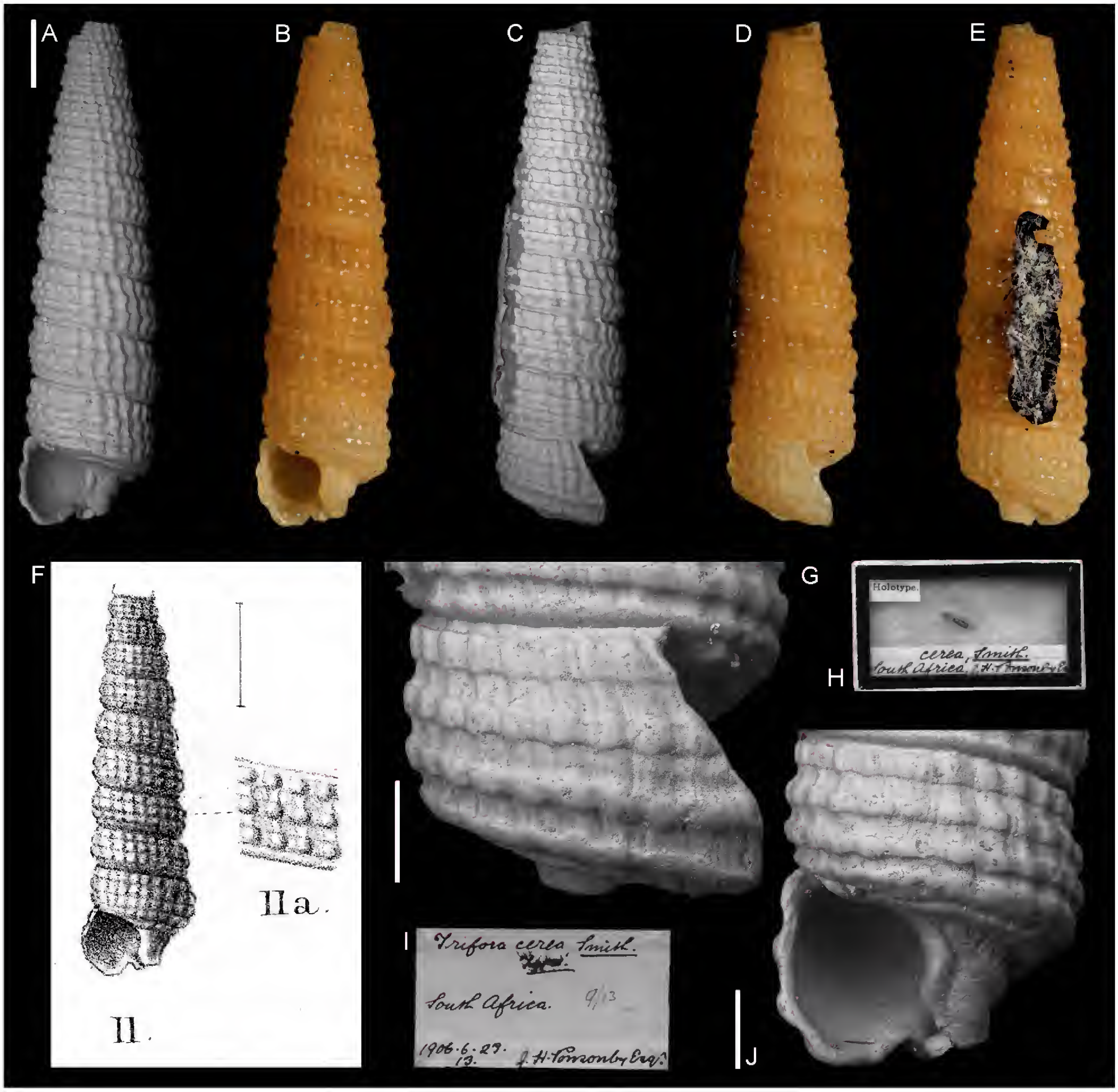

Figure 83. *Trifora cerea* E.A. Smith, 1906, South Africa. **A–E, G, J** Syntype NHMUK 1906.6.23.13: front (**A, B**), side (**C, D**), back (**E**), peristome (**G**), aperture (**J**). **F** Original figures. **H** Original box. **I** Original label. Scale bars: **A–E**: 1 mm; **G, J**: 0.5 mm.

with at least nine whorls bearing three spiral cords with tubercles at the intersection with slightly prosocline axial ribs. The second cord is less pronounced in the first whorl of the type specimen, suggesting that the second cord develops later than the others. A fourth smooth spiral cord is visible suprasuturally. Peristome showing a faint additional spiral cord between the second and the third, but too worn to enable the description of the posterior sinus. Siphonal canal short. The fourth spiral cord is smooth on the base, which bears a fifth, again smooth, cord. The periphery of the last whorl is quite angulated. Protoconch absent in the syntype. Teleoconch yellow to light orange.

Remarks. The date of publication of this paper follows Trew (1993).

Triphoris conspersus E.A. Smith, 1875 ex A. Adams ms

Figure 84

Triphoris conspersus E.A. Smith 1875: 106, not illustrated.

Type locality. "Cape Sima" (Shima Peninsula, Mie Prefecture), Japan.

Type material. Syntypes: NHMUK 1873.8.6.135, Cape Sima, Japan: 1 specimen; NHMUK 196545, Japan: 3 specimens (ex H. Cuming coll.).

Additional material. NHMUK 1878.1.28.435, Japan: 2 specimens (ex A. Adams coll.); *Triphora* sp. (not *conspersus*), NHMUK 1878.1.28.450, Japan (ex A. Adams coll.).

Original description. *Testa parva, elongata, lateribus levissime convexis; anfractus circiter 16 granulorum seriebus tribus cincti (*suprema *albida, hic illic fusco-maculata,* mediana *quam caeteris longe tenuiore, albida,* infima *pallide violacea); sutura distincta, canaliculata; anfr. ultimus infra granula carinis tribus cinctus; apertura rotunde ovata; canalis brevis recurvus.*

Long. 8½ mill., diam. 2.

Hab. Cape Sima, 18 fathoms, sand and broken shells.

This is a very pretty species, and appears to be undescribed hitherto, the above name being probably but a manuscript one attached to specimens in Cuming's collection.

Translation of the Latin text. Small shell, elongated, slightly convex; about 16 whorls encircled by three series of granules (the apical whitish and brownish spotted, the intermediate fainter than the others, whitish, the abapical light violet); distinct suture, canaliculated; last whorl with three carinae under the rows of granules; aperture round ovate; anterior siphon short, curved.

Height 8½ mm, diameter 2 mm.

Diagnosis. Syntypes ranging between 4.5 and 6.5 mm high. Shell conical, with flat whorls. Teleoconch up to 13 whorls bearing three spiral cords bearing tubercles at the intersection with prosocline axial ribs. The second cord develops on the seventh whorl and attains full size only on the last whorl. Suture impressed. Not a single specimen of the type series bears a complete peristome which can be described. Base with two additional smooth thin spiral cords. Siphonal canal long. Protoconch multispiral. The last three whorls present in a specimen of the type series bear a single strong spiral keel and axial riblets. Background teleoconch colour white with orange-brown blotches and the third spiral row which can tend to purple. Protoconch brown.

Remarks. E.A. Smith stated that this name was "a manuscript one attached [by A. Adams] to specimens in the Cuming's collection". Only lot NHMUK 196545 comes from the Cuming's collection, as reported on a modern label; it bears only "Japan" as the locality. However, the lot NHMUK 1873.8.6.135 bears an old label with the same locality data as stated in the original description ("Cape Sima, 18 fms", Fig. 84H) and another one with the name of J.G. Jeffreys on it. Two additional lots come from the H. Adams collection: 1878.1.28.435 and 1878.1.28.450. Their inventory numbers suggest they were deposited in the NHMUK after the species was described. Moreover, the latter at least (Fig. 84K) does not seem to be *T. conspersus* because of its smaller tubercles, which are whitish on a brown teleoconch background colour instead of white with brown spots ("*suprema albida, hic illic fusco-maculata*"). Due to the uncertainty about what material E.A. Smith had examined at the time of preparing the species' description, we refrain from selecting a lectotype.

Trifora convexa E.A. Smith, 1904

Figure 85

Trifora convexa E.A. Smith 1904: 37, pl. 3, fig. 9.

Type locality. "Port Alfred, Cape Colony" (Cape of Good Hope, South Africa).

Type material. Syntypes: NHMUK 1903.12.19.1084–1086: 3 specimens (glued on cardboard), Port Alfred, South Africa.

Original description. *Testa parva, fusca, ad apicem albida; anfractus 10 convexi, supremi duo pallidi, laeves, caeteri tricingulati, cingulis granosis, duobus inferioribus magis conspicuis, sutura filiformi sejuncti, ultimus ad peripheriam rotundatus, cingulis sex instructus; labrum subpatulum; columella callo crasso pellucido induta, supra incurva.*

Longit. 5.5 millim., diam. fere 2.

The suture is marked by the lira which encircles the periphery of the body-whorl, and winds up the spire at, but above the actual suture.

Translation of the Latin text. Small shell, brown, with whitish apex; 10 convex whorls, the uppermost two pale, light, the other with three granulated cords, the lower two more conspicuous, separated by a threadlike suture, the last rounded at its periphery, with six cords; extended lip; columella covered by a large translucent callus, curved above.

Height 5.5 mm, diameter about 2 mm.

Diagnosis. Syntype NHMUK 1903.12.19.1084 (Fig. 85A–F) 5 mm high. Shell conical with seven rounded whorls bearing three solid spiral cords with weak nodules at the intersection with orthocline axial ribs. A fourth thin smooth cord can be seen suprasuturally. Peristome incomplete, apparently without additional spiral cords. Base with three large flat spiral cords similar in appearance to those on the whorls. Siphonal canal short. Protoconch paucispiral. The transition between protoconch and teleoconch is very difficult to recognize because the apex is worn, but the protoconch is apparently less than two whorls, the first being smooth and the second with a fine suprasutural smooth spiral cord. Teleoconch brown to orange; protoconch lighter, almost white.

Trifora fuscescens E.A. Smith, 1904

Figure 86

Trifora fuscescens E.A. Smith 1904: 37, pl. 3, fig. 6.

Type locality. "Port Alfred, Cape Colony" (Cape of Good Hope, South Africa).

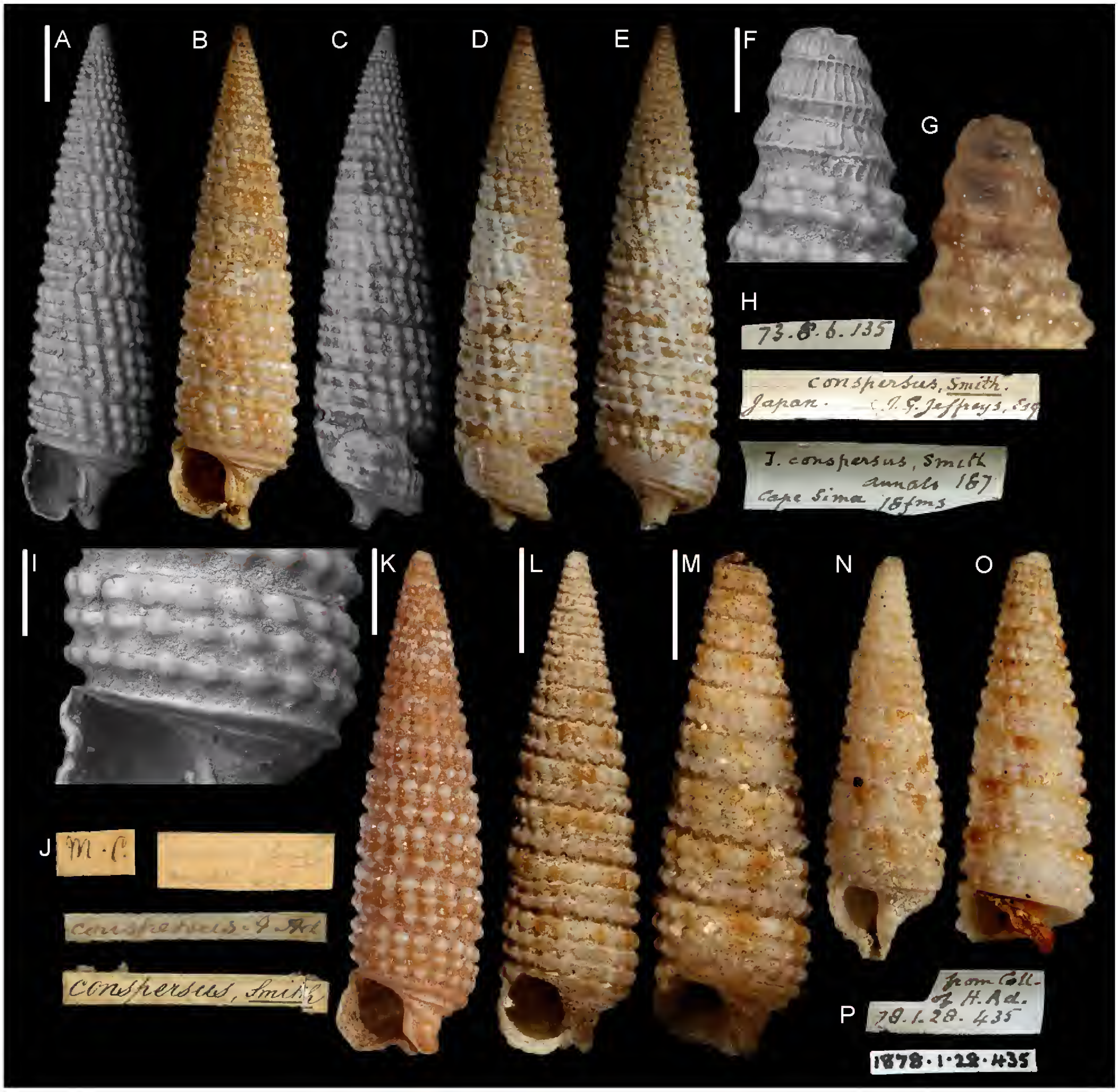

Figure 84. *Triphoris conspersus* E.A. Smith, 1875. **A–I** Syntype NHMUK 1873.8.6.135, Cape Sima, Japan: front (**A, B**), side (**C, D**, the apex seems bent in C but it is a deformation due to SEM imaging), back (**E**), protoconch (**F, G**), original labels (**H**), microsculpture (**I**). **J, L, M** Syntypes NHMUK 196545, Japan (coll. H. Cuming): original labels (**J**), front views (**L, M**). **K** *Triphora* sp. (not *conspersus*), NHMUK 1878.1.28.450, Japan (**H**. Adams coll.): front. **N–P** *T. conspersus*, NHMUK 1878.1.28.435, Japan (**H**. Adams coll.): front views (**N–O**), original labels (**P**). Scale bars: **A–E, K–M**: 1 mm; **F, G**: 0.2 mm; **I**: 0.5 mm.

Type material. Syntypes: NHMUK 1903.12.19.1087–1092: 6 specimens, Port Alfred, South Africa.

Original description. *Testa parva, gracilis, fuscescens, quadricingulata, cingulo supremo aliis majori, planiusculo, caeteris subaequalibus rotundatis; anfractus circiter 18, fere plani, ultimus cingulis septenis prope aperturam lineis incrementi sectis et subgranosis cinctus; apertura parva, rotunde quadrata, antice brevissime oblique canaliculata; labrum tenue, postice ad suturam sinuatum, in medio subpatulum, ad marginem leviter crenulatum.*

Longit. 11.5 millim., diam. 2.25.

Some of the specimens named *T. cingulatus*, A. Ad., by Mr. Sowerby (Marine Shells of S. Africa, p. 36), belong to the present species. None of them agree with Adams' species, which was described from the Red Sea, and has strong longitudinal sculpture between the spirals.

Translation of the Latin text. Small shell, slender, brownish, with four spiral cords; the uppermost row larger than the others, almost flat, the others rather similarly rounded; about 18 whorls, nearly flat, the last with seven weakly granulated cords crossed by growth lines near

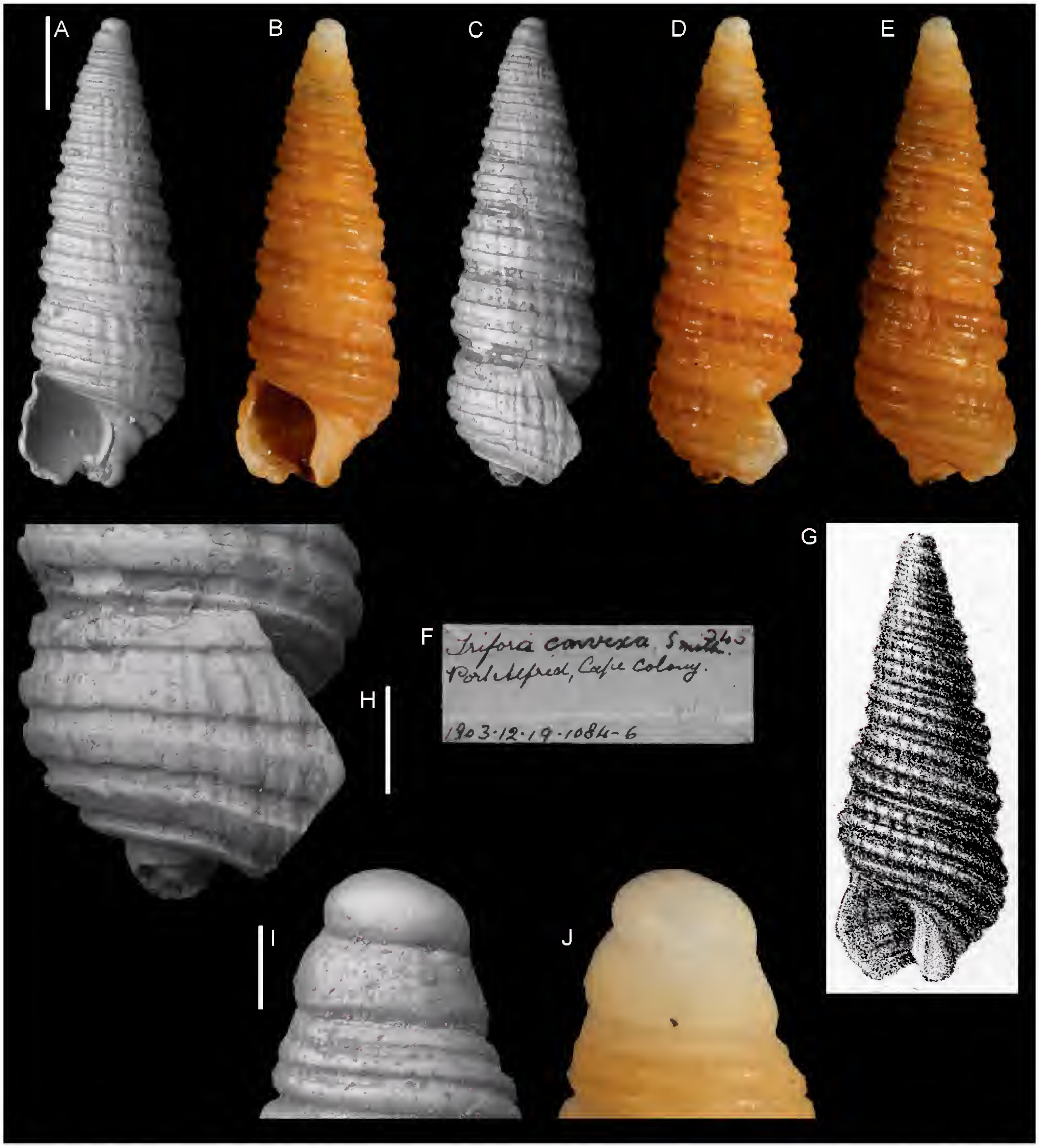

Figure 85. *Trifora convexa* E.A. Smith, 1904, Port Alfred, South Africa. **A–F, H–J** Syntype NHMUK 1903.12.19.1084: front (**A, B**), side (**C, D**), back (**E**), original label (**F**), peristome (**H**), protoconch (**I, J**). **G** Original figure. Scale bars: **A–E**: 1 mm; **H**: 0.5 mm; **I, J**: 0.2 mm.

the aperture; small subquadrate aperture, anteriorly with a very short oblique sinus; thin lip, posteriorly indented near the suture, in the middle lightly flared, with faint marginal crenulations.

Height 11.5 mm, diameter 2.25 mm.

Diagnosis. Syntype NHMUK 1903.12.19.1087 (Fig. 86A–E) 9.1 mm high. Very slender shell, slightly cyrtoconoid. Teleoconch of 14 flat whorls bearing four thick flat spiral cords made up of coalescent tubercles. A fifth thin smooth cord is visible between the second and the third on the last few whorls but never attains full size. A thin smooth cord is also visible suprasuturally. Base with three additional cords similar in appearance to those on the whorls. Peristome with a deep posterior sinus. Siphonal canal short. Protoconch paucispiral with a large smooth first whorl followed by two whorls with three smooth spiral cords. Transition with teleoconch poorly marked. Teleoconch orange to brown; protoconch white.

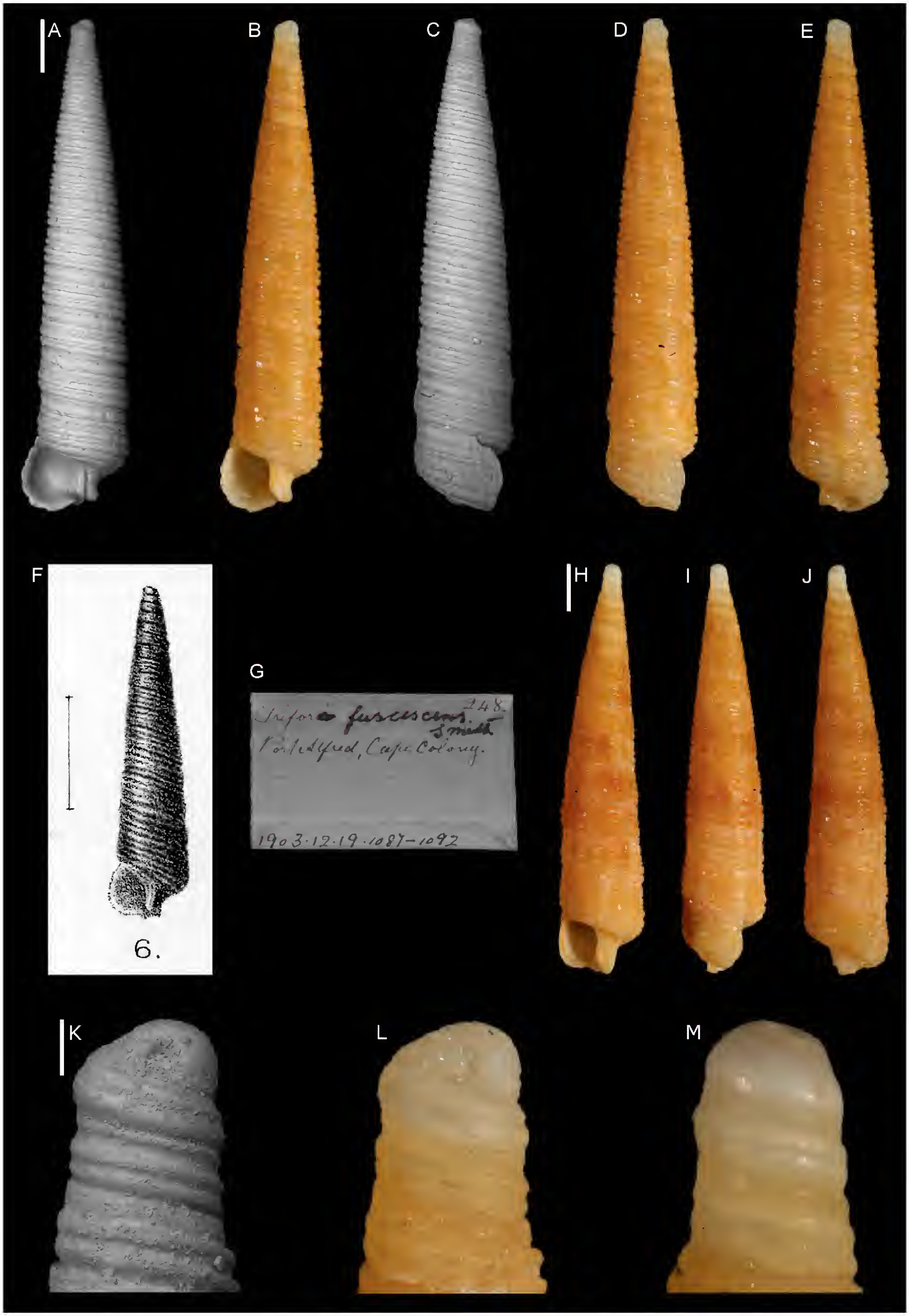

Figure 86. *Trifora fuscescens* E.A. Smith, 1904, Port Alfred, South Africa. **A–E, K, L** Syntype NHMUK 1903.12.19.1087: front (**A, B**), side (**C, D**), back (**E**), protoconch (**K, L**). **H–J, M** Syntype NHMUK 1903.12.19.1088: front (**H**), side (**I**), back (**J**), protoconch (**M**). **F**. Original figure. **G** Original label. Scale bars: **A–E, H–J**: 1 mm; **K–M**: 0.2 mm.

Trifora fuscomaculata E.A. Smith, 1904

Figure 87

Trifora fuscomaculata E.A. Smith 1904: 37, pl. 3, figs 7, 8.

Type locality. "Port Alfred, Cape Colony" (Cape of Good Hope, South Africa).

Type material. Lectotype: NHMUK 1903.12.19.1078, here designated. Paralectotype: NHMUK 1903.12.19.1079, 1 specimen, Port Alfred, South Africa.

Additional material. *Triphora* sp. (*T. fuscomaculata* var. of E.A. Smith, but not conspecific), NHMUK 1903.12.19.1080–1083, 4 specimens, Port Alfred, South Africa.

Original description. *Testa elongata, gracilis, alba, fusco irregulariter maculata; anfractus circiter 20 planiusculi, lente accrescentes, quadricingulati, cingulis tuberculatis, duobus medianis aliis majoribus, longitudinaliter sulcati, subcancellati, ultimus infra peripheriam cingulis tribus haud granosis ornatus; apertura rotunde quadrata, antice breviter oblique canaliculata; columella supra arcuata, callo tenui induta.*

Longit. 17 millim., diam. 3.5.

Var. (Pl. iii, fig. 8) Testa angustior, minor, cingulis tribus, superioribus aequalibus, distinctius et confertim tuberculatis.

Longit. 15 millim., diam. 3

The typical form is more distinctly blotched with brown than the variety.

Translation of the Latin text. Elongated shell, slender, white, with irregular brown spots; about 20 nearly flat whorls, growing slowly, with four tuberculated cords, the two in the middle larger than others, longitudinally grooved, subcancellated, the last with three granulated cords under its periphery; aperture subquadrate, anteriorly with a very short oblique sinus; columella superiorly arched covered by a thin callus.

Height 17 mm, diameter 3.5 mm.

Variety in pl. iii, fig. 8, shell more slender, smaller, with three cords. The uppermost of the same size, clearly tightly tuberculated.

Diagnosis. Lectotype 14.4 mm high. Shell conical with flat sides and obsolete sutures. The lectotype lacks the apical part. The remaining teleoconch has 12 whorls bearing four thin spiral cords with faint tubercles at the intersection with faint prosocline axial ribs. Numerous fine spiral striae are visible in the wide interspaces. Peristome badly damaged. Periphery angulated at the base, which bears four additional weakly sculptured spiral cords. Siphonal canal damaged but apparently short. Protoconch missing. Teleoconch white with orange blotches.

Remarks. In the box of this lot there is a capsule with two specimens of *T. fuscomaculata* s.s. and a second capsule with four specimens of a variety that E.A. Smith cited but not fully described in his work (1904). These four shells (Fig. 87K–N) have well-defined tubercles and an impressed suture which qualify them as a distinct species. Therefore, we have designated a lectotype which closely matches the original figure to stabilize the nomenclature.

Triforis gracilior E.A. Smith, 1903

Figure 88

Triforis gracilior E.A. Smith 1903: 614, pl. 35, figs 18, 19.

Type locality. S. Nilandu Atoll, 1–36 fathoms, Maldives.

Type material. Syntypes: NHMUK 1903.9.17.16: 1 specimen, Maldive Islands.

Original description. *Testa* T. excellenti *similis, sed gracilior, cingulis duobus inferioribus subundulatis, alba, hic illic fusco maculata.*

Longit. 28 mm., diam. 5½ mm.

Like *T. excellens*, this species has three keels upon each whorl, but they are not so equal, the uppermost being a trifle more slender than the others. The latter also are slightly affected by faint longitudinal depressions giving them an obscurely beaded appearance. The body-whorl is bicarinate at the periphery and has three or four lirae beneath. As in the preceding species, the space between the second and third keel is a little broader than that which separates the first and second, and the suture is filo-lirate.

Translation of the Latin text. Shell similar to *T. excellens*, but more slender, the two lower cords are slightly undulated, white with irregular brown spots.

Height 28 mm, diameter 5½ mm.

Diagnosis. Syntype 29.4 mm high. Shell conical, very elongated; apical part missing. The remaining teleoconch has 23 whorls bearing two main thin weakly tubercled spiral cords; two more thin ones are visible sub- and suprasuturally. Base with three additional faint spiral cords. Peristome with a shallow posterior sinus. Siphonal canal slightly elongated. Protoconch missing. Teleoconch white with narrow orange vertical flecks.

Remarks. The general appearance and sculpture is very similar to *T. smithi* G.B. Sowerby III, 1904, although the latter lacks the orange flecks observable in *T. gracilior*. E.A. Smith (1916) suggested that *T. smithi* is a synonym of *T. gracilior*.

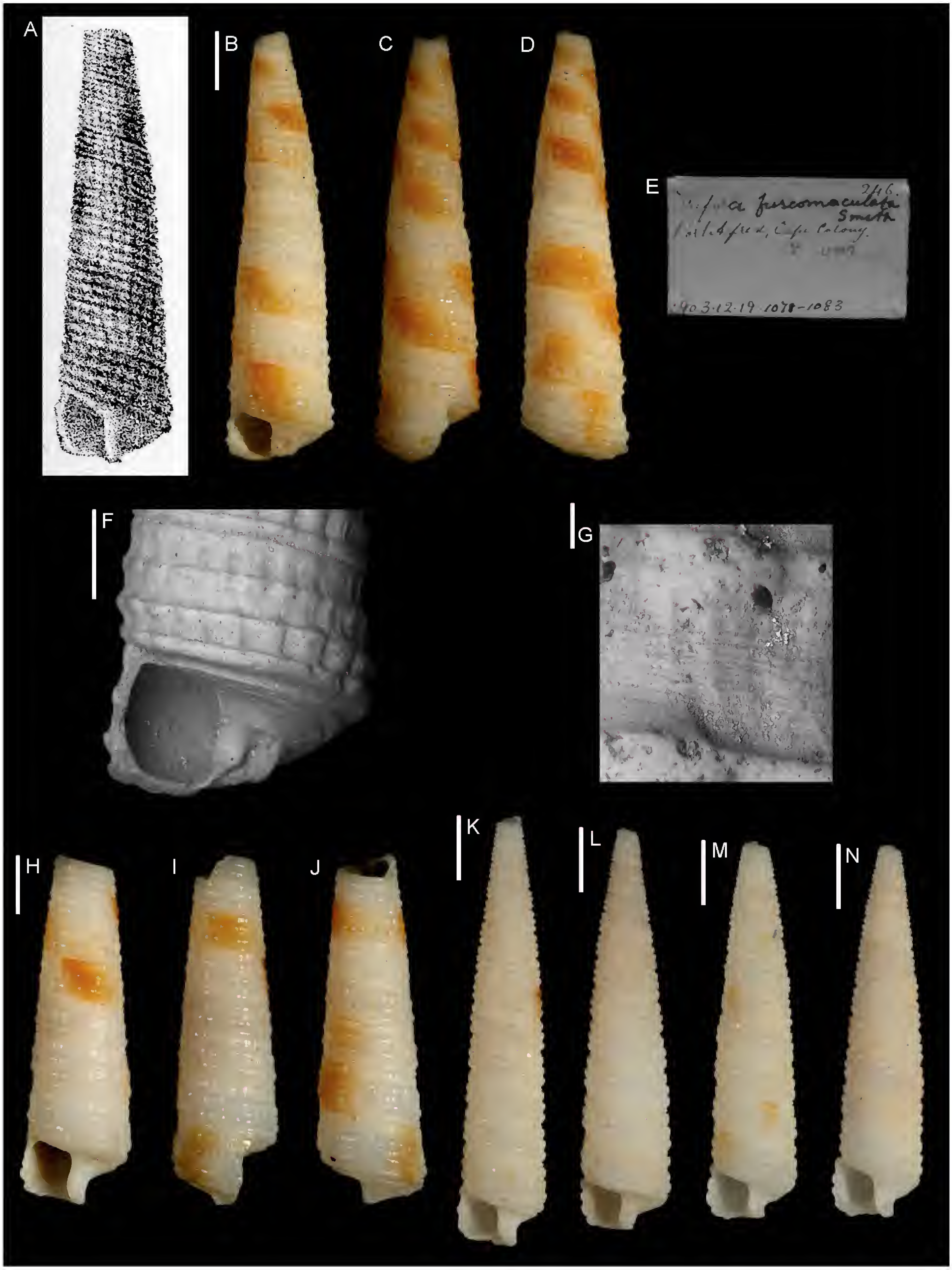

Figure 87. *Trifora fuscomaculata* E.A. Smith, 1904. **A** Original figure. **B–D, F, G** Lectotype NHMUK 1903.12.19.1078, Port Alfred, South Africa: front (**B**), side (**C**), back (**D**), aperture (**F**), microsculpture (**G**). **E** Original label. **H–J** Paralectotype, NHMUK 1903.12.19.1079, Port Alfred, South Africa: front (**H**), side (**I**), back (**J**). **K–N** *Triphora* sp. (*fuscomaculata* var., sensu E.A. Smith 1904), NHMUK 1903.12.19.1080–1083, Port Alfred, South Africa. Scale bars: **B–D, H–N**: 2 mm; **F**: 0.2 mm; **G**: 0.1 mm.

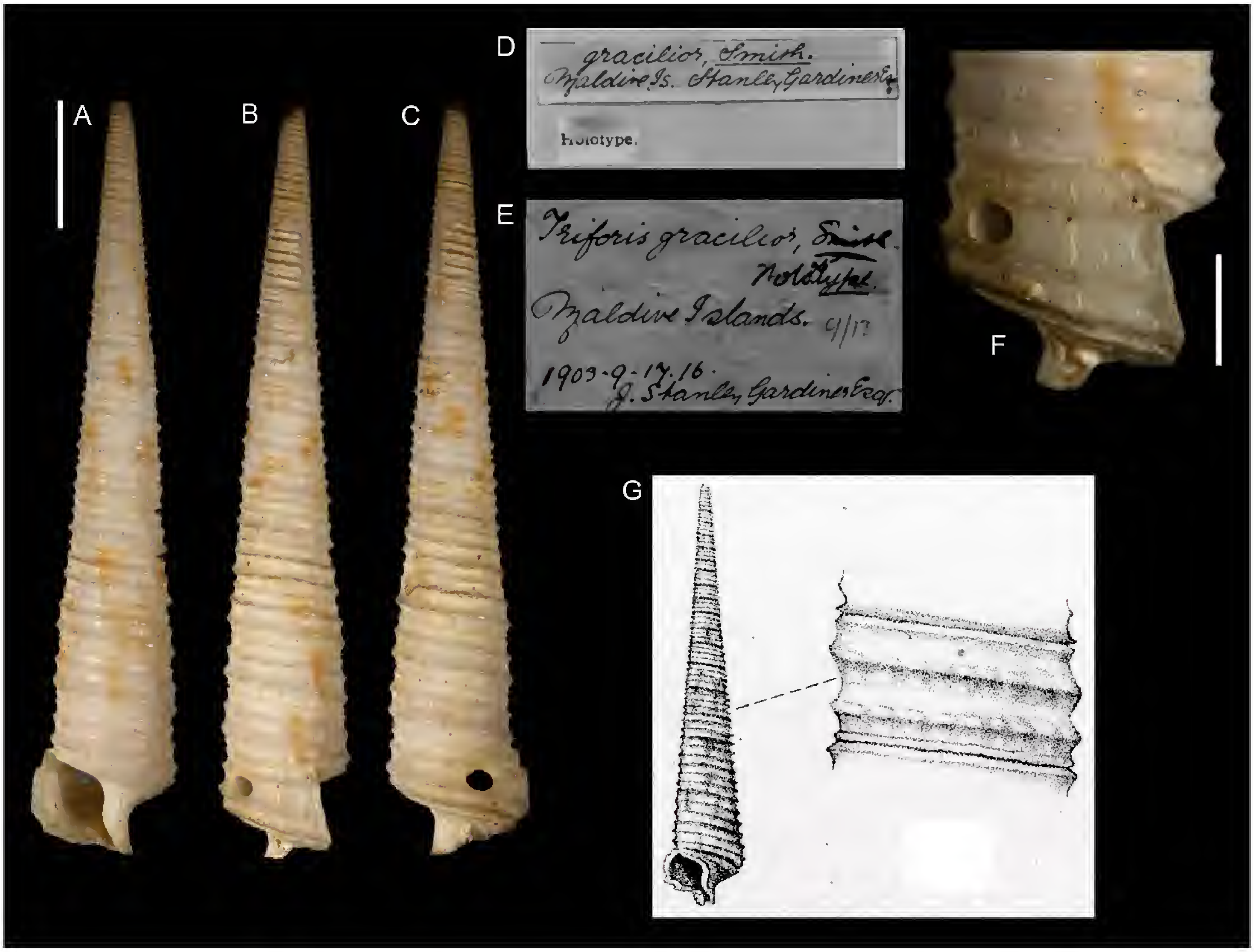

Figure 88. *Triforis gracilior* E.A. Smith, 1903, South Nilandu Atoll, Maldives. **A–F** Syntype NHMUK 1903.9.17.16: front (**A**), side (**B**), back (**C**), original labels (**D, E**), peristome (**F**). **G** Original figures. Scale bars: **A–C**: 4 mm; **F**: 2 mm

Triforis lilaceocinctus E.A. Smith, 1903

Figure 89

Triforis lilaceocinctus E.A. Smith 1903: 613, pl. 35, fig. 15.

Type locality. Miladumadulu Atoll, 3–28 fathoms, Maldives.

Type material. Syntypes: NHMUK 1903.9.17.13: 1 specimen, Maldive Islands.

Original description. *Testa elongato-pupoidea, supra acuminata, granulis flavescentibus et albis, lirata, inter granula rufo punctata; anfractus circiter 15, superiores liris duabus granosis aequalibus instructi, pauci anteriores lira graciliore mediana, dilute lilacea, vix granulata ornata, sutura lineari sejuncti, microscopice spiraliter striati, ultimus circa basim lilaceus, liris aliis tribus nodulosis, rufo punctatis, instructus; apertura obliqua, piriformis; canalis parvus, dextrorsus, semiclausus.*

Longit. 10½ mm., diam. 3½ mm.

A general glance at this pretty species gives the impression that the whorls have each two adjacent rows of large granules. Such however is not the case. It is the lower row in one whorl being adjacent to the upper one in another (the linear suture being between) that gives this appearance, the unspotted and more slender median lirae also lending to the effect. This lira gradually dies out as it ascends the spire, so that the upper whorls have only two rows of equal sized granules. This species also occurs at the Mauritius (Brit. Mus.).

Translation of the Latin text. Shell pupoid-elongate, pointed at the top, yellowish and white tuberculated cords, spotted with red among tubercles; about 15 whorls: the upper ones with two equal tuberculated cords; a few lower ones with a median thin cord, lightly lilac and barely granose, separated by a linear suture, microscopically spirally striated; the last lilac near the base, which has three additional nodose cords, spotted by red; oblique aperture, pyriform; small anterior siphon, dextral, semiclosed.

Length 10½ mm, diameter 3½ mm.

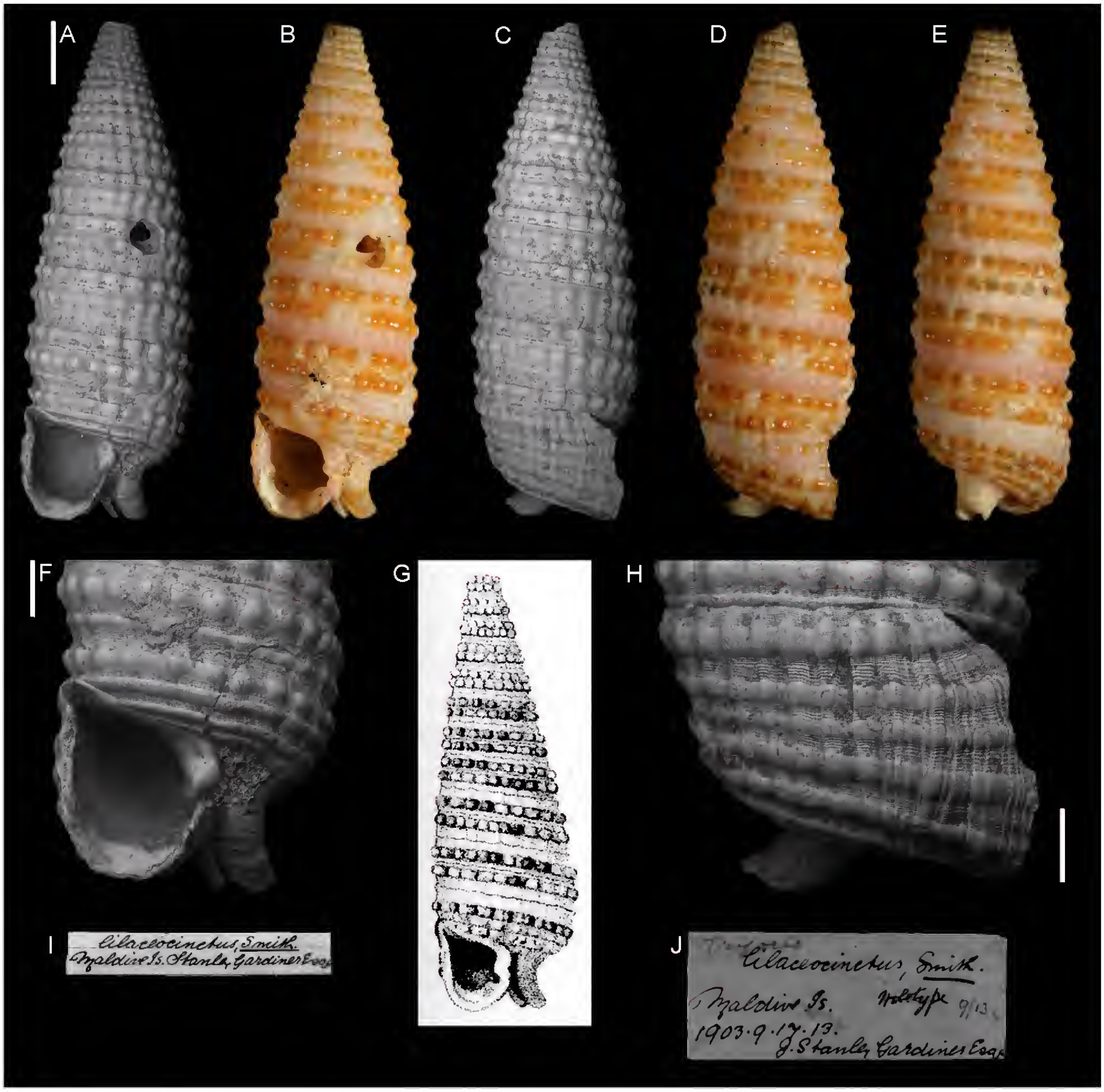

Figure 89. *Triforis lilaceocinctus* E.A. Smith, 1903, Miladumadulu Atoll, Maldives. **A–F, H** Syntype NHMUK 1903.9.17.13: front (**A, B**), side (**C, D**), back (**E**), aperture (**F**), peristome (**H**). **G** Original figure. **I, J** Original labels. Scale bars: **A–E**: 1 mm; **F, H**: 0.5 mm.

Diagnosis. Syntype 7.8 mm high. Shell cyrtoconoid, apex missing in the syntype. Teleoconch with 11 flat whorls with two main spiral cords bearing tubercles at the intersection with orthocline axial ribs. Another spiral cord develops at mid shell height in the wide interspace between the main two, but remains much thinner than the others. An additional fourth narrow smooth cord is visible suprasuturally. The interspaces are filled by numerous thin spiral and axial threads giving a cancellate microsculpture until the penultimate whorl, where the axial sculpture fades away. Peristome with one additional spiral cord and a deep posterior sinus. Siphonal canal long. Base showing a fifth and sixth weakly sculptured spiral cords. Protoconch missing. Teleoconch white to pink with the main spiral cordswith orange blocks with interspaces between tubercles usually darker.

Triforis pura E.A. Smith, 1903

Figure 90

Triforis pura E.A. Smith 1903: 614, pl. 35, figs 20, 21.

Type locality. Mahlos Atoll, 4–24 fathoms, Maldives.

Type material. Syntypes: NHMUK 1903.9.17.14: 1 specimen (glued on paper), Maldive Islands.

Original description. *Testa elongata, alba, clathrata, granulata; anfractus circiter 20, fere plani, costis spiralibus tribus granosis inaequalibus (costa mediana minima) cincti, inter costas longitudinaliter costati, ultimus costis senis (prope labrum duabus intercalatis) ornatus; canalis dextrorsus, clausus, laevis; apertura irregulariter ovata, obliqua; labrum antice prominens, postice recedens; columella callo crassiusculo reflexo induta.*

Longit. 14 mm., diam. 3.

Of the three spirals the uppermost is a little stouter than the lowermost and the central one is rather finer than the latter. The granules form oblique rows of three, being connected by the longitudinal costae. The suture is thread-like.

Translation of the Latin text. Elongated shell, white, cancellated, granose; about 20 whorls, nearly flat, encircled by three unequal tuberculated spiral rows (the intermediate the least), ribbed longitudinally among the rows, the last whorl with six cords (with two additional ones near the lip); anterior siphon dextral, closed, slender; aperture irregularly ovate, oblique; lip anteriorly projecting, posteriorly retracting; columella covered by a rather thick bent callus.

Height 14 mm, diameter 3 mm.

Diagnosis. Syntype 14.1 mm high. Shell slightly cyrtoconoid, syntype without the apex. Teleoconch of minimum 13 flat whorls with three spiral cords with faint tubercles at the intersections with prosocline axial ribs; the first cord is remarkably thicker than the other two. A fourth smooth suprasutural cord is easily visible. Peristome with an additional spiral cord and a shallow posterior sinus. Base with two weakly tubercled spiral cords and an additional narrow one between the fourth and the fifth. Siphonal canal long. Protoconch missing. Teleoconch pure white.

Trifora shepstonensis E.A. Smith, 1906

Figure 91

Trifora shepstonensis E.A. Smith 1906: 43–44, pl. 7, figs 12, 12a.

Type locality. Port Shepstone, Kwa-Zulu Natal, South Africa.

Type material. Lectotype: NHMUK 1906.6.23.11, here designated. Paralectotype: NHMUK 1906.6.23.12.

Additional material. *Triphora* sp. (not *shepstonensis*), NHMUK 1927.2.9.323–325, 3 specimens, Port Alfred, South Africa (coll. Turton).

Original description. *Testa elongata, subulata, fuscescens; anfractus circiter 15, plani, tricingulati, cingulis plus minus moniliformibus, mediani caeteris minori, in sulcis liris longitudinalibus decussati, ultimus liris 5 ornatus; apertura parva, albida; labrum tenue interdum productum, columellam antice attingens; columella supra arcuata, callo crassiusculo reflexo induta; canalis brevis, obliquus, recurvus. Longit. 10 mm., diam. 2.5.*

Hab.– Port Shepstone (Burnup).

The spiral ridges are crossed by oblique shallow sulci so as to produce a somewhat beaded appearance.

Translation of the Latin text. Elongated shell, subulate, brownish; about 15 flat whorls, with three cords more or less moniliform, the intermediate less than the others, crossed by longitudinal striae inside the cord interspaces, last whorl with 5 cords. Small aperture, white; lip thin sometimes projecting, reaching anteriorly the columella; columella arched above, covered by a rather thick bent callus; anterior siphon short, oblique, curved. Height 10 mm, diameter 2.5 mm.

Diagnosis. Lectotype 7.9 mm high. Shell slightly cyrtoconoid. Teleoconch of 11 whorls with three spiral cords bearing coalescent tubercles. A very fine smooth spiral cord is visible suprasuturally. Peristome damaged and repaired in the lectotype. Siphonal canal short. Base with a fifth weakly sculptured spiral cord. The apex is very worn in the lectotype, but based on the very broad first teleoconch whorl, the species may bear a paucispiral protoconch. Teleoconch pinkish with a brown suture.

Remarks. The date of publication of E.A. Smith's (1906) paper follows Trew (1993). The type collection contained also lot NHMUK 1927.2.9.323–325 (Fig. 91I–K) whose specimens lack the typical coalescent tubercles of *T. shepstonensis* and certainly belong to a different species. Therefore, we designated a lectotype which closely matches the original figure to stabilize the nomenclature.

Species described by G.B. Sowerby III

George B. Sowerby III described eight species of Triphoridae, of which only *Triforis innocens* G.B. Sowerby III, 1921 was not found in NHMUK; this species was described from Port Alfred, South Africa, and based on the material from W.H. Turton. Sowerby also described *Triforis abnormalis* in 1903, which is a member of the Newtoniellidae (currently: *Ataxocerithium abnormale*).

Triphora eupunctata G.B. Sowerby III, 1907

Figure 92

Triphora eupunctata G.B. Sowerby III 1907: 301, pl. 25, fig. 7.

Type locality. New Caledonia.

Type material. Lectotype: NHMUK 1907.8.28.46, here designated. Paralectotype: NHMUK 1907.8.28.47: 1 specimen, New Caledonia. A third specimen NHMUK 1907.8.28.48 may not belong to this species; see Remarks.

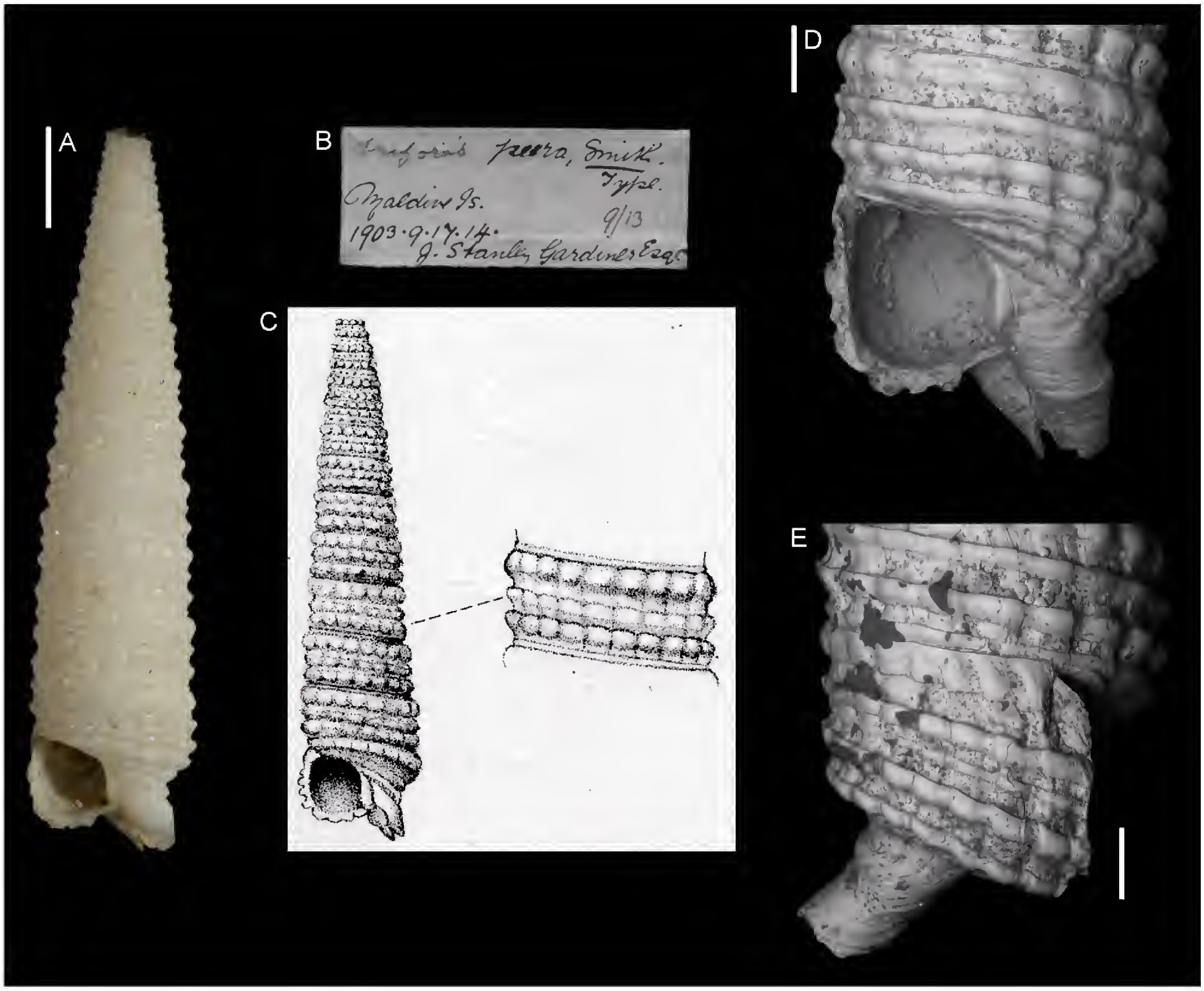

Figure 90. *Triforis pura* E.A. Smith, 1903, Maldive Islands. **A, D, E** Syntype NHMUK 1903.9.17.14: front (**A**), aperture (**D**), peristome (**E**). **B** Original label. **C** Original figures. Scale bars: **A**: 1 mm; **D, E**: 0.5 mm.

Original description. Testa sinistrorsa, elongata, convexiuscula, ad apicem acuminata, pallide rufo-fusca, nitens, fusco seriatim punctate; anfractus 16–17, planati, vix convexi, cingulis 3 eximie gemmiferis, cingula tertia gemmis fusco interpunctatis ornati, sutura canaliculata creno-lirata discreti; ultimus brevis, infra obtuse angulatus, ad basin liris 2 angustis crenulatis munitus; rostrum breve, crassum, obliquum; apertura oblique subquadrata. Long. 10, diam. 2.5 mm.

Hab.—*New Caledonia (Bouge).*

Shell light reddish brown, shining, closely and beautifully beaded in three rows on each whorl, spotted with brown between the beads of the lower rows; the whorls are separated by a channelled suture, in which may be observed a crenulated ridge; the last whorl has two narrow crenulated keels at the base.

Translation of the Latin text. Elongated and rather convex sinistral shell with acuminate apex, shining, light reddish brown spotted with brown; 16–17 strongly convex whorls with three strong beaded rows, with the third row spotted with brown between the beads, channelled suture with a crenulated ridge; last whorl obtusely angulated and with two narrow crenulated keels at the base; siphonal canal short, large, deviate; subquadrate, oblique peristome. Length 10, diameter 2.5 mm.

Locality: New Caledonia (Bouge)

Diagnosis. Lectotype height 7.6 mm. Shell slightly cyrtoconoid with flat whorls. Teleoconch of 12 whorls with three spiral cords with tubercles at the intersection with orthocline axial ribs. The second cord starts on the fifth whorl as a fine thread and is fully developed on the last three whorls only. A fourth smooth suprasutural cord is visible as well as very fine spiral and faint axial threads in interspaces. An additional spiral cord runs on the peristome between the second and the third. Siphonal canal short. The base has one additional weakly granulated spiral cord and an obsolete one running on the siphonal canal. Protoconch missing in the type series. Background colour yellowish to light brown; the third spiral cord bears a characteristic colouration of white tubercles and brown interspaces.

Remarks. The lot NHMUK 1907.8.28.46–48 contains three specimens: the lectotype (1907.8.28.46) and the paralectotype (1907.8.28.47), here designated, and a

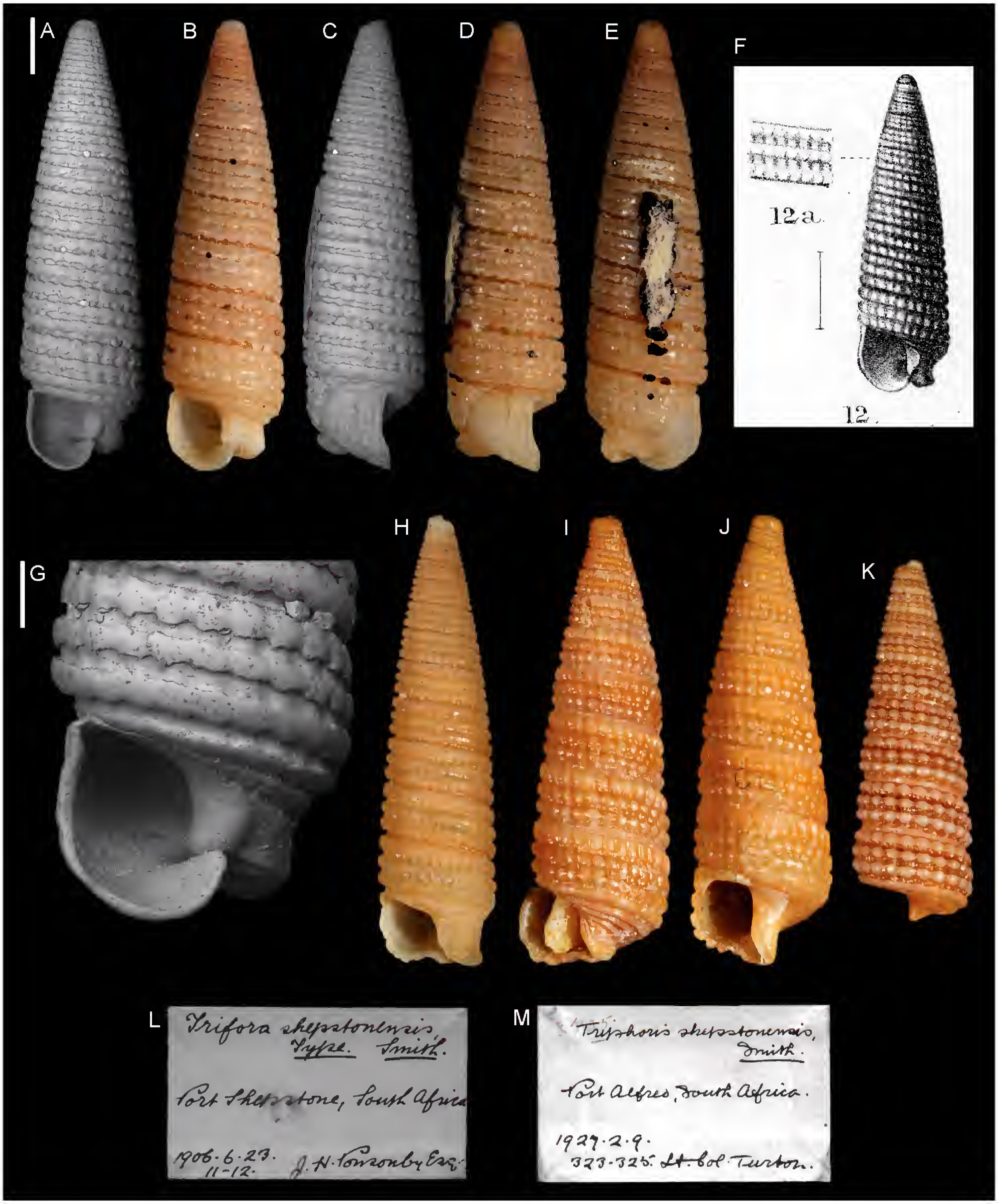

Figure 91. *Trifora shepstonensis* E.A. Smith, 1906. **A–E, G** Lectotype NHMUK 1906.6.23.11, Port Shepstone, South Africa: front (**A, B**), side (**C, D**), back (**E**), aperture (**G**). **F** Original figures. **H** Paralectotype, NHMUK 1906.6.23.12, Port Shepstone, South Africa: front. **I–K** *Triphora* sp. (not *shepstonensis*), NHMUK 1927.2.9.323–325, Port Alfred, South Africa (coll. Turton). **L, M** Original labels. Scale bars: **A–E**: 1 mm; **G**: 0.5 mm.

third specimen (1907.8.28.48) very similar in overall shape and sculpture, but with a thin brown line on the third spiral cord rather than white tubercles with brown interspaces. It is unclear if this difference has relevance to discriminate between species, but because Sowerby clearly specified the presence of brown spots between the tubercles rather than a continuous line, we have selected a lectotype fitting the original description to stabilize the nomenclature.

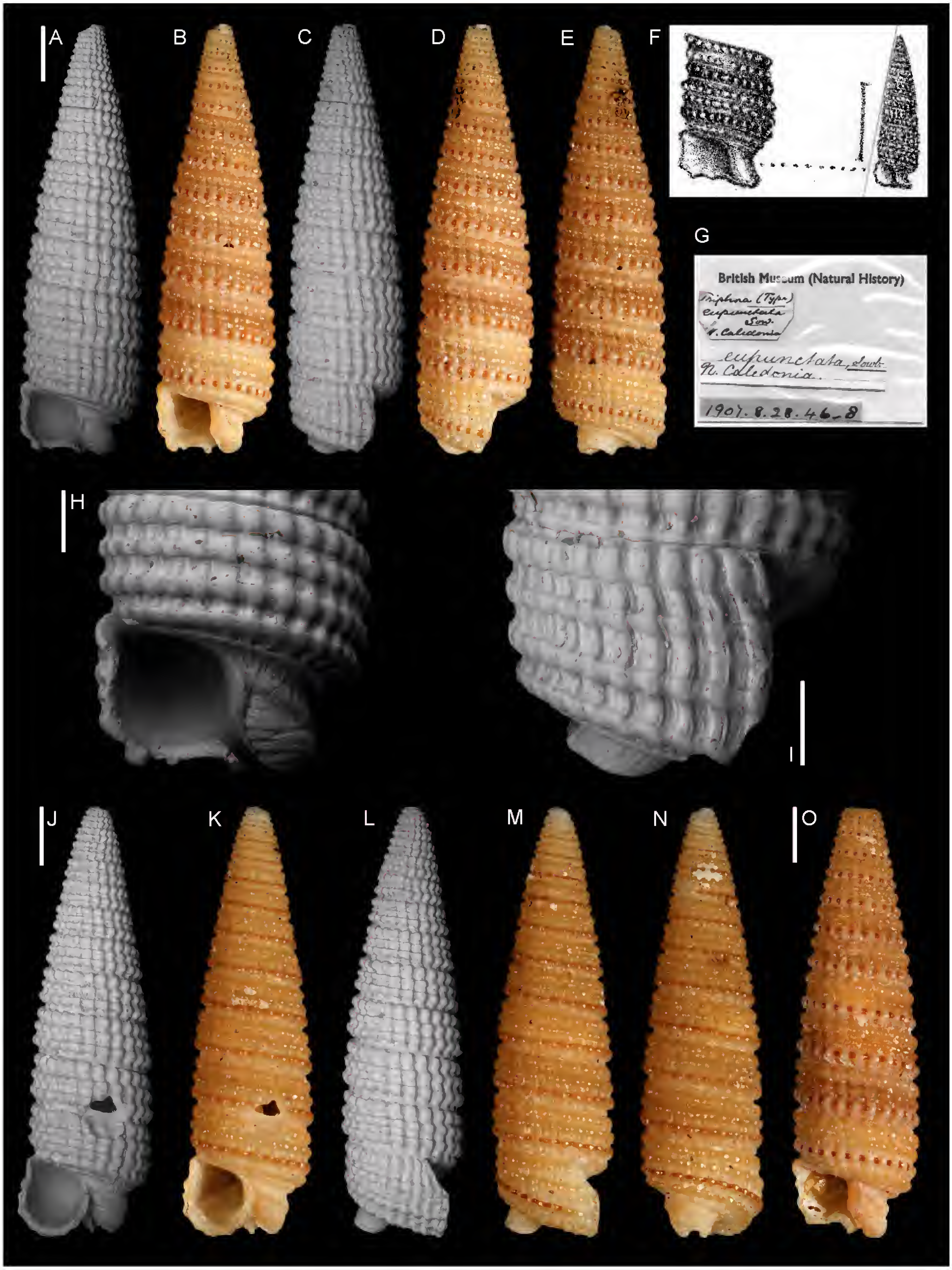

Figure 92. *Triphora eupunctata* G.B. Sowerby III, 1907, New Caledonia. **A–E, H, I** Lectotype NHMUK 1907.8.28.46: front (**A**, **B**), side (**C, D**), back (**E**), aperture (**H**), peristome (**I**). **F** Original figures. **G** Original labels. **J–N** NHMUK 1907.8.28.48 (probably not *T. eupunctata*): front (**J, K**), side (**L, M**), back (**N**). **O** Paralectotype, NHMUK 1907.8.28.47: front. Scale bars: **A–E, J–O**: 1 mm; **H, I**: 0.5 mm.

Triphora fuscoapicata G.B. Sowerby III, 1907
Figure 93

Triphora fuscoapicata G.B. Sowerby III 1907: 301, pl. 25, fig. 9.

Type locality. Cebu Island, Philippines.

Type material. Syntypes: NHMUK 1907.8.28.38–40: 3 specimens, Cebu Island, Philippines.

Original description. Testa sinistrorsa, elongato-acuminata, ad apicem acutissima, albida, hic illic fusco minute punctata, ad apicem brunnea; anfractus circa 18, embryonales 5–6 planato-declives, leaves, sequentes cingulis spiralibus gemmates 2 (interdum lira minuta interveniente) ornate, sutura impressa discreti; ultimus quadriseriatim gemmatus, infra angulatus, prope aperturam tubulatim forato munitus, ad basin depressus; rostrum crassiusculum, oblique recurvum; aperture parva, subcircularis; labrum tenue. *Long. 5.5, diam. 1.12 mm.*

Hab.—*Island of Cebú, Philippines.*

The principal feature distinguishing this species is that the embryonic whorls, numbering 5 or 6, are dark brown, showing conspicuously against the whiteness of the subsequent whorls.

Translation of the Latin text. Elongate slender sinistral shell with a very sharp apex, whitish with sparse small brown dots, and with a brown apex; about 18 whorls, 5–6 flat-sloping away embryonic, subsequent with two beaded spiral rows (sometimes with a fine lira in between), impressed suture; last whorl with four rows, angulated at the base, with a tubular aperture near the peristome, with a depressed base; rather obtuse, recurved siphonal canal; small subcircular aperture, thin external lip. Length 5.5, diameter 1.12 mm.

Locality: Insland of Cebú, Philippines.

Diagnosis. Syntypes ranging between 4.6 and 5.9 mm high and show considerable variation in adult shell size. Shell cyrtoconoid with flat whorls. Teleoconch of 10–13 whorls, with three spiral cords bearing tubercles at the intersections with prosocline axial ribs. The second cord appears on the fifth whorl as a narrow thread and always remains smaller than the other cords. A fourth smooth suprasutural cord is visible throughout the shell. Between the main cords run numerous fine finely tubercled spiral ribs. The peristome is well developed with additional spiral cords between the main ones. Posterior sinus well developed and protruding as a very short canal. Anterior canal quite long. Base almost flat, with a sharp angle at the periphery marked by a faint smooth spiral cord. Multispiral protoconch of six whorls; the first almost smooth, the second with numerous pustules abapically and short axial riblets apically, and the third with numerous riblets and a single spiral keel which become two in the remaining whorls. Teleoconch whitish to very light brown, first two or three whorls pure white; protoconch brown.

Triphora fuscozonata G.B. Sowerby III, 1907
Figure 94

Triphora fuscozonata G.B. Sowerby III 1907: 301, pl. 25, fig. 8.

Type locality. New Caledonia.

Type material. Syntypes: NHMUK 1907.8.28.36: 1 specimen, New Caledonia.

Original description. *Testa sinistrorsa, elongata, acute acuminata, nigro-fusco fasciata; anfractus 18, leviter convexi, gemmis rotundatis confertis biseriatis (lira angusta interveniente) ornate, sutura impressa discreti; ultimus curtus, liris 6 minute gemmulatis, prope basin leviter obliquum; apertura parva, oblique subtrigona; labrum tenue, postice sinuatum. Long. 6, diam. 1.5 mm.*

Hab.—*New Caledonia.*

This species may be recognized by the dark-brown bands on each whorl; the gem-like nodules common to many species are arranged in two prominent rows, with a narrow intervening crenulated ridge; on the last whorl they are smaller and closer, forming six ridges.

Translation of the Latin text. Elongate sinistral shell with a sharp apex, dark-brown banded; 18 light convex whorls with two rows of gem-like rounded nodules (a narrow intervening ridge), impressed suture; last whorl short, with 6 small gemmulated lirae, slightly slanting near its basis; small aperture, obliquely subtrigonal; thin external lip with a posterior sinum. Length 6, diameter 1.5 mm.

Locality: New Caledonia.

Diagnosis. Syntype 5.3 mm high. Shell conical with flat whorls. Teleoconch of 12 whorls with three spiral cords with tubercles at the intersection with slightly prosocline axial ribs. The second cord starts in the lower part of the shell as a fine thread and never fully develops to the size of the others. Fine axial threads are visible in the interspaces. Peristome incomplete in the syntype, with faint additional spiral cords. Siphonal canal short. The base bears two additional smooth spiral cords. Protoconch incomplete, but clearly multispiral; the three visible whorls have numerous axial ribs and a single spiral keel. Teleoconch whorls dark brown apically and light brown to whitish abapically. Base very light brown to white, siphonal canal brown. Protoconch hyaline, but worn in the syntype.

Triphora hungerfordi G.B. Sowerby III, 1914
Figure 95

Triphora hungerfordi G.B. Sowerby III 1914: 477–478, pl. 19, fig. 10.

Type locality. Hong Kong.

Type material. Syntypes: NHMUK 1919.12.31.17: 1 specimen, Hong Kong.

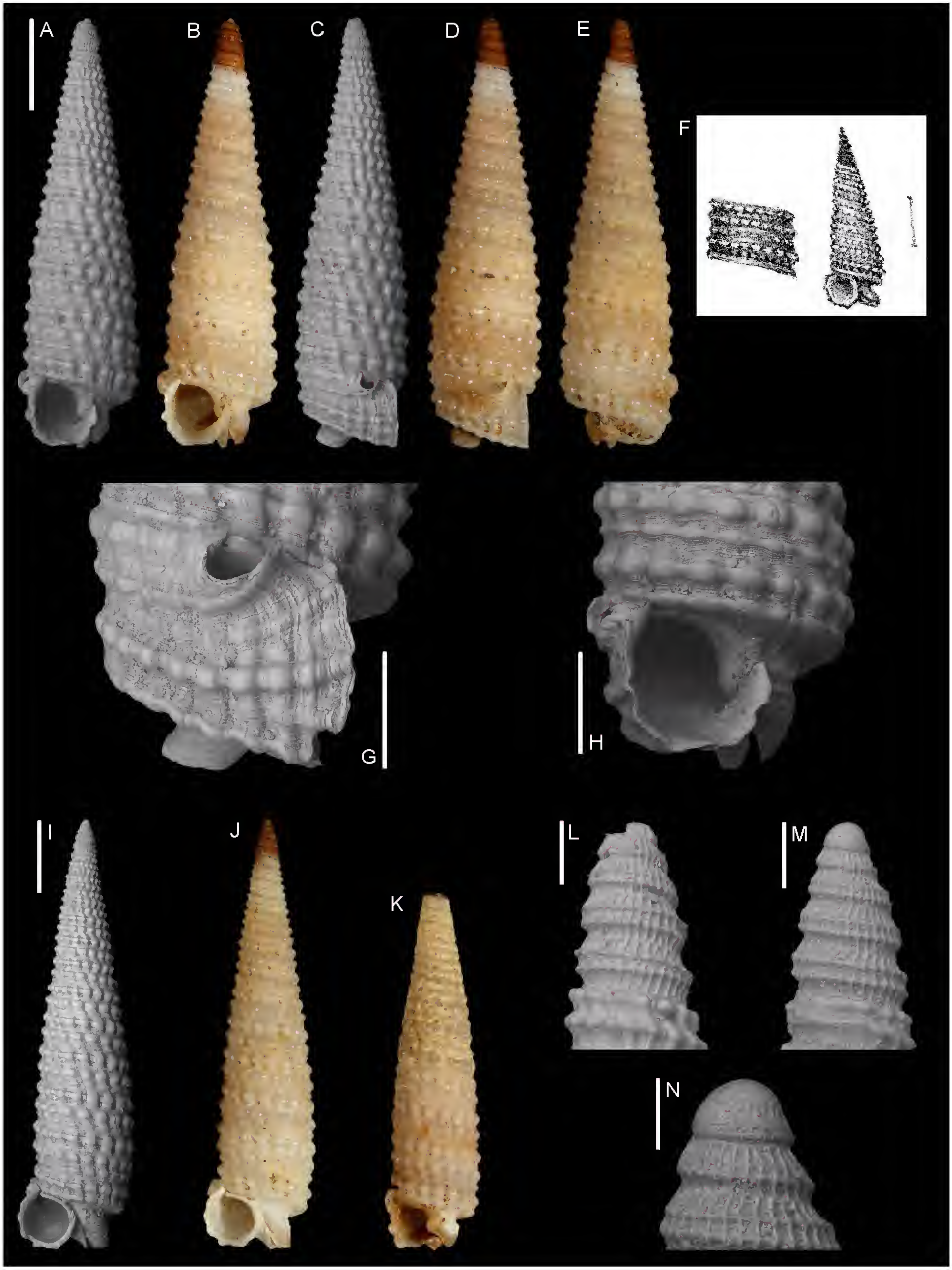

Figure 93. *Triphora fuscoapicata* G.B. Sowerby III, 1907. Cebu Island, Philippines. **A–E, G, H, L** Syntype NHMUK 1907.8.28.38: front (**A, B**), side (**C, D**), back (**E**), peristome (**G**), aperture (**H**), protoconch (**L**). **I, J** Syntype NHMUK 1907.8.28.39: front. **K, M, N** Syntype NHMUK 1907.8.28.40: front (**K**), protoconch (**M, N**). **F** Original figures. Scale bars: **A–E, I–K**: 1 mm; **G, H**: 0.5 mm; **L, M**: 0.2 mm; **N**: 0.1 mm.

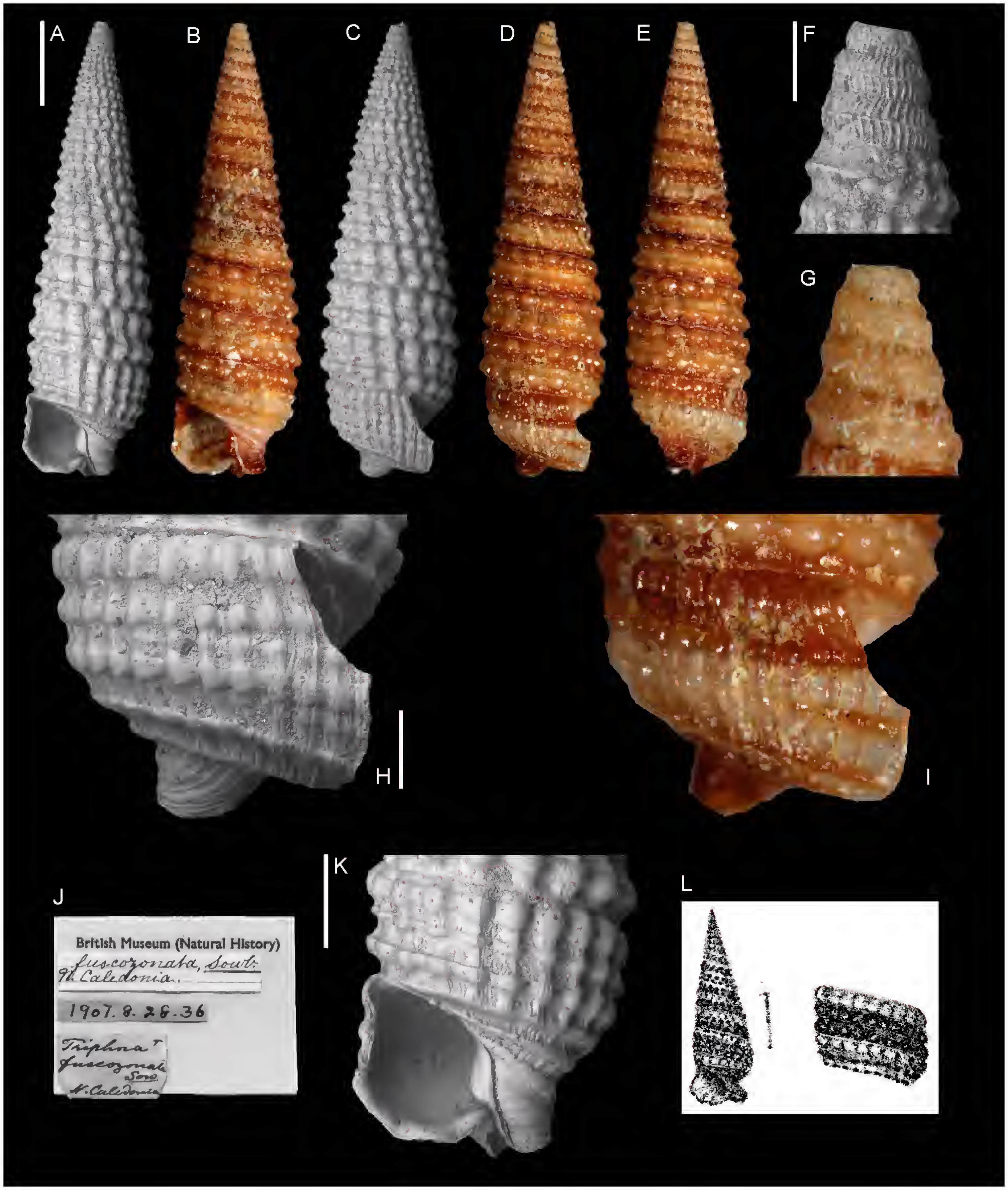

Figure 94. *Triphora fuscozonata* G.B. Sowerby III, 1907, New Caledonia. **A–K** Syntype NHMUK 1907.8.28.36: front (**A, B**), side (**C, D**), back (**E**), protoconch (**F, G**), peristome (**H, I**), original labels (**J**) aperture (**K**). **L** Original figures. Scale bars: **A–E**: 1 mm; **F, G**: 0.2 mm; **H, I**: 0.3 mm; **K**: 0.5 mm.

Original description. Testa sinistrorsa, elongato-acuminata, nigro-fusca; spira elata, leviter convexa; anfractus 12, bi-seriatim pustulati; pustulis rotundatis, glabratis, inaequalibus; anfractus ultimus breviusculus, circiter sex-soriatim pustulatus; rostrum valide reflexum. Apertura subquadrata; labrum tenue, minute crenulatum; columella obliqua.

Long. 12, diam. $2\frac{1}{4}$ mm.

Hab.—*Hongkong.*

In general form and appearance this shell differs but little from small dark-coloured specimens of the European T. perversa, *but the nodulous spiral ridges are more unequal* *and irregular, and not interrupted by longitudinal furrows. A few specimens of this species were brought from Hong-kong many years ago by the late Surgeon-Major R. Hungerford, but until now it has remained nameless.*

Translation of the Latin text. Elongate slender dark-brown sinistral shell; high spire slightly convex; 12 whorls with two ridges of rounded smooth irregular pustules; rather short last whorl with about six series of pustules; anterior siphon very reflected. Subquadrate aperture; light external lip slightly crenulated; slanting columella.

Length 12, diameter 21/4 mm.

Locality: Hong Kong.

Diagnosis. Syntype 5.6 mm. Shell conical, with flat sides. Teleoconch of 11 whorls bearing two spiral cords with tubercles at the intersection with slightly prosocline axia ribs. Beginning on the seventh whorl, a fine spiral thread develops between the two major cords but fully develops only on the last whorl. A very fine smooth suprasutural cord is also visible as well as fine axial threads in the interspaces. Peristome with a shallow posterior sinus and additional spiral cords between the main ones. Siphonal canal short. Base with two smooth spiral cords. Protoconch missing. Teleoconch brown with lighter first whorls and tubercles.

Remarks. The original description refers to "a few specimens", but only one was found in the NHMUK. The other specimens may have been sold and dispersed. *Trifora hungerfordi* closely resembles *Triforis fusca* Dunker, 1860 (Albano and Bakker 2016). However, caution is necessary in establishing these as synonyms because of the lack of the protoconch. In the Indo-Pacific, species with morphologically indistinguishable teleoconchs may have entirely different protoconch types (P.G. Albano and P.A.J. Bakker pers. obs.).

Triforis picturatus G.B. Sowerby III, 1901

Figure 96

Triforis picturatus G.B. Sowerby III 1901: 210, pl. 22, fig. 11.

Type locality. Cebu, Philippines.

Type material. Syntypes: NHMUK 1901.10.3.89–90: 2 specimens, Cebu Island, Philippines.

Original description. *Testa sinistrorsa, elongata, gracilis, albida, nigro-fusco maculata, ad apicem fusca; anfr. 18, planati, vix concavi, liris tribus acutiusculis cincti, inferne angulati ad angulum pustulati, pustulis albidis fusco interpunctatis; anfractus ultimus breviculus, biangulatus, ad basim vix concavus, rostro fusco oblique dextrorsus reflexo instructus; apertura parva, subquadrata; labrum tenue, serratum. Long. 9, diam. 2.5 mm.* A pretty species, neatly sculptured and nodule, streaked and spotted with blackish brown; with a brown tubular rostrum placed obliquely away from the aperture, on the right hand side of the shell.

Translation of the Latin text. Elongate sinistral slender shell, white with blackish-brown spots and dark apex; 18 flat, barely concave whorls with three sharp spiral lirae, angulated and pustulated anteriorly with alternating dark-brown and white pustules; last whorl short, biangulated, barely concave, dark siphonal canal placed obliquely right from aperture; small subquadrate aperture; light serrated external lip. Length 9, diameter 2.5 mm.

Diagnosis. Syntypes 7.6 and 9.4 mm high. Conical shell with flat whorls. Teleoconch of 12 whorls with three spiral narrow cords that bear oblong tubercles in the first whorls. Such tubercles soon become a continuous weakly ondulated spiral cord. A fourth smooth cord is barely visible suprasuturally. Between the main cords, many fine spiral and axial threads are visible. Peristome rebuilt after breakage in one syntype and incomplete in the other but it apparently bears additional spiral cords and a shallow posterior sinus. Base with two additional undulate spiral cords and foliaceous axial riblets. Siphonal canal large and moderately long. Protoconch missing. Teleoconch brown with white blotches and tubercles. Base brown. Operculum horny, thin, ovate, paucispiral of about 2 whorls, nucleus a little eccentric, periphery thinner and only very little upturned.

Remarks. Syntype NHMUK 1901.10.3.89 was collected live and contains the dried animal inside. The operculum was extracted and photographed.

Triphora princeps G.B. Sowerby III, 1904

Figure 97

Triphora princeps G.B. Sowerby III 1904: 174–175, figured.

Type locality. Not reported.

Type material. Holotype: NHMUK 1904.12.23.147, fixed by monotypy.

Original description. *Testa perelongata, sinistrorsa, straminea, postice fusco-tincta, lineis rufo-fuscis numerosis longitudinalibus parum obliquis picta; anfractus circa 40, planulati, sulcis longitudinalibus parum obliquis hic illic foveolatis insculpti, cingulis 4 interruptis pseudo-nodulosis, aliquanto irregularibus, inaequalibus, duo inferioribus majoribus, instructi; anfractus ultimus infra sub-acute angulatus, ad angulum bicarinatus, infra angulum subconcavo-constrictus, carinis 2 aliquanto robustis munitus; rostrum longiusculum, contort-reflexum; apertura subquadrata; labrum tenue. Long. 57, diam. maj. 7 mm.*

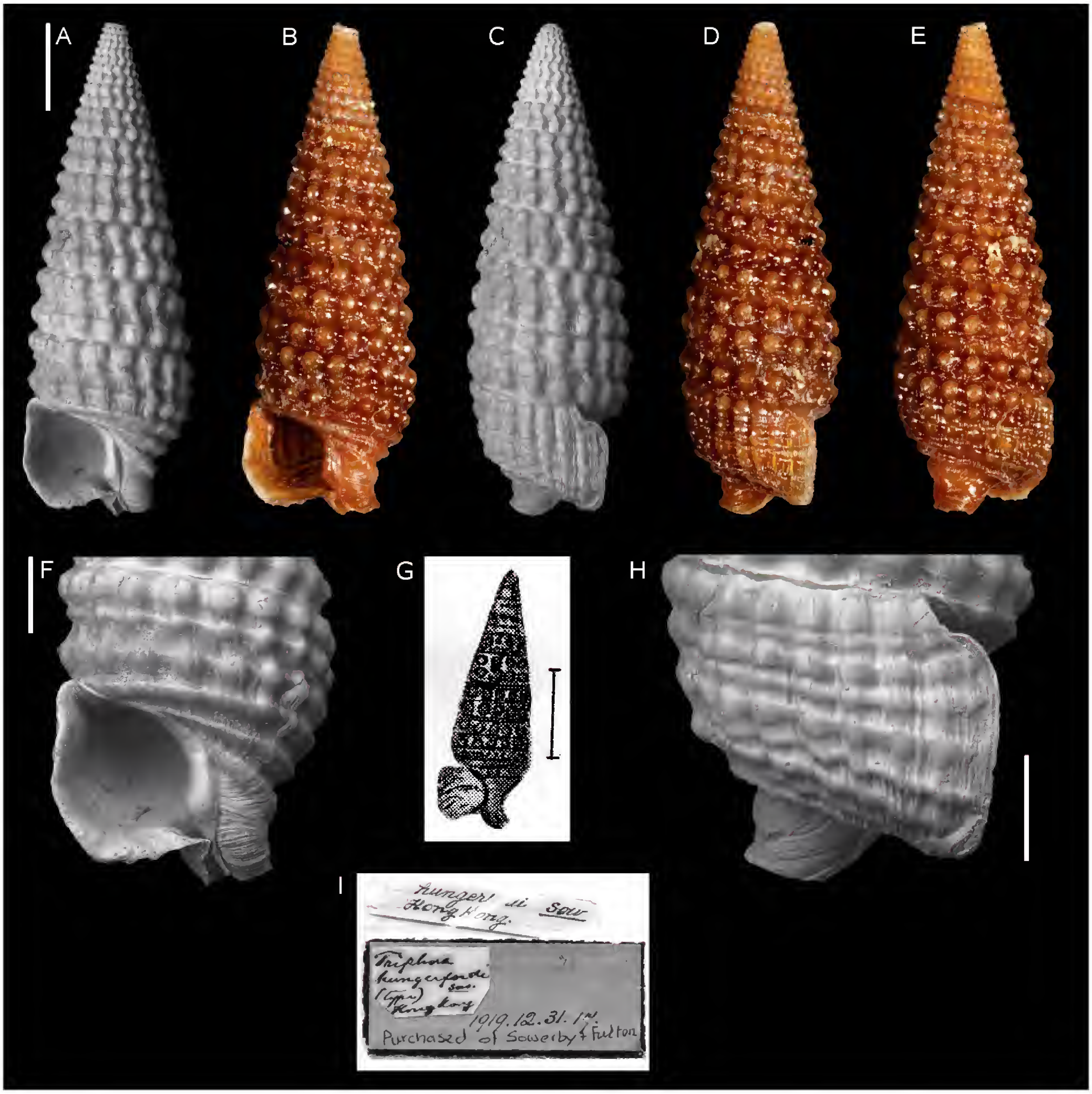

Figure 95. *Triphora hungerfordi* G.B. Sowerby III, 1914, Hong Kong. **A–F, H, I** Syntype NHMUK 1919.12.31.17: front (**A, B**), side (**C, D**), back (**E**), aperture (**F**), peristome (**H**), original labels (**I**). **G** Original figure. Scale bars: **A–E**: 1 mm; **F**, **H**: 0.5 mm.

Hab.—?

This is by far the largest known species of the genus. Unfortunately, with the unique specimen there is no indication of its habitat, but it is not improbable it may have been dredged off Ascension Island, as it was found in Admiral Keppel's cabinet in close proximity to shells so labelled. Besides its remarkable size, the shell is very distinct in character. The longitudinal brown pitted grooves intersect the spiral ridges, causing the most prominent ones to assume the form of transversely oblong nodules. There is a very small young shell of this species in the British Museum, from the Cuming Collection.

Translation of the Latin text. A straw-like very elongated sinistral shell posteriorly dark-brown with several a little obliquely longitudinal lines dark red in colour; about 40 flat whorls with longitudinal scars slightly slanting and pitted here and there, four pseudo-nodulose spiral cords somewhat irregular, unequal, being the two anterior more developed; last whorl rather sharply angulated at the base with a bicarinated edge, restricted and concave under the periphery, two rather strong carinae; bent long siphonal canal, subquadrate aperture; thin outer lip. Length 57, greater diameter 7 mm.

Diagnosis. Holotype 58 mm, among the largest Triphoridae. Extremely elongated conical shell, with

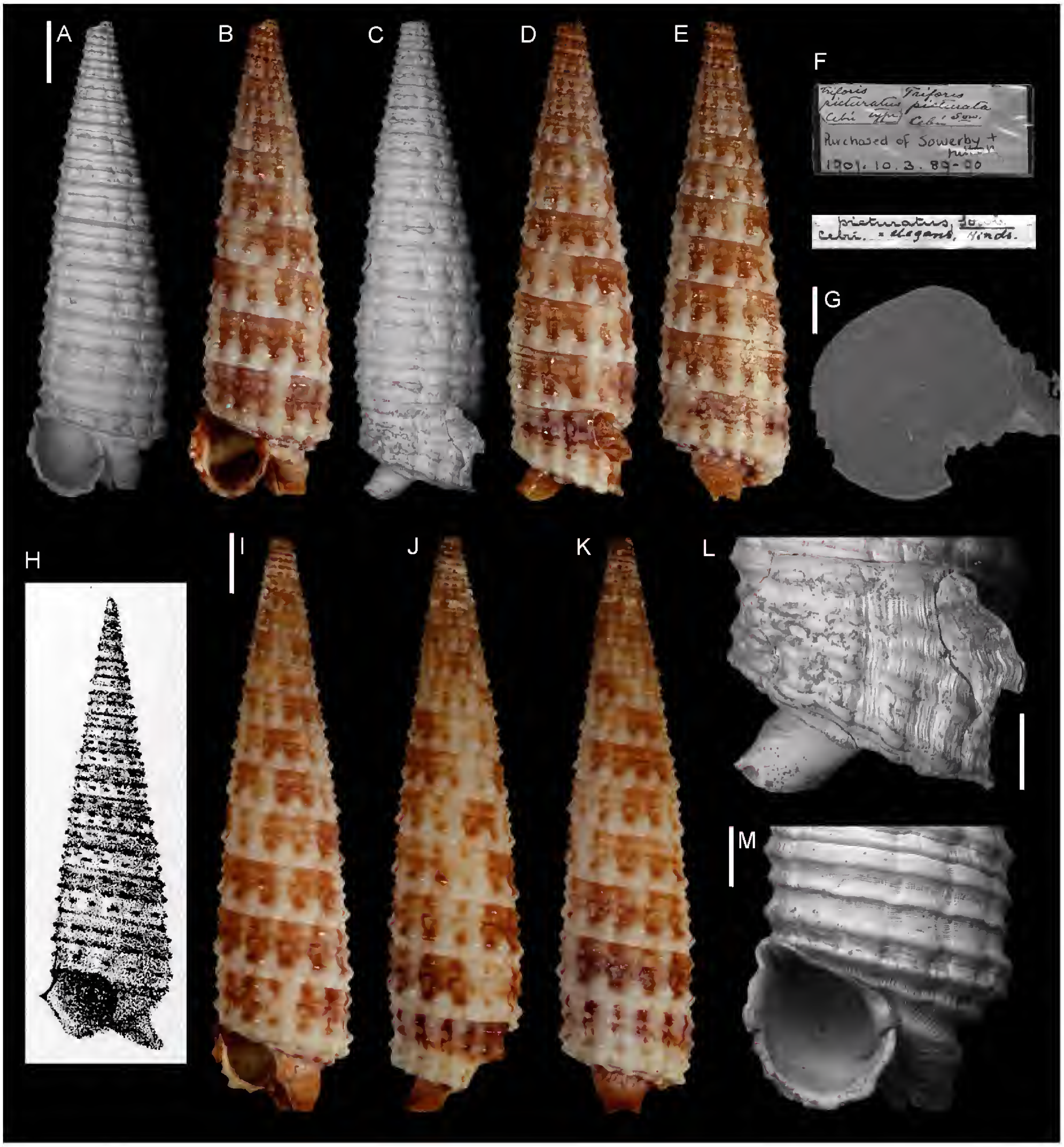

Figure 96. *Triforis picturatus* G.B. Sowerby III, 1901, Cebu Island, Philippines. **A–E, G, L, M** Syntype NHMUK 1901.10.3.89: front (**A, B**), side (**C, D**), back (**E**), operculum (**G**), peristome (**L**), aperture (**M**). **F** Original labels. **H** Original figure. **I–K** Syntype NHMUK 1901.10.3.90: front (**I**), side (**J**), back (**K**). Scale bars: **A–E, I–K**: 1 mm; **G**: 0.2 mm; **L, M**: 0.5 mm.

flat whorls. Teleoconch of ca 40 whorls, initially with three weakly nodulose spiral cords. In the lower part of the shell, a fourth cord between the second and third and a fifth suprasutural cord are visible, both weakly nodulose. The holotype is a subadult and, therefore, the peristome is not fully developed. Siphonal canal long with two smooth cords on it. Base with one prominent but weakly sculptured additional cord and two faint ones. Protoconch incomplete in the holotype, but may be paucispiral; the visible whorl has two strong smooth keels. Teleoconch elegantly coloured, with a brown background and white flammules, dark brown interspaces.

Remarks. The NHMUK 196547 specimen (Fig. 97F) is most likely the "very small young shell of this species in the British Museum, from the Cuming collection" cited by Sowerby as also S.P. Dance observed in 1965 (note on labels accompanying the specimen). However, this specimen has a coarser sculpture and different colour pattern and we do not consider it conspecific.

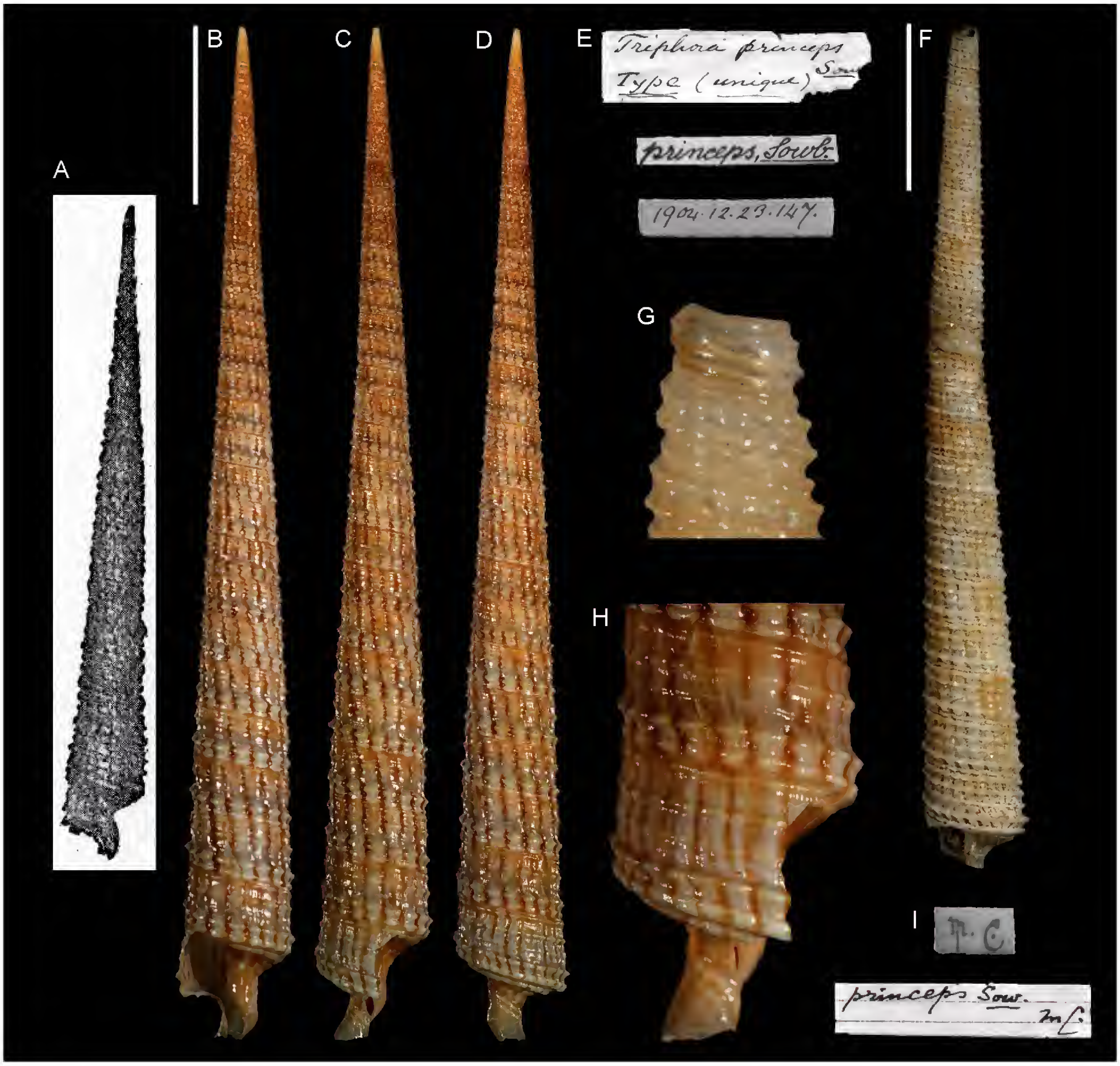

Figure 97. *Triphora princeps* G.B. Sowerby III, 1904, unknown locality. **A** Original figure. **B–E, G, H** Holotype, NHMUK 1904.12.23.147: front (**B**), side (**C**), back (**D**), original labels (**E**), protoconch (**G**), peristome (**H**). **F, I** Specimen NHMUK 196547 cited by Sowerby as "very small young shell" but belonging to a different species: front (**F**), original labels (**I**). Scale bars: **B–D**: 10 mm; **F**: 5 mm.

Triphora smithi G.B. Sowerby III, 1904

Figure 98

Triphora smithi G.B. Sowerby III 1904: 175, figured.

Type locality. Not reported.

Type material. Holotype: NHMUK 1904.12.23.146, fixed by monotypy.

Original description. *Testa elongato-acuminata, pallide, straminea, anfractus circiter 35, planulati, cingulis spiralibus 2–4 acutiusculis laevibus instructi, aliter laeviusculi; anfractus ultimus obtuse angulatus, ad angulum bicarinatus, infra angulum leviter convexus, triliratus; rostrum breviusculum, leviter contortum; apertura subquadrata; labrum tenue. Long. 33, diam. maj. 5 mm.*

Hab.—*?*

Although much smaller than *t. princeps,* this shell is larger than any other known species of the genus. It is broader in proportion to its length than *T. princeps*, and both the spiral ridges and the interstices between them are remarkably smooth, showing only irregular growth-lines. The specimen is at present unique.

Translation of the Latin text. A straw-like pale elongated sharp sinistral shell, about 35 plain whorls with 2–4 light and acute spiral cords differently slender; trilirate last whorl obtusely angulated with a bicarinate angle and a light convexity under it; bend siphonal canal rather short; subquadrate aperture; thin outer lip. Length 33, larger diameter 5 mm.

Diagnosis. Holotype 32 mm, but lacks the apex. Elongated conical shell with flat whorls. Teleoconch of 21 whorls (but the original description states 35, suggesting that the apical part may have got broken after the description). Whorls with three smooth spiral cords, the first smaller, but present since the early teleoconch. A fourth smooth suprasutural cord is also visible. Peristome not fully developed in the holotype. Siphonal canal long. Base with one additional smooth spiral cord. Protoconch missing. Teleoconch whitish with greyish interspaces between cords.

Remarks. The general appearance and sculpture is very similar to *T. gracilior* E.A. Smith, 1903, although the latter has orange flecks not observable in *T. smithi*. E.A. Smith (1916) suggested that *T. smithi* is a synonym of *T. gracilior*.

Species described by J.R. le B. Tomlin

Four species of Triphoridae were described by John Read le Brockton Tomlin. The type material of three of these species was found in the NHMUK: *Viriola alboguttata* Tomlin, 1926, *Triphora alexandri* Tomlin, 1931, and *T. hemileuca* Tomlin, 1931. No type material was found of *Euthymia latisinuata* Tomlin, 1931. *Triphora barnardi* Tomlin, 1945 was introduced as a *nomen novum* for *T. capensis* Thiele, 1925, which is preoccupied by *Triphoris capensis* Bartsch, 1915. The Tomlin collection was deposited in NMW (Trew 1990); we refrain from making any lectotype designations here until we are able to see that material.

Viriola alboguttata Tomlin, 1926

Figure 99

Viriola alboguttata Tomlin 1926: 294, pl. 16, fig. 7.

Original localities. Scottburgh and Port Shepstone, Natal, South Africa.

Type material. Syntypes: NHMUK 1926.12.6.7, Scottburgh, Natal, South Africa, 1 specimen (glued on paper); NMW 1955.158.1124, 1 specimen (fide Trew 1990; not seen).

Original description. Shell sinistral, consisting of 13½ whorls, 4½ of which form the protoconch; the whorls of the protoconch have an extremely sharp, central, raised keel, from each side of which numerous short, raised, waved lines run to the sutures at right angles; the other nine whorls have a series of three outstanding spiral cords equally spaced; the two outer cords are of much the same strength throughout, but the central one starts as quite a fine line and approximates gradually to the strength of the other two; the interstices between the cords are crossed at right angles by fine raised lines, which are more distant than those on the protoconch and not waved.

The colour of the protoconch is dark reddish, that of the rest of the shell light chocolate brown, the uppermost of the 3 spiral cords being spotted broadly with white at regular intervals—about 4 or 5 times on each whorl.

At the summit of the aperture there is a strong sinus, and the interior is marked with three pairs of brown lines running outwards to the edge of the peristome.

Length 5 mm., max. diam. 1.75 mm.

Hab.—Scottburgh (C.W. Alexander), apparently living; Port Shepstone (Burnup).

This distinct little species belongs, together with *ima* Bartsch and *fuscescens* Smith, to Jousseaume's genus *Viriola*, which is exactly analogous to *Seila* in having a spiral ribs plain, without tubercles.

Diagnosis. Syntype 4.4 mm high. Shell conical with flat sides. Teleoconch of eight whorls with three smooth spiral cords. The second cord develops initially as a fine thread and attains full size only on the last whorl. Among the spiral cords, orthocline obsolete axial ribs are visible. Peristome with additional spiral cords and a pronounced posterior sinus. Siphonal canal short. Base with four additional smooth spiral cords. Protoconch multispiral of five whorls; the first two with tiny granules, the last three with a strong spiral keel and axial riblets. Colour brown with white blotches more pronounced on the first spiral cord.

Remarks. *Viriola fallax* Kay, 1979 (p. 215) is a junior synonym.

Triphora alexandri Tomlin, 1931

Figure 100

Triphora alexandri Tomlin 1931: 425–426, pl. 33, fig. 3.

Type locality. Umhlali, Natal, South Africa.

Type material. Syntypes: NHMUK 1931.7.23.8: 1 specimen, South Africa.

Original description. Shell with 15½ whorls, whereof 1½ are protoconch—the extreme apex is missing and would probably add one more whorl to protoconch; what is left shows a sharp, central keel with rather distant axial lines. This sculpture gradually develops on the postnuclear whorls into two rows of very regular tubercles, the upper row pale brown and the lower white; the last seven whorls have three rows, of which the upper two are pale brown; the white row throughout is obviously the strongest. Sutures marked by a raised line; periphery with a tubercled keel; base pale brown, with 3 keels encircling the canal; canal reflexed.

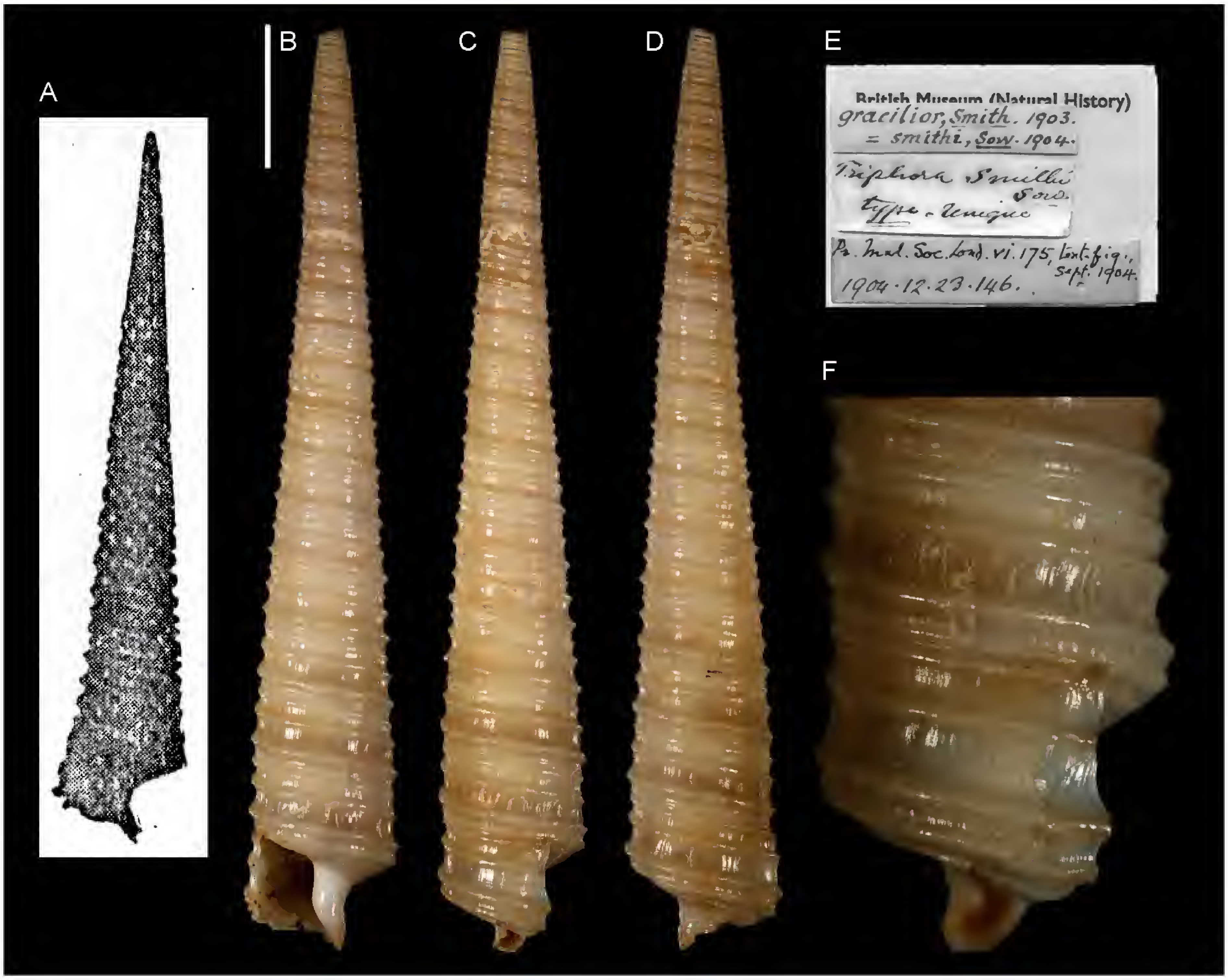

Figure 98. *Triphora smithi* G.B. Sowerby III, 1904, unknown locality. **A** Original figure. **B–F** Holotype, NHMUK 1904.12.23.1476: front (**B**), side (**C**), back (**D**), original labels (**E**), peristome (**F**). Scale bar: **B–D**: 5 mm.

Alt. 8.75 mm.; diam. max. vix 2 mm.
Hab.—Umhlali (Alexander).
Readily distinguished by its coloration.

Diagnosis. Available syntype 7.4 mm high. Shell cyrtoconoid. Teleoconch of 13 whorls with three spiral cords bearing tubercles at the intersection with prosocline axial ribs. Suture deep. Peristome incomplete without additional spiral cords. Posterior sinus not observable. Siphonal canal long. Base with three narrow, almost smooth spiral cords. Protoconch broken in the available syntype, but its last whorl is present and suggests a multispiral type with one spiral keel and axial riblets. Background teleoconch colour light brown, with lighter tubercles and white third spiral cord and first two teleoconch whorls. The remaining protoconch whorl light brown.

Remarks. The original figure closely matches with this specimen, including also in having the protoconch incomplete. No other type specimens were reported in the NMW (Trew 1990).

Triphora hemileuca Tomlin, 1931

Figure 101

Triphora hemileuca Tomlin 1931: 426, pl. 33, fig. 4.

Type locality. Port Shepstone, Natal, South Africa.

Type material. Holotype: NHMUK 1931.7.23.6, fixed by monotypy.

Original description. Shell with a protoconch of 3 whorls, which are irregularly crossed by axial riblets; protoconch and next three whorls cream-white, last six whorls brown-black; there are twelve whorls in all, of which nos. 4 to 7 have a prominent central keel, cut into tubercles by numerous axial riblets, and fine spi-

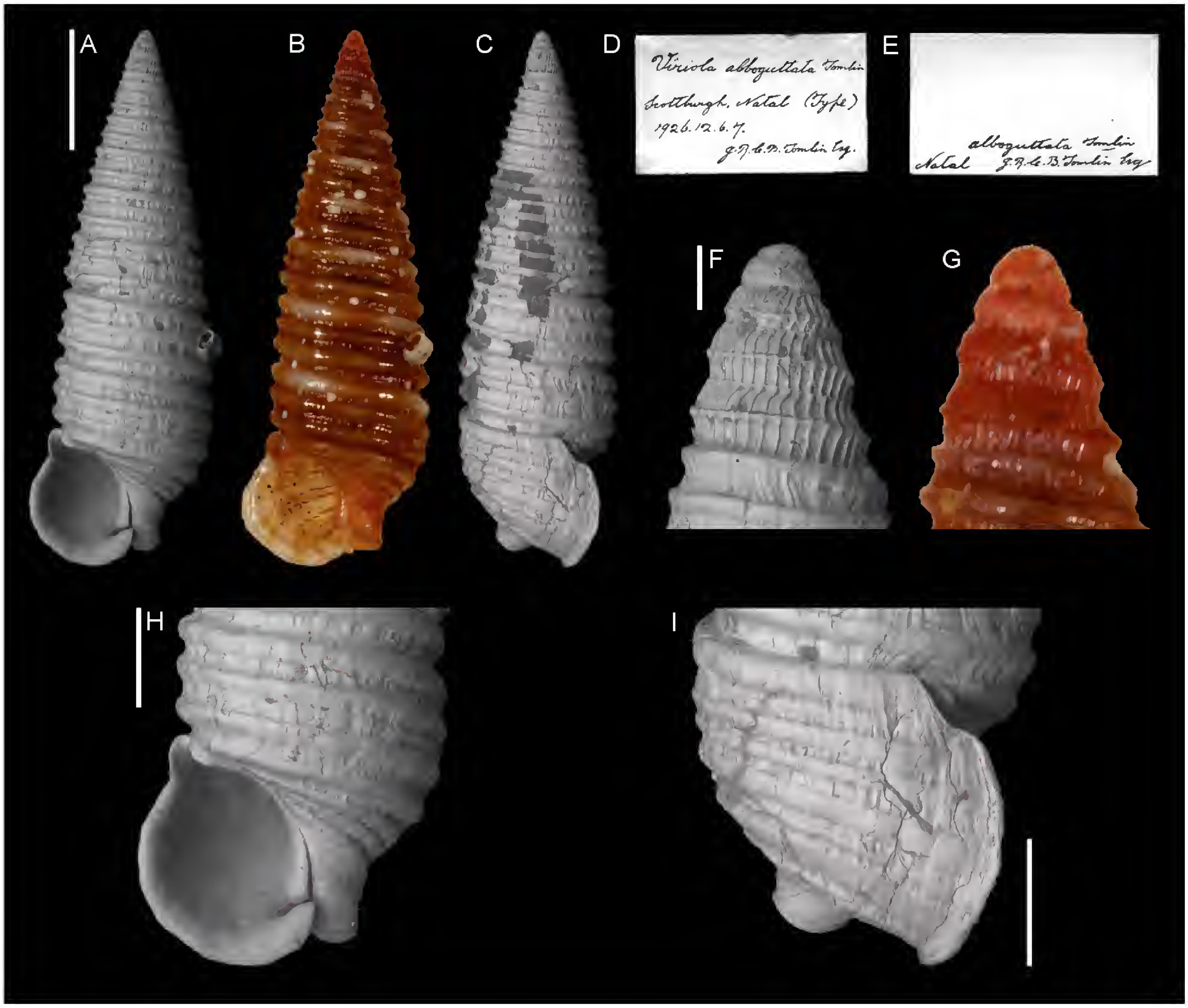

Figure 99. *Viriola alboguttata* Tomlin, 1926, Scottburgh, Natal, South Africa. **A–C, F–I** Syntype NHMUK 1926.12.6.7: front (**A, B**), side (**C**), protoconch (**F, G**), aperture (**H**), peristome (**I**). **D, E** Original labels. Scale bars: **A–C**: 1 mm; **F, G**: 0.1 mm; **H, I**: 0.5 mm.

ral lines above and below the keel. The last five whorls have three tuberculiferous keels, one immediately below the suture, and two on the lower half of the whorl very close together and only separated by a fine groove, the interspaces being filled with fine spirals as before. Periphery sharply keeled; base of shell and canal much lighter brown.

Alt. 6 mm.; diam. max. 1.5 mm.

Hab.—Port Shepstone (Burnup).

This specimen is unique, but is so extraordinarily perfect in every way that I do not hesitate to describe it. There is the usual raised line round the suture, and a considerable interval between the uppermost keel and the two lower ones on each whorl. The coloration will at once be recognizable.

Diagnosis. Holotype height 5.4 mm. Shell cyrtoconoid, with eight weakly rounded teleoconch whorls with three spiral cords. The second develops on the fourth whorl. Tubercles are present at the intersection with orthocline axial ribs. Two or three fine spiral threads are visible in the interspace between the main spiral cords. Peristome with a moderately deep posterior sinus and no additional spiral cords. Siphonal canal short. Base with two additional weakly tubercled spiral cords. Protoconch paucispiral with 2.5 whorls with wavy thick axial ribs and interspaces smaller than the ribs. Colour deep brown. The proconch and the first two teleoconch whorls are pure white.

Remarks. No other type specimens were reported for the NMW (Trew 1990).

Species described by W.H. Turton

William H. Turton deposited large sets of his South African collections in the OUMNH in Oxford including "… the *Types* of the 625 new species and varieties, which I have named myself…" (Turton 1932: xiv). Turton depos-

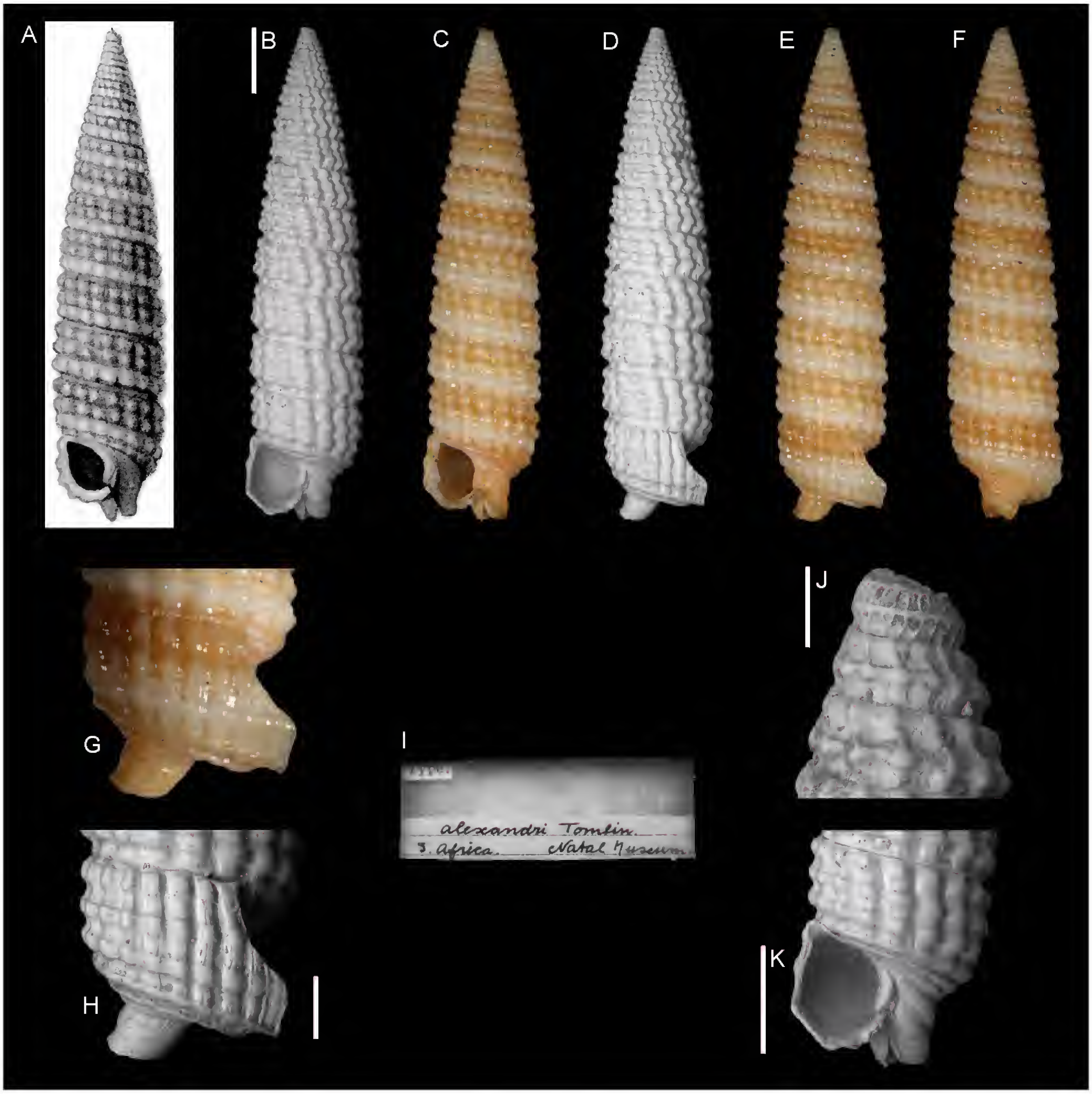

Figure 100. *Triphora alexandri* Tomlin, 1931, Umhlali, S. Africa. **A** Original figure. **B–H, J, K** Syntype NHMUK 1931.7.23.8: front (**B, C**), side (**D, E**), back (**F**), peristome (**G, H**), protoconch (**J**), aperture (**K**). **I** Original label. Scale bars: **B–F, K**: 1 mm; **G, H**: 0.5 mm; **J**: 0.2 mm.

ited material at the USNM and repeatedly tried to send shells to the NHMUK, but they were often refused with his great disappointment. Eventually, however, he managed to send material to the NHMUK (Turton 1932: x). Unfortunately, the type material of his South African triphorids was prepared for loan to the first author in 2014 but the package apparently never left the Museum and was not found any more. All types should be regarded as lost (S. De Grave pers. comm. October 2015). Therefore, we here illustrate and describe the lots of Turton's species present in the NHMUK; such shells, however, shall not be considered type specimens, because Turton clearly stated that the the type material was sent to Oxford. We found specimens of three species: *T. apicibulbus* Turton, 1932, *T. retusa* Turton, 1932, and *T. rufanensis* Turton, 1932.

Triphora apicibulbus Turton, 1932

Figure 102

Triphora apicibulbus Turton 1932: 118, pl. XXV, fig. 863.

Type locality. Port Alfred, South Africa.

Type material. OUMNH: lost.

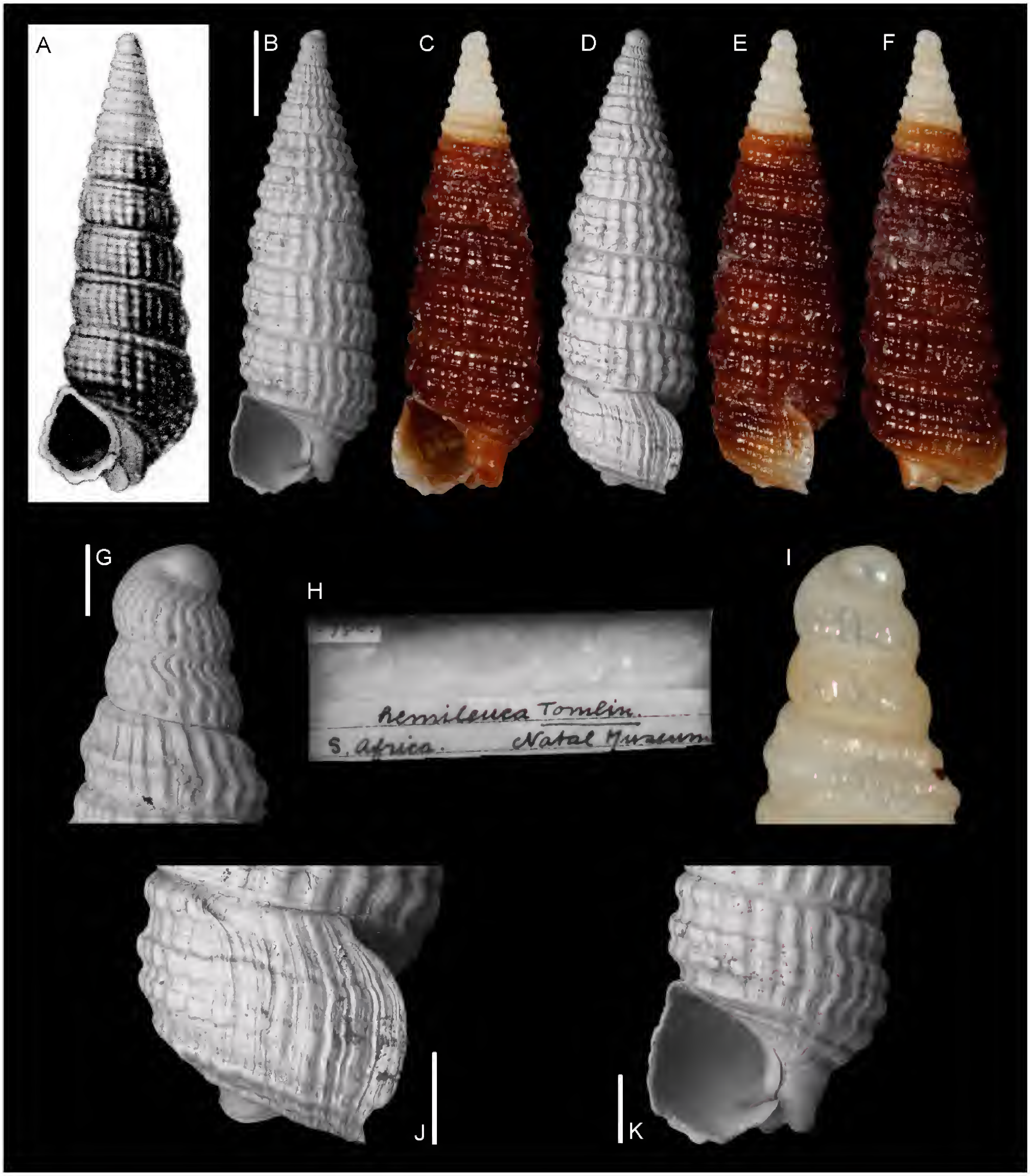

Figure 101. *Triphora hemileuca* Tomlin, 1931, South Africa. **A** Original figure. **B–G, I–K** Holotype, NHMUK 1931.7.23.6: front (**B**, **C**), side (**D, E**), back (**F**), protoconch (**G, I**), peristome (**J**), aperture (**K**). **H** Original label. Scale bars: **B–F**: 1 mm; **G, I**: 0.2 mm; **J, K**: 0.5 mm.

Additional material. NHMUK 1933.9.4.34–36: 3 specimens, Port Alfred, South Africa (coll. W.H. Turton).

Original description. *The* shape *of the shell is narrowly conic; 1 minute and 2 bulbous nuclear whorls, the remaining 8 very slightly globular. The* surface *is marked by 3 rows of tubercles on each whorl, and there are 2 basal cords. The* colour *is white, except the base, which is light brown. The* size *of the type is 6 ×1.5 mm. The shell grows up to 8 mm, but the larger ones do not show the sculpturing so plainly.* Characteristics. *Near 860, [Triphora] madria, though wider, with only 2 basal cords. It is wider than 858, [Triphora] innocens. But the brown colour at the base best distinguishes it; and also the very bulbous protoconch, the last nuclear whorl being larger than the succeeding one. This gives it a curious appearance, and*

I think justifies the name. It is true that [T.] madria has something like it, as noticed by Bartsch, but not nearly so pronounced. I attach two photos, the smaller shell, 4 mm, showing this better than the other.

Diagnosis. Height range 5.5–6.1 mm. Shell slightly cyrtoconoid, with flat sides. Teleoconch of ca 10 whorls with three strong spiral cords, all visible since the first whorl, with coalescent tubercles which on the last whorls look like continuous bands. Siphonal canal short. Base with two-three additional smooth spiral cords. Paucispiral protoconch of 1.5 whorls, apparently smooth but the specimens are worn. Shell white in colour.

Triphora retusa Turton, 1932

Figure 103

Triphora retusa Turton 1932: 117, pl. XXV, fig. 855.

Type locality. Port Alfred, South Africa.

Type material. OUMNH: lost.

Additional material. NHMUK 1933.9.4.37: 1 specimen, Port Alfred, South Africa (coll. W.H. Turton).

Original description. *The* shape *is broadly conic; 1 very small nuclear whorl, with 5 others nearly straight; aperture large, nearly circular, and rather projecting; apex very blunt. The* surface *is covered with 3 rows of tubercles on each whorl. The* colour *is yellowish brown; and the* size *2 × 1 mm.* Characteristics. *A little shell near [Triphora] sabita but smaller, more broadly conic, with a much blunter apex, and more projecting aperture. Though so small it seems to be full-grown, as I found about a dozen specimens, the type being the largest.*

Diagnosis. Specimen 1.1 mm high, but it is clearly a juvenile with just three post-metamorphic whorls, which bear two spiral cords with granules at the intersection with faint orthocline axial ribs. Paucispiral protoconch of one whorl, apparently smooth, but very worn. Shell brown in colour.

Triphora rufanensis Turton, 1932

Figure 104

Triphora rufanensis Turton 1932: 118, pl. XXV, fig. 862.

Type locality. Port Alfred, South Africa.

Type material. OUMNH: lost.

Additional material. NHMUK 1933.9.4.22–23: 2 specimens, Port Alfred, South Africa (coll. W.H. Turton).

Original description. *The* shape *of the shell is narrowly conic; with rather a blunt apex; 1 nuclear whorl, broken, and 10 others which are straight. The* surface *is marked by 3 nodulous cords on each whorl, and there are 3 basal cords. The* colour *is white, and glistening; and the* size *5 × 1.6 mm.* Characteristics. *It is near 869, whitechurchi, but more broadly conic, and much smaller.*

Diagnosis. The available specimen is 4.7 mm high, but subadult. Conical shell with flat sides. Teleoconch of eight whorls with three spiral cords clearly visible since the first whorl and with nodules at the intersection with the slightly prosocline axial ribs. Peristome not preserved and the specimen is subadult, thus without base. Apex badly worn, but apparently paucispiral of 1.5 whorls which bears three smooth spiral cords on after the first half whorl. White shell with small brown marks.

Species described by J.C. Verco

Joseph C. Verco introduced 16 new triphorid names. In the NHMUK, we found specimens of eight species. Although Verco donated his collection to the South Australian Museum (Dance 1966; Cotton 1933), he sent some specimens to the NHMUK, as reported in the museum's register. This register contains entries of several families, suggesting that Verco sent several lots of many taxa to the NHMUK, as reported by E.A. Smith (1906) for some "Pleurotomidae" (Turridae s.l.). Verco often listed several specimens as part of the type series. Moreover, some labels and register entries report that the shells in the NHMUK are "co-types", which shall be considered syntypes according to Article 72.4.6 of the Code (ICZN 1999). In his work on South Australian Triphoridae, Marshall (1983) discussed most of Verco's names but probably was not aware of these syntypes. Most of Marshall's "holotype" records are actually lectotype designations according to Article 74.6 of the Code (ICZN 1999), and the syntypes are now paralectotypes according to Article 74.1.3. Marshall included accurate descriptions; therefore, we refrain here from adding additional diagnostic notes.

Triphora armillata Verco, 1909

Figure 105

Triphora armillata Verco 1909: 283–284, pl. XXII, fig. 5.

Type locality. Gulf St Vincent, South Australia.

Type material. Lectotype: SAM D.13448 (fide Marshall 1983; not seen, see Remarks). Paralectotypes: NHMUK 1910.3.29.40–42, 3 specimens, Gulf St Vincent, South Australia.

Original description. *Shell solid, elongate-conic. Protoconch of 4 whorls, convex, centrally carinate, the fourth with two approximate carinae; crowded fine axial bars, concave forward above the carinae, straight below. Spire-whorls twelve, sloping, the first four with two spiral rows*

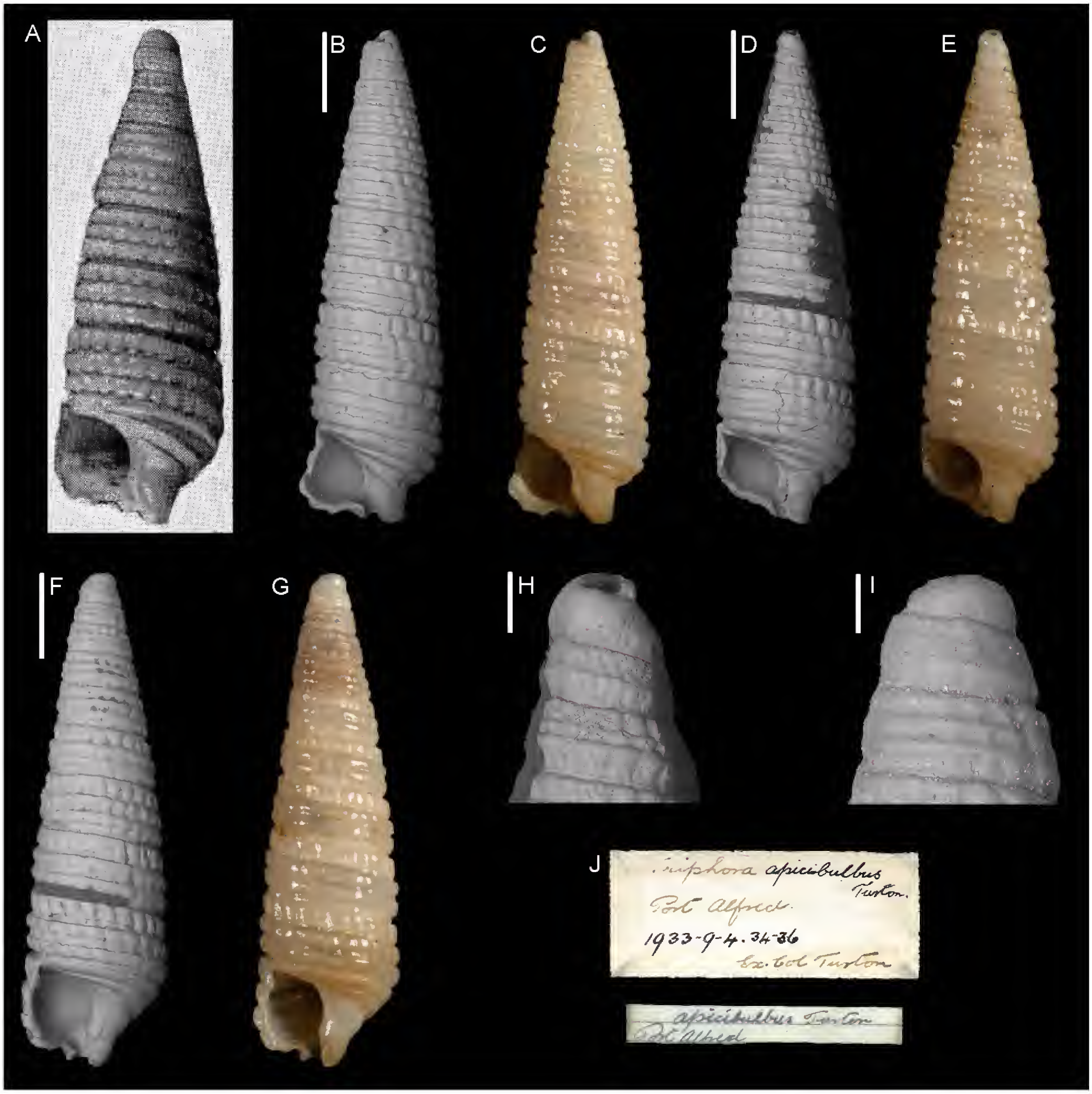

Figure 102. *Triphora apicibulbus* Turton, 1932, Port Alfred, South Africa, NHMUK 1933.9.4.34–36. **A** Original figure. **B, C** NHMUK 1933.9.4.34: front. **D, E, H** NHMUK 1933.9.4.35: front (**C, D**), protoconch (**H**). **F, G, I** NHMUK 1933.9.4.36: front (**F, G**), protoconch (**I**). **J** Original labels. Scale bars: **B–G**: 1 mm; **H, I**: 0.2 mm.

Figure 103. *Triphora retusa* Turton, 1932, Port Alfred, South Africa. **A, B** NHMUK 1933.9.4.37. **C** Original labels. **D** Original figure. Scale bar: **A, B**: 0.3 mm.

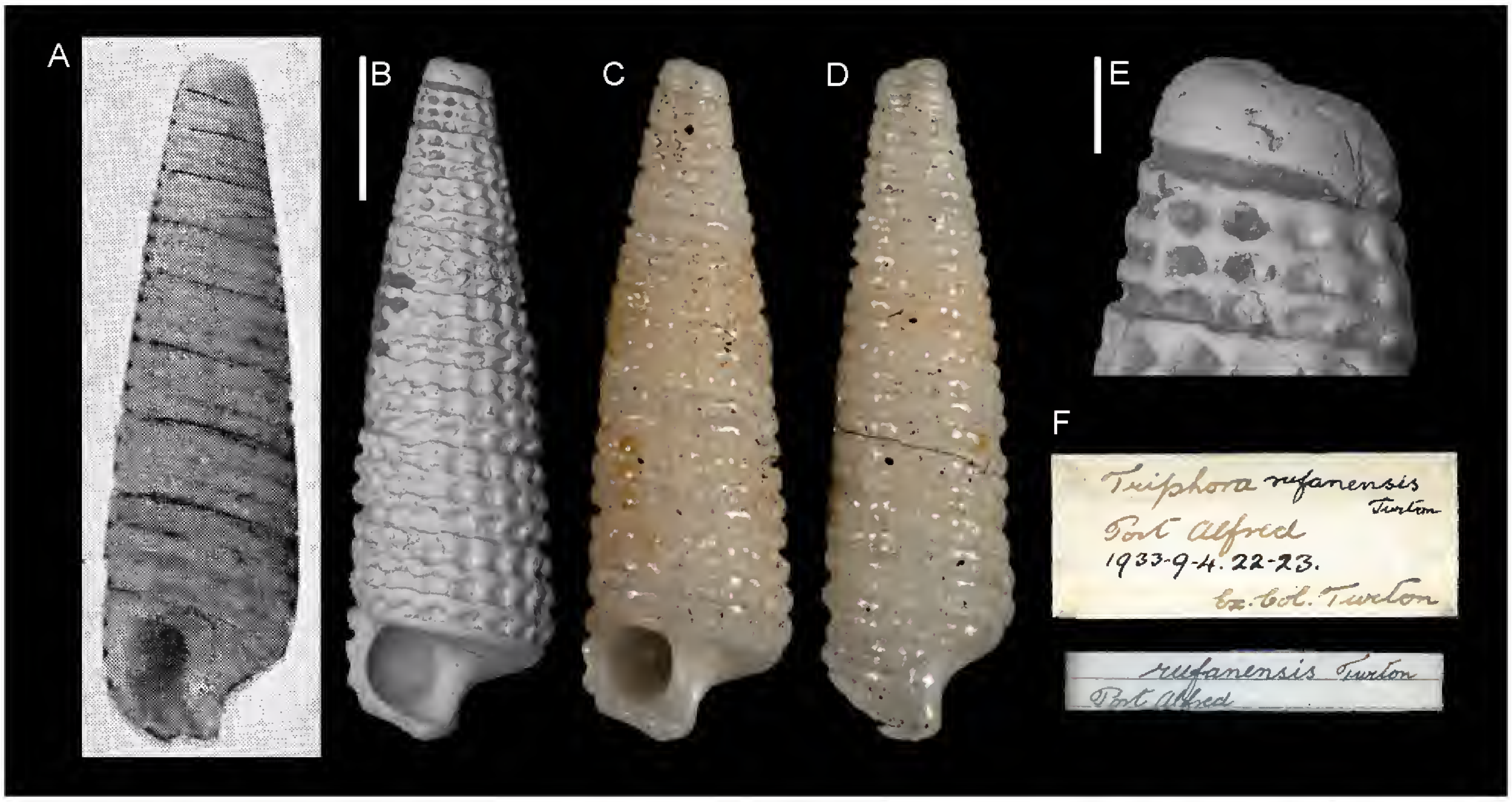

Figure 104. *Triphora rufanensis* Turton, 1932, Port Alfred, South Africa. **A** Original figure. **B–F** NHMUK 1933.9.4.22: front (**B**, **C**), side (**D**), protoconch (**E**), original labels (**F**). Scale bars: **B–D**: 1 mm; **E**: 0.2 mm.

of pearls; in the fifth a lira appears between them, and becomes gradually as large as the others; the tubercles are large, about twenty in a row in the penultimate, joined by short bars transversely, and by narrower axial bars directed obliquely forwards towards the lower suture. Sutural spaces distinct, as wide as a pearl row; in the eighth a supra-sutural thread arises, which grows distinct and slightly tuberculate. Base flatly convex, with the sutural lira, and two basal lirae; the first with valid transversely oval tubercles, joined by very broad axial bands to much lower tubercles in the second, and by vanishing bands to the nearly smooth third lira. Aperture round, pinched at the suture into a sinus, and with a short well recurved canal in front; outer lip thin, simple, slightly reflected at its margin, retrocurrent at the suture, crossing the columella in front and flattened out over the base of the canal, so as to close it here. The outer lip has eight nodulous spirals on its outer surface, viz., *three as on the spire, the peripheral and one basal, and three others intercalated on the bodywhorl. Colour, protoconch light-brown, shell white, but for the fifth and sixth whorls which are dark-brown, so as to form a sort of bracelet, whence the name.*

Dim.—*Length, 7,9 mm.; breadth, 2,2 mm.*

Locality.—*Type, Gulf St. Vincent, dredged in 20 fathoms, with many other good ones; also in 6 and in 15 to 20 fathoms off St. Francis Island, 9 good in each; in 22 fathoms, Investigator Strait, 2 good and 4 poor; in 22 fathoms, outside Backstairs Passage, 3 poor; in 40 fathoms off Beachport, 2 moderate, 3 poor; in 55 fathoms off Cape Borda, 4 poor. Also taken on the beach in Gulf St. Vincent, Venus and Scales Bay, West Coast, and many and good on St. Francis Island. It is a shallow-water species, ranging up to about 40 fathoms.*

Remarks. Verco referred to a type series consisting of multiple specimens in the original description of *T. armillata*. Marshall (1983) reported the "holotype" in SAM, but this should be considered a lectotype designation according to Article 74.6 of the Code (ICZN 1999). The NHMUK collection register reports the type locality and the wording "Co-types", which suggests that the accompanying specimens are part of the type series. Because of Marshall's lectotype designation, these and all other syntypes are now paralectotypes.

Triphora tasmanica var. *lilacina* var. *aureovincta* Verco, 1910

Figure 106

Triphora tasmanica var. *lilacina* var. *aureovincta* Verco 1910: 126, not illustrated.

Type locality. "off Cape Borda" (Kangaroo Island, South Australia).

Type material. Holotype: SAM D.13444, fixed by monotypy (not seen, fide Marshall 1983).

Additional material. NHMUK 1911.8.12.3–4: 2 specimens (glued on cardboard), Rottnest Is. Western Australia.

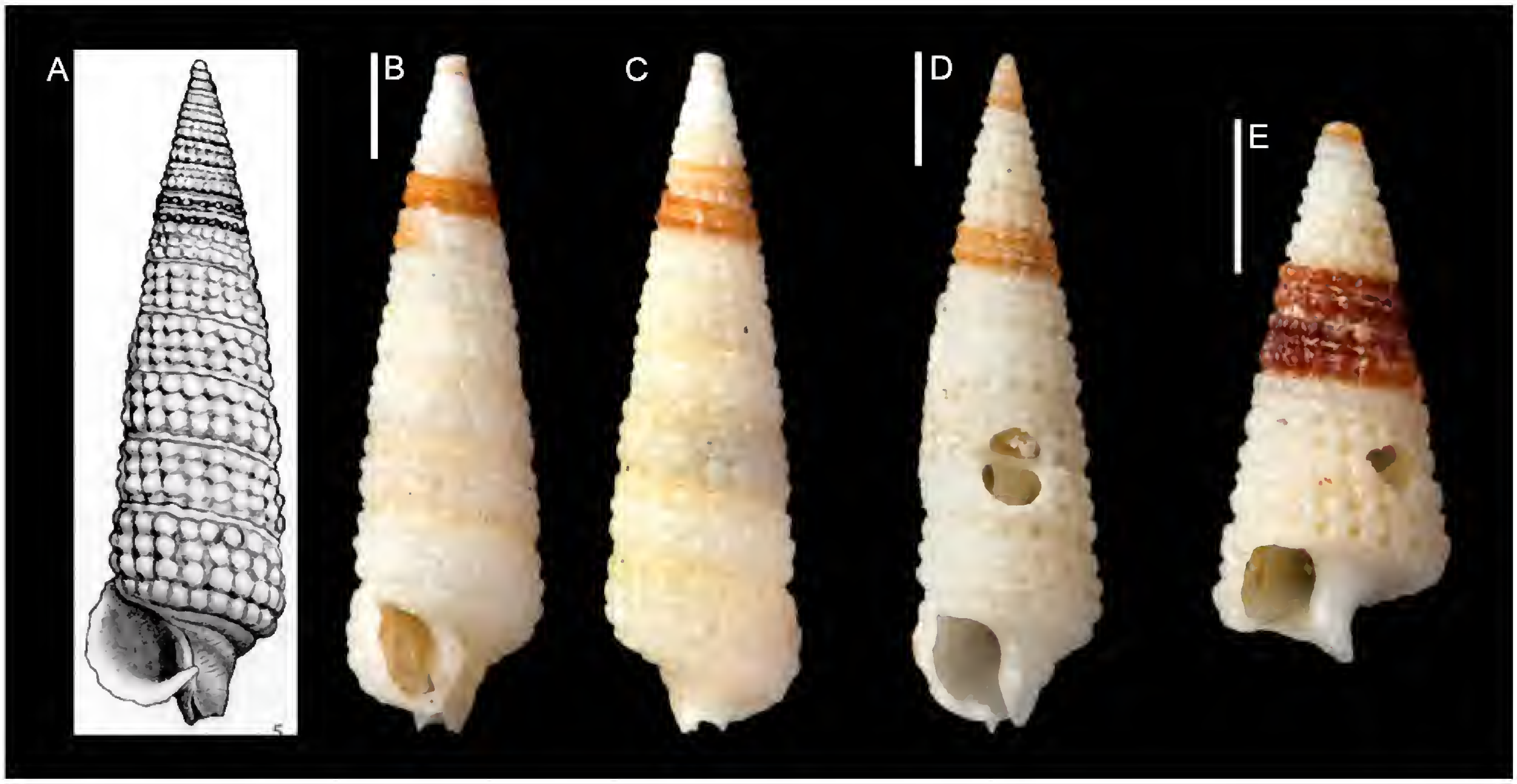

Figure 105. *Triphora armillata* Verco, 1909, Gulf St. Vincent, South Australia. **A** Original figure. **B, C** NHMUK 1910.3.29.40: front (**B**), back (**C**); **D** NHMUK 1910.3.29.41: front; **E** NHMUK 1910.3.29.42 front. Scale bar: 1 mm (photo courtesy: Kevin Webb, NHMUK Photographic Unit).

Original description. *This exquisitely pretty little shell was taken in perfect condition in 55 fathoms off Cape Borda.*

It has a golden band like T. regina, *Hedley, but instead of colouring the most anterior spiral of pearls, it ornaments the smooth spiral plait in front of this, and so is found in the suture and on the base of the body-whorl. Its protoconch is that of* T. tasmanica, *and has not the spicular form of* T. regina. *It is very deeply-coloured purple, like the var.* lilacina, *Verco. One example, perfect, of eight whorls, was taken.*

Type in my collection.

Remarks. Marshall (1983) considered this variety a valid taxon: *Isotriphora aureovincta*. Because the original description clearly refers to a single specimen examined at the time of description, Marshall's record of the holotype is correct and the material in the NHMUK does not belong to the type series.

Triphora cana Verco, 1909

Figure 107

Triphora cana Verco 1909: 289, pl. XXIII, figs 2–4.

Type locality. "Gulf St. Vincent" (South Australia).

Type material. Lectotype: SAM D. 13439 (fide Marshall 1983; not seen, see Remarks). Paralectotypes: NHMUK 1910.3.29.43–44: 2 specimens, Gulf St. Vincent, South Australia.

Original description. *Shell sinistral, solid, of 12 whorls, elongate-conical. Protoconch slightly mamillate, of two whorls; the second the larger, convex, with sigmoid axial bars, 16 in a whorl. Spirewhorls, the first with one nodulous carina, the second with two, the third with three, the last arising between the other two. Whorls sloping, the last three subconvex. Sutural space distinct, with a supra-sutural thread in the last six spaces, remaining nearly smooth. Tubercles close, about 18 in the penultimate, joined transversely and axially (obliquely forwards) by stout bars which lattice the surface. Aperture roundly rhomboidal, scarcely pinched behind. Outer lip slightly retrocurrent towards the suture; basal lip in contact with the erect, solid inner lip, and crossing the columella, where it closes in the short recurved notched, otherwise open canal. Base flatly convex, bounded by the nearly smooth peripheral lira, with a second smooth basal lira and a third encircling the base of the canal. The protoconch and first four spire-whorls are white, the rest light-brown.*

Dim.—*Length, 71 mm.; breadth, 2.1 mm.*

Locality. —*Type, Gulf St. Vincent, depth unrecorded, with 15 good and 34 moderate examples; 35 fathoms, St. Francis Island, 1 good; 40 fathoms off Beachport, 1 good and 1 poor; 55 fathoms off Cape Borda, 3 good and 5 poor; 62 fathoms off Cape Borda, 1 moderate and 3 poor; 110 fathoms off Beachport, 2 moderate; St. Francis Island beach, 5 good, 1 poor.*

The species varies a great deal—

1. In colour. The first six whorls may be white, and all the rest a blackish-brown. The first three whorls (in-

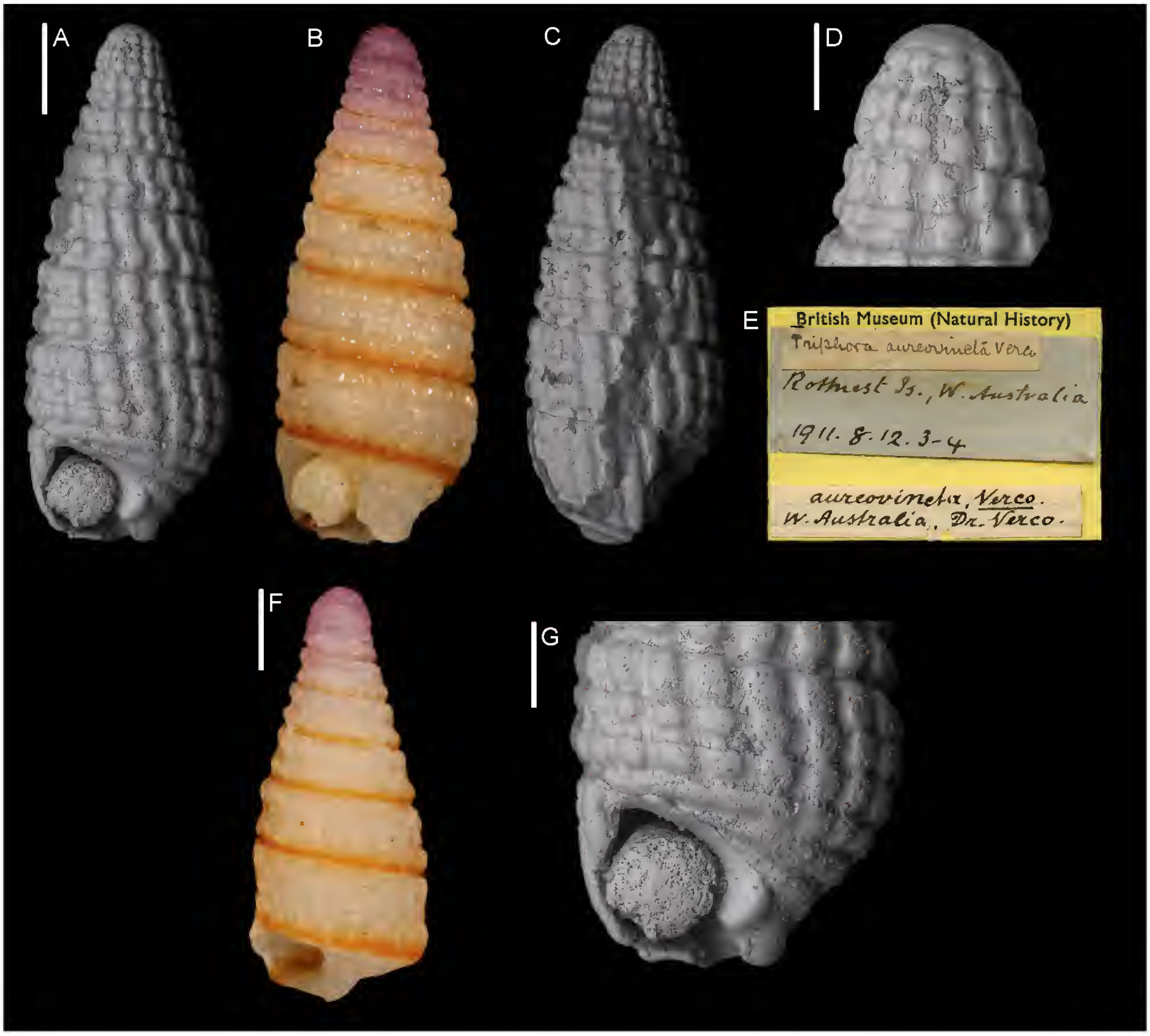

Figure 106. *Triphora tasmanica* var. *lilacina* var. *aureovincta* Verco, 1910, Rottnest Is., Western Australia. **A–D, G** NHMUK 1911.8.12.3: front (**A, B**), side (**C**), protoconch (**D**), aperture (**G**). **E** Original labels. **F** NHMUK 1911.8.12.4: front (**F**). Scale bars: **A–C, F**: 0.5 mm; **D**: 0.2 mm; **G**: 0.3 mm.

cluding the protoconch) may be dark-brown, and all the rest light-brown, with no white whorls. The three apical whorls may be brown, the next three white, and the rest brown, so connecting the previous shell with the type. The three apical whorls may be brown, and the seven remaining whorls quite white. The infra-sutural pearl row in the coloured portion may be dark-purple or barely tinted, the others brown, or the highest and lowest row may be purple and the central brown.

2. In shape. In most examples, though not in the type, the posterior pearl row becomes larger than the others, the pearls being greater, and consequently closer, and are somewhat axially elongate. When this is marked the whorl may be wider below the suture than above it, so as to give a more or less gradate appearance to the whorls.

Remarks. Verco referred to a type series consisting of multiple specimens in the original description. Marshall (1983) reported of the "holotype" in SAM but this specimen should be considered a lectotype according to Article 74.6 of the Code (ICZN 1999). The label accompanying this lot reports the type locality and the wording "Cotypes", which suggests that the accompanying specimens indeed belong to the type series. Because of Marshall's lectotype designation, these and all other syntypes are now paralectotypes.

Triphora latilirata Verco, 1909

Figure 108

Triphora latilirata Verco 1909: 283, pl. XXVI, fig. 1.

Type locality. "Gulf St. Vincent" (South Australia).

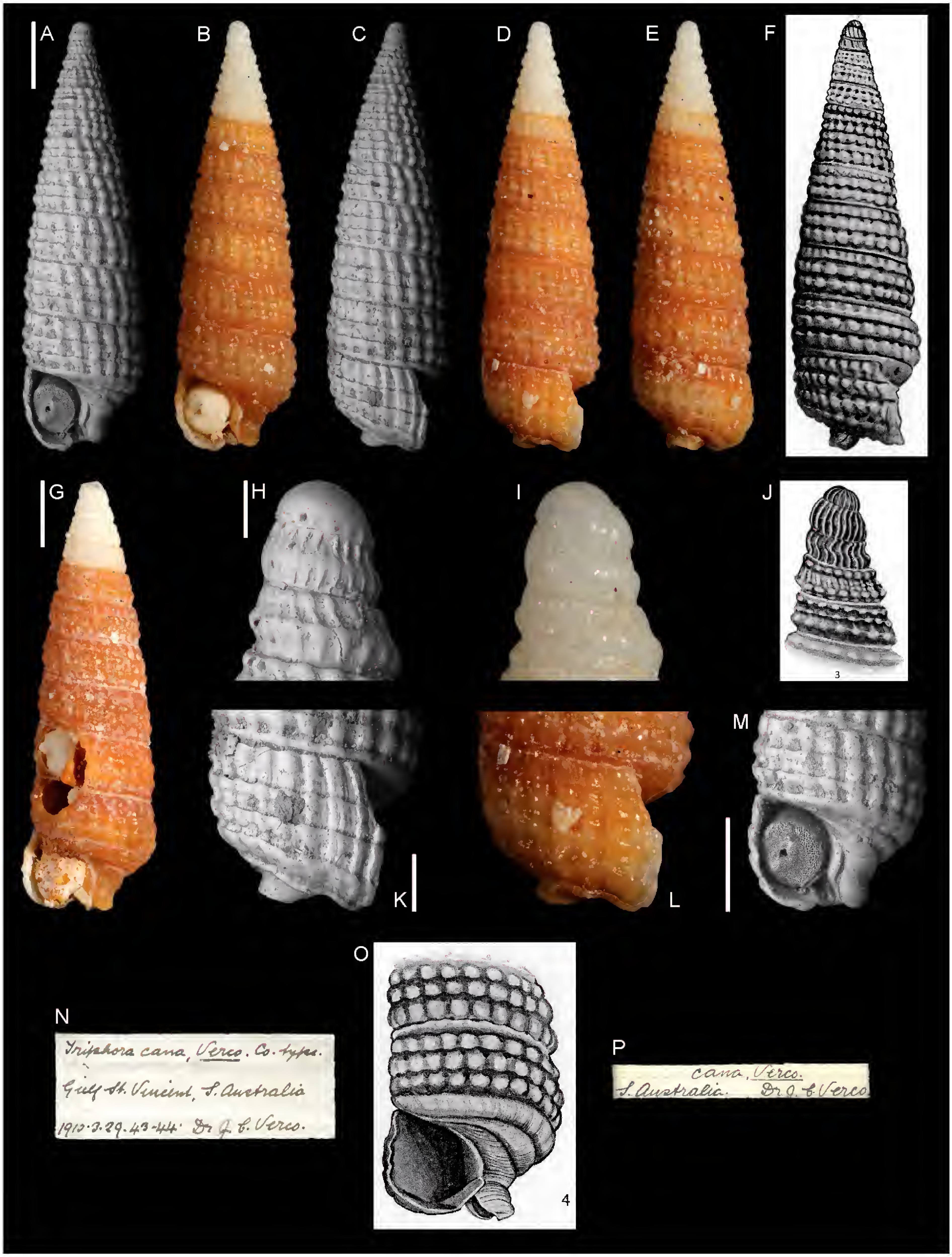

Figure 107. *Triphora cana* Verco, 1909, Gulf St. Vincent, South Australia. **A–E, H, I, K–M** Paralectotype, NHMUK 1910.3.29.43: front (**A, B**), side (**C, D**), back (**E**), protoconch (**H, I**), peristome (**K, L**), aperture (**M**). **G** Paralectotype, NHMUK 1910.3.29.44: front. **F, J, O** Original figures. **N, P** Original labels. Scale bars: **A–E, G, M**: 1 mm; **H, I**: 0.2 mm; **K, L**: 0.5 mm.

Type material. Lectotype: SAM D. 13447 (fide Marshall 1983; not seen, see Remarks). Paralectotype: NHMUK 1910.3.29.45: 1 specimen, Gulf St Vincent, South Australia.

Original description. *Shell sinistral, solid, elongate-conic. Protoconch of 5 whorls, smooth and round. Spire-whorls 13, flat, sloping; suture rather wider than the spaces between the spiral ribs. Spirals 3, flat, wide, nearly smooth on the surface; interstices narrow, pimctated by close-set axial incisions, which also cut the sides of the lirae. Body-whorl rhomboidal, with three spiral ribs, towards the aperture the interspaces are occupied each by a short, rapidly-widening spiral; the axial incisions are more distinct towards the aperture. Base convex with a peripheral spiral, rounded, smooth keel, and a second more anterior, punctated between. Aperture roundly quadrate: outer lip sloping, straight, ascending at the suture and pinched into a tiny sinus, anteriorly circular and effuse; in profile straight, minutely retrocurrent at the suture, obliquely very slightly antecurrent anteriorly. Canal well marked, nearly closed, especially at the junction with the aperture, markedly recurved. Inner lip distinct, slightly erect. Colour, white.*

Dim.—*Length, 10.5 mm; breadth, 2.5 mm.*

Locality. —*Type, Gulf St. Vincent, (?) depth, with 23 others moderate: in 15 to 20 fathoms off St. Francis Island, 1 moderate; in 24 fathoms off Newland Head, 1 moderate; in 55 fathoms off Cape Borda, 1 good.*

Variations.—*In the shell from 55 fathoms, in the antepenultimate whorl an interstitial thread arises between the middle and anterior spirals, and becomes a definite though small lira. In some large shells a thin sutural lamina is seen between the later whorls. A large broken specimen would measure 15 mm if complete. In one individual the posterior spiral lira throughout the shell is tinged brown.*

Remarks. Verco referred to a type series consisting of multiple specimens in his original description. Marshall (1983) reported the “holotype” in SAM but this should be considered a lectotype designation according to Article 74.6 of the Code (ICZN 1999). The label accompanying this lot reports the type locality and the wording “Co-types”, which suggests that the specimens indeed belong to the type series. Because of Marshall’s lectotype designation, these and all other syntypes are now paralectotypes.

Triphora albovittata var. *mamillata* Verco, 1909

Figure 109

Triphora albovittata var. *mamillata* Verco 1909: 285–286, not illustrated.

Type locality. Gulf St Vincent, South Australia (fide Marshall 1983, by lectotype designation).

Type material. Lectotype: SAM D.13446 (fide Marshall 1983; not seen, see Remarks).

Additional material. NHMUK 1910.3.29.49–51: 3 specimens, Gulf St Vincent, South Australia.

Original description. *Instead of having the elongate four-whorled protoconch of the type, it has a mamillate two-whorled apex. The first whorl is round and smooth, the second has a central carina and subdistant axial bars. Generally the second is swollen and lies somewhat out of the axis of the shell, causing the mamillate form. Rarely the first whorl may be as large as the second. This protoconch seems complete, and not the base of a spiculate protoconch, whose terminal whorls have fallen. The shell varies in shape, being short, broad, and pupaeform, or long, narrow, and elongate-pyramidal.*

Dredged in Gulf St. Vincent, 7 perfect and 7 poor; in 90 fathoms off Cape Jaffa, 2 good; in 150 fathoms off Beachport, 2 poor. Taken on the beach MacDonnell Bay, 1; Gulf St. Vincent, 23, in varying condition; Venus Bay, 2, good.

The very different protoconch makes me diffident about calling this a variety, inasmuch as the characters of the protoconch are generally regarded as very certain specific diagnostics; but the shells are otherwise indistinguishable.

Remarks. Marshall (1983) considered this variety a valid taxon: *Obesula mamillata*, distinguished by *O. albovittata* by its paucispiral protoconch. Verco referred to a type series of multiple specimens in his original description. Marshall’s (1983) report of the “holotype” in the SAM should be considered a lectotype designation according to Article 74.6 of the Code (ICZN 1999).

The specimens in NHMUK represent two strikingly different colour forms: a white form (Fig. 109A, B) and a form with light brownish shell, white first spiral cord and brown base (Fig. 109C, D). Marshall (1983) reported that also *O. albovittata* occurs in two colour forms, similar to the ones illustrated here for *O. mamillata* and suggested that the only differentiating character between the two species is the protoconch type.

The NHMUK collection register does not indicate that these are “Co-types”, although the specimens were part of Verco’s collection and come from the type locality. Until additional evidence is available, we do not consider these specimens as belonging to the original type series.

Triphora novapostrema Verco, 1910

Figure 110

Triphora novapostrema Verco 1910: 126–127, pl. XXX, figs 1, 2.

Type locality. “off Cape Borda” (Kangaroo Island, South Australia) (fide Marshall 1983).

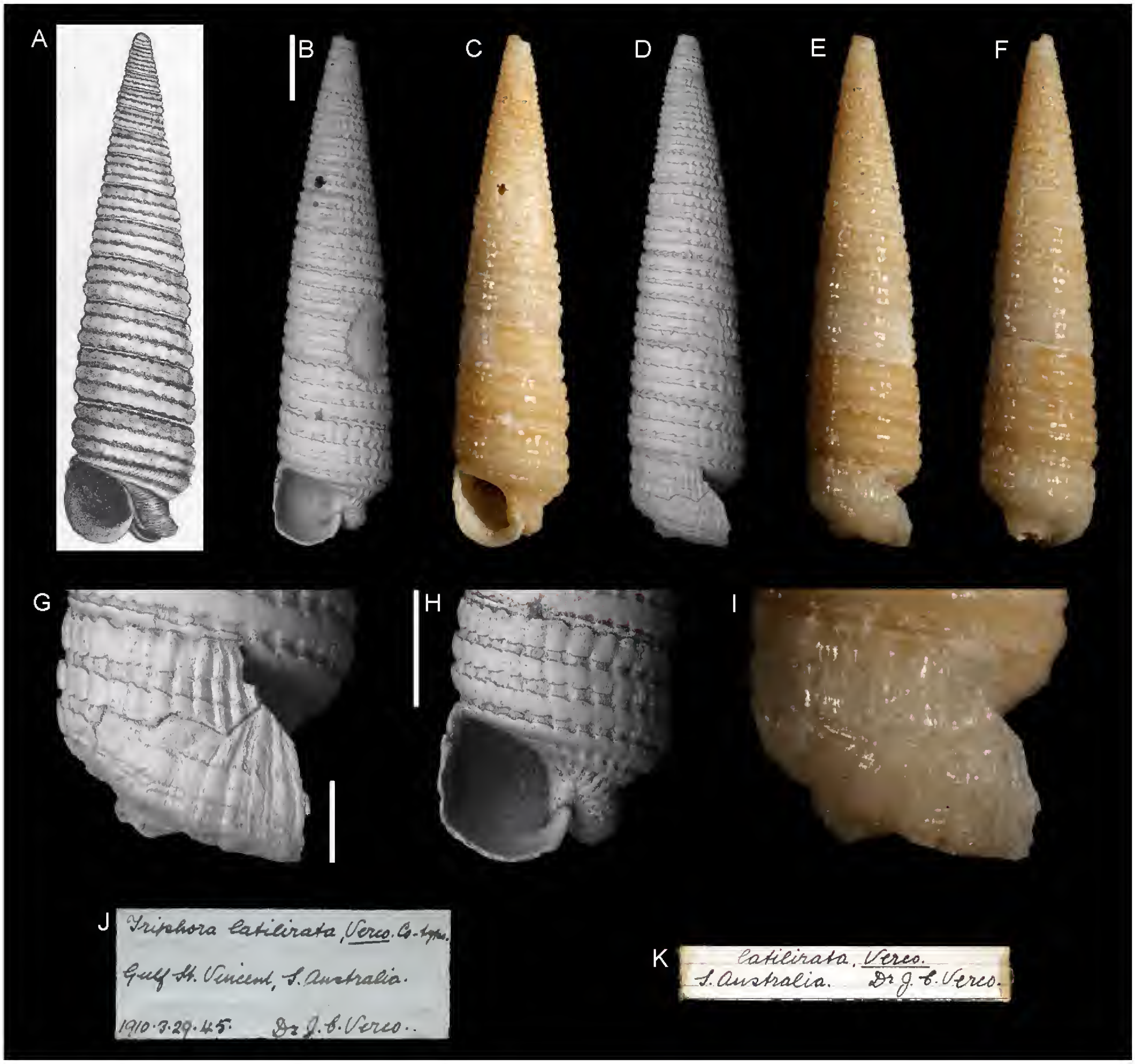

Figure 108. *Triphora latilirata* Verco, 1909, Gulf St. Vincent, South Australia. **A** Original figure. **B–K** Paralectotype, NHMUK 1910.3.29.45: front (**B, C**), side (**D, E**), back (**F**), peristome (**G, I**), aperture (**H**), original labels (**J, K**). Scale bars: **B–F, H**: 1 mm; **G, I**: 0.5 mm.

Type material. Lectotype: SAM D. 13450 (fide Marshall 1983; not seen, see Remarks).

Additional material. NHMUK 1911.8.12.1–2: 2 specimens (glued on cardboard), off Cape Borda, Kangaroo Island, South Australia.

Original description. *Shell immature, of eight whorls, including the protoconch of two whorls, the first nearly smooth with a round projecting apex, the second with two stout prominent keels, gradually becoming nodular. In the first spire-whorl arises a faint third spiral, posterior to the others (whence the specific name), which continuously enlarges till it nearly equals them in size. They are crossed by axial liras, about fourteen in the last whorl, both axials and spirals being well marked, the latter the stouter, and being tuberculate at their intersection. The peripheral spiral is prominent and subtuberculate, it is visible in the earlier sutures, but not in the later; two flat obsolete plaits curve round the base. Colour white.*

Dim.—*Length, 3.1 mm; breadth, 1.2 mm. The largest example, immature, is 5.2 mm.*

Locality.—*Dredged in 55 fathoms off Cape Borda, type with 7 others, some quite fresh, all immature; in Gulf St. Vincent, 1.*

Diagnosis.—*Its special characters are its blunt protoconch with two carinae, and the third spiral arising behind the others; in most* Triphora *it arises between them as in* T. angasi, tasmanica, cana, *etc.*

Type in my collection.

Remarks. In the original description, Verco referred to multiple specimens in the type series. Marshall's (1983) re-

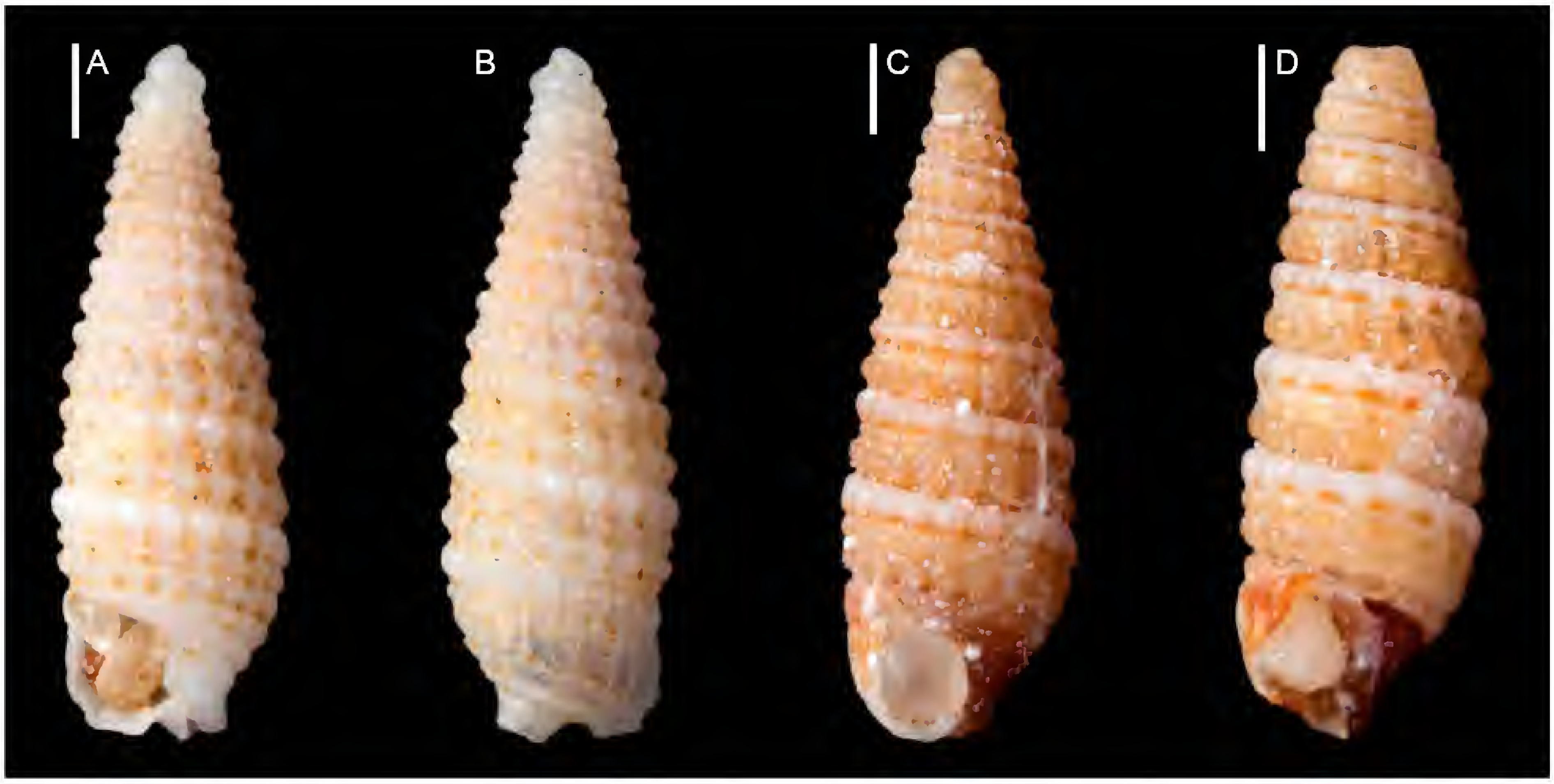

Figure 109. *Triphora albovittata* var. *mamillata* Verco, 1909, Gulf St. Vincent, South Australia. **A, B** NHMUK 1910.3.29.49: front (**A**), back (**B**). **C, D** NHMUK 1910.3.29.50–51: front views. Scale bar: 0.5 mm (photo courtesy: Kevin Webb, NHMUK Photographic Unit).

port of the "holotype" in the SAM should be considered a lectotype designation according to Article 74.6 of the Code (ICZN 1999). The two NHMUK shells come from the type locality. However, neither the label nor the register entry states that they are co-types. Their type status is uncertain.

Triphora spica Verco, 1909

Figure 111

Triphora spica Verco 1909: 281, pl. XXIII, fig. 1.

Type locality. "off Beachport" (South Australia).

Type material. Lectotype: SAM D. 13453 (fide Marshall 1983; not seen, see Remarks). Paralectotypes: NHMUK 1910.3.29.54–55: 2 specimens, Cape Borda, Kangaroo Island, South Australia.

Original description. *Shell solid, long, narrow, upper third elongate-conical, the rest nearly cylindrical. Protoconch of 5 whorls, convex, with two central closely approximate spiral threads and numerous axial bars. Spire-whorls 17, the first three with two nodulate spiral ribs, and an infra-sutural small, smooth cord. In the fourth whorl this becomes nodulate; and getting thicker equals the other spirals in the sixth whorl. Between the twelfth and thirteenth whorls a supra-sutural thin threadlet appears and gradually enlarges and grows subnodular. The nodules in a spiral row on the penultimate are 17, transversely elliptical, and are joined spirally by a bar about one-third of their width, and vertically by obsolete bars nearly their own width. The body-whorl has three spiral ribs, a subnodulated peripheral riblet, a distinct smooth, stout, basal spiral, and an obsolete one at the base of the canal. The lip is broken. Colour, lightbrown, with axial streaks of darker-brown from suture to suture; sometimes these happen to be continuous over two or more whorls, sometimes not; the protoconch is of darker brown.*

Dim.—*Length, 97 mm; breadth, 1.55 mm; length of protoconch, 0.55 mm.*

Locality.—*Type, 40 fathoms off Beachport, with 4 others; 55 fathoms off Cape Borda, 10 good, many poor; 62 fathoms off Cape Borda, 1 poor; Gulf St. Vincent, under 25 fathoms, 7 poor. The habitat would appear to be in 40 to 50 fathoms.*

Diagnosis.—*From* T. kesteveni, *Hedley, it differs in its nodulated spirals and in its colour.*

Remarks. In the original description, Verco referred to multiple specimens in the type series. Marshall's (1983) report of the "holotype" in the SAM should be considered a lectotype designation according to Article 74.6 of the Code (ICZN 1999). The label accompanying this lot reports Cape Borda as the locality, as listed in the original description, and the wording "Co-types", which suggests that these specimens indeed belong to the type series. Because of Marshall's lectotype designation, these and all other syntypes are now paralectotypes.

Triphora spina Verco, 1909

Figure 112

Triphora spina Verco 1909: 280–281, pl. XXII, figs 2–4.

Type locality. "off Beachport" (South Australia).

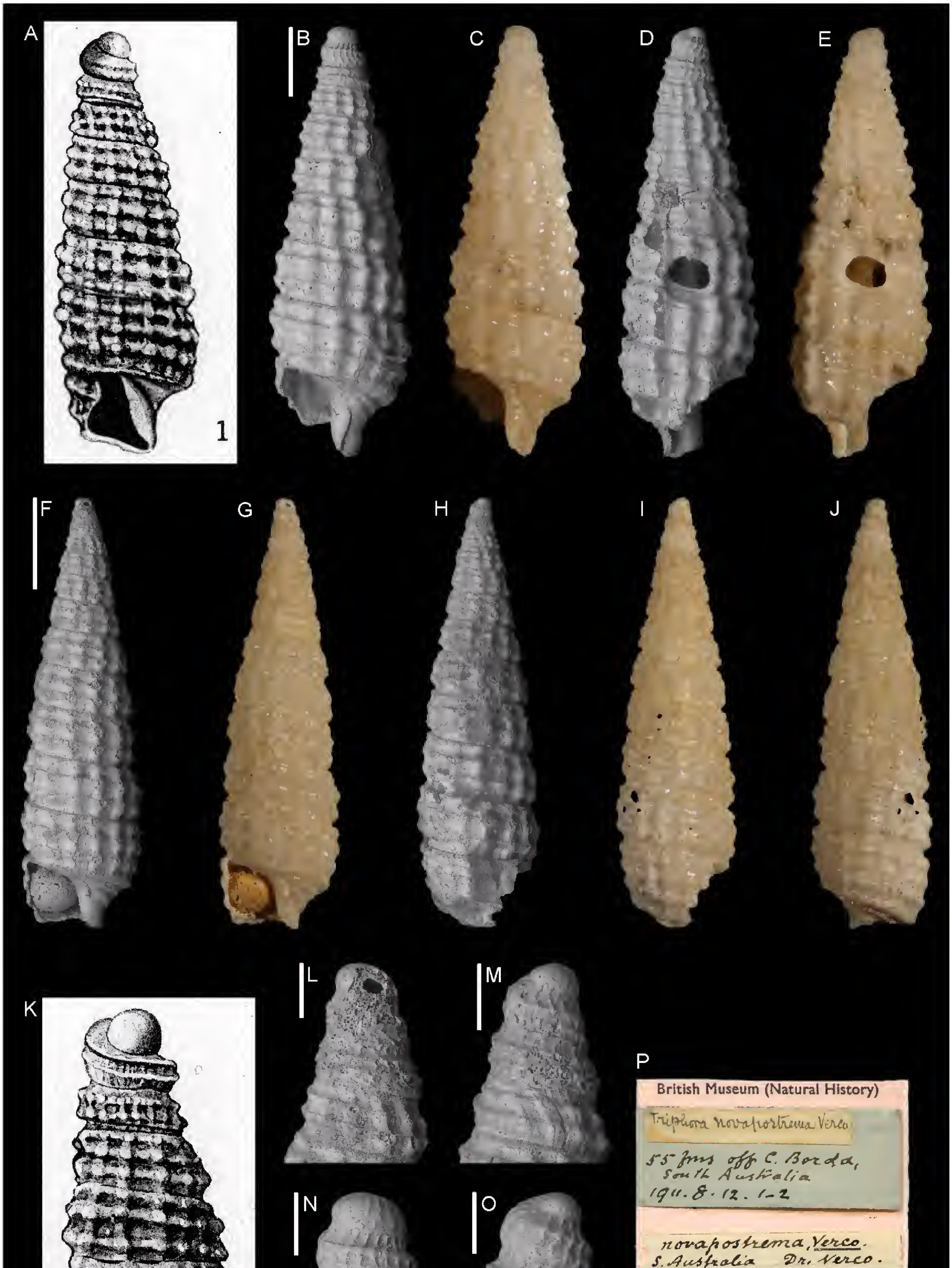

Figure 110. *Triphora novapostrema* Verco, 1910, off Cape Borda, South Australia. **A, K** Original figures. **B–E, N, O** NHMUK 1911.8.12.1: front (**B, C**), side (**D, E**), protoconch (**N, O**). **F–J, L, M** NHMUK 1911.8.12.2: front (**F, G**), side (**H, I**), back (**J**), protoconch (**L, M**). **P**. Original labels. Scale bars: **B–E**: 0.5 mm; **F–J**: 1 mm; **L–O**: 0.2 mm.

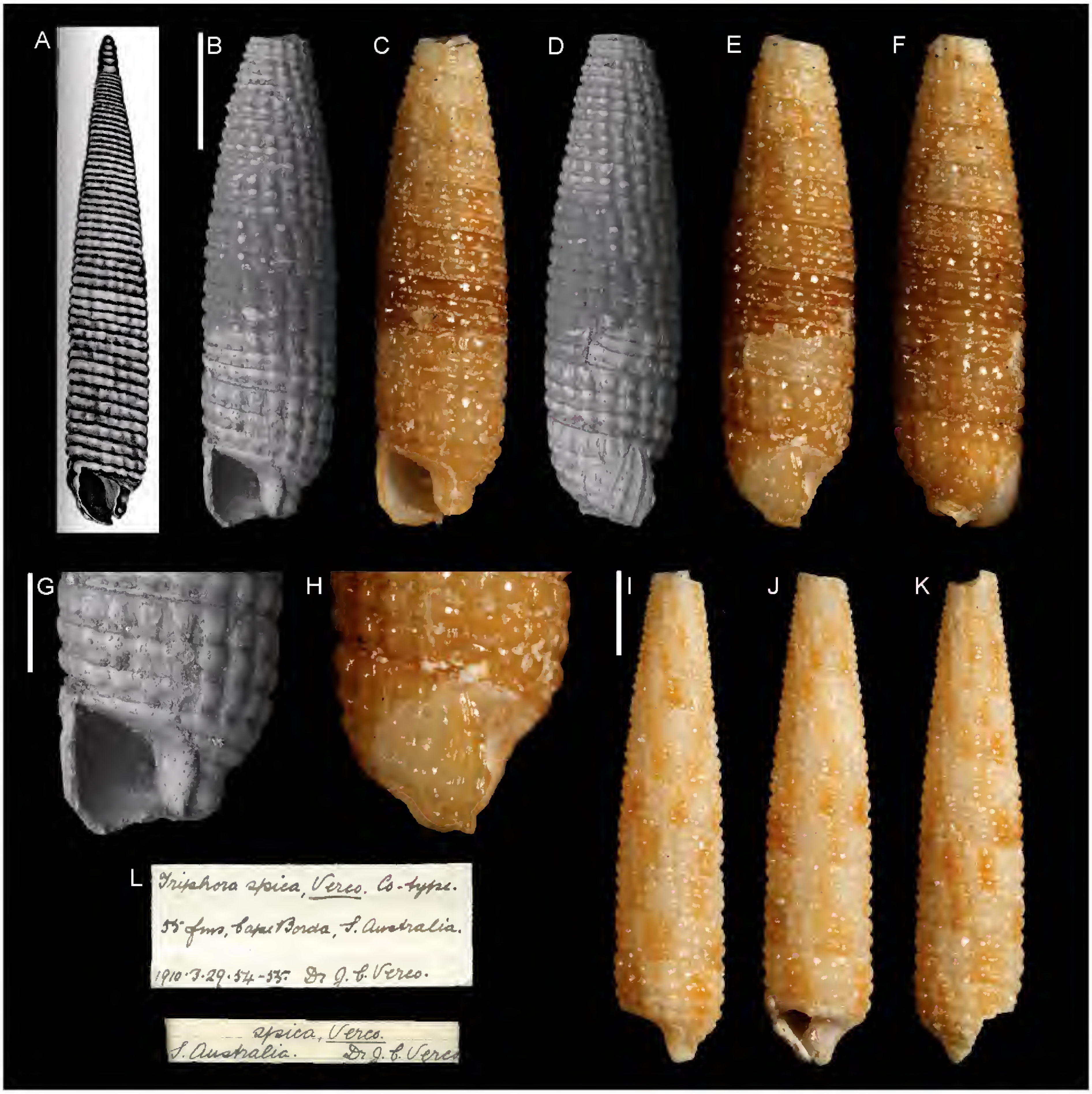

Figure 111. *Triphora spica* Verco, 1909, Cape Borda, South Australia. **A** Original figure. **B–H** Paralectotype, NHMUK 1910.3.29.54: front (**B, C**), side (**D, E**), back (**F**), aperture (**G**), peristome (**H**). **I–K**: Paralectotype, NHMUK 1910.3.29.55: front (**I**), side (**J**), back (**K**). **L** Original labels. Scale bars: **B–F, I–K**: 1 mm; **G, H**: 0.5 mm.

Type material. Lectotype: SAM D. 13449 (fide Marshall 1983; not seen, see Remarks). Paralectotype: NHMUK 1910.3.29.39: 1 specimen, off Beachport, South Australia.

Original description. *Shell sinistral, elongate-subulate-pyramidal. Protoconch of 4 turns, apex prominent and tongue-like, whorls smooth, centrally boldly angled, concave between the median angulations. Suture linear. Spire-whorls 17, with four ribs; the largest is the continuation of the nuclear angulation; above this is a much smaller infra-sutural rib, below it the shell wall seems thinner and less opaque; then comes a bold rib, and close below it a supra-sutural rib. They are slightly tuberculate with low transverse nodules, united by low broad oblique axial costae, most marked between the upper two ribs, but connecting the upper three; the supra-marginal rib is smooth, and wedged in between the two adjacent ribs. Aperture roundly rhomboidal; outer lip crenulated by the spirals, antecurrent into a spur towards the front canal nearly closed at this point, curved to the left, and reflected; back of the aperture pinched at the suture, but no sutural notch. Base smooth, with one spiral. Colour, light-amber tint.*

Dim.—*Length, 12.4 mm; width, 1.9 mm.*

Locality.—*Type, 110 fathoms off Beachport, with 2 others perfect and 11 broken, in 150 fathoms 6 moderate, and in 200 fathoms 3 poor; in 90 fathoms off Cape Jaffa, 7 perfect and 14 broken, and in 130 fathoms 3 broken.*

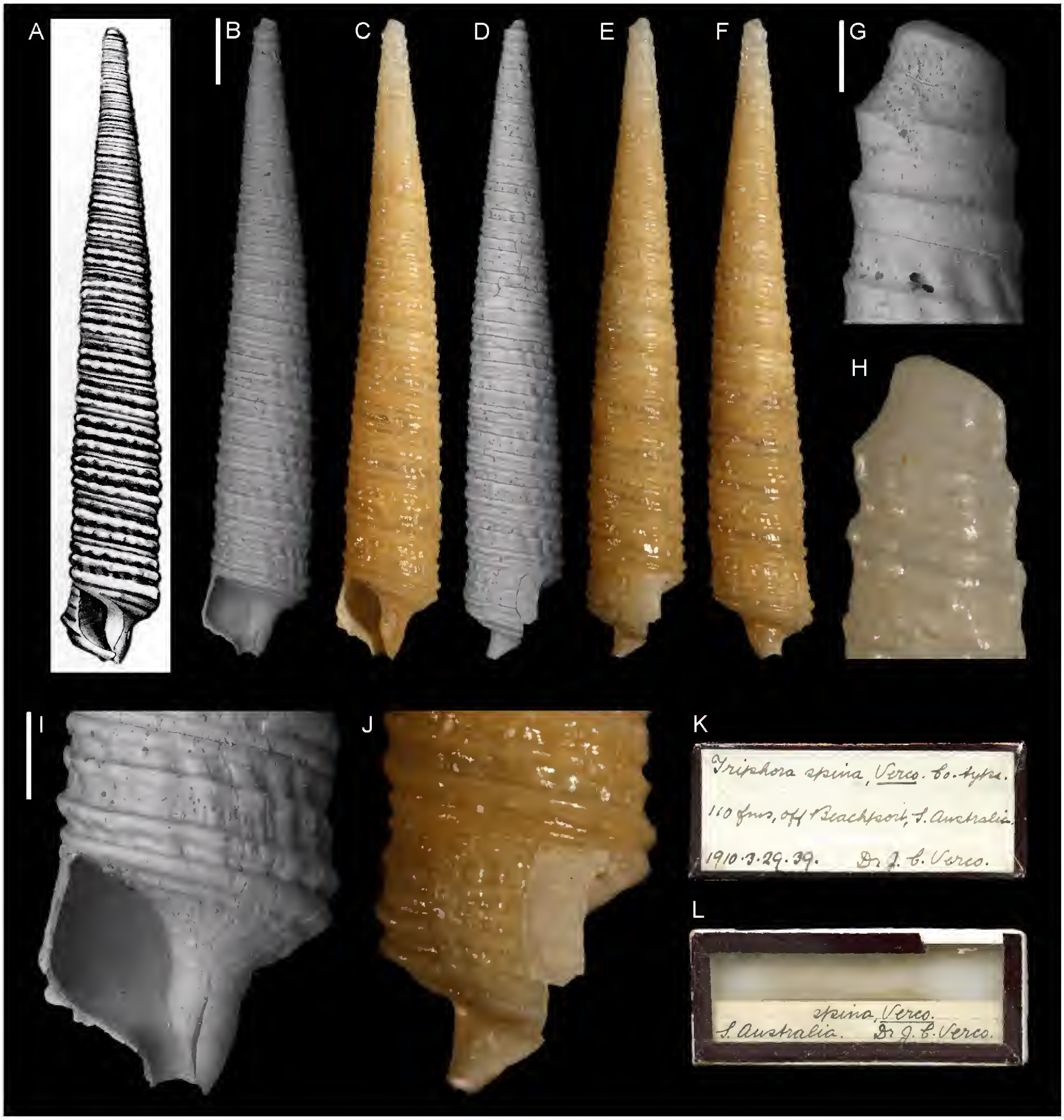

Figure 112. *Triphora spina* Verco, 1909, off Beachport, South Australia. **A** Original figure. **B–L** Paralectotype, NHMUK 1910.3.29.39: front (**B, C**), side (**D, E**), back (**F**), protoconch (**G, H**), aperture (**I**), peristome (**J**), original labels (**K, L**). Scale bars: **B–F**: 1 mm; **G, H**: 0.2 mm; **I, J**: 0.5 mm.

It differs from T. subula *in its unicarinate protoconch, and in having the 4 ribs throughout.*

Remarks. In his original description, Verco referred to multiple specimens in the type series. Marshall's (1983) report of the "holotype" in the SAM should be considered a lectotype designation according to Article 74.6 of the Code (ICZN 1999). The label accompanying this lot reports the type locality and the wording "Co-types", which suggests that the specimens indeed belong to the type series. Because of Marshall's lectotype designation, these and all other syntypes are now paralectotypes.

Species described by R.B. Watson

Robert B. Watson described seven species of Triphoridae. All the types are in the NHMUK. We follow Low and Evenhuis (2013) in dating Watson (1886).

Cerithium (*Bittium*) *abruptum* Watson, 1880

Figure 113

Cerithium (Bittium) abruptum Watson 1880: 119–120, not illustrated. Illustration available in Watson (1886): 551, pl. XLI, fig. 4.

Type locality. Lat. 38°38'N, long. 28°28'30"W, Fayal, Azores.

Type material. Syntypes: NHMUK 1887.2.9.1709–11: 3 specimens, type locality.

Original description. *St. 75. July 2, 1873. Lat. 38°38'N., long. 28°28'30"W. Fayal, Azores. 450–500 fms. Sand.*

Shell.—*Small, narrow, conical, blunt, in general form very like a decollated* Cerithiopsis metaxa, *solid, translucent, white.* Sculpture. *Longitudinals—there are on the last whorl about thirteen, on the earlier, fewer longitudinal ribs, which are low and narrow, and are parted by flat and broader furrows. They come down the spire, from whorl to whorl, with a strong sinistral twist. The embryonic whorls have ten or twelve small ribs. Spirals—except on the first two whorls there are on each whorl four narrow, rounded, prominent spiral threads, which rise, as they cross the longitudinals, into pointed high tubercles. The furrows which part them (except that between the third and the fourth) are narrower than the spirals. The highest of these spirals is the weakest and least prominent, being pinched in by the superior contraction of the whorl into the suture. Close above this highest spiral runs the suture. The base of each whorl is roundly but rather abruptly contracted, so that the sutural furrow has its upperside abruptly, its underside gradually, declining. The base, which is oblique, concave, and contracted, has a strong plain spiral thread round its edge, and a very minute thread encircling the base of the pillar, the scar of the siphonal cut. Besides the larger systems of sculpture, there are some faint and irregular traces of microscopic rounded longitudinals and sharper spirals.* Colour *translucent white.* Spire *high, narrow, with very straight outlines, and scarcely contracted.* Apex *excessively blunt and abrupt, the extreme point being rounded and barely rising into view; it is quite smooth and polished. The second whorl is longitudinally ribbed and polished; on the third the ordinary sculpture begins.* Whorls *11, convex, constricted suddenly below and gradually above.* Suture *excessively minute and faint in itself, but its place strongly marked by the constriction of the whorls above and below.* Mouth *very small, oval, perpendicular, pointed above, and with a large open rounded slit in front, whose edge is hardly reverted.* Outer lip *thin, advancing on the base much beyond the point of the pillar.* Inner lip *a thin glaze, with microscopic corrugations on the pillar.* Pillar *very short, with a broad base spreading out to meet the outer lip, straight, with a broad but sharp point. H. 0.23. B. 0.05. Penultimate whorl, height 0.03. Mouth, length 0.028, breadth 0.02.*

This species in general aspect is very like Cerithiopsis metaxa, *della Chiaje, but differs in not having the sharp sculptured apex; the whorls, in consequence of the sutural contraction, are more rounded; the longitudinals are swellings of the whole shell, not, as in that other, mere projecting tubercles; the spirals are more definitely continuous; the longitudinal rows of tubercles run less definitely from whorl to whorl, and have a strong sinistral twist as they proceed down the spire, while in* C. metaxa *their continuous lines are very straight.*

Remarks. Bouchet (1985) accurately described the species and, therefore, we refrain from adding additional diagnostic notes.

Cerithium (*Triforis*) *bigemma* Watson, 1880

Cerithium (*Triforis*) *bigemma* Watson 1880: 101–102, not illustrated. Illustration available in Watson (1886): 562–563, pl. XLIII, fig. 6.

Type locality. "Lat. 18°38'30"N, long. 65°5'30"W, St. Thomas, North of Culebra Island, Danish West Indies" (Puerto Rico).

Type material. Lectotype: NHMUK 1887.2.9.1762, designated by Rolán and Fernández-Garcés (2008) (not seen).

Original description. St. 24. Mar. 25, 1873. Lat. 18°38'30"N., long. 65°5'30"W. St. Thomas, N. of Culebra Island, Danish West Indies. 390 fms. Coral-mud.

Shell.—*Sharply conical, high and narrow, solid, opaque, brilliant, yellowish white.* Sculpture. *Longitudinals—the whorls are crossed by rows of tubercles with broad and rounded hollows between; of these longitudinal rows there are 17 to 18 on the last, and about 14 on a great many of the preceding whorls; besides these the surface is sharply, distinctly, and pretty closely scored by minute lines of growth. Spirals—a prominent spiral band encircles the whorls formed by two rows of rounded tubercles, which in each row are connected by a spiral thread; of these threads the lower is rather the larger, sharper, and more prominent. The distance between these threads is very nearly the same as that between the longitudinal rows, so that each group of four adjoining tubercles forms nearly a rhomb. Round the upper part of each whorl is an impressed flat surface, in which, very near the suture, lies another smaller spiral, which becomes minutely tubercled where it crosses the longitudinal rows. At the bottom of each whorl is a very minute spiral thread, which forms a pouting edge to the suture. Besides these the surface is faintly reticulated by microscopic spirals crossing the longitudinal lines of growth. This reticulation is best seen on the flat and glossy base, which is unbroken except by a small sharp spiral, about 0.012 in. within the edge.* Colour *yellowish white, pure white on the upper part of the spire; round the base of each whorl is a suffused pale tint of brown, which is more or less the colour of the base of the shell; the point of the pillar is white.* Spire *high, narrow, and conical, slightly slewed to the left; so that while the left slope is straight, almost concave, the right slope is just perceptibly convex.* Whorls *probably 22, but of these the 3 or 4 apical ones are broken off; they are of very slow increase, flat, constricted on their upper part, flatly prominent in the middle, and contracted at the lower part; the base of the shell is flatly conical.* Suture *strongly defined by the de-*

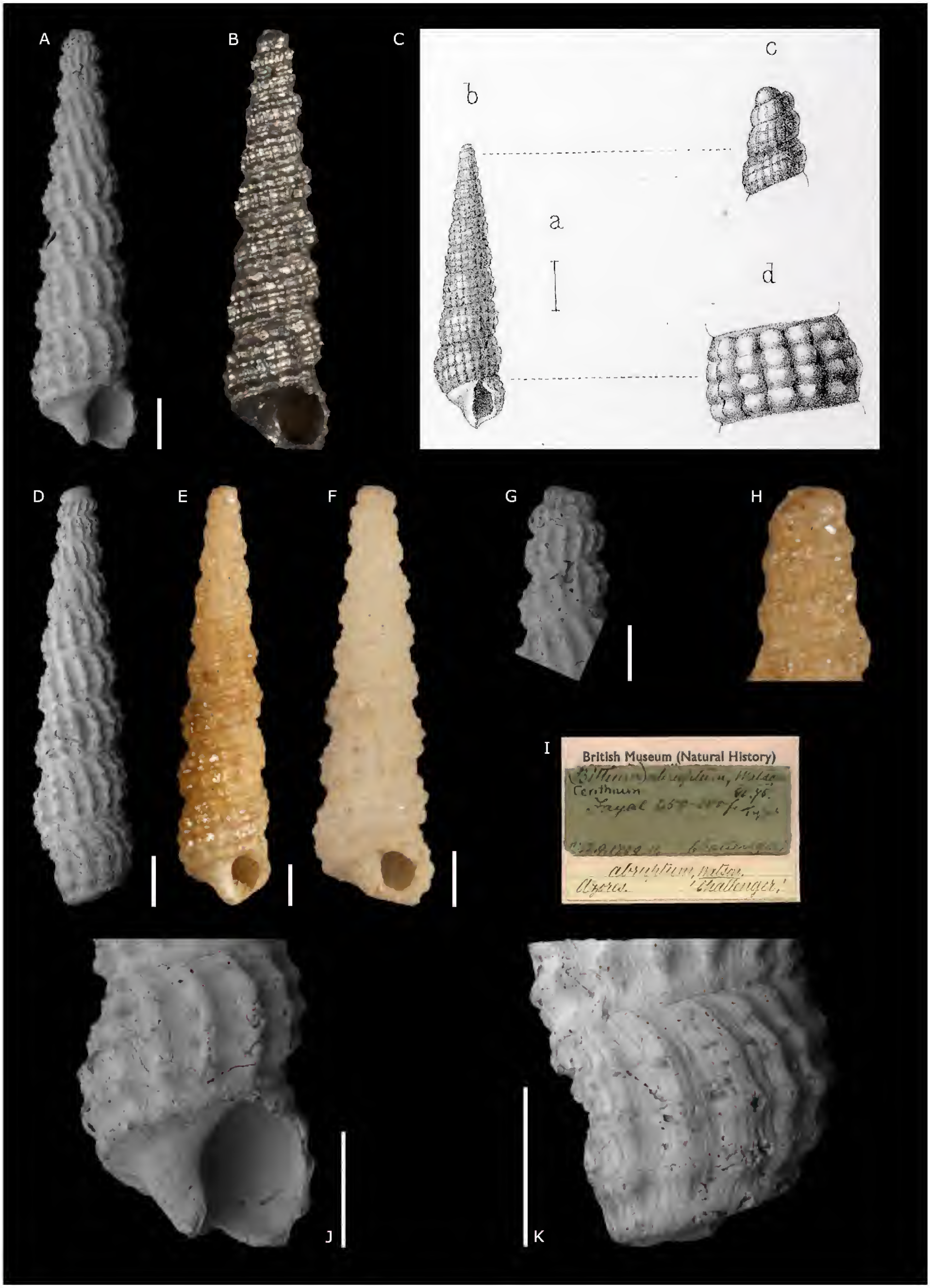

Figure 113. *Cerithium* (*Bittium*) *abruptum* Watson, 1880, Fayal, Azores. **A, B, D, G, J, K** Syntype NHMUK 1887.2.9.1709: front (**A, B**), side (**D**), protoconch (**G**), aperture (**J**), peristome (**K**). **C** Original figure. **E, H** Syntype NHMUK 1887.2.9.1710: front (**E**), protoconch (**H**). **F** Syntype NHMUK 1887.2.9.1711: front. **I** Original labels. Scale bars: **A, B, D–F, J, K**: 0.5 mm; **G**, **H**: 0.1 mm.

pression in which it lies, but itself linear and projecting, being minutely marginated both above and below. Mouth *squarely oval, pointed above and at the front of the pillar by the canal, which is small.* Outer lip *broken.* Pillar *short, small, straight, scarcely excavated or twisted, at the point sharp and slightly advancing outwards.* Inner lip. *A very thin layer of glaze is carried across the body, and turns round the pillar in a few microscopic lines, by which alone it can be traced. H. 0.6. B. 0.12. Penultimate whorl 0.072. Mouth, length 0.08, breadth 0.06.*

This has a good deal the proportions of C. metula, *Lov., with a narrower base. It slightly resembles the* Triforis Pfeifferi, *Crosse, and (apparently, for the B. M. tablet has more than one species on it) the* T. scitula, *A. Ad., both from S. Australia; but these have only one series of gemmules, the upper row being very much smaller, and in both the whole shell is very much smaller and slenderer.* T. gigas, *Hinds, is a much thinner and less strongly tubercled and sutured shell.* T. angustissima, *Desh. (Moll. de Bourbon), is larger, broader in proportion, has the lower (in his description "supérieure", as he reverses the shell) row of tubercles larger, and lacks the infrasutural flat constriction with its small and finely tubercled spiral.*

Remarks. Rolán and Fernández-Garcés (2008) recently treated this species and illustrated the lectotype.

Triforis dolicha Watson, 1886

Figure 114

Triforis dolicha Watson (1886): 565–566, pl. XLII, fig. 1.

Type locality. "Lat. 9°59'S, long. 139°42'E West of Cape York, North-east Australia"

Type material. Syntypes: NHMUK 1887.2.9.1767: 1 specimen, type locality.

Original description. *Station 188. September 10, 1874. Lat. 9°59'S., long. 139°42'E. West of Cape York, North-east Australia. 28 fathoms. Green mud.*

Shell.—*Long and narrow, conical, pale, spotted with brown, with three rows of fine tubercles on the later whorls and two on the earlier, a furrowed suture, a small regularly tapering apex, and a square barely produced base.* Sculpture*: Longitudinals—there are on each whorl about 16 riblets, which originate at the upper row of tubercles, and swell down to the lower; they are parted from each other by little shallow pits, and they but feebly and doubtfully run down the spire, being not quite coincident in the adjoining whorls, and being parted by the sutural furrow; near the outer lip the riblets subside into continuous bars, which are prolonged to the base. Spirals—on the last four whorls there are three, on the earlier two, rows of tubercles set upon the longitudinals, and slightly connected in each row by a fine thread; round the angle of the base runs a sharp rounded thread; at the top of the pillar is another finer; on the pillar itself there are two folds.* Colour *pale brownish, with darker stains.* Spire *high and narrow, conical.* Apex *conical, consisting of five rather sharply angulated and carinated whorls, which are ornamented by minute not quite regular longitudinal bars; the extreme tip is small, rounded, quite smooth, polished, and not very prominent, but rather spread out than immersed.* Whorls*: there are 11½ regular whorls, which are short and of very gradual increase; the edge of the base is bevelled off, but the base itself is flat, with a slight hollowing in the middle.* Suture *furrowed, but in itself invisible, rather oblique.* Mouth *somewhat squarely rounded, small, bluntly pointed above.* Outer lip *is very thin and sharp; has at its insertion a small deep rounded sinus, below which it advances very much into a scoop-like form on the base, and is on the right sharply bent in upon the pillar, the forward edge of which it inwraps.* Pillar *very short indeed; its point is twisted, and very sharply bent to the right, infolding the generic canal.* Inner lip *concave, very short, with a thickened edge; there is a minute nick at its junction, with the outer lip on the pillar. H. 0.184 in. B. 0.048. Mouth, height 0.027, breadth 0.022. Apex, height 0.018, breadth 0.013.*

This species is not at all unlike the smaller forms of Triforis perversa *(Linne), of Europe; but, besides very many minute points of distinction, the base is squarer, with two not three threads, the labral sinus is much deeper, the mouth is rounder, the basal lip more produced, and the pillar tip more bent and elongated; the sutural furrow, too, is deeper, wider, and less oblique, and while the apex is slightly broader, the extreme tip is a very little smaller.*

Diagnosis. Syntype 4.3 mm high. Shell slightly cyrtoconoid with flat whorls. Teleoconch of 11 whorls with three spiral cords, the second as a narrow thread until the last whorl, with tubercles at the intersection with the prosocline axial ribs. A fourth smooth suprasutural cord is visible in the second half of the shell. Numerous prosocline growth lines are visible in the interspaces between the cords. Peristome with a shallow posterior sinus and additional spiral cords. Siphonal canal long. Base rather flat and concave with two additional smooth spiral cords. Protoconch incomplete in the syntype, but clearly multispiral with at least four whorls. The last three bear a single strong spiral keel and axial riblets. Teleoconch apparently whitish, but the syntype is worn; the "darker stains" described by Watson may be again due to taphonomic damage. Protoconch light brown.

Cerithium (*Triforis*) *hebes* Watson, 1880

Figure 115

Cerithium (*Triforis*) *hebes* Watson 1880: 103, not illustrated. Illustration available in Watson (1886): 551, pl. XLIII, fig. 7.

Type locality. "Nightingale Island, Tristao da Cunha Islands, S. Atlantic"

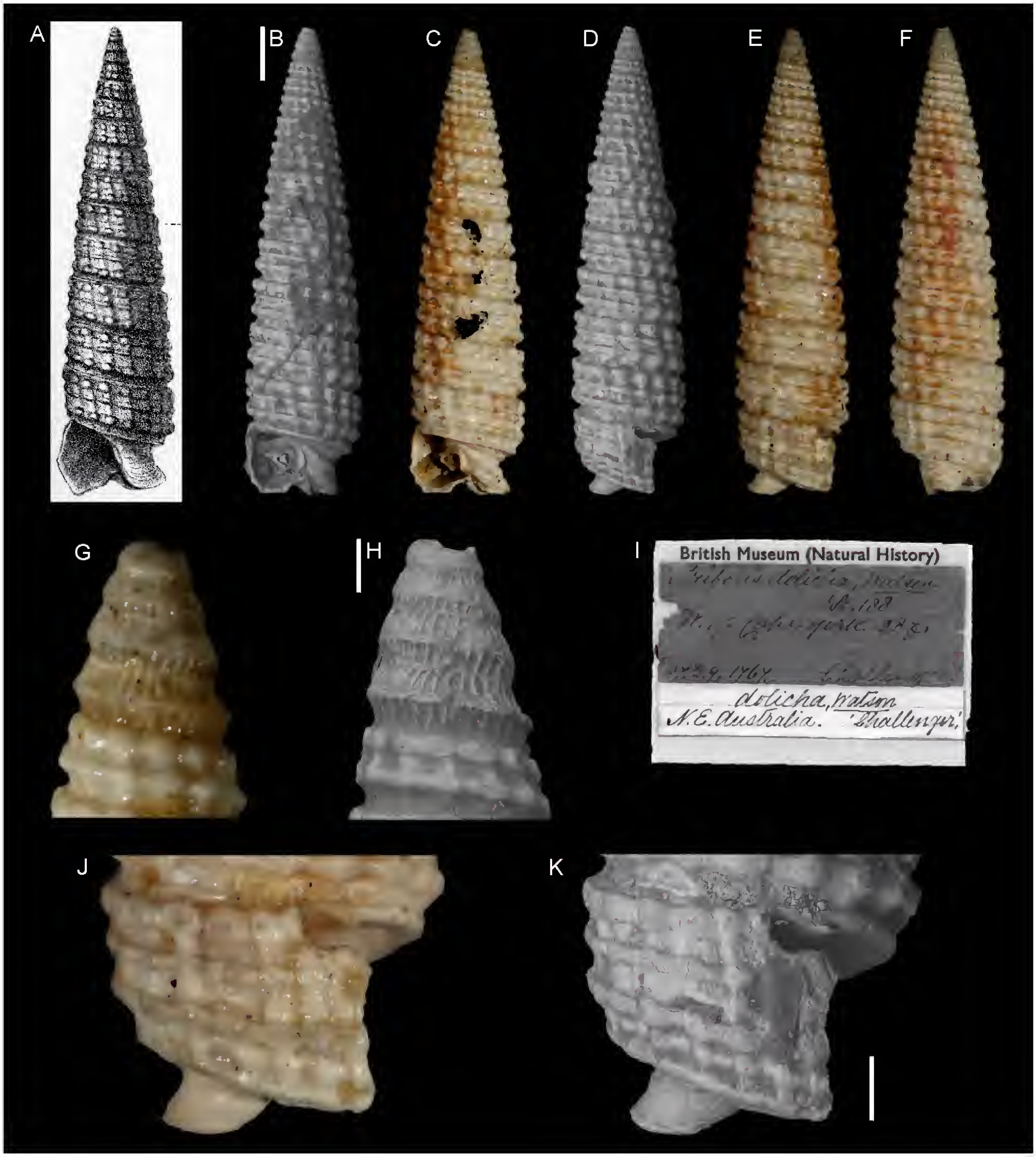

Figure 114. *Triforis dolicha* Watson, 1886, West of Cape York, North-East Australia. **A** Original figure. **B–H, J, K** Syntype NHMUK 1887.2.9.1767: front (**B, C**), side (**D, E**), back (**F**), protoconch (**G, H**), peristome (**J, K**). **I** Original labels. Scale bars: **B–F**: 0.5 mm; **G, H**: 0.1 mm; **J, K**: 0.2 mm.

Type material. Syntypes: NHMUK 1887.2.9.1763–5: 3 specimens, type locality.

Original description. *St. 135. Oct. 18, 1873. Nightingale Island, Tristao da Cunha Islands, S. Atlantic. 100–150 fms. Rock; shells.*

Shell.—*Cylindrically conical, blunt, uncontracted towards the base, strong, translucent, hardly glossy.* Sculpture. *Longitudinals—on the last whorl there are about 20 longitudinal rows of rounded tubercles, parted by depressions of much the same breadth and form as themselves; they run more or less continuously and straight up the spire from whorl to whorl. There are indistinct lines of growth. Spirals— on each whorl the tubercles are arranged in three spiral rows, parted by rather deep but narrow squarish furrows. The highest row is rather smaller and less prominent than the others. The base of each whorl is sharply but not deeply constricted; the edge of this constriction appears on* *the margin of the base as a rounded thread, defined by a slight furrow, which, with the exception of microscopic radiating lines of growth, is the only ornament of the flat and very slightly conical base.* Colour *pure somewhat translucent white.* Spire *high and conical, but contracting very little, and hence more cylindrical than usual.* Apex *very blunt, but almost mucronated; this arises from the three embryonic whorls, which are smooth, being formed of two tumid threads, of which the lower is the larger, but the upper is at first the more prominent, and at its origin stands up minute, round, and prominent, like a small eccentric blunt spike, reminding one of the mucronated mamillary plug of some of the Caecums. It is not a plug, however, but the true embryonic form. This embryonic shell is smooth and glossy, but has some faint trace of spiral sculpture.* Whorls *12, of very gradual increase, flat on the sides, constricted below, flat and hardly conical on the base.* Suture *well defined by the contraction of the whorl above it, and by a minute thread on which it projects.* Mouth *angulately oval, with a small straight canal in front.* Outer lip *broken.* Pillar *perpendicular, straight, short, narrow, pointed.* Inner lip *a thickish porcellanous glaze. H. 0.24. B. 0.06. Penultimate whorl 0.03. Mouth, length 0.032, breadth 0.02.*

This species has some resemblance to T. suturalis, *Ad. & Rve., but is easily distinguished from that by its blunt apex and the less sunken suture.*

Diagnosis. Syntypes ranging in height between 3.7 and 5.3 mm; none looks fully mature. Shell conical with slightly curved sides. The largest specimen has ca 9 whorls bearing three strong spiral cords from the beginning of the teleoconch; tubercles are present at the intersection with the orthocline axial ribs. A fourth smooth narrow cord is visible suprasuturally. Growth lines are visible between the cords. Due to the subadult stage, the peristome and the base are not fully developed. Siphonal canal short. The large protoconch is certainly paucispiral, with two whorls: the first bears a strong spiral keel and possibly some thick axial ribs, but all syntypes have very worn apexes. Teleoconch and protoconch white.

Cerithium (*Triforis*) *inflata* Watson, 1880

Cerithium (*Triforis*) *inflata* Watson 1880: 103–104, not illustrated. Illustration available in Watson (1886): 564–565, pl. XL, fig. 1.

Type locality. "Lat. 18°38'30"N, long. 65°5'30"W, St. Thomas, North of Culebra Island, Danish West Indies" (Puerto Rico).

Type material. Lectotype: NHMUK 1887.2.9.1766, designated by Rolán and Fernández-Garcés (2008) (not seen).

Original description. *St. 24. Mar. 25, 1873. Lat. 18°38'30"K, long. 65°5'30"W. St. Thomas, N. of Culebra Island, Danish West Indies. 390 fms. Mud.*

Shell.—*Small, narrow, conical, with a blunt inflated apex, solid, opaque, glossy.* Sculpture. *Longitudinals—there are on the last whorl 16 rows of small rounded but not blunt tubercles, which more or less continuously run obliquely down the spire in lines from right to left; the hollows which part them are in form much like themselves; there are also faint microscopic scratches on the lines of growth. Spirals—on each whorl the tubercles are arranged in two spiral rows, in which the tubercles have their sharp tips tilted up the spire, and they are parted by a triangular shaped furrow, narrower than the spirals of tubercles. Below the under row of tubercles is a broader furrow, in the bottom of which runs the suture on the spireward face of a fine rounded thread occupying the extreme upper edge of the subjacent whorl. This thread is undulated rather than tubercled where it crosses the longitudinal rows; on the spireward side this thread is defined by a minute deep square-bottomed trench, while on the basal side it lies close in to the foot of the upper spiral row of tubercles. Round the edge of the base is a slight sharp narrow keel, which the succeeding whorl as it grows buries in the spiral thread mentioned above. At 0.004 from the edge, and there forming a ledge, the whole centre of the base is slightly projected: with this exception, the flat and scarcely conical base has no ornamentation beyond the radiating lines of growth and the microscopic spirals, which, though visible on the rest of the shell, are, as usual, more distinct on the base.* Colour *dull translucent white.* Spire *high, narrow, and conical.* Apex *blunt and inflated. The two embryonic whorls are larger, but otherwise very much like those of* C. metula, *Lov., being turban-shaped and projecting beyond the succeeding whorls; they are glossy and quite smooth but for some very faint microscopic longitudinal and spiral lines.* Whorls *13, of very gradual increase, flat on the sides; the base, too, is flat, and very little conical.* Suture *linear, almost hidden by the overlap of the subjacent whorl.* Mouth *very small and square, with a minute, round, very short canal in front, whose edges are reverted all round.* Outer lip *broken.* Pillar *very small, extremely short, straight, but reverted at the point.* Inner lip *not fully formed. H. 0.2. B. 0.06. Penultimate whorl 0.02. Mouth, length 0.028, breadth 0.025.*

This species, which in shape resembles T. suturalis, *Ad. & Rve., may be easily distinguished from that species by the absence of the deep suture and by the inflated apex. From* C. *(*T.*)* hebes, *W., its sculpture and its apex distinguish it at once.*

Remarks. Rolán and Fernández-Garcés (2008) recently treated this species and illustrated the lectotype.

Cerithium (*Triforis*) *levukense* Watson, 1880

Figure 116

Cerithium (*Triforis*) *levukense* Watson 1880: 100, not illustrated. Illustration available in Watson (1886): 551, pl. XXIX, fig. 4.

Type locality. "Levuka, Fiji".

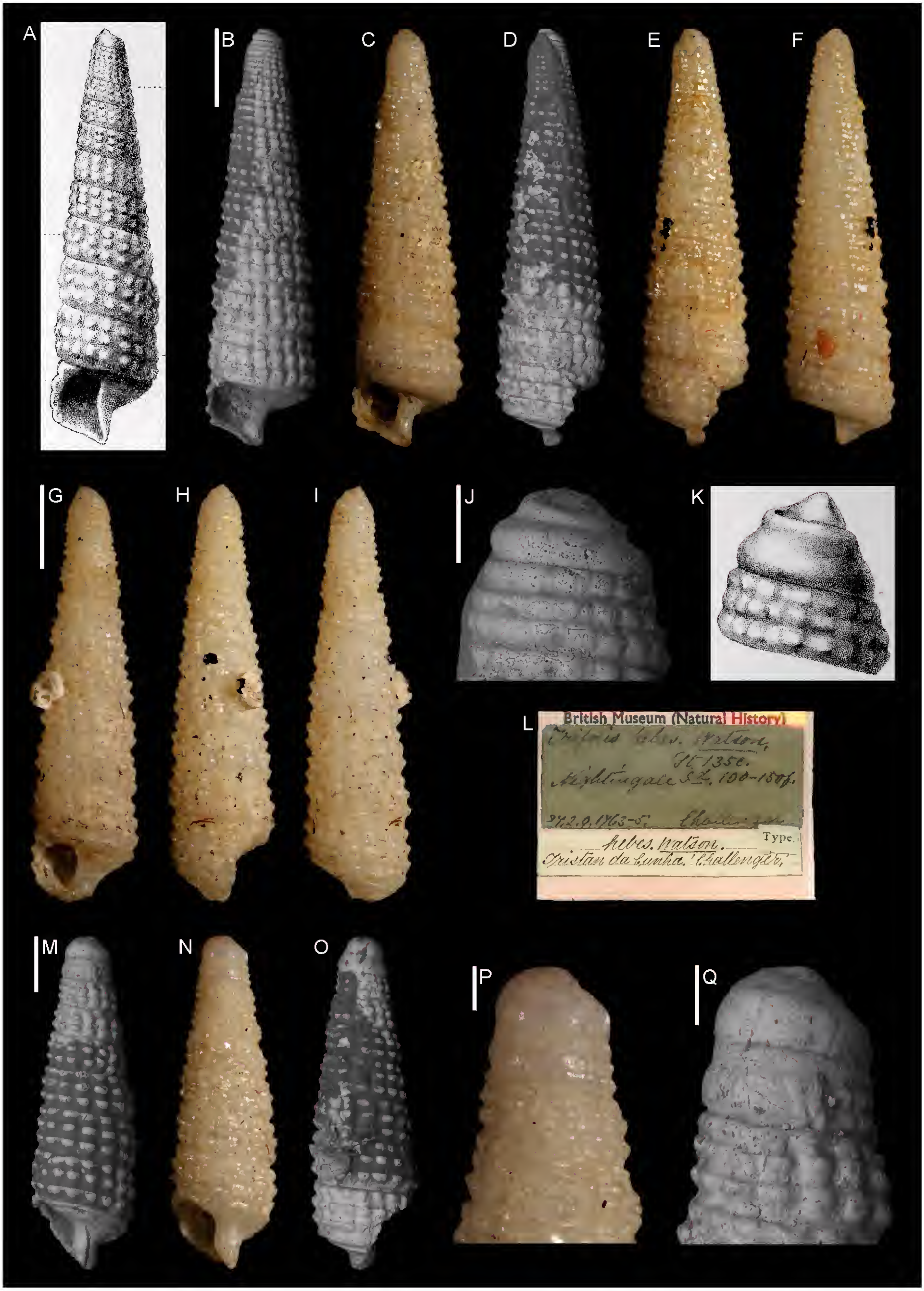

Figure 115. *Cerithium* (*Triforis*) *hebes* Watson, 1880, Nightingale Island, Tristan da Cunha, South Atlantic. **A, K** Original figures. **B–F, J** Syntype NHMUK 1887.2.9.1763: front (**B, C**), side (**D, E**), back (**F**), protoconch (**J**). **G–I** Syntype NHMUK 1887.2.9.1764: front (**G**), side (**H**), back (**I**). **M–Q** Syntype NHMUK 1887.2.9.1765: front (**M, N**), side (**O**), protoconch (**P, Q**). **L** Original labels. Scale bars: **B–I**: 1 mm; **H, P, Q**: 0.2 mm; **M–O**: 0.5 mm.

Type material. Syntypes: NHMUK 1887.2.9.1760–1: 2 specimens, type locality.

Original description. *July 29, 1874. Levuka, Fiji. 12 fms.*

Shell.—*Sinistral, sharply conical, with a narrow and produced base, solid, yellowish white, glossy.* Sculpture. *Longitudinals.— there are (on the last whorl) about twenty longitudinal rows of round tubercles, which rows form a small rib across the whorl, and are more or less continuous up the spire; these continue on the base as strongly as on the upper part of the whorls. These rows are parted by shallow rounded depressions. Spirals—the longitudinal rows are cut by narrow little rounded grooves, whose intersection with them forms the tubercles. On the upper whorls there is only one such spiral groove, so that there are only two tubercled spirals, but the groove gradually widens, and there appears in the bottom of it a minute additional spiral, which finally becomes as large as the other two; on the base are 3 equally divided tubercled spiral threads, of which the inmost is the smallest, and it ceases at the siphonal tube. The* apex *consists of 6 small rather elongated narrow whorls, of which the first 1½ have about ten rows of minute tubercles faintly connected by spirals; the next 4½ whorls are crossed by about 24 longitudinal sharp little ribs, rising into points at the carina, which is a continuous spiral thread. This carina on the first of these whorls is near the base, but later it rises so as to encircle the upper part of the whorl. The minute spiral rows of tubercles, which alone appear on the first whorl and half, cover the whole surface (both ribs and interstices) on the later apical whorls. The regular sculpture does not begin abruptly and at once, but a tongue of this new sculpture breaks across the top of the whorl, while the lower part retains the earlier ornamentation.* Colour. *The apical whorls are amber, the rest of the shell yellowish white, with a narrow amber-coloured thread within the contraction of the base of each whorl; this spiral thread is not continuous, being interrupted by each of the longitudinal rows of tubercles.* Spire *high, sharply conical, with a very slight convexity in its lines of profile, which are not perfectly alike.* Apex *a narrow and perfect cone, ending in a small rounded point.* Whorls *17, of very regular increase, flat on the side; the whole last whorl is contracted and a little elongated; the base is narrow and flat.* Suture *sharply impressed, and broader than the spiral grooves, being marginated on its upperside by a minute flat surface, which runs round the base of the superior whorl.* Mouth *almost more than perpendicular, square, with a largish auricle at its upper corner, and a small and very transverse rift at the pillar.* Outer lip *sharp, thin, straight, perpendicular, angulated at the basal corner, flat across the base, turned in towards the mouth and pinched in at the pillar, where it joins the pillar-lip, closing in the side of the small siphonal canal, whose edge is sharp and straight, or a very little contracted all round.* Pillar *straight in front, then very much bent back, so that its posterior line almost stands on the edge of the base.* Pillar-lip *expanded but abruptly defined on the base, blunt but projecting on the pillar, where it is covered by and cemented to the outer lip. H. 0.22. B. 0.075 least 0.06. Penultimate whorl 0.032. Mouth, length 0.037, breadth 0.035. This beautiful little species is very like in general aspect to* C. perversum, *L.; but, apart from other obvious differences, the sculpture of the apex is quite distinct. In that species the extreme apex has about seven spiral scatches, parted by roughened threads, and the following whorls are beset with much closer-set and more numerous riblets, and they have two close-set spirals at the carina. The whole of this sculptured apex (in* C. perversum*) is stumpier, and the whorls are not so angulated, and the extreme point is blunter.* T. Hindsii, *Desh. (Bourbon Moll. p. 99), is very near, but is less contracted in front towards the base, has not there near the mouth four rows of pearls, has the pearls white on a brown ground, has not the single amber thread, and is a little narrower in proportion.*

Diagnosis. The adult syntype is 4.4 mm high. Shell cyrtoconoid with flat whorls. Teleoconch with at least 11 whorls, but the apical part is missing. Three spiral cords are present with the second developing initially as a narrow thread and attaining full size only on the last whorl. A fourth smooth suprasutural cord is visible. Peristome incomplete in the adult syntype. Siphonal canal short. Base flat, with two weakly sculptured spiral cords. Protoconch present only in the juvenile syntype and likely multispiral as illustrated by Watson. Teleoconch light yellowish with a narrow orange-brown line on the lower part of the third spiral cord.

Triforis rufula Watson, 1886

Figure 117

Triforis rufula Watson (1886): 566–567, pl. XLII, fig. 2.

Type locality. "Lat. 10°30'S, long. 142°18'E. Off Wednesday Island, Cape York, North-east Australia".

Type material. Lectotype: NHMUK 1887.2.9.1768, here designated. Paralectotypes: NHMUK 1887.2.9.1769–71: 3 specimens (at least one certainly not belonging to this species, see remarks).

Original description. *Station 186. September 8, 1874. Lat. 10°30'S., long. 142°18'E. Off Wednesday Island, Cape York, North-east Australia. 8 fathoms. Coral mud.*

Shell.—*High, ruddyish, with convexly conical outlines, a slightly convex base, three rows of tubercles on each whorl, a small furrowed suture, and a conical and high apex.* Sculpture*: Longitudinals—there are on the last whorl about 18 (on the earlier whorls fewer) direct riblets, which run down the spire pretty continuously, and cross the base; the parting furrows are wide open and rounded. Spirals—on each whorl there are three very slightly raised square threads, which swell into strongish tubercles as they cross the riblets; they are parted by squarish somewhat narrower furrows; at the angle of the base, barely within its contraction, is a slightly weaker subtubercled thread; another, weaker and undulated rath-*

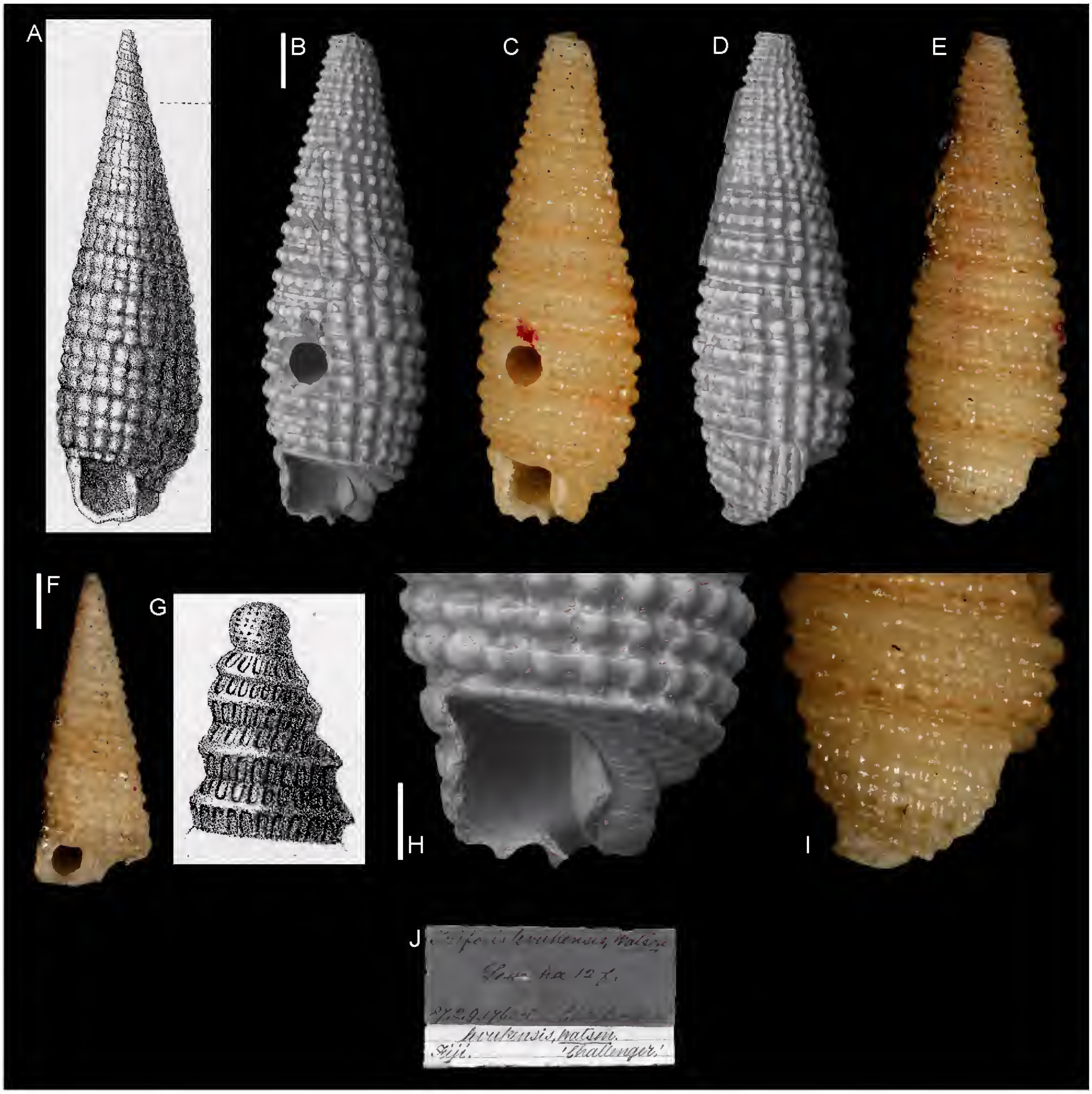

Figure 116. *Cerithium* (***Triforis***) *levukense* Watson, 1880, Levuka, Fiji. **A, G** Original figure. **B–E, H, I** Syntype NHMUK 1887.2.9.1760: front (**B, C**), side (**D, E**), aperture (**H**), peristome (**I**). **F** Syntype NHMUK 1887.2.9.1761: front. **J** Original labels. Scale bars: **B–F**: 0.5 mm; **H**: 0.3 mm.

er than tubercled, occupies the middle of the base; round the top of the pillar is another weaker still. Colour *yellow, more or less ruddy.* Spire *high, very slightly tumid, the lateral outlines being convex.* Apex *has a small blunt rounded tip, is translucent white and conical, and consists of five short convex whorls, on each of which, above the middle, are two fine flat slightly raised threads; their surface is also scored longitudinally with fine regular bard.* Whorls *8, besides those of the apex; they are flat on the sides, of slow and regular increase, and are parted by a strong sutural furrow; the last whorl is little larger than the penultimate, and has a short rounded base.* Suture *oblique, strongly defined by its furrow, but in itself invisible.* Mouth *oblique, irregularly four-sided, very acute-angled above at the sinus, and below at the canal.* Outer lip *thin and sharp, angulated but not sinuated at its insertion; from this point its edge advances all the way to the base of the shell, at the corner of which it turns in a distinct angle, and across which it is prominent; the lip of the canal does not touch the pillar point, so that the round canal is not closed.* Pillar *short, twisted but very shortly reverted at the point.* Inner lip *well defined, with a slightly thickened edge, concave. H. 0.192 in. B. 0.057. Mouth, height 0.037, breadth 0.027. Apex, height 0.02, breadth 0.014.*

This species is in a vague way very like a great many others of the genus, but is distinct from any known to me.

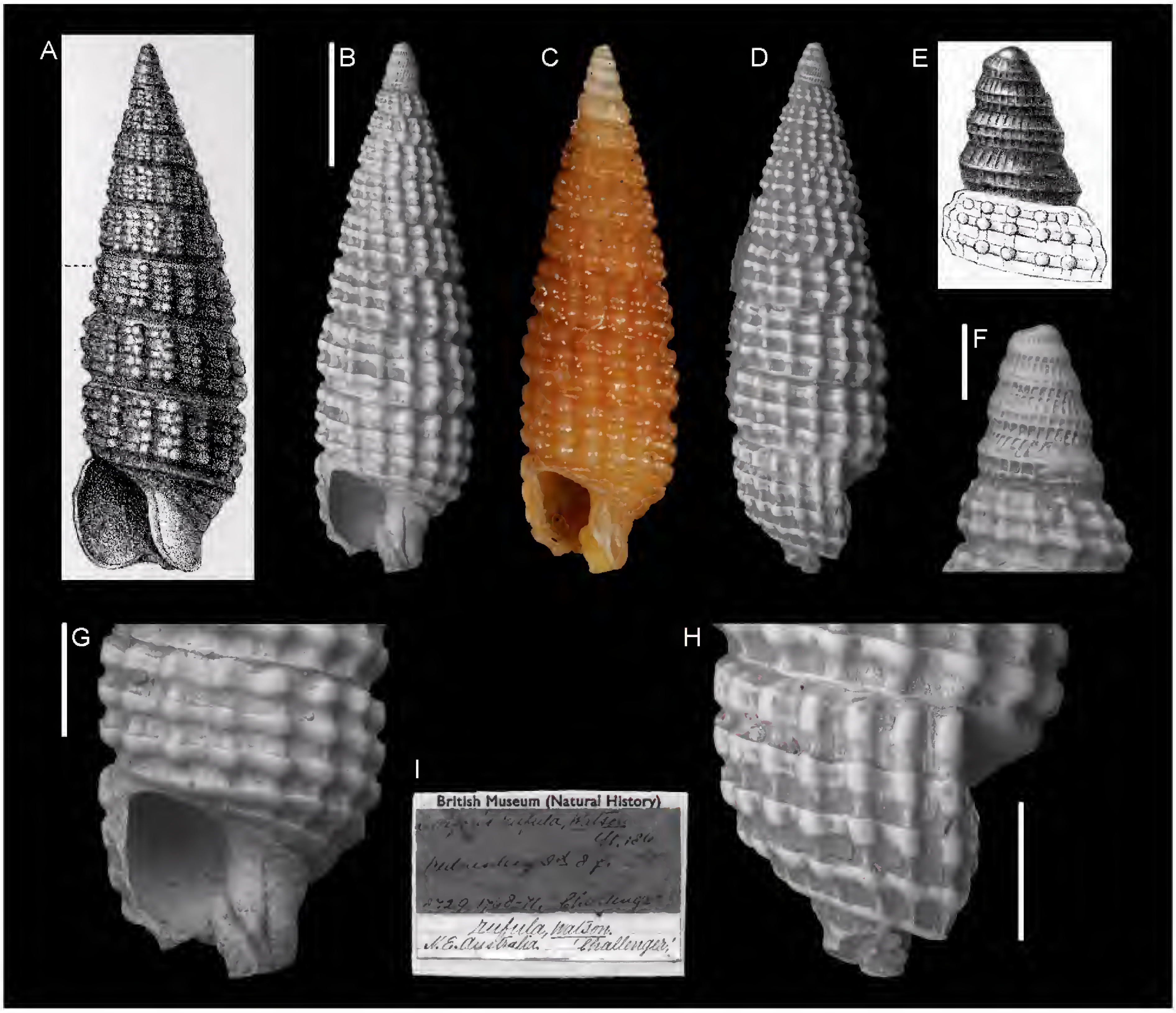

Figure 117. *Triforis rufula* Watson, 1886, off Wednesday Is., Cape York, north-east Australia. **A, E** Original figures **B–D, F–H** Lectotype NHMUK 1887.2.9.1768: front (**B, C**), side (**D**), protoconch (**F**), aperture (**G**), peristome (**H**). **I**. Original labels. Scale bars: **B–D**: 1 mm; **F**: 0.2 mm; **G, H**: 0.5 mm.

Diagnosis. Lectotype 4.2 mm high. Shell cyrtoconoid with flat whorls. Teleoconch of eight whorls with three spiral cords well developed from the first whorl onward and bearing tubercles at the intersection with orthocline axial ribs. A fourth smooth suprasutural cord is visible in the lower half of the shell. Growth lines are visible between the cords. Peristome incomplete in the lectotype. Siphonal canal short. On the base, the fourth cord becomes strong and slightly tubercled and two more smooth cords are visible. Protoconch multispiral of at least four whorls, but the first whorls are missing. These whorls bear two spiral keels and axial riblets. Teleoconch brown, protoconch white.

Remarks. Lot NHMUK 1887.2.9.1768–71 contains four specimens, with one specimen clearly matching the original drawing. Another specimen is obviously not conspecific because it has the second spiral cord developing later along the spire in contrast to *T. rufula* in which the three spiral cords are evident throughout the teleoconch. The other two specimens are juveniles and difficult to associate to this taxon due to their state of preservation. A lectotype is designated to stabilise the nomenclature.

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References

Adams A (1854) Descriptions of new species of *Eulima*, *Triphoris*, etc., from the Collection of Hugh Cuming, Esa. Proceedings of the Zoological Society of London 19: 276–279. https://doi.org/10.1111/j.1096-3642.1851.tb01178.x

Adams A (1861) On some new species of *Eulima*, *Leiostraca* and *Cerithiopsis* from Japan. Annals and Magazine of Natural History (Series 3) 7: 125–131

Adams A, Reeve L (1848–1850) Mollusca. In: Adams A (Ed.) The zoology of the voyage of H.M.S. Samarang; under the command of Captain Sir Edward Belcher, C.B., F.R.A.S., F.G.S., during the years 1843–1846. Reeve and Benham, London, 87 pp.

Albano PG, Bakker PAJ (2016) Annotated catalogue of the types of Triphoridae (Mollusca, Gastropoda) in the Museum für Naturkunde, Berlin, with lectotype designations. Zoosystematics and Evolution 92(1): 33–78. https://doi.org/10.3897/zse.92.5936

Albano PG, Sabelli B, Bouchet P (2011) The challenge of small and rare species in marine biodiversity surveys: microgastropod diversity in a complex tropical coastal environment. Biodiversity and Conservation 20(13): 3223–3237. https://doi.org/10.1007/s10531-011-0117-x

Albano PG, Bakker PAJ, Janssen R, Eschner A (2017) An illustrated catalogue of Rudolf Sturany's type specimens in the Naturhistorisches Museum Wien, Austria (NHMW): Red Sea gastropods. Zoosystematics and Evolution 93(1): 45–94. https://doi.org/10.3897/zse.93.10039

Barnard KH (1963) Contributions to the knowledge of South African marine Mollusca. Part III. Gastropoda: Prosobranchiata: Taenioglossa. Annals of the South African Museum 47(1): 1–199.

Biggs HEJ (1973) The marine Mollusca of the Trucial coast, Persian Gulf. Bulletin of the British Museum Natural History (Zoology) 24(8): 343–421.

Bouchet P (1985) Les Triphoridae de Mediterranee et du proche Atlantique (Mollusca, Gastropoda). Lavori della Società Italiana di Malacologia 21: 5–58.

Bouchet P, Guillemot H (1978) The *Triphora perversa*-complex in Western Europe. Journal of Molluscan Studies 44: 344–356.

Bouchet P, Strong EE (2010) Historical name-bearing types in marine molluscs. An impediment to biodiversity studies? In: Polaszek A (Ed.) Systema Naturae 250. CRC Press, London, 63–74. https://doi.org/10.1201/EBK1420095012-c6

Bouchet P, Lozouet P, Maestrati P, Héros V (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. Biological Journal of the Linnean Society 75: 421–436.https://doi.org/10.1046/j.1095-8312.2002.00052.x

Carpenter PP (1857) Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Report of the British Association for the Advancement of Science 26 [for 1856]: 159–368. https://doi.org/10.5962/bhl.title.60613

Cotton BC (1933) Obituary and bibliography of conchological works of Sir Joseph Cooke Verco. The South Australian Naturalist 14(4): 121–124.

Crosse H, Fischer P (1865) Description d'espèces nouvelles de l'Australie meridionale. Journal de Conchyliologie 13: 38–55.

Dance SP (1966) Shell Collecting. An Illustrated History. University of California Press, London, 344 pp.

De Folin L (1867) Espèces nouvelles. Les Meleagrinicoles, Havre, 74 pp.

Dickinson EC (2005) The Proceedings of the Zoological Society of London, 1859–1900: an exploration of breaks between calendar years of publication. Journal of Zoology 266: 427–430. https://doi.org/10.1017/S0952836905007077

Duncan FM (1937) On the dates of publication of the Society's 'Proceedings', 1859–1926. With an appendix containing the dates of publication of 'Proceedings' 1830–1858, compiled by the late F.H. Waterhouse, and of the 'Transactions' 1833–1869, by the late Henry Peavot, originally published in the P.Z.S. 1893, 1913. Proceedings of the Zoological Society of London 107: 71–84.

Fernandes F, Rolán E (1988) A família Triphoridae (Mollusca: Gastropoda) no Arquipélago de Cabo Verde. Publicações ocasionais da Sociedade Portuguesa de Malacologia 11: 17–32.

Fernandes F, Rolán E (1993) Nuevas aportaciones a la familia Triphoridae (Mollusca, Gastropoda) para el Archipiélago de Cabo Verde. Iberus 10(1): 143–148.

Herbert DG (2013) *Turritella declivis* Adams & Reeve, in Reeve, 1849 (Mollusca: Gastropoda) – a South African not an Australian species, and a characteristic component of the Agulhas Bank benthos. African Zoology 48(2): 412–417. https://doi.org/10.1080/15627020.2013.11407611

Hertlein LG, Strong AM (1947) Eastern Pacific expedition of the New York Zoological Society. XXXVI. Mollusks from the west coast of Mexico and Central America. Part V. New York Zoological Society, Zoologica 31(4): 129–150.

Hertlein LG, Strong AM (1950) Eastern Pacific expedition of the New York Zoological Society. XLII. Mollusks from the west coast of Mexico and Central America. Part IX. New York Zoological Society, Zoologica 35(4): 217–252.

Higo S, Callomon P, Goto Y (2001) Catalogue and bibliography of the marine shell-bearing Mollusca of Japan. Gastropoda. Bivalvia. Polyplacophora. Scaphopoda. Type figures. Elle Scientific Publications, Osaka, 196 pp.

Hinds RB (1843a) Descriptions of two new species of shells from the collection of Hugh Cuming. Proceedings of the Zoological Society of London 11: 22–23.

Hinds RB (1843b) Descriptions of new shells from the collection of Captain Belcher, R.N., C.B.. Annals and Magazine of Natural History 11: 16–21. https://doi.org/10.1080/03745484309445254

Hinds RB (1844) The Zoology of the Voyage of H.M.S. Sulphur, Under the Command of Captain Sir Edward Belcher, R.N., C.B., F.R.G.S., etc. during the years 1836–42. Smith, Elder and Co., London, 72 + iv pp.

ICZN (1999) International Code of Zoological Nomenclature, 4th edition. The International Trust for Zoological Nomenclature, London, 306 pp.

Jeffreys JG (1885) On the Mollusca procured during the ‘Lightning’ and ‘Porcupine’ expeditions, 1868–1870. Part IX. Proceedings of the Zoological Society of London 1885: 27–63.

Johnson RI (1994) Types of shelled Indo-Pacific mollusks described by W.H. Pease. Bulletin of the Museum of Comparative Zoology 154(1): 1–61. https://doi.org/10.3099/0027-4100(2003)158[1:MTABOW]2.0.CO;2

Jousseaume F (1884) Monographie des Triforidae. Bulletins de la Société Malacologique de France 1: 217–270.

Kay EA (1965) Marine molluscs in the Cuming collection, British Museum (Natural History) described by William Harper Pease. Bulletin of the British Museum Natural History (Zoology) Supplement 1: 1–96.

Kay EA (1965) Hawaiian marine shells. Reef and Shore Fauna of Hawaii. Section 4: Mollusca. Bishop Museum Press, Honolulu, XVII–653 pp.

Keen AM (1966) West American mollusk types in the British Museum (Natural History). II. Species described by R.B. Hinds. The Veliger 8(4): 265–275.

Kisch BS (1960) Les mollusques décrites par de Folin – a part les Caecidae et Chemnitzidae – avec catalogue. Journal de Conchyliologie 100(4): 137–162.

Kosuge S (1962a) Descriptions of 10 new species and 1 new subspecies of the family Triphoridae (Mollusca) from Shiono-misaki, Kii Peninsula, Central Japan with a list of hitherto known species. Bulletin of the National Science Museum 6(2): 78–89.

Kosuge S (1962b) On the family Triphoridae (Gastropoda) from Amami Islands (3). Venus 22(2): 119–129.

Kosuge S (1963a) On the family Triphoridae (Gastropoda) from Amami Islands (4). Venus 22(3): 240–257.

Kosuge S (1963b) On the family Triphoridae (Gastropoda) from Amami Islands (5). Venus 22(3): 257–263.

Le Renard J (1995) Révision des mollusques paléogènes du bassin de Paris. III – Chronologie des créatures de références primaires. Cossmanniana 3(4): 133–150.

Le Renard J, Pacaud J-M (1995) Révision des mollusques paléogènes du bassin de Paris. II – Liste des références primaires des espèces. Cossmanniana 3(3): 65–132.

Low MEY, Evenhuis NL (2013) Dates of publication of the Zoology parts of the Report of the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–76. Zootaxa 3701 (4): 401–420. https://doi.org/10.11646/zootaxa.3701.4.1

Marshall BA (1977) The dextral triforid genus *Metaxia* (Mollusca: Gastropoda) in the south-west Pacific. New Zealand Journal of Zoology 4: 111–117. https://doi.org/10.1080/03014223.1977.9517944

Marshall BA (1983) A revision of the recent Triphoridae of Southern Australia. Records of the Australian Museum Supplement 2: 1–119. https://doi.org/10.3853/j.0812-7387.2.1983.102

Marshall BA (1994) Results of the Rumphius Biohistorical Expedition to Ambon (1990). Part 2. An unusual triphorid (Mollusca: Gastropoda) from the Moluccas, Indonesia. Zoologische Mededelingen 68: 39–43.

Melvill JC (1904) Descriptions of twenty-eight species of Gastropoda from the Persian Gulf, Gulf of Oman, and Arabian Sea, dredged by Mr. F.W. Townsend, of the Indo-European Telegraph Service, 1900–1904. Proceedings of the Malacological Society of London 6: 158–169. https://doi.org/10.1093/oxfordjournals.mollus.a066056

Melvill JC (1909) Report on the marine Mollusca obtained by Mr. J. Stanley Gardiner F.R.S., among the Islands of the Indian Ocean in 1905. Transactions of the Linnean Society of London, series 2, 13: 65–138. https://doi.org/10.1111/j.1096-3642.1909.tb00411.x

Melvill JC (1918) Descriptions of thirty-four species of marine Mollusca from the Persian Gulf, Gulf of Oman and Arabian Sea. Annals and Magazine of Natural History (Series 9) 1: 137–158. https://doi.org/10.1080/00222931808562296

Melvill JC, Standen R (1899) Report on the marine Mollusca obtained during the first expedition of Prof. A.C. Haddon to the Torres Straits, in 1888–89. Journal of the Linnean Society 27: 150–206.

Melvill JC, Standen R (1901) The Mollusca of the Persian Gulf, Gulf of Oman and Arabian Seas as evidenced mainly through the collections of Mr. F.W. Townsend, 1893–1900, with descriptions of new species. Part 1. Cephalopoda, Gastropoda and Scaphopoda. Proceedings of the Zoological Society of London 11: 327–460. https://doi.org/10.1111/j.1469-7998.1901.tb08181.x

Pease WH (1861) Descriptions of forty-seven new species of shells from the Sandwich Islands, in the collection of Hugh Cuming. Proceedings of the Zoological Society of London 28: 431–438.

Pease WH (1868). Synonymy of marine gastropodae inhabiting Polynesia. American Journal of Conchology 4(3): 103–132.

Petit RE (2007) Lovell Augustus Reeve (1814–1865): malacological author and publisher. *Zootaxa* 1648: 1–120. https://doi.org/10.11646/zootaxa.1648.1.1

Rolán E (2005) Malacological fauna from the Cape Verde Archipelago. Part 1. Polyplacophora and Gastropoda. ConchBooks, Hackenheim, 455 pp.

Rolán E, Cruz-Abrego FM (1995) A new triphorid species (Gastropoda, Triphoridae) from Nichupté lagoon, Yucatán peninsula, Mexico. Iberus 13(2): 87–92.

Rolán E, Espinosa J (1994) The family Triphoridae (Mollusca, Gastropoda, Prosobranchia) in Cuba. 3. The genus *Isotriphora*, with description of a new species. Basteria 58: 63–68.

Rolán E, Fernández-Garcés R (1992) Famiglia Triphoridae (Mollusca: Gastropoda) en la isla de Cuba. 1. El genero *Metaxia* Monterosato, 1884. Bollettino Malacologico 28(5–12): 169–176.

Rolán E, Fernández-Garcés R (1993) The family Triphoridae (Mollusca, Gastropoda, Prosobranchia) in Cuba. 2. The genus *Iniforis* Jousseaume. Apex 8(3): 95–106.

Rolán E, Fernández-Garcés R (1994) The Family Triphoridae (Mollusca, Gastropoda) in Cuba. 4. The genera *Monophorus*, *Nototriphora*, *Cosmotriphora* and *Cheirodonta*, with the description of three new species. Apex 9(1): 17–27.

Rolán E, Fernández-Garcés R (1995) The family Triphoridae (Mollusca, Gastropoda) in Cuba. 5. The genera *Marshallora*, *Mesophora*, *Similiphora*, *Eutriphora*, *Latitriphora*, *Aclophora* and other species without generic affiliation. Apex 10(1): 9–24.

Rolán E, Fernández-Garcés R (2008) New data on the Caribbean Triphoridae (Caenogastropoda, Triphoroidea) with the description of 26 new species. Iberus 26(1): 81–170.

Rolán E, Fernández-Garcés R (2009) Two new species of *Iniforis* (Gastropoda: Triphoridae) from the Caribbean. Novapex 10(3): 103–108.

Rolán E, Peñas A (2001) Two new species of the genus *Monophorus* (Gastropoda, Triphoridae) in the east Atlantic and Mediterranean Sea. Iberus 19(2): 31–40.

Sclater PL (1893) List of the date of delivery of the sheets of the ‘Proceedings’ of the Zoological Society of London, from the commencement in 1830 to 1859 inclusive. Proceedings of the Zoological Society of London 1893: 435–440.

Sherborn CD (1922) Index Animalium 1801–1850. Volume A and B. Bibliography. Cambridge University Press, London, xv–cxxxi pp.

Smith EA (1875) A list of the Gastropoda collected in Japanese Seas by Commander H.C. St. John, R.N. Annals and Magazine of Natural History, Series 4, 16: 103–115. https://doi.org/10.1080/00222937508681135

Smith EA (1890) Report on the marine molluscan fauna of the Island of St. Helena. Proceedings of the Zoological Society of London 1890: 247–317.

Smith EA (1903) Marine Mollusca. In: Gardiner JS (Ed.) The fauna and geography of the Maldive and Laccadive Archipelagoes, being an account of the work carried on and of the collections made by an expedition during the years 1899 and 1900. Cambridge University Press, Cambridge, 2(2): 589–630.

Smith EA (1904) On a collection of marine shells from Port Alfred, Cape Colony. Journal of Malacology 11: 21–44.

Smith EA (1906) The history of the collections contained in the natural history departments of the British Museum. Vol. II. Separate historical accounts of the several collections included in the Department of Zoology. British Museum, Clowes and Sons, London, 782 pp.

Smith EA (1906) On South African marine mollusca, with descriptions of new species. Annals of the Natal Government Museum 1: 19–71.

Smith EA (1910) On South African marine Mollusca, with descriptions of new species. Annals of the Natal Museum 2: 175–219.

Smith EA (1916) Note on *Triphora smithi*, Sowerby, and *T. gracilior*, Smith. Proceedings of the Malacological Society of London 12(2–3): 60. https://doi.org/10.1093/oxfordjournals.mollus.a063615

Sowerby GB III (1901) Descriptions of new species of marine Mollusca collected by the late Otto Koch at the Island of Cebú, Philippines. (Second paper). Proceedings of the Malacological Society of London 4(5): 208–211. https://doi.org/10.1093/oxfordjournals.mollus.a065816

Sowerby GB III (1903) Descriptions of fourteen new species of marine Mollusca from Japan. Annals and Magazine of Natural History, series 7, 12: 496–501. https://doi.org/10.1080/00222930308678886

Sowerby GB III (1904) Descriptions of six new species of marine Mollusca from the collection of the late admiral Keppel. Proceedings of the Malacological Society of London 6(3): 174–177. https://doi.org/10.1093/oxfordjournals.mollus.a066058

Sowerby GB III (1907) Descriptions of new marine Mollusca from New Caledonia, etc. Proceedings of the Malacological Society of London 7(5): 299–303.

Sowerby GB III (1914) Descriptions of new Mollusca from New Caledonia, Japan, Philippines, China, and West Africa. Annals and Magazine of Natural History, series 8, 14: 475–480. https://doi.org/10.1080/00222931408693604

Sowerby GB III (1921) New shells from Port Alfred, collected by Lieut.-Colonel W. H. Turton. Proceedings of the Malacological Society of London 14(4): 125–127.

Steger J, Stockinger M, Ivkić A, Galil BS, Albano PG (2018) New records of non-indigenous molluscs from the Eastern Mediterranean Sea. Bioinvasions Records 7(3): 245–257. https://doi.org/10.3391/bir.2018.7.3.05

Tomlin JR le B (1926) On South African marine Mollusca, with descriptions of new species. Annals of the Natal Museum 5(3): 283–301.

Tomlin JR le B (1931) On South African marine Mollusca, with descriptions of new genera and species. Annals of the Natal Museum 6(3): 415–450.

Tomlin JR le B (1941) Shell sales. Proceedings of the Malacological Society of London 24(4): 157–160. https://doi.org/10.1093/oxfordjournals.mollus.a064409

Trew A (1987) James Cosmo Melvill's New Molluscan Names. Amgueddfa Genedlaethol Cymru, National Museum of Wales, Cardiff, 84 pp.

Trew A (1990) John R. le B. Tomlin's New Molluscan Names. Amgueddfa Genedlaethol Cymru, National Museum of Wales, Cardiff, 101 pp.

Trew A (1992) Henry and Arthur Adams New Molluscan Names. National Museum of Wales, Cardiff, 63 pp.

Trew A (1993) Edgar Albert Smith's New Molluscan Names. National Museum of Wales, Cardiff, 86 pp.

Turton WH (1932) The Marine Shells of Port Alfred, S. Africa. Oxford University Press, London, 331 pp.

Verco JC (1909) Notes on South Australian marine Mollusca, with description of new species. Part XI. Transactions of the Royal Society of South Australia 33: 277–292.

Verco JC (1910) Notes on South Australian marine Mollusca, with description of new species. Part XIII. Transactions of the Royal Society of South Australia 34: 115–131.

Warén A (1980) Marine Mollusca described by John Gwyn Jeffreys, with the location of the type material. Conchological Society of Great Britain and Ireland, Special Publication 1: 1–60.

Watson RB (1880) Mollusca of H.M.S. 'Challenger' Expedition. Part V. Journal of the Linnean Society 15: 87–126. https://doi.org/10.1111/j.1096-3642.1880.tb00346.x

Watson RB (1886) Report on the Scaphopoda and Gasteropoda collected by H.M.S. Challenger during the years 1873–76. Reports of the scientific results of the voyage of H.M.S. "Challenger", Zoology 15(42): 1–756.

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