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Instructions for authors

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Zoosystematics and Evolution (formerly Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe) edited by the *Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin* is an international, peer-reviewed, life science journal, devoted to whole-organism biology. It mainly publishes original research and review articles in the field of Metazoan taxonomy, biosystematics, evolution, morphology, development and biogeography at all taxonomic levels. Its scope encompasses primary information from collection-related research, viz. taxonomic descriptions and discoveries, revisions, annotated type catalogues, aspects of the history of science, and contributions on new methods and principles of systematics. Entomological papers will also be accepted for review, but authors should first consider submission to the Deutsche Entomologische Zeitschrift. Articles whose main topic is ecology, functional anatomy, physiology, or ethology are only acceptable when of clear systematic or evolutionary relevance and perspective. Review articles and contributions to a discussion forum are welcome, but authors are asked to contact the editors beforehand.

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- Materials and Methods
- Results
- Discussion
- Acknowledgements
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- Tables with captions
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In Focus

The cover picture shows a female of *Nothobranchius insularis* sp. n. from eastern Tanzania.

See paper of **Costa WJEM** Redescription of *Nothobranchius lucius* and description of a new species from Mafia Island, eastern Tanzania (Cyprinodontiformes, Aplocheilidae)

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Bryanites graeffii sp. n. (Coleoptera, Carabidae): museum rediscovery of a relict species from Samoa

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Abstract

Bryanites graeffii **sp. n.** is described from Samoa based on a single male specimen collected between 1862–1870 that was recently discovered in the Muséum national d'Histoire naturelle, Paris. Cladistic analysis based on 127 morphological characters from 49 exemplars of the carabid beetle tribe Platynini in the Austral-Pacific region, places the new species as adelphotaxon to *Bryanites samoaensis* Valentine, type species of the genus *Bryanites* Valentine, 1987. *Bryanites* comprises, along with *Vitagonum* Moore, 1998 of Fiji and *Ctenognathus* Fairmaire, 1843 of New Zealand, a clade that diverged early in the evolutionary history of Pacific platynine Carabidae. *Bryanites graeffii* exhibits very large body size among taxa of Platynini—16.2 mm standardized body length—with the genus characterized by vestigial flight wings and metathoracic apomorphies that are associated with flight-wing loss. Along with *Blackburnia* Sharp, 1878 of Hawaii, the origins of *Bryanites*, *Vitagonum*, and *Ctenognathus* are hypothesized to date to the Miocene, with their radiations beginning long before the origins of the geographically widespread, flight-capable species of *Metacolpodes* Jeannel, 1948 that colonized numerous island systems across the western Pacific. Given the numerous platynine taxa collected by extensive biotic surveys of Samoa during the first quarter of the 20th Century, the absence of any specimens of *B. graeffii* since the initial collection of the unique holotype prior to 1871 suggests that this species may be extinct. Such extirpation of large platynine carabid beetles has also been documented for Hawaii, where the time of extinction of seven *Blackburnia* species represented only by subfossil fragments coincides with the time of human colonization and attendant introduction of the Pacific rat, *Rattus exulans* (Peale).

Introduction

It is undeniable that natural history museums represent invaluable and irreplaceable archives of biological diversity on Earth. Firstly these institutions serve as repositories for many millions of studied and described specimens: i.e. type specimens and associated subsequent collections of named species. Secondly museums also hold uncounted, unstudied specimens that have been collected and processed, but never adequately examined or understood by a taxonomic specialist. Predictably, examination of unidentified material collected long ago can produce surprising results, especially when the historical museum specimens represent the only evidence we have for existence of that particular species. For example, two Samoan species of flying fox, genus *Pteropus* Brisson, 1762 (Chiroptera: Pteropodidae), are known only from museum specimens collected between 1839 and 1856 (Helgen et al. 2009). In this contribution, a Samoan carabid beetle specimen collected prior to 1871, and subsequently deposited in the Paris Natural History Museum, is shown to represent the only specimen known of a new species. Moreover, the genus to which the new species is assigned is known previously only from two species based on two specimens collected in 1924 (Valentine 1987). That the new species is being described only now, over 140 years after its collection from nature, attests to the contextual information that is required to interpret biodiversity, for it is not the simple naming of organisms that occupies systematists, but more importantly, the organized naming and placing in context of all organisms. A scientific name presented in isolation from any detailed taxonomic framework is nearly useless, being suspect as a natural entity, devoid of biological context provided by knowledge of its sister group (Hennig 1966), and at best representing a single datum indexing a gross estimate of biodiversity.

The specimen described in this contribution is a member of the carabid beetle tribe Platynini belonging to the genus *Bryanites* Valentine, 1987 (Valentine 1987). This genus was previously known only from specimens collected by E. H. Bryan, Jr., 23-v-1924, at Salaʻilua, Savaiʻi Island, Samoa. Though the holotype specimens of *Bryanites samoaensis* Valentine and *B. barri* Valentine are assignable to the Platynini, they are aberrant representatives of that tribe. In contrast to many platynine carabid beetles, which as the name suggests are flattened dorsally, the bodies of *Bryanites* beetles are fusiform with a broad pronotum, their bodies convex dorsally. The two *Bryanites* spp. also exhibit patterns of setation on the elytra and pronotum unusual among platynine taxa. H. E. Andrewes, formerly at the Natural History Museum, London and a worldwide authority on Carabidae, placed determination labels on both specimens subsequently described by Valentine that read "? Pterostichini gen. nov." He did this presumably because the specimens appear superficially like the larger-bodied, more robust beetles of that tribe, though their lack of a critical diagnostic feature of most Pterostichini—i.e. an externally visible plica, or fold, along the apical elytral margin—fits members of the tribe Platynini. Andrewes' tentative, incorrect guess as to tribal membership is also understandable because the two *Bryanites* beetles appear nothing like the other Samoan species of Platynini that he had previously described (Andrewes 1927).

This paper first traces the provenance of the newly described Samoan beetle specimen from its collection in nature to the present day. We cannot be certain why the specimen avoided description until now. But the documented timing of expeditions and subsequent taxonomic publications coupled with the temporal connections of the various taxonomists, and how the beetle could have passed from hand to hand, make a strong case for how a large carabid beetle from a tropical island could be ignored for well over a century to be rediscovered within a natural history museum. In order to be certain how best to classify the new species, cladistic analysis using morphological characters is used to phylogenetically place the species. After adding the new species to a little-known clade of Samoan Carabidae, the question regarding the fate of this lineage in nature is investigated, with parallels from the platynine carabid beetle fauna of the Hawaiian Islands suggesting a likely scenario for this species leading from the 19th to the 21st Century.

Materials and methods

Taxonomic material. Specimens treated in this contribution were borrowed from the Muséum national d'Histoire naturelle, Paris (MNHN), Mdm. Helène Perrin and Dr. Thierry Deuve curators, and the B. P. Bishop Museum, Honolulu (BPBM), James Boone collection manager. Placement of the new species within the context of platynine phylogeny (Suppl. material 1) utilized an updated version of the character matrix previously presented in Liebherr (2005), with that paper citing institutional sources that provided specimens for initial matrix development. Taxa included in the analysis are distributed in the southwest Pacific region, including Australia and Asia, northeastward through Melanesia and Polynesia to the Hawaiian Islands.

Several taxa were added to complement the previous analysis. *Colpodes kanak* Fauvel (Fauvel 1903) of New Caledonia was added to the analysis based on examination of a female (MNHN) determined by Fauvel in 1906. *Vitagonum apterum* Moore of Fiji was added because it, like *Bryanites*, represents an aberrant, taxonomically isolated platynine lineage in the Pacific (Moore 1998). The male holotype of *Bryanites samoaensis* serves to represent the genus in the analysis. The female holotype of *B. barri* Valentine was also studied, and external anatomy of prothorax and elytra is consistent with Valentine's (1987) taxonomic decision placing both species together in the genus. However the type specimen of *B. barri* is heavily damaged. The beetle was extensively disarticulated during description, demonstrated by Valentine's illustrations of an isolated mentum, maxilla, and labium (Valentine 1987: Fig. 3). The resulting disarticulated structures were then mounted on two acetate sheets using Canada balsam as a fixative. Several isolated flecks of mounting medium remain on the sheet without any associated sclerite, suggesting strongly that flexure of the acetate caused the balsam to pop off the acetate. This interpretation explains the absence of the head capsule, mandibles, and antennae from the mounting cards. The female ovipositor is also damaged and the internal reproductive tract not present. Given this destruction of the specimen, 26 characters of the female reproductive tract and 11 characters of the head cannot be scored. Coupling that loss with the inability to score the 21 characters of the male reproductive system from the female holotype leads to at least 58 of the 127 characters necessarily being coded as missing. The poor mounting condition of the remaining sclerites cemented to the specimen cards limits confidence in assessing microsculpture covered by the Balsam, adding further uncertainty to the assessment of character states. This lack of information precludes a precise placement of this taxon in the analysis, at the same time seriously reducing resolution in a strict consensus cladogram when the taxon is included in the analysis. As *B. samoaensis* is the type species of *Bryanites*, it was decided to limit the focus of the analysis to the question of where the taxon herein classified as *B. graeffii* fits phylogenetically relative to an array of fully informative exemplar specimens. As we have no evidence to overturn Valentine's (1987) decision to place *B. barri* in *Bryanites*, that decision is allowed to stand.

Laboratory Techniques. Dissection protocols used throughout development of the present character matrix are detailed in Liebherr (2015: 18–20). An ocular ratio is used to quantify eye size: the maximum width of head across eyes divided by the minimum breadth of frons between eyes. Male genitalia are preserved in polyethylene vials placed on the specimen pin. Standardized body length comprises the sum of three measurements: 1, head length measured from the medioanterior margin of the labrum to the cervical ridge; 2, median pronotal length; and 3, elytral length measured from base of elevated scutellar apex to apex of longer elytron adjacent to the suture.

Character data. The cladistic analysis was based on 127 characters, 26 scored from the female reproductive tract and gonocoxae (i.e. ovipositor), 21 scored from male genitalic structures, and 80 derived from external anatomical structures (Suppl. material 2). Six of the characters are autapomorphic for a single terminal, however these were retained as other taxa could not be scored for these characters, due either to missing female or damaged specimens. Given additional material these characters could become potentially synapomorphous.

Cladistic methods. The character matrix was developed in WinClada (Nixon 2002) (Suppl. material 2), and analyzed by Nona (Goloboff 1999) using the ratchet (Nixon 1999). Results from an initial analysis using 200 iterations of the ratchet were compared to subsequent analyses using 1000 ratchet iterations, and then 10,000 ratchet iterations. After each ratchet run all trees were hard collapsed—i.e. collapsing nodes on trees when they are not supported under all optimizations—and then non-optimum (longer) trees were deleted. The strict consensus was then generated from those remaining hard-collapsed trees. Identical results at the 200, 1000 and 10,000 ratchet levels permitted the conclusion that all most parsimonious trees had been discovered.

Results

Provenance. The specimen rediscovered in the Paris Museum (Fig. 1) bears three labels (Fig. 2). The collector/locality label specifies that the beetle was collected in Samoa by "Dr. Graffe." A second label reads "8284", and a third label notes accession by the Paris Museum. "Dr. Graffe" is no doubt Eduard Gräffe, or Graeffe, a Swiss zoologist and naturalist who lived in Samoa from 1862-1870 (Graeffe 1917, Clunie and Snow 1986). Graeffe was employed by Johann Cesar VI Godeffroy, a wealthy shipping magnate in Hamburg who founded the Museum Godeffroy. The Museum Godeffroy published a journal, within which Graeffe published treatises on Samoan geography and birds (Graeffe 1873a, 1873b). He also published on the invertebrates including the insects of Fiji (Graeffe 1866). He maintained contact with scientists in Europe, including the ornithologists Otto Finsch and Gustav Hartlaub, to whom he sent a manuscript describing the birds of Tonga (Graeffe 1870). After Graeffe's return to Hamburg, Leon Fairmaire described new species and redescribed numerous previously described beetle species from Australia, Fiji, Tonga, and Samoa (Fairmaire 1879a), many deposited in Museum Godeffroy. Fairmaire's (1879a) paper documents a connection between Graeffe and Fairmaire via the Museum Godeffroy, and supports the transfer of the specimen described herein to Fairmaire, either by loan or by purchase, after 1870 but prior to 1879. Fairmaire described or revised other carabid beetles from Fiji and Tonga (Fairmaire 1878, 1879b, 1881a, 1881b), though no more from Samoa. When his collection passed to the Paris Museum upon his death in 1906, the "MUSEUM PARIS" accession label was placed on the specimens (e.g. Fig. 2), with all of his carabid specimens maintained together in boxes as the "Fairmaire Collection." When Erwin and Erwin (1971) assessed the condition of the Paris Museum carabid beetle holdings, they cited shelving unit B13, shelves 1-2; "23 boxes of the Fairmaire Collection, misc. carabids in very poor condition with no or poor labels, 'a mess'! (p. 10)." It is within this set of boxes that the specimen described below was found.

Cladistic Analysis. Subjecting the taxon-character matrix to Nona (Goloboff 1999) within the WinClada shell (Nixon 2002) resulted in 47 hard-collapsed, multiple equally parsimonious trees (MEPT) of 566 step-length under 200, 1000, or 10,000 iterations of the ratchet (Nixon 1999). These trees were constrained to be fully resolved under all character optimizations; i.e. fast or slow optimization. The strict consensus cladogram of 607 steps (Fig. 3) was rooted so that the species of *Lorostema* Motschulsky, 1865 comprise outgroups to the other Pacific platynine taxa. This decision was based on plesiomorphic presence of two testes in male beetles of *Lorostema* spp. versus the derived monorchid, or single-testis configuration (character 46, Suppl. material 2) in males of species of *Blackburnia* Sharp, 1878, *Notagonum* Darlington, 1952, *Colpodes* W. S. MacLeay, 1825, and *Metacolpodes* Jeannel, 1948 (Will et al. 2005). The cladistic relationships indicate that the newly described species should be combined as *Bryanites graeffii* sp. n. (Fig. 3). The two *Bryanites* examples are members of a clade, under all possible MEPTs, that includes *Vitagonum apterum* Moore of Fiji as adelphotaxon. These two genera are in turn sister group to *Ctenognathus* Fairmaire, 1843 of New Zealand.

Other relationships inherent in the tree are very similar to those discussed in Liebherr (2005, fig. 78), although the inclusion of the two *Bryanites* spp. plus *V. apterum* in this analysis results in the *Ctenognathus* spp. joining with those taxa much closer to the root node the cladogram (Fig. 3). Also, *Notagonum kanak* (Fauvel) comb. n. is placed such that it must be removed from the genus *Colpodes* and newly combined with *Notagonum*.

Taxonomic challenges remain regarding monophyletic classification of species in the genera *Colpodes* and *Notagonum*, and these must be addressed via a more comprehensive and informative phylogenetic analysis, such as those that include DNA-molecular characters (e.g. Maddison 2012). *Colpodes* is certainly polyphyletic. The genus is based on Co*lpodes brunneus* (W. S. MacLeay), placed here as sister species to a second Javan species, *C. latus* Louwerens (Fig. 3). A third Javan species, *C. brittoni* Louwerens, is also closely related, with beetles of all three species exhibiting exceedingly protruded compound eyes and very broad pronotal lateral margins (Liebherr 1998). Other species combined with *Colpodes* in this analysis—from Fiji and Tahiti (Fig. 3)—must be recombined with different generic names to accommodate the monophyletic taxa *Helluocolpodes* Liebherr, 2005 and *Metacolpodes*. *Notagonum* has been a genus of convenience since Darlington (1952) proposed it. In his words, "It must be admitted that it is hard to draw a line between *Colpodes* in my partly restricted sense and some of the forms which I am including in *Notagonum*, but I am convinced that when *Colpodes* is broken up the various species of *Notagonum* will properly form at least one and perhaps more separate genera (Darlington 1952: 129)."

Taxonomy

Bryanites Valentine, 1987

Type species. *Bryanites samoaensis* Valentine (by original designation).

Diagnosis. These beetles can be diagnosed from other Pacific platynine taxa by the much reduced subapical sinuation of the elytra, with the elytral margins straight to convex near the apex (Fig. 1). The pronotum is broadly orbiculate, with the lateral margins convex to only slightly concave anterad the rounded hind angles. The pronotum has the basal seta present and situated anterad the rounded hind angle. The elytra are moderately narrowed basally, with the basal elytral groove meeting the lateral elytral depression at an angle; i.e. the humeri are angulate. The male aedeagus exhibits characters typical of tribe Platynini (Fig. 4): 1, both parameres are rounded apically, or conchoid in shape; 2, the right paramere is smaller than the left, and the aedeagus lies with the right side ventral in repose; 3, the basal bulb is closed and bears a sagittal crest; and 4, the internal sac is tubular and unarmored, with slightly more melanized spicules present apically near the gonopore.

Beetles of all three *Bryanites* species are brachypterous, with the wing rudiments narrow and elongate stenopterous straps, the length of the rudiments more than 4× the rudiment breadth. Beetle size is moderate to large, ranging from 11.7 mm in *B. barri* (measurement of Barr 1987) to 16.2 mm in *B. graeffii*.

Key to the Adults of *Bryanites* Valentine

1. Beetles of moderate size, standardized body length 11.7–12.5 mm; pronotum quadrisetose both lateral and basal setae present; parascutellar seta present 2
– Larger beetles, standardized body length 16.2 mm; pronotum bisetose, only basal seta present both sides; parascutellar seta absent .... *B. graeffii* sp. n.
2. Third elytral interval with 6 setae along length, the anterior seta associated with the third stria, the trailing five setae associated with the second stria; elytral basal groove meeting lateral elytral depression at right angle; pronotum without any evident laterobasal depressions, at most a slight depression near hind margin (left side of holotype) .... *B. samoaensis* Valentine
– Third elytral interval with 3 setae along length, the anterior seta associated with the third stria, the posterior two setae associated with the second stria; elytral basal groove meeting lateral elytral depression at acute angle; pronotum with broad, shallow linear laterobasal depressions extended from hind angles toward center of pronotal disc .... *B. barri* Valentine

Bryanites graeffii sp. n.

http://zoobank.org/F82C8023-8E56-4563-AB2E-8A208F41E984
Figs 1, 2, 4

Diagnosis. Besides the very large size of this beetle—standardized body length 16.2 mm—the elytral and pronotal setation are diagnostic. The elytra lack the parascutellar seta and any dorsal elytral setae, though both subapical and apical setae are present in the seventh stria near the rounded sutural apex. The pronotum has only the basal seta present, with this seta's position 0.14× the median pronotal length anterad a transverse line drawn across the median pronotal base. The pronotal lateral marginal depression is broad and upraised to a smooth, unbeaded margin. The prosternal process is flat between the procoxae, with four to five setae each side approaching the process apex. Cuticular microsculpture is particularly well developed, with the frons and clypeus bearing distinct, upraised isodiametric sculpticells, and the vertex covered with more transverse, though equally well-developed sculpticells. The pronotal and elytral discs are covered with very small transverse sculpticells, the sculpticells' small size giving the surface a velvety or velour-like reflection.

Description. Head broad, robust, ocular ratio 1.61; antennae elongate, as long as distance from antennal socket to elytral midlength; scape stout, maximal breadth 0.5× distance from basal constriction to apex; antennomeres 2–3 apparently glabrous, but sparsely covered with very short microsetae, an apical ring of setae on antennomere 3; antennomere 4 apparently glabrous in basal ¼ of length, though also with very short microsetae, remainder of antennomere and antennomeres 5–11 pilose with darker

Figure 1. Male holotype, *Bryanites graeffii*, dorsal view.

Dr Graffe
Samoa

8284.

MUSEUM PARIS
Samoa
Collection Léon Fairmaire,
1906

Figure 2. Specimen labels associated with holotype specimen of *Bryanites graeffii*.

brunneous, glabrous longitudinal ridge on each anterior and posterior surface; frontal grooves very shallow, ending posteriorly anterad the anterior supraorbital seta; posterior supraorbital setal position behind posterior margin of eye and 3× as far from eye margin as anterior seta; frons and clypeus not demarked by suture, surfaces convex, continuous, only three very shallow transverse wrinkles medially at position of frontoclypeal suture; labral anterior margin straight, only slightly incurved medially; mentum tooth broad, apex flattened medially, mentum setae positioned posterad curved mentum margin each side of midline; submentum with two setae each side. Pronotum broad, maximal width 1.08× median length; lateral margins only slightly incurved anterad rounded hind angles; broadly longitudinal laterobasal depressions joined by well-defined transverse depression anterad basal convexity; median longitudinal impression very finely incised, absent on basal convexity, continuous to beaded front margin; front angles projected anteriorly, their apex tightly rounded; lateral marginal depression of equal breadth from midlength to front angles, about twice as broad in basal half of pronotum; proepisternum smooth, proepimeron very narrow. Elytra flattened overall, sutural intervals upraised at suture in apical half of length; elytral apex evenly rounded; elytral striae finely incised, completely smooth, the intervening intervals nearly flat; humeri narrowed, with elytral basal groove meeting lateral depression at obtuse-angulate juncture, i.e., the humerus; seventh stria with two setae near strial apex; eighth striae with 33–37 lateral elytral setae more or less continuously distributed along elytral length, but with greater intersetal distances near midlength. Legs gracile, elongate; profemur with eight setae along anteroventral margin; mesofemur with 8–11 setae along posteroventral margin; metacoxa bisetose, two lateral setae present anteriorly and posteriorly, median seta absent; metafemur with eight setae along posteroventral margin, three setae on anterodorsal surface near apex from 0.7–0.8× femoral length; metatarsomeres 1–3 convex dorsally, without evident inner or outer dorsal sulci; metatarsomere 4 lobate apically, length of outer apical lobe 0.4× median tarsomere length, length of inner lobe 0.25× median length; tarsomeres 1-4 with two parallel longitudinal rows of elongate ventrolateral setae each side of a central space, the setae of inner rows each side about half as long as setae of outer rows; metatarsomere 5 apparently with eight ventrolateral setae, equal in length to tarsomere depth, set in two longitudinal rows (several setae broken off). The pronotum and elytra of the type specimen are covered with a varnish-like substance that can be scraped off with diffi-

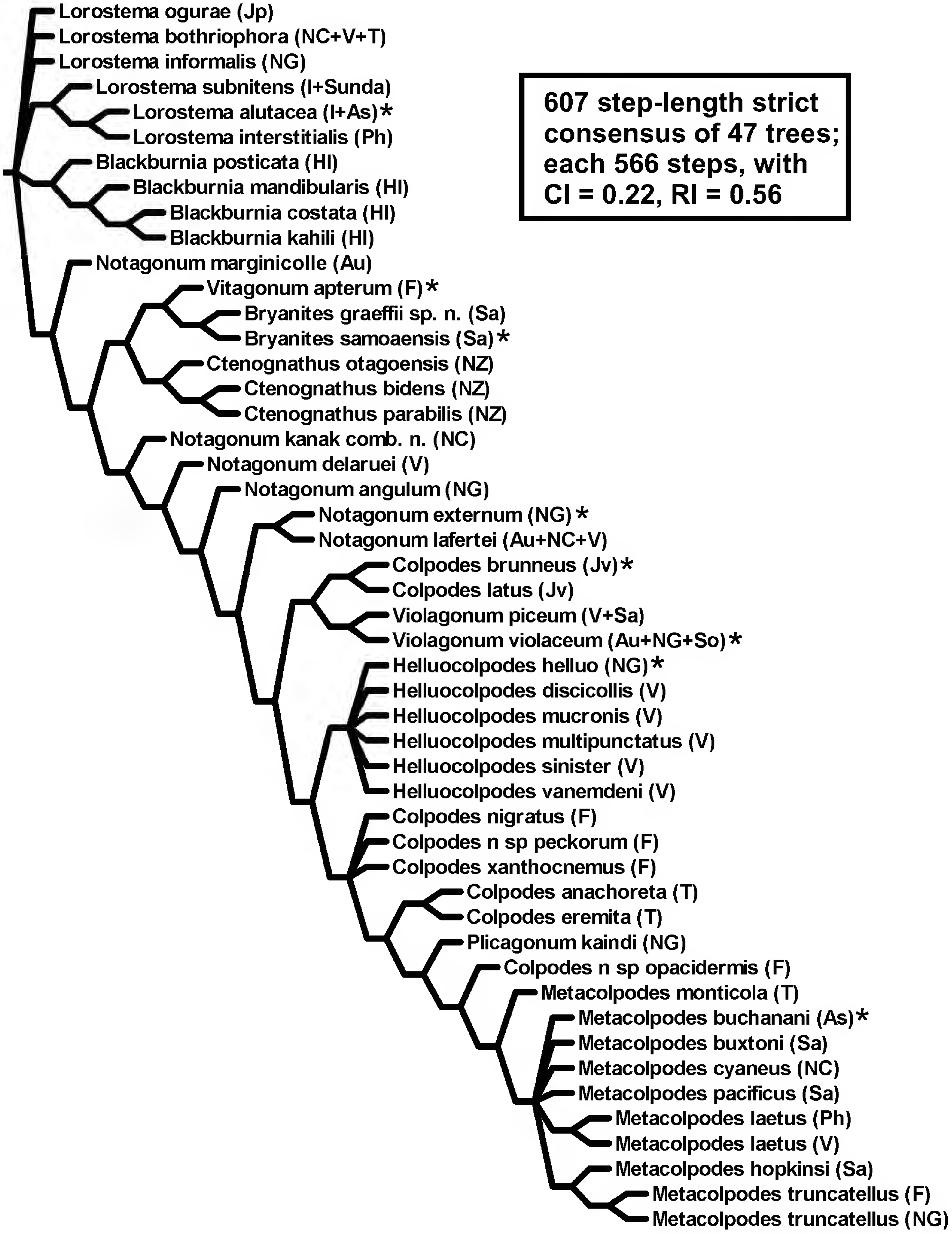

Figure 3. Strict consensus cladogram of 49 taxa of Pacific platynine carabid beetles. Type species, where included, indicated by asterisks. See text for further explanation of cladistic analysis. Distributional areas of species include: As, Asia; Au, Australia; F, Fiji; HI, Hawaiian Islands; I, India including Sri Lanka; Jp, Japan; Jv, Java; NC, New Caledonia; NG, New Guinea; NZ, New Zealand; Ph, Philippine Islands; R, Rapa; Sa, Samoa; So, Solomon Islands; Sunda, Sunda Islands; T, Tahiti and Society Islands; V, Vanuatu.

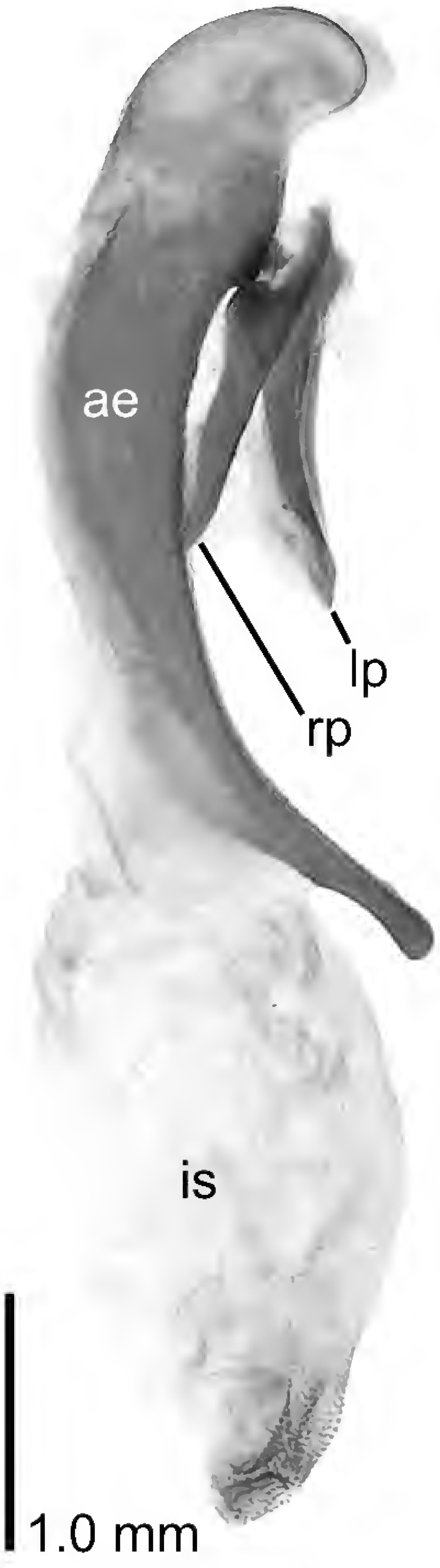

Figure 4. Male aedeagus, internal sac everted, of *Bryanites graeffii* male holotype, right lateral view. Abbreviations include: ae, aedeagal median lobe; is, internal sac; lp, left paramere; rp, right paramere.

culty (Fig. 1). The head, ventral surface, legs, and elytral lateral marginal depression are not so covered, suggesting that this coating is associated with the specimen in life, not an artifact of preservation.

Male genitalia. Aedeagal median lobe elongate, evenly narrowed from midlength to apex extended 4.0× its dorsoventral breadth beyond the apex of the ostial opening (Fig. 4); aedeagal tip slightly expanded, apical surface of tip tightly rounded; right paramere slightly shorter and narrower than left; aedeagal internal sac fusiform (flattened under cover slip), with a field of more heavily sclerotized spicules distributed apically near gonopore.

Type. Holotype male (MNHN): Dr Graffe / Samoa // 8284 // MUSEUM PARIS / Samoa / Collection Léon Fairmaire / 1906 // HOLOTYPE / Bryanites / graeffii / J.K. Liebherr 2016 (black-margined red label). The type locality is designated as the mountains near Apia, Upolu island, based on Graeffe (1917); his autobiography notes his residing at Apia during his tenure in Samoa. He visited other islands in the Fijian and Tongan archipelagos, but did not mention any visits within Samoa to the islands of Savaiʻi or Tutuila. Moreover, the following passage for the year 1869, after he had published his popular book describing a trip to Viti Levu (Graeffe 1868), suggests the time period during which he could have collected the specimen here described as *Bryanites graeffii*: "Es wurde nun wieder tüchtig geforscht und zog ich fast täglich mit meinem Gewehr in die Waldungen des Apiaberges, Vögel und grosse Fledermäuse, *Pteropus samoaensis* Peale erlegend, Insekten und Landschnecken, sowie Pflanzen sammelnd (Graeffe 1917: 31) [It was now again time for me to diligently conduct research, going almost daily with my rifle into the woods of the Apia mountains to gather birds and big bats, *Pteropus samoaensis* Peale, insects and snails, as well as plants]." A collection made in 1869 would have had to wait only a year before Graeffe left Samoa to return to Hamburg, allowing safe preservation of a specimen held in the humid tropical Pacific. In an ironic coincidence, Apia is also the type locality of the extinct flying fox, *Pteropus allenorum* Helgen, Helgen and Wilson, 2009 (Mammalia: Chiroptera) , known from a unique holotype collected in 1856 that was recently rediscovered in the Academy of Natural Sciences of Philadelphia (Helgen et al. 2009).

Etymology. The species epithet honors Dr. Eduard Graeffe, zoologist and naturalist from Zurich, Switzerland who collected the type specimen while working in Samoa from 1862–1870 (Clunie & Snow 1986). The species epithet is formed from Gräffe converted to Latin iconography, and without the terminal letter. This formation is consistent with several other honorific epithets for Eduard Gräffe; e.g. *Epeira graeffii* Keyserling (Arachnida: Araneidae), now combined with *Phonographa* Simon, 1894, *Lamellidoris graeffii* Bergh (Nudibranchia: Dorididae), and *Pachycephala pectoralis graeffii* Hartlaub (Aves: Pachycephalidae).

Nomenclatural note

Based upon the results of the cladistic analysis, *Colpodes kanak* Fauvel is newly combined with the genus *Notagonum* Darlington: *Notagonum kanak* (Fauvel) comb. n. (Suppl. material 1). This taxonomic decision is based on *N. kanak* exhibiting the following character states that place it within the *Notagonum* grade (Fig. 5, Suppl. material 2): 1, frons with evident isodiametric microsculpture that is visible through the surface reflection; 2, pronotal basal bead visible laterally but effaced at midline; 3, pronotal laterobasal depressions smooth, not punctate; 4, pronotal disc with evident transverse mi-

Figure 5. *Notagonum kanak* female (MNHN), label data: Ncalédonie / ile d. Pins / f. Faustien // MUSEUM PARIS / Ex. Coll. M. MAINDRON / Coll. G. BABAULT 1930 // Colpodes / kanak / Fauvel dedit 1906 (card mounted, abdomen removed, female genitalia and reproductive tract in vial on pin).

crosculpture; 5, margins of prosternal process rounded on posterior face; 6, short elytral sutural tooth present, subapical tooth absent; 7, metatarsomere 4 with shallow apicomedial ventral invagination and short lateral lobes, the outer, or lateral lobe, less than twice the length of the inner lobe.

Discussion

The results of the cladistic analysis succeed in the goal of placing the new species as a member of a Samoan lineage, *Bryanites*, that exhibits a close biogeographic relationship to the Fijian relict, *Vitagonum* (Moore 1998). This clade, and its sister group *Ctenognathus* of New Zealand, diverged early in the history of Pacific Platynini. Previously, Liebherr (2005) concluded that the Hawaiian genus *Blackburnia* colonized the Hawaiian Island chain long before the origins of the present high islands, and perhaps as long ago as 28 Mya when Kure became the first in a consistently present subaerial chain of islands generated by the Hawaiian Island volcanic hotspot (Duncan and Clague 1985). In the Samoan Island chain, the Alexa Bank seamount is hypothesized to have originated as a subaerial island 22 Ma (McDougall 2010), setting the earliest date possible for colonization of the Samoan Islands hotspot volcanic chain by a *Bryanites* ancestor. Subaerial origin of the Fijian archipelago is dated to a similar time—22–25 Ma (Gill and McDougall 1973, Whelan et al. 1985)—establishing a maximal time of origin for the ancestor of *Vitagonum*. And volcanism along the Kermadec-Lau-Tonga Ridge system would have enhanced colonization prospects for the ancestor of New Zealand *Ctenognathus* 10—15 Mya. Thus all area relationships among the early diverging Pacific platynine lineages, including *Bryanites*, occupy continental areas or island chains available for colonization in the Miocene. This supports Valentine's (1987) hypothesis that *Bryanites* is a relict Samoan lineage.

The question of whether any or all of the *Bryanites* species are extinct is necessarily open ended. Nevertheless, examination of the circumstances of their collections taken within the context of other biological surveys of Samoa paint a grim picture as to the possibility of their continued existence in nature. The single specimen of *Bryanites graeffii* was collected prior to 1871 by a naturalist principally interested in birds and marine invertebrates (Graeffe 1917). Nonetheless, we know that he collected insects during his trips to Fiji (Graeffe 1868), and during 1869 near Apia (Graeffe 1917). But only the one specimen of *B. graeffii* described herein is known to have passed to Leon Fairmaire for eventual deposition in the Paris Museum. The British Museum survey of 1924–1925 (Kami and Miller 1998), summarized for Carabidae by Andrewes (1927), led to description of five other platynine carabids— *Colpodes buxtoni* Andrewes, *C. pacificus* Andrewes, *C. hopkinsi* Andrewes, *C. piceus* Andrewes, and *C. anomalus* Andrewes, the first three of which are now assigned to *Metacolpodes* (Fig. 3, Suppl. material 1; Liebherr 2005). Andrewes (1927) also examined previously collected taxonomic material, including that from 1905 collections for the Vienna Museum (Rechinger 1914) and 1912–1913 collections for the Berlin Museum (Friedrichs 1914).

The Bishop Museum's Whitney South Seas Expedition of 1924, including E. H. Bryan, Jr. as entomologist, also visited Samoa (Evenhuis 2007). Bryan's field notes for 23 May 1924–the date labeled on the two specimens later described as *Bryanites* (Valentine 1987)–included: "Put away large quantity of specimens collected yesterday (Evenhuis 2007: 125)." Some of those "yesterday's" specimens were collected when he "Dug several things from partly rotten bank *[sic bark]* of large tree:- centipedes, termites, sowbugs, tree cricket and moderately large slender fuscous Carabid (Evenhuis 2007: 125)." Given that the description of a "moderately large slender fuscous Carabid" on Samoa can only fit a *Bryanites* beetle, it appears that *Bryanites*, either the *B. barri* or *B. samoaensis* individual that Bryan collected, was associated with a downed log covered with rotten bark. Bryan described the situation within which he was collecting at that camp as "Two large Ac[h]atinella [*sic*] landshells on Orange tree in banana patch at about 2200'. [Met] Mr. Beck and returned to hut. Mosquitoes not bad, but rats after our provisions. Very good collecting at this elevation (Evenhuis 2007: 125)." Being a field biologist based on Oahu, Bryan no doubt mistook a native Samoan *Samoana* or *Eua* land snail (Pilsbry 1909–1910, Cowie 1992) for the precinctive Oahu genus *Achatinella*, but his sighting of native land snails in proximity to rats in 1924 suggests that the native elements did not have long to exist at the site given the presence of invasive rats. There is both indirect and direct evidence that rats prey on native brachypterous carabid beetles. Deposits in Makauwahi Cave on Kauai include abundant subfossil fragments of extinct, brachypterous *Blackburnia* carabid beetles in stratigraphic layers deposited prior to human colonization and the associated introduction of the Pacific rat, *Rattus exulans* (Peale) (Liebherr and Porch 2015). Subfossil fragments of those presently extinct taxa are absent from the stratigraphic column in deposits laid down from shortly after the time of human colonization up to the present. More directly, stomach contents of alien black rats (*Rattus rattus* L.) have been shown to include fragments of a native Hawaiian *Blackburnia* beetle species, as well as native katydids, weevils and spiders (Shiels et al. 2013). The presence of predatory, climbing, night active rats is uniformly deleterious to native communities on tropical islands (Harper and Bunbury 2015), with Samoa not a likely exception to this rule.

Given these various lines of data, it seems unlikely that *Bryanites* beetles currently exist in nature. Only through the perspicuous collecting by E. H. Bryan, Jr. and the passing of his two specimens to J. Manson Valentine could the first two species of this genus be described (Valentine 1987). The subsequent discovery of a single additional specimen collected over 140 years ago that traveled a circuitous route from Samoa, to the Museum Godeffroy, to the Paris Museum adds another entry point to study of the *Bryanites* radiation. Are we better for knowing about this evolutionary story even after all known players have likely left the scene? To the degree that the hotspot volcanic chain of Samoa supported a very unique radiation of platynine Carabidae, as did Hawaii, we have learned that the *Blackburnia* radiation of Hawaii had an analog in Samoa, with Samoan species inhabiting the islands of Savaiʻi and Upolu. We have characterized a large-bodied, distinctive species that may turn up in Samoan subfossil deposits, much like the large-bodied subfossil *Blackburnia* spp. of Kauai (Liebherr and Porch 2015). And should these or any other *Bryanites* beetles have survived forest conversion, and the plagues of rats and other invasive species so that they may be collected during a future biological survey, that sample will be connected to specimens held in two other biodiversity hotspots on Earth.

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Supplementary material 1

Taxonomic checklist

Authors: James K. Liebherr
Data type: Adobe PDF file
Explanation note: Taxa included in cladistic analysis taxonomically placing *Bryanites graeffii* sp. n. are listed along with their taxonomic authorities.

Supplementary material 2

Computer file for cladistic analysis

Authors: James K. Liebherr
Data type: Adobe PDF file
Explanation note: The NONA format data file that supports the cladistic analysis of *Bryanites* and Pacific Platynini is provided for export to a plain text editor.

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The diversity of acorn barnacles (Cirripedia, Balanomorpha) across Thailand's coasts: The Andaman Sea and the Gulf of Thailand

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Abstract

The acorn barnacle is a sessile crustacean, inhabiting the intertidal areas of tropical and temperate regions worldwide. According to current practices on Cirripedia morphology, shell, opercular valves, and arthropodal characters including cirri and mouthparts are used as a tool for taxonomic classification, and using these characteristics the present study aimed to provide better resolution for the barnacle diversity and geographical distribution within coastlines of Thailand: the Andaman Sea and the Gulf of Thailand. A total of ten species belonging to three families (Chthamalidae, Tetraclitidae, and Balanidae) were identified in this study. Subsequently, five species were newly recorded for the first time from Thailand's coasts: *Newmanella spinosus* Chan & Cheang, 2016, *Euraphia hembeli* Conrad, 1837, *Euraphia depressa* (Poli, 1795), *Tetraclita kuroshioensis* Chan, Tsang & Chu, 2007, and *Tetraclita singaporensis* Chan, Tsang & Chu, 2007. The others, already mentioned in previous records, include: *Tetraclita squamosa* (Bruguière, 1789), *Chthamalus malayensis* Pilsbry, 1916, *Amphibalanus amphitrite* (Darwin, 1854), *Amphibalanus reticulatus* (Utinomi, 1967), and *Megabalanus tintinnabulum* (Linnaeus, 1758). Interestingly, acorn barnacles along the Andaman Sea occur abundantly, and are much higher in number of species (up to 8 species) than those found in the Gulf of Thailand's coast (up to 6 species). This biased trend of species' preferences is possibly due to the differences in oceanographic nature between two coastlines and the history of barnacle colonization.

Introduction

Acorn barnacles, a member of marine crustaceans, inhabit a diverse array of substrates (e.g. calcareous rock or limestone, mollusk shells, corals, sponges, mangrove roots, turtle shells, and whale skins) along intertidal zones of temperate and tropical coastlines worldwide, as sessile form throughout their adulthood (Frith et al. 1976; Sophia Rani et al. 2010; Brickner and Høeg 2010; Brickner et al. 2010; Chen et al. 2012; Hayashi 2013; Chen et al. 2014; Yu et al. 2016). It is known as a marine fouling or biofouling organism and it has been considered as a problematic or invasive species for oyster farming, aquaculture, the reforestation of mangrove swamps, and for the support structures of offshore oil rig platforms and ship transport (Santhakumaran and Sawant 1991; Rawangkul et al. 1995; Molnar et al. 2008; Sophia Rani et al. 2010; Holm 2012). Although the presence of hard calcareous plates covering acorn barnacles' bodies limits its abilities to search for food and new habitats, the species are still tremendously successful in occupying the coastline of tropical and temperate regions due to their free-swimming and planktonic larval stages: high-feeding nauplius and non-feeding cyprid. The nauplius larva develops in successive manner with ecdysis or molting to shed their exoskeleton and allow growth of larva, a characteristic used to classify acorn barnacles into Ecdysozoa of Protostomia clade. The metamorphosis (settlement process) alters a cyprid larva to a sessile juvenile and subsequently an adult form growing inside the ring of shell plates (4–8 in number depending on the species), homologous structure to carapace of other crustaceans (Høeg and Møller 2006; Maruzzo et al. 2012; Martin et al. 2014). The sessile body of adult barnacles has six pairs of featherly throracic appendages called cirri (legs or feeding appendages), so named suborder Cirripedia constituted inside order Sessilia and superorder Thoracica. With highly suitable habitats and temperature ranges, diverse forms of acorn barnacles occur along coastlines in both the Andaman Sea and the Gulf of Thailand. However, the taxonomic classification alongside geographical distribution information of acorn barnacles has received little attention in Thailand. Here we aim to investigate taxonomy, shell morphology, and geographical distribution by firstly relating the taxonomic key of acorn barnacles to their distribution records along the Andaman Sea and the Gulf of Thailand coasts to elucidate the diversity of the species across the coastlines of Thailand.

Material and methods

Study sites

Acorn barnacles were collected from the rocky coastal areas of two distinct geographic regions of Thailand: the Andaman Sea and the Gulf of Thailand, during May 2015-July 2016.

The Andaman Sea located in the eastern part of the Indian Ocean is bordered by the coastlines of Myanmar, Thailand, Malaysia, Indonesia and India. In the Andaman Sea, the tide is semidiurnal. Its water temperature and salinity range 25.9–30.4°C and 29–33 ppt, respectively (Limpsaichol et al. 1991). Five sampling sites along the Andaman Sea coast comprised of (1) Ao Khoei beach, Khura Buri district, Phang-nga province, (2) Na Tai beach, Takua Thung district, Phang-nga province, (3) Kalim beach, Katu district, Phuket province, (4) Ao Yon beach, Mueang Phuket district, Phuket province, and (5) Panwa beach, Mueang Phuket district, Phuket province.

The Gulf of Thailand, a semi-enclosed sea, is bordered by the coastlines of Vietnam, Cambodia, Thailand, and Malaysia with a connection to the South China Sea in the south. In the Gulf of Thailand, the tide is mixed diurnal. Its water temperature and salinity range 29–32°C and 30–33 ppt, respectively (Pollution Control Department 2001). Five sampling sites along the coastline of the Gulf of Thailand were investigated, comprising (1) Khao Sam Muk beach, Mueang Chon Buri district, Chon Buri province, (2) Si Racha beach, Si Racha district, Chon Buri province, (3) Ko Kham Yai beach, Ko Si Chang district, Chon Buri province, (4) Ban Krut beach, Bang Saphan district, Prachuap Khiri Khan province, and (5) Hin Ngam beach, Sichon district, Nakhon Si Thammarat province.

A synopsis and illustration of all the sampling locations are given in Table 1 and Figure 1.

Table 1. Sampling locations, arranged from north to south.

Locality		Habitat characteristics	Coordinates
Andaman Sea coast			
Ao Khoei	AK	Large boulders on sandy shores	09°16’44.18”N 98°22’07.01”E
Na Tai	NT	Rocky shores	08°14’15.39”N 98°16’51.22”E
Kalim	KL	Small to large rocks on sandy shores	07°55’25.47”N 98°15’47.68”E
Ao Yon	AY	Rocky shores	07°52’09.79”N 98°26’08.29”E
Panwa	PW	Large boulders on sandy shores	07°48’05.09”N 98°24’28.80”E
Gulf of Thailand coast			
Khao Sam Muk	KS	Rocky shores	013°18’38.88”N 100°54’07.81”E
Si Racha	SR	Large boulders on sandy shores	013°10’33.92”N 100°55’33.74”E
Ko Kham Yai	KK	Small rocks on sandy shores	013°09’59.30”N 100°49’18.00”E
Ban Krut	BK	Rocky shores	011°21’26.07”N 099°34’42.86”E
Hin Ngam	HN	Rocky shores	009°00’00.68”N 099°55’09.45”E

Sampling collection

The barnacles were collected from each station by surveying along rocky shores of an intertidal zone during both low and high tides. Whole acorn barnacle individuals were removed from the substratum and immediately preserved in ethyl alcohol (95%v/v) for further examination. All work was done under certified supervision of S.K. (Certificate from Institute of Animal for Scientific Purposes Development-IAD, Royal Thai Government: U1-03104-2559).

Morphology analysis

Samples were primarily identified based on their shell morphology using an Olympus SZ51 stereomicroscope and was photographed with digital camera. For better species identification in some families, arthropodal characters were observed. Soft bodies were removed from the shells and dissected. Cirri and mouthparts were mounted onto slides for light microscopy observation and imaging using digital camera. Taxonomic identification was performed using keys of Newman and Ross (1976) and Chan et al. (2009). The general terminology of shell morphology and the important characters used in this paper follow Chan et al. (2009). All voucher specimens from each station were deposited in the collection of Laboratory of Zoology, Department of Biology, Faculty of Science, Burapha University, Thailand.

Results

Based on shell morphology, total ten species (6 genera) of acorn barnacles along the coastlines of Thailand in both the Andaman Sea and the Gulf of Thailand were identified and are categorized into three families: Chthamalidae (2 subfamilies: Chthamalinae and Euraphiinae), Tetraclitidae (2 subfamilies: Newmanellinae and Tetraclitinae), and Balanidae (2 subfamilies: Amphibalaninae and Megabalaninae). The descriptions of the identified barnacles are as follows:

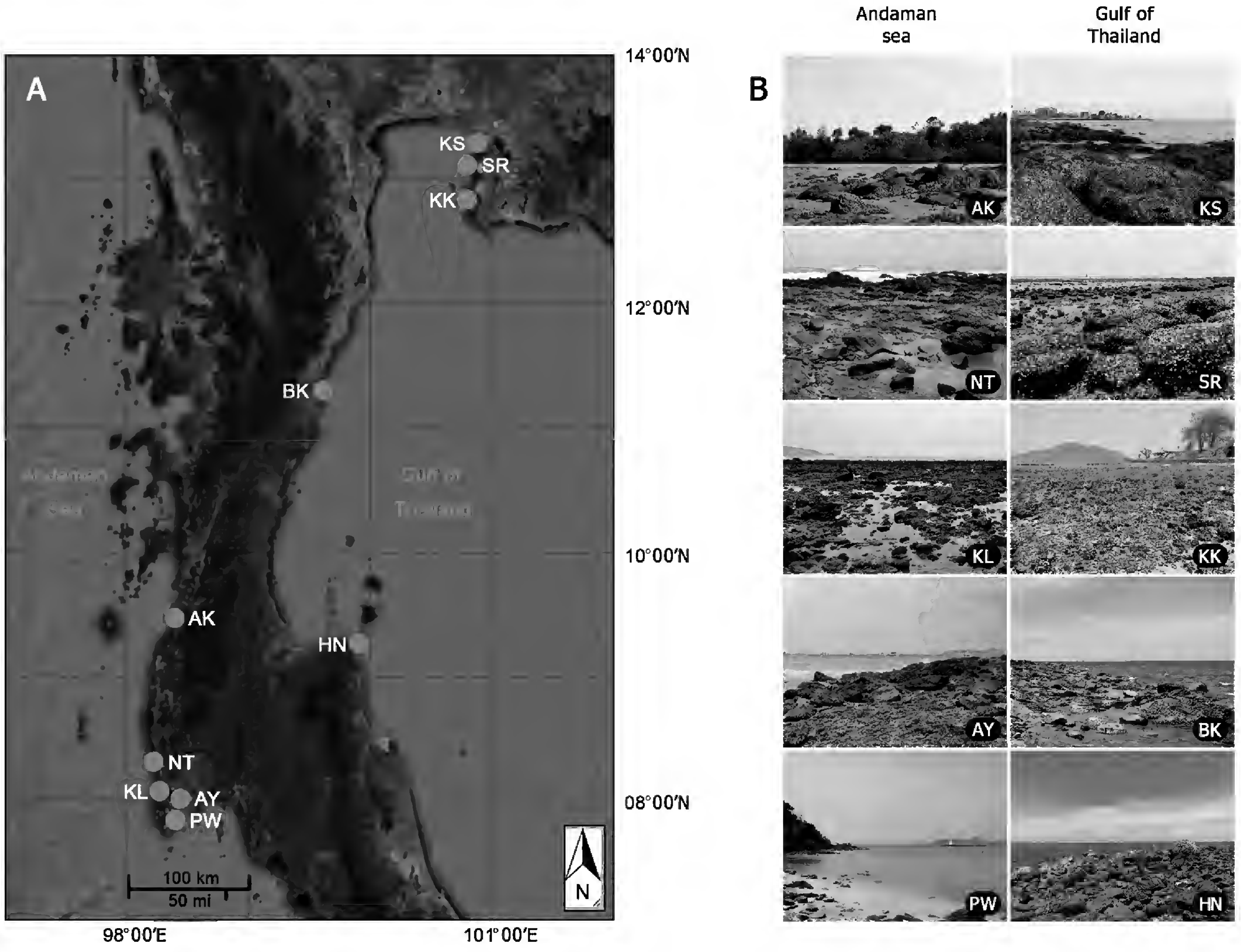

Figure 1. Map showing all sampling locations (**A**) and habitat characteristics (**B**) of acorn barnacles found along the coastlines of the Andaman Sea and the Gulf of Thailand. See Table 1 for acronyms of sampling sites. (modified from http://marinegiscenter.dmcr.go.th/gis/)

Systematic taxonomy

Superorder Thoracica Darwin, 1854
Order Sessilia Lamarck, 1818
Suborder Balanomorpha Pilsbry, 1916
Superfamily Chthamaloidea Darwin, 1854
Family Chthamalidae Pilsbry, 1916
Subfamily Chthamalinae Darwin, 1854

Genus *Chthamalus* Ranzani, 1817

Type species. *Chthamalus stellatus* (Poli, 1791)

1 genus, 1 species recorded: *Chthamalus malayensis* Pilsbry, 1916.

Chthamalus malayensis Pilsbry, 1916

Figure 2; Tables 2–3

Chthamalus malayensis Pilsbry, 1916: 310–311; Hiro, 1939: 249–251; Utinomi, 1954: 18; Karande & Palekar, 1963: 231; Pope, 1965: 51–63; Newman & Ross, 1976: 42; Dong et al., 1980: 125; Ren, 1984: 151–153; Southward et al., 1998: 123.
Chthamalus stellatus: Hoek, 1913: 267–269.
Chthamalus challenger: Broch, 1931: 53–55; 1947: 5.
Chthamalus antennatus: Rossel, 1972: 174, pl. 13, figs. 1–7, pl. 14, fig. 1–5.

Non-type material examined. Andaman Sea: 3 specimens, Phang-nga province, Takua Thung district, Na Tai beach, 16.V.2015, A. Pochai (BUU16.CH.CM01-03). 2 specimens, Phuket province, Mueang Phuket district, Ao Yon beach, 15.VII.2015, A. Pochai (BUU16.CH.CM04-05). 1 specimen, Phuket province, Mueang Phuket district, Panwa beach, 16.VII.2015, S. Khachonpisitsak (BUU16.CH.CM06). 3 specimens, Phuket province, Katu district, Kalim beach, 15.VII.2015, A. Pochai (BUU16.CH.CM07-09).

Gulf of Thailand: 2 specimens, Chon Buri province, Ko Si Chang district, Ko Kham Yai beach, 05.VII.2015, S. Khachonpisitsak (BUU16.CH.CM10-11).

Description. Peduncle absent; body length 3–10 mm; base membranous. Shell elongated oval/shield-shaped, shell white to grey with 6 plates (1 carina, 2 carinal latus, 2 latus and 1 rostrum), carina bigger than rostrum, parietes symmetrical, calcareous and solid, radii solid, inner surface of parietes smooth and white-grey to pale-violet; orifice kite-shaped. Operculum plates symmetrical, articulation of opercular valves deep, scutum and tergum separable. Tergum smaller than scutum, tergum higher than wide, tergum with 4 distinct crests for lateral depressor muscles. Scutum elongated and triangular, adductor pit deep. Mandible with 4 teeth, lower margin pectinated, three large setae at the edge; cirri I with conical spines; cirri II with multi-cuspidate setae and basal guard.

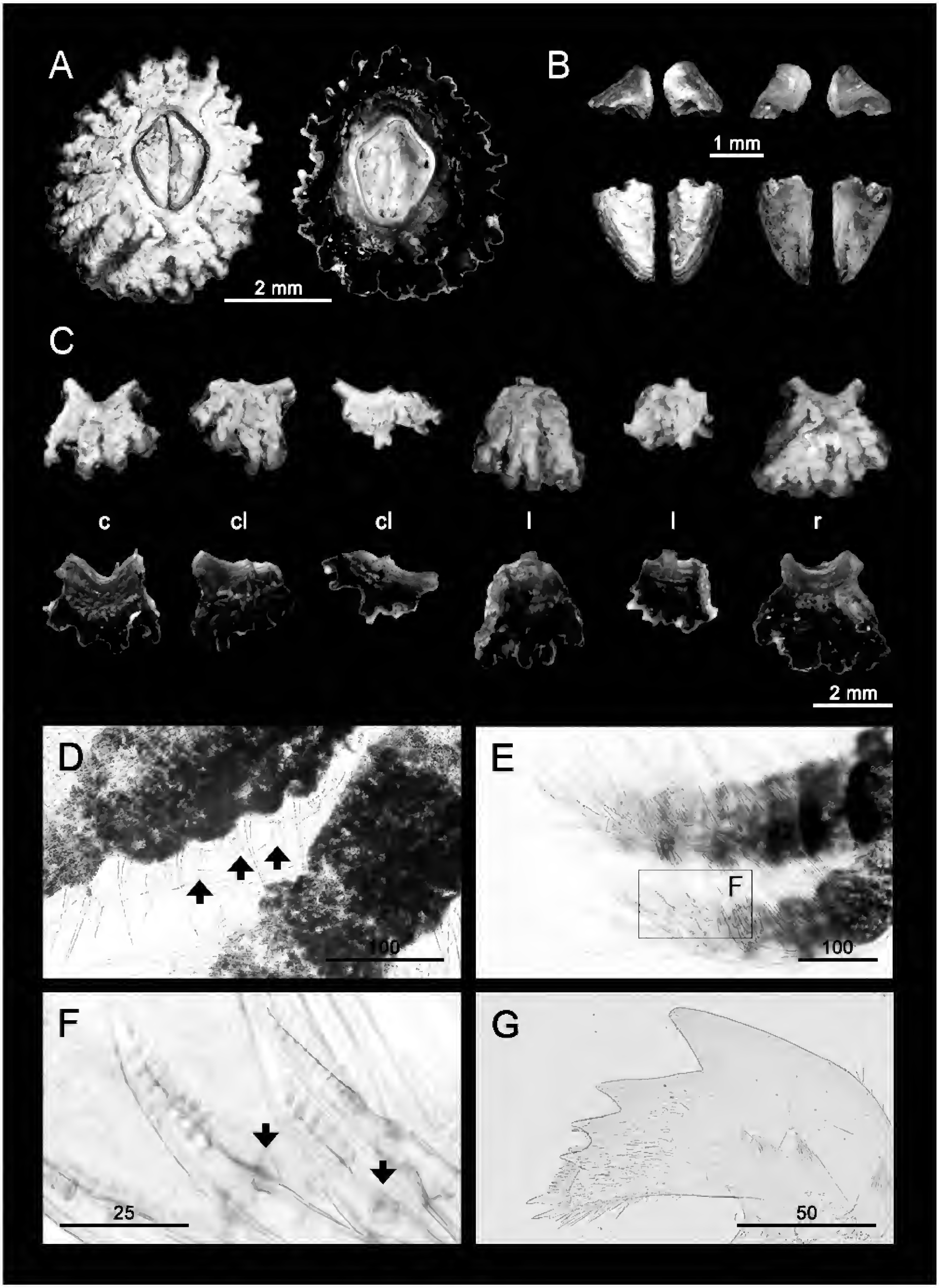

Figure 2. *Chthamalus malayensis* collected from Ka Lim beach, Phuket (BUU16.CH.CM07). **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** External (upper panel) and internal (lower panel) view of shell plates, **D–G.** Light microscopy on mouthparts, **D.** Close up of cirri I showing conical spines(🡅), **E.** Cirri II, **F.** Close up on cirri II showing multi-cuspidate setae with basal guard(🡇), **G.** Mandible with four large teeth. **D-G.** Scale bars in μm. Abbreviations: c, carina; cl, carinal latus; l, latus; r, rostrum.

Table 2. Species list and distribution of acorn barnacles found in ten sampling sites along the coastlines of the Andaman Sea and the Gulf of Thailand. Abbreviations: +, presence; abs, absence. See Table 1 for acronyms of sampling sites.

Species	Sampling sites									
	Andaman Sea					Gulf of Thailand				
	AK	NT	KL	AY	PW	KS	SR	KK	BK	HN
Chthamalus malayensis	abs	+	+	+	+	abs	abs	+	abs	abs
Euraphia depressa	abs	abs	abs	abs	abs	+	abs	abs	abs	abs
Euraphia hembeli	abs	+	abs	abs	abs	abs	abs	abs	abs	abs
Newmanella spinosus	abs	+	abs	abs	abs	abs	abs	abs	abs	abs
Tetraclita kuroshioensis	+	+	+	+	abs	abs	abs	+	+	abs
Tetraclita singaporensis	abs	+	abs	abs	abs	abs	abs	abs	abs	abs
Tetraclita squamosa	abs	abs	abs	abs	abs	abs	abs	abs	abs	+
Amphibalanus amphitrite	+	+	+	+	+	+	+	+	+	+
Amphibalanus reticulatus	abs	+	abs	abs	abs	+	+	+	abs	abs
Megabalanus tintinnabulum	abs	+	abs	abs	abs	abs	abs	abs	abs	abs
Total number of species	**2**	**8**	**3**	**3**	**2**	**3**	**2**	**4**	**2**	**2**

Distribution. *Chthamalus malayensis* is widely distributed in the Indo-West Pacific region. It has been previously recorded in Taiwan, Thailand, China, Philippines, Vietnam, Malaysia, India and Australia (Jones 2004; Tsang et al. 2008; Tsang et al. 2012). From the previous observation, *C. malayensis* presented in both the Andaman Sea (Phuket) and the Gulf of Thailand (Si Chang and Samui Islands) (Tsang et al. 2012). In this study, *C. malayensis* were also found in both coastlines: the Andaman Sea (Na Tai, Kalim, Ao Yon, Panwa) and the Gulf of Thailand (Ko Kham Yai) (Table 2).

Remarks. *Chthamalus malayensis* has usually 4 crests for lateral depressor muscles while *Euraphia hembeli* and *Euraphia depressa* contains distinct 10–12 crests at the tergum and 3 small crests, respectively. The size of *C. malayensis* ranges from 3–10 mm similar to *E. depressa* while that of *Euraphia hembeli* is much bigger (10–33 mm). In addition, *C. malayensis* differs from *E. depressa* in two main characters diagnosed in this study: shape of external shell and jointing pattern of tergum and scutum. The shape of the external shell of *C. malayensis* shows a distinct and rather uniform ribbed surface from the lower region to the apex; on the other hand, *E. depressa* exhibits smooth surface that is never ribbed. Secondly, marked articulation and sinous jointing of tergum and scutum can be clearly noticed in *C. malayensis* while *E. depressa* shows less articulation. However, these shell morphology is not reliable tool for species identification among Chthamalids; hence, we further investigate arthropodal characters. It is clear that *Chthamalus* has four teeth on the mandible while *Euraphia* has three teeth on the mandible. In addition, to further identify *Chthamalus* into the correct species, setae on cirri I and cirri II were observed. Our specimens of Chthamalids have conical spines on cirri I and multi-cuspidate setae with basal guard on cirri II (Figure 2F); hence, our specimens are confirmed as *C. malayensis*.

Moreover, *C. malayensis* distributes above the vertical zonation of *Tetraclita* population. The overlapping of habitats can be seen among these species and even *C. malayensis* were found to attach to *Tetraclita* at the overlapping regions of high shore and middle shore.

Subfamily Euraphiinae Newman & Ross, 1976

Genus *Euraphia* Conrad, 1837

Type species. *Euraphia hembeli* Conrad, 1837

1 genus, 2 species recorded: *Euraphia depressa* (Poli, 1795) and *Euraphia hembeli* Conrad, 1837.

Euraphia depressa (Poli, 1795)

Figure 3; Tables 2–3

Chthamalus depressus Poli, 1791
Chthamalus stellatus var. *depressus*: Darwin, 1854.
Euraphia depressa: Utinomi (1959); Southward (1964).

Non-type material examined. Gulf of Thailand: 2 specimens, Chon Buri province, Mueang Chon Buri district, Khao Sam Muk beach, 05.VII.2016, W. Sukparangsi (BUU16.CM.ED01-02).

Description. Peduncle absent; body length 3–10 mm; base membranous. Shell light brown-yellowish brown with 6 plates (1 carina, 2 carinal latus, 2 latus and 1 rostrum), shell flatted and thin-walled; parietes symmetrical and solid, external surface of shell without ribbed, inner surface of parietes smooth and light brown and white with small horizontal striations around aperture, parietes separable, suture distinct and easily parted; orifice rhomboidal. Opercular plates symmetrical, tergum smaller than scutum, scutum and tergum separable jointing between tergum and scutum with slightly sinous. Scutum triangular with slightly curved basal margin, external surface with shallow and horizontal striations from occludent margin to tergal margin, occludent margin of scutum without teeth, tergal margin slightly sinous from interior view; tergum with 2–3 lateral depressor crests. Mandible with 3 teeth, lower margin pectinated with 8 setae, three

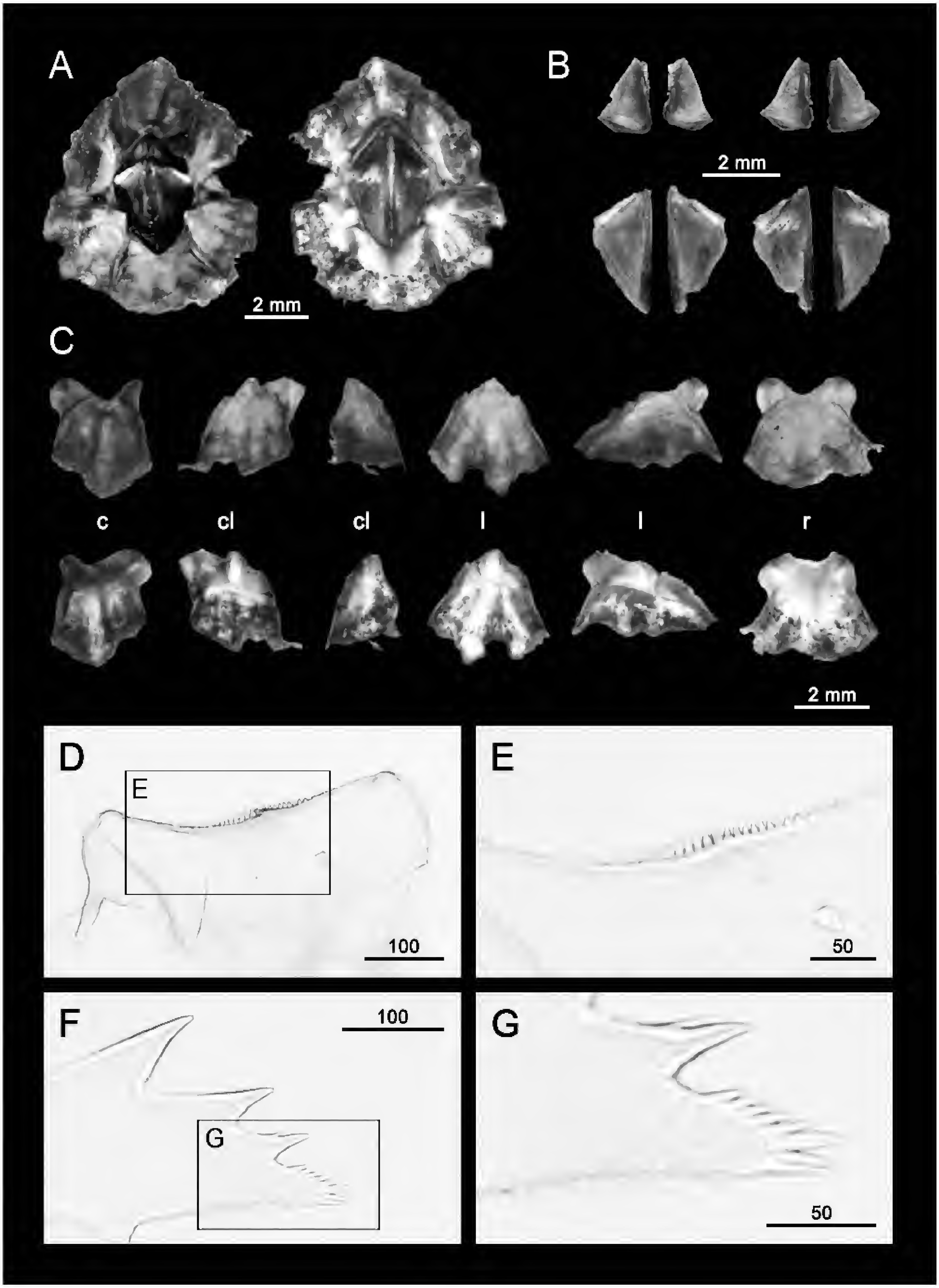

Figure 3. *Euraphia depressa* collected from Khao Sam Muk beach, Chon Buri (BUU16.CH.ED01). **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** External (upper panel) and internal (lower panel) view of shell plates, **D-G.** Light microscopy on mouthparts, **D.** Labrum, **E.** Close up on the teeth of the labrum, **F.** Mandible with three large teeth, **G.** Close up on the pectinated lower margin of mandible. **D–G.** Scale bars in µm. Abbreviations: c, carina; cl, carinal latus; l, latus; r, rostrum.

Table 3. Distribution of acorn barnacles on different habitat types of intertidal zone (vertical zonation): low shores/ sublittoral zone (LS), middle Shores/ littoral zone (MS), and high shores/ supralittoral zone (HS).

Scientific name	Habitat type			Settlement pattern on habitats
	LS	MS	HS	
Family Chthamalidae				
Chthamalus malayensis			+	Attached to rock platform, shell of *Tetraclita* spp. and other substrates
Euraphia depressa			+	Attached to sheltered sites of rock
Euraphia hembeli	+	+		Attached to rocky shore exposed to heavy wave action
Family Tetraclitidae				
Newmanella spinosus	+			Attached to rocks on a wave exposed shore
Tetraclita kuroshioensis		+		Attached to rock platform and sheltered sites of rock
Tetraclita singaporensis		+		Attached to rock platform and sheltered sites of rock
Tetraclita squamosa		+		Attached to rock platform and sheltered sites of rock
Family Balanidae				
Amphibalanus amphitrite	+	+	+	Attached to rocks on a wave exposed shore, shell of oyster and Asian green mussel, offshore vessel and various substrates
Amphibalanus reticulatus	+	+		Attached to shell of Asian green mussel, oyster, ridged Venus clam and other substrates
Megabalanus tintinnabulum	+			Attached to rocky shore exposed to heavy wave action

large setae at the edge; labrum with obvious teeth; caudal appendage absent.

Distribution. In previous records, *Euraphia depressa* was found to inhabit along Mediteranean localities, including Spain (Punta Carnero, Punta de la Chullera, Malago, Salobrena and Calpe), France (Cap Bear, La Couronne, and Cassis), Italy (Pegli and Lido), Greece (Amnisso), the Black Sea and Suez canal (Utinomi 1959; Southward 1964; Achituv and Safriel 1980; Crisp 1981). In this study, the presence of *E. depressa* in Khao Sam Muk station (Chon Buri) in Thailand was unexpected as it was previously unrecorded along Thailand's coastal areas. They were found along rocky shores exposed to heavy wave action inhabiting sheltered crevices of the rocky platform and high shore. The abundance of *E. depressa* is much less than that of the cosmopolitan barnacle *Amphibalanus amphitrite* in the same area of observation.

Remarks. *Euraphia depressa* (Poli, 1795) was the reassigned name from *Chthamalus depressus* (Poli, 1795). According to Southward (1964), *Euraphia depressa* can be distinguished from *Chthamalus stellatus*, based on the shell morphology showing smooth unribbed shell on the external surface from younger specimens to more adult stage and the operculum characters, showing joints between tergum and scutum without sinous or slightly sinous, and smaller tergum. In addition, a barnacle of the genus *Euraphia* is distinguished from the genus *Chthamalus* based on the number of teeth on mandible and as described in Southward (1964) our specimens have mandible with three large teeth and three large setae on the lower edge (Figure 3F & G) and lacking of caudal appendages, leading to species identification of our specimens as *Euraphia depressa*. However, the number of setae at the pectinated margin of mandible in our specimens is different. Only small 5 setae after larger three setae were found in our specimens while up to 12 setae were mentioned in Southward (1964).

Euraphia hembeli Conrad, 1837

Figure 4; Tables 2–3

Euraphia hembeli Conrad, 1837: 261.

Non-type material examined. Andaman Sea: 2 specimens, Phang-nga province, Takua Thung district, Na Tai beach, 16.V.2015, A. Pochai (BUU16.CH.EH01-02).

Description. Peduncle absent; base membranous; body length larger than *Chthamalus* and range from 10–30 mm. Shell brownish grey with 6 plates (1 carina, 2 carinal latus, 2 latus and 1 rostrum), carina bigger than rostrum, carinal latus bigger than latus. External surface of shell irregularly ribbed around basal margin, inner surface of parietes smooth and white with dark brown and pale violet horizontal striations around aperture. Parietes symmetrical, calcareous and solid, parietes separable, sutures coarsely serrate or with interlocking toothed structure. Orifice rhomboidal. Operculum plates symmetrical, tergum smaller than scutum, tergum and scutum separable. Scutum triangular, occludent margin of scutum with strong teeth. Tergum strongly marked with 10–12 lateral depressor crests, scutal margin strongly articulated.

Distribution. Barnacles in the genus *Euraphia* were recorded in several regions including West Africa, the Mediterranean, Hawaii and Southern Japan (Newman and Ross 1976). *Euraphia hembeli* was previously recorded in California around San Diego (Barrett and Freeman 2016). In this study, we report the presence of *Euraphia hembeli* distributing along low and middle shore of the intertidal zone, which was only found at Na Tai station, the Andaman Sea (Tables 2 and 3). In addition, this is the first report of its presence in Thailand.

Remarks. Based on the shell and opercular valve morphology (Newman and Ross 1976; Kim and Yamaguchi 1996), two candidates: *Euraphia hembeli* Conrad, 1837 and *Euraphia*

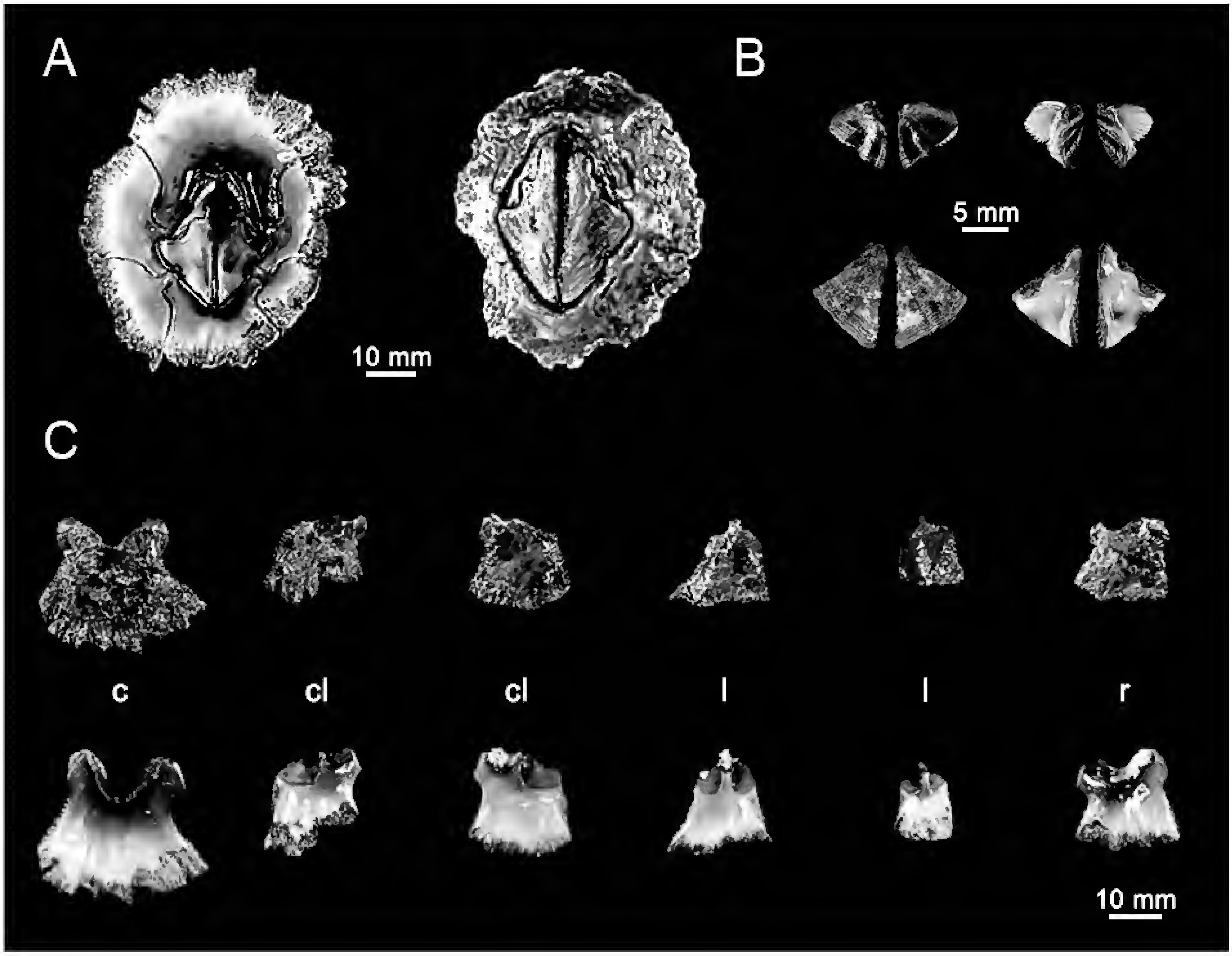

Figure 4. *Euraphia hembeli* collected from Na Tai beach, Phang-nga (BUU16.CH.CH01). **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** External (upper panel) and internal (lower panel) view of shell plates. Abbreviations: c, carina; cl, carinal latus; l, latus; r, rostrum.

pilsbryi Hiro, 1936 (reassigned as *Hexechamaesipho pilsbryi* (Hiro, 1936)) show similar patterns of opercular plates to our collected specimens. Based on Newman and Ross (1976), description of *Euraphia hembeli* in Barrett and Freeman (2016) and Chan et al. (2008), our specimens fit more into *E. hembeli* and differ from other *Euraphia* in its gigantic appearance (up to 30 mm) and the presence of strong marked lateral depressor crests (10–12 in number, less in *H. pilsbryi*).

Superfamily Tetraclitoidea Gruvel, 1903
Family Tetraclitidae Gruvel, 1903
Subfamily Newmanellinae Ross & Perreault, 1999

Genus *Newmanella* Ross, 1969

Type species. *Newmanella radiata* (Bruguiere, 1789)

1 genus, 1 species recorded: *Newmanella spinosus* Chan & Cheang, 2016.

Newmanella spinosus Chan & Cheang, 2016

Figure 5; Tables 2–3

Newmanella spinosus Chan & Cheang, 2016: 212–220, figs 9–15.

Non-type material examined. Andaman Sea: 4 specimens, Phang-nga province, Takua Thung district, Na Tai beach, 16.V.2015, A. Pochai (BUU16.TC.NS01-04).

Description. Peduncle absent; base calcareous. Shell greyish green, shell with 4 plates (1 carina, 2 latus, 1 rostrum); parietes low conical, 3–4 rows of irregular parietal tubes (parietes multiple tubiferous), radii board with horizontal striation and summit oblique. External surface with deep longitudinal/radiating lines from base to apex, internal surface of parietes smooth and white with greyish green striations close to operculum. Orifice pentagonal, diamond-shaped. External surface of operculum brownish grey, internal surface of operculum white. Scutum triangular, external surface of scutum with horizontal striations; tergum high and narrow, tergum with numerous depressor crests.

Distribution. *Newmanella spinosus* was previously recorded from low intertidal to subtidal levels on rock shores along the coastlines of Taiwan and the Philippines and they were also collected from the surfaces of buoys

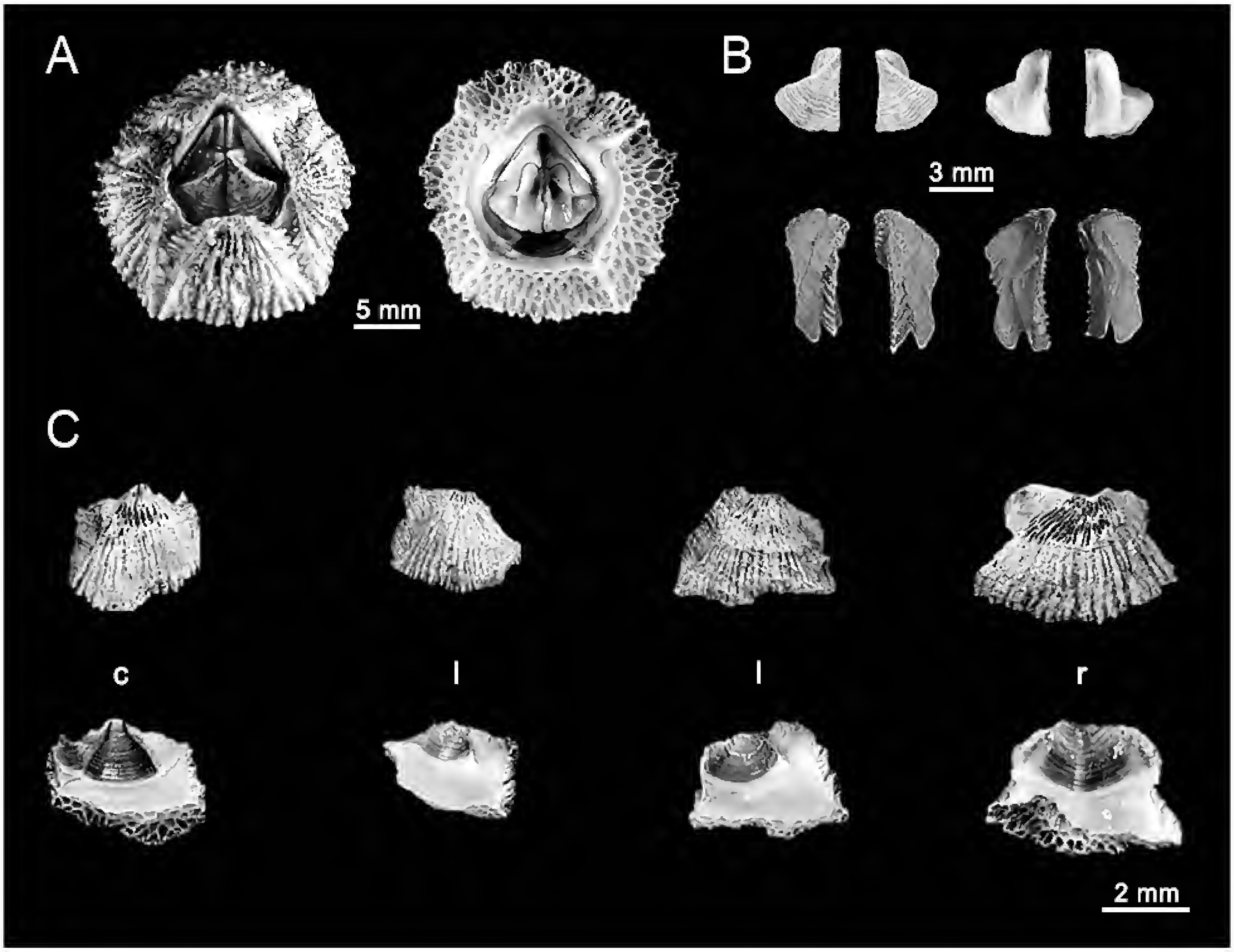

Figure 5. *Newmanella spinosus* collected from Na Tai beach, Phang-nga (BUU16.TC.NS01). **A**. Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** External (upper panel) and internal (lower panel) view of shell plates. Abbreviations: c, carina; l, latus; r, rostrum.

used in fishing cages in the open sea (Chan and Cheang 2016). In this present study, *N. spinosus* specifically distributes along low shores, and the intertidal zones of Na Tai beach, Takua Thung District, Phang-nga (the Andaman Sea).

Remarks. *N. spinosus* is morphologically similar to *N. radiata,* based on shell and scutum. The shell of *N. spinosus* is green while those of *N. radiata* is white. In addition, lateral scutal depressor muscle crest is shallow in the scutum of *N. radiata*, but deep in *N. spinosus*. The distribution of *N. spinosus* is around the North Pacific Ocean, from Okinawan Japan to Taiwan and the Philippines (Chan and Cheang 2016). The presence of *N. spinosus* in Thailand is surprising in our study, and creates the first record of this species distributing specifically in Na Tai beach, Takua Thung district, Phang-nga province.

Subfamily Tetraclitinae Newman & Ross, 1976

Genus *Tetraclita* Schumacher, 1817

Type species. *Tetraclita squamosa* (Bruguiére, 1789)

1 genus, 3 species recorded: *Tetraclita kuroshioensis* Chan, Tsang & Chu, 2007, *Tetraclita singaporensis* Chan, Tsang & Chu, 2007 and *Tetraclita squamosa* (Bruguiere, 1789).

Tetraclita kuroshioensis Chan, Tsang & Chu, 2007

Figure 6; Suppl. material 1; Tables 2–3

Tetraclita squamosa viridis: Hiro, 1936: 635; 1937: 469; 1939: 271.
Tetraclita squamosa squamosal: Utinomi, 1968: 178.
Tetraclita pacifica Chan et al., 2007b: 88.

Non-type material examined. Andaman Sea: 2 specimens, Phang-nga province, Khura Buri district, Ao Khoei beach, 30.VII.2015, A. Pochai (BUU16.TC.TK01-02). 3 specimens, Phang-nga province, Takua Thung district, Na Tai beach, 16.V.2015, A. Pochai (BUU16.TC.TK03-05). 2 specimens, Phuket province, Mueang Phuket district, Ao Yon beach, 15.VII.2015, A. Pochai (BUU16.TC.TK06-07). 3 specimens, Phuket province, Katu district, Kalim beach, 15.VII.2015, A. Pochai (BUU16.TC.TK08-10).

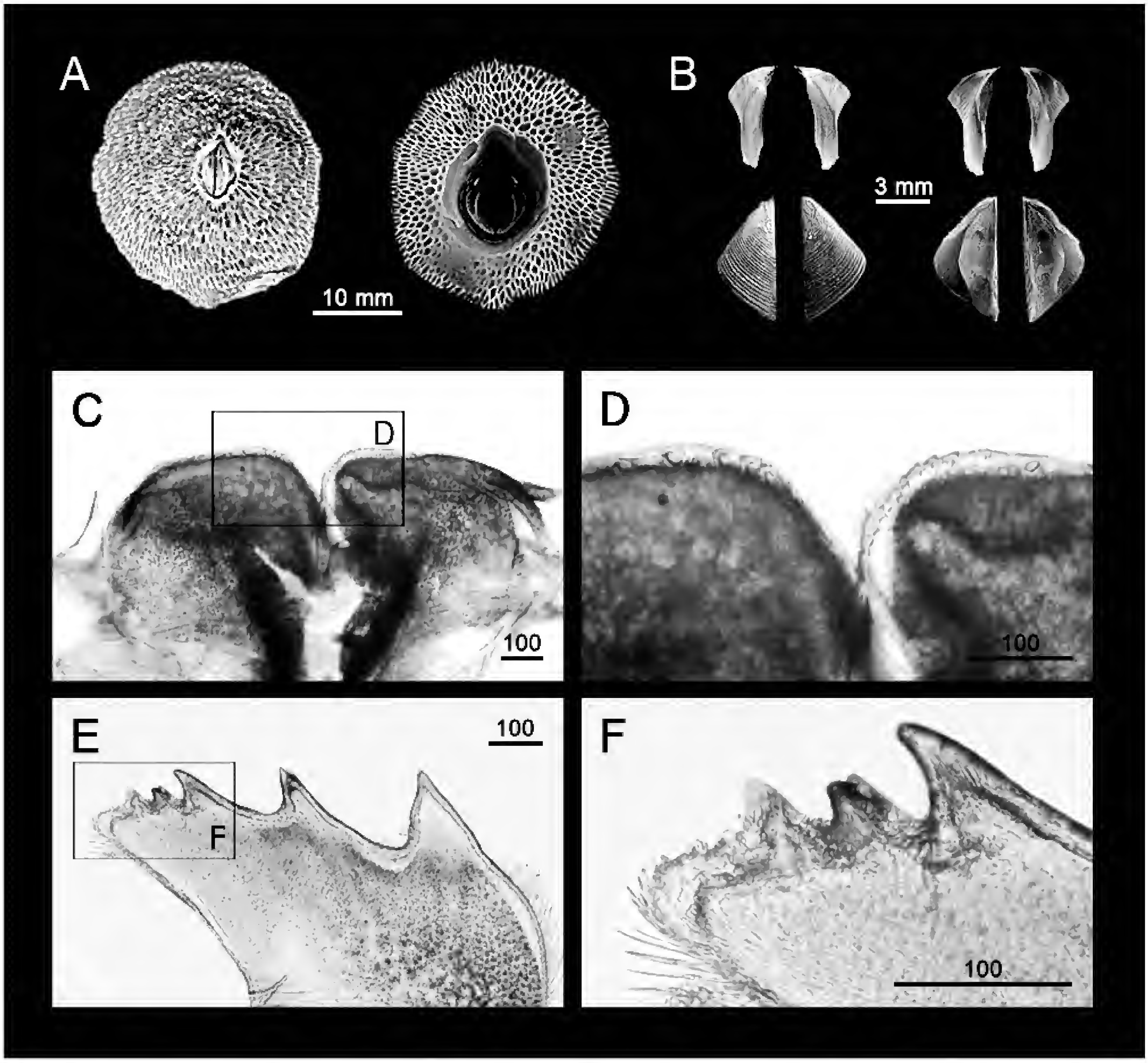

Figure 6. *Tetraclita kuroshioensis* collected from (BUU16.TC.TK01) from Na Tai beach, Phang-nga. **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C–F.** Light microscopy on mouthparts, **C.** Labrum, **D.** Close up on the teeth of the labrum, **E.** Mandible, **F.** Close up on the lower margin of mandible. **C–F.** Scale bars in μm.

Gulf of Thailand: 3 specimens, Prachuap Khiri Khan province, Bang Saphan district, Ban Krut beach, 06.IX.2015, A. Pochai (BUU16.TC.TK11-13). 3 specimens, Chon Buri province, Ko Si Chang district, Ko Kham Yai beach, 05.VII.2015, S. Khachonpisitsak (BUU16.TC.TK14-16).

Description. Peduncle absent; base membranous; shell greyish black to purplish-grey with 4 plates (1 carina, 2 latus, 1 rostrum), parietes conical, plates inseparable, 7–8 rows of parietal tubes (parietes multiple tubiferous), external surface with mosaic scales pattern radiating randomly from base to apex, internal surface of parietes smooth and white with dark grey striations around aperture. External surface of operculum mixed grey and yellowish-light brown, internal surface of operculum greyish-dusky green. Scutum bigger than tergum, scutum triangular, external surface of scutum with horizontal striations, occludent margin of scutum with obvious shallow and rough teeth, short articular ridge-basal margin, angle between basal margin and tergal margin is quite perpendicular. Tergum higher than wide, basi-scutal angle 158°, tergum with broad spur, spur angle 30°. Mandible with 4 big teeth, 1st tooth smaller; maxillule not notched with 11 setae; labrum with 5 small teeth on each side; cirri I possessing serrulate setae.

Distribution. *Tetraclita kuroshioensis* is reassigned the name from *Tetraclita squamosa* which were collected from Taiwan, and Okinawa and Honsu of Japan, and *Tetraclita pacifica*. The distribution of this species occurs in broad area along north-west Pacific region (Chan et al. 2007a, b; Chan 2009). In this present study, the species distribution occurs along littoral intertidal zones in both the Andaman Sea (Ao Yon, Ao Khoei, Na Tai, and Kalim) and the Gulf of Thailand (Ban Krut and Ko Kham Yai).

Remark. *Tetraclita kuroshioensis* is quite similar to *Tetraclita singaporensis* in following characteristics: tergum without beak and with wide spur, scutum with short articular ridge-basal margin. However, angle between tergal margin and basal margin of *T. kuroshioensis* is more perpendicular (90°) or shaper while that of *T. singaporensis* is curved.

Tetraclita singaporensis Chan, Tsang & Chu, 2007

Figure 7; Suppl. material 2; Tables 2–3

Tetraclita singaporensis Chan, Tsang & Chu, 2007: 52–53, figs 1–3.

Non-type material examined. Andaman Sea: 2 specimens, Phang-nga province, Takua Thung district, Na Tai beach, 16.V.2015, A. Pochai (BUU16.TS.TSG01-02).

Description. Peduncle absent; base membranous; shell purplish-dusky green with 4 plates (1 carina, 2 latus, 1 rostrum), parietes conical, plates inseparable, 5–6 rows of parietal tubes (parietes multiple tubiferous), external surface with deep and irregular longitudinal striations from apex to base and small radiating lines, internal surface of parietes smooth and white with greyish-green horizontal striations around aperture. External surface of operculum yellowish brown mixed with dusky green, internal surface of operculum dusky green-purplish and white around spur of the tergum. Scutum bigger than tergum, scutum triangular, short articular ridge-basal margin, external surface of scutum with horizontal striations, occludent margin of scutum with rough teeth. Tergum higher than wide, tergum with broad spur and not beaked, spur angle 30–35°, basi-scutal margin 148–150°. Mandible with 4 big teeth, 2nd and 3rd teeth consisting double teeth, 1st tooth with small spines, lower margin pectinate with 8 small teeth and obvious double bigger teeth at the edge; maxillule notched, two large setae above notch, 13–17 setae below notch; labrum with 4–5 large teeth on each side; cirri I possessing bidenate serrulate setae.

Distribution. *Tetracliata singaporensis* has been reassigned the name from previously known as *Tetraclita squamosa*, which were collected from Singapore. Hence, the distribution of this species is firstly marked at Singapore, Indo-West Pacific region (Chan et al. 2007a). In this present work, the specimens were collected from Na Tai, Andaman Sea and it distributes in the mid shore.

Remarks. *Tetraclita singaporensis* differs from *Tetraclita squamosa* in that it has tergum without beak and broader spur, and scutum with short articular ridge-basal margin.

Tetraclita squamosa (Bruguiére, 1789)

Figure 8; Suppl. material 3; Tables 2–3

Balanus squamosa Bruguiére, 1789: 170.
Lepas porosa Gmelin, 1791: 3212.
Tetraclita porosa var. *viridis*: Darwin, 1854: 329; Borradaile, 1900: 799; Gruvel, 1905: 228; Krüger, 1911: 61, pl. 4, fig. 41b; Hoek, 1913: 254;
Tetraclita squamosa: Stebbing, 1910: 570; Barnard, 1924: 90; Oliveira, 1941: 6.
Tetraclita squamosa squamosa: Pilsbry, 1916: 251; Kolosváry, 1943: 96; Henry, 1957: 33; Stubbings, 1967: 294; Newman & Ross, 1976: 48; Ren & Liu, 1979: 339, pl. 1, figs. 1–11.
Tetraclita squamosa forma viridis: Broch, 1922: 337; 1931: 116.
Tetraclita porosa perfecta Nilsson-Cantell, 1921: 364.
Tetraclita squamosa: Yamaguchi, 1987: 344; Chan, 2001: 625, fig. 8; Chan et al., 2007b: 82, fig. 4.

Non-type material examined. Gulf of Thailand: 2 specimens, Nakhon Si Thammarat province, Sichon district, Hin Ngam beach, 04.VII.2015, A. Pochai (BUU16.TC.TSS01-02).

Description. Peduncle absent; base membranous; shell green mixed with brownish grey, shell with 4 plates (1 carina, 2 latus, 1 rostrum); parietes conical, plate fused, inseparable, 8 rows of parietal tubes (parietes multiple tubiferous), external surface with longitudinal lines from base to apex, internal surface of parietes smooth and white with purplish grey striations close to aperture, External surface of operculum brownish grey, internal surface of operculum purplish grey. Scutum larger than tergum, scutum triangular, long articular ridge-basal margin, external surface of scutum with horizontal striations, occludent margin of scutum with very shallow teeth; tergum higher than wide, basi-scutal margin 158–160°, tergum apex obviously beaked, tergum with spur long and sharp, spur angle 25°. Mandible with 4 big teeth, 1st tooth with three small spines, lower margin pectinate; maxillule notched, two large setae above notch, 11 big setae below notch and some smaller setae at the edge; labrum with 4 large teeth on each side; cirri I possessing bidenate serrulate setae.

Distribution. *Tetraclita squamosa* is widespread in tropical and subtropical waters from West Africa, the Indo-Pacific, the Indian Ocean, Australia, Indonesia and Singapore (Newman and Ross 1976; Ren and Liu 1979; Jones et al. 2000; Chan et al. 2007b). Its distributions in Thailand were previously recorded in two places: the Andaman Islands and the Gulf of Siam (recently called the Gulf of Thailand) (Jones 2000). In this present study, *T. squamosa* has restricted areas of distribution and it was found specifically at Hin Ngam beach, the Gulf of Thailand coast. Regarding vertical zonation, *T. squamosa* found in Thailand occurs on the mid shore.

Remark. As described in Chan et al. 2007a, b, *T. squamosa* (southern China) has unique tergum characteristics including tergum with beak and long spur, and scutum with long articular ridge-basal margin. Our specimens

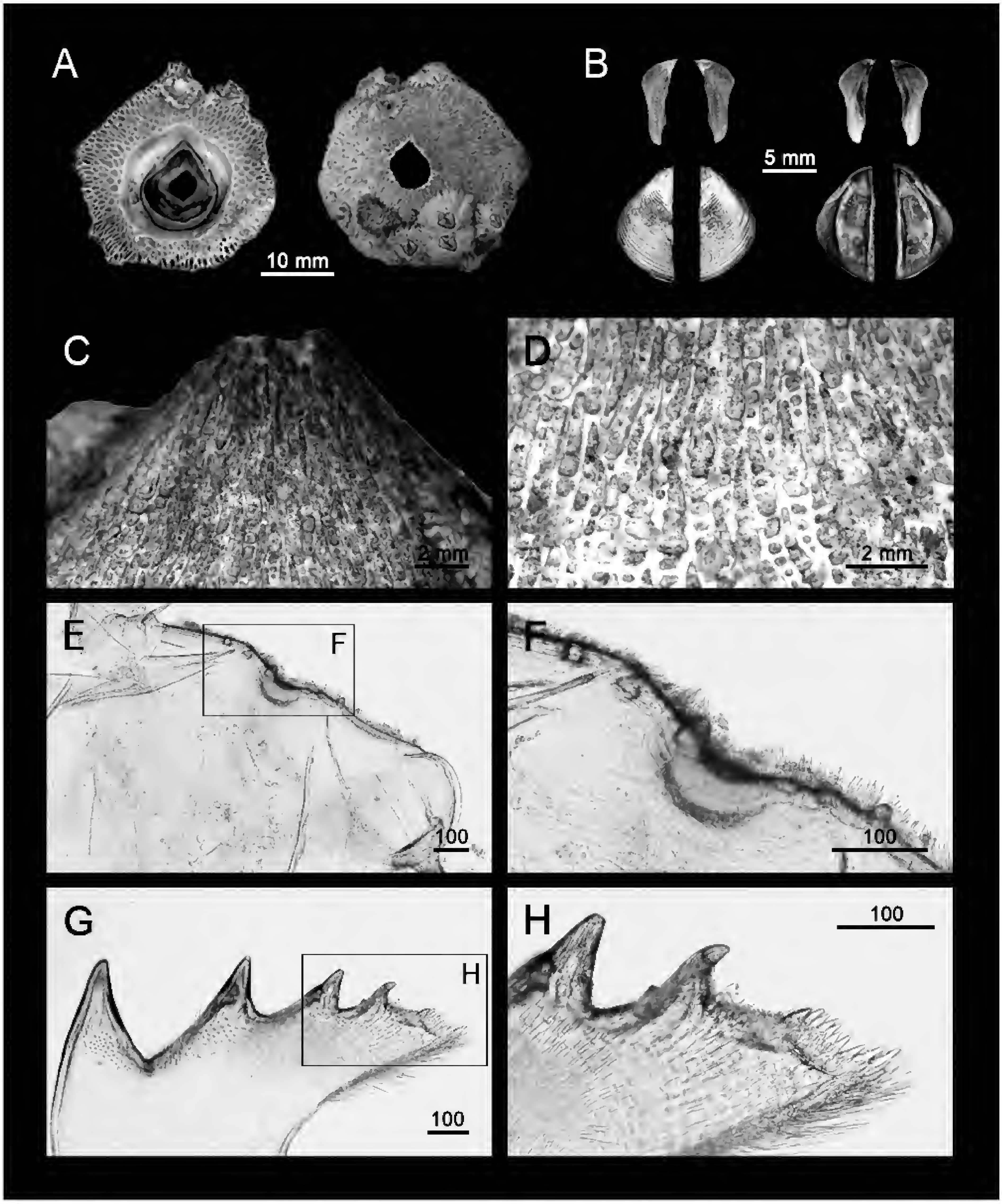

Figure 7. *Tetraclita singaporensis* collected from (BUU16.TC.TSG02) from Na Tai beach, Phang-nga. **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** Lateral side showing external surface of shell, **D.** Close up on the external surface of shell, **E–H.** Light microscopy on mouthparts, **E.** Labrum, **E.** Close up on the teeth of the labrum, **G.** Mandible, **G.** Close up on the pectinated lower margin of mandible. **E–H.** Scale bars in µm.

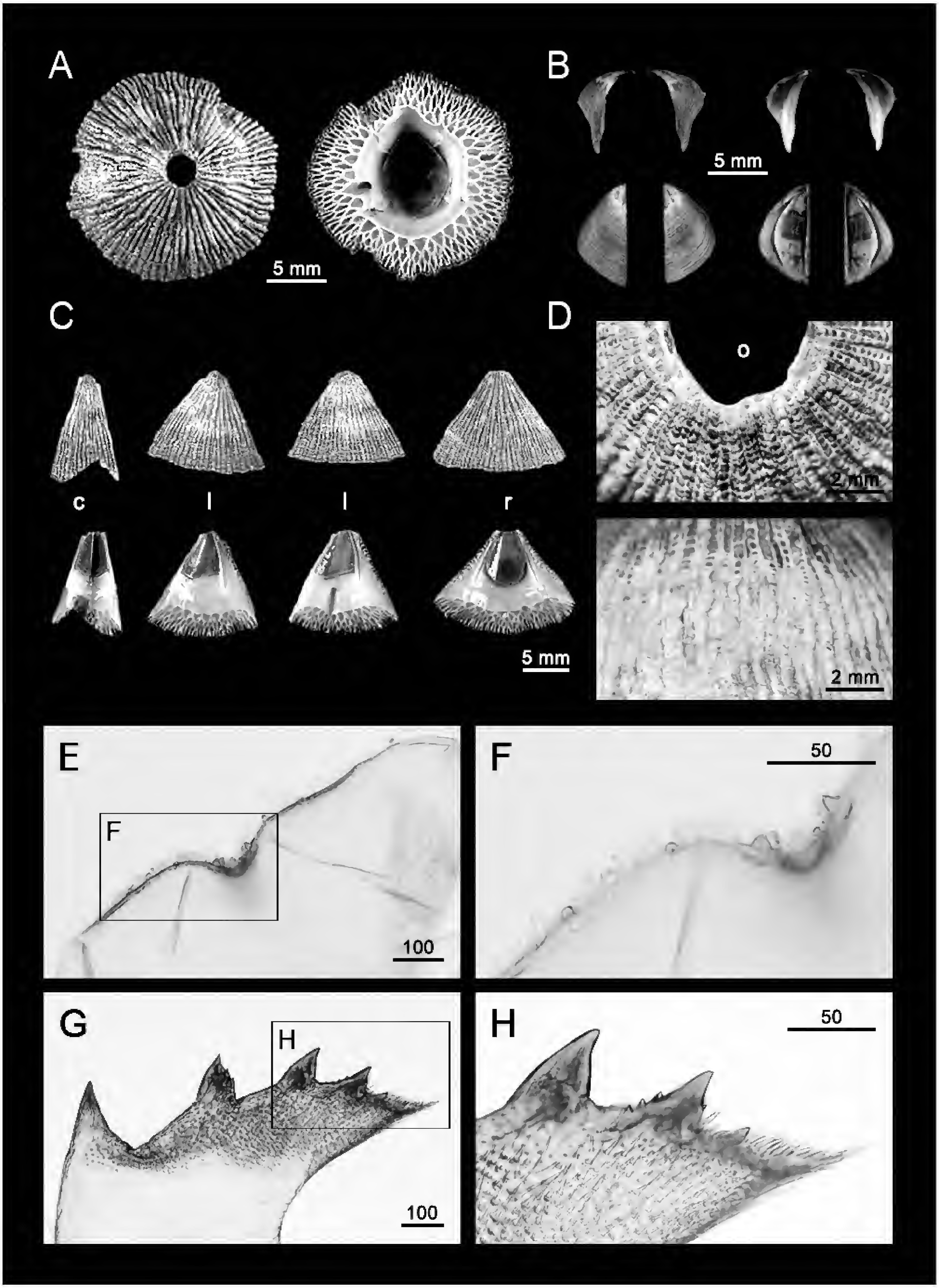

Figure 8. *Tetraclita squamosa* collected from Hin Ngam beach, Nakhon Si Thammarat (BUU16.TC.TS01). **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** External (upper panel) and internal (lower panel) view of shell plates, **D.** Close up on external surface of shell, **E–H.** Light microscopy on mouthparts, **E.** Labrum, **E.** Close up on the teeth of the labrum, **G.** Mandible, **G.** Close up on the pectinated lower margin of mandible. **E–H.** Scale bars in μm. Abbreviations: c, carina; l, latus; r, rostrum.

from Hin Ngam beach have all of these characteristics; hence, it is more fitted into *T. squamosa* (Southern China) rather than *T. squamosa* (Singapore), which is reassigned as *T. singaporensis*.

Superfamily Balanoidea Leach, 1817
Family Balanidae Leach, 1817
Subfamily Amphibalaninae Pitombo, 2004

Genus *Amphibalanus* Pitombo, 2004

Type species. *Amphibalanus amphitrite* (Darwin, 1854)

1 genus, 2 species recorded: *Amphibalanus amphitrite* (Darwin, 1854) and *Amphibalanus reticulatus* (Utinomi, 1967).

Amphibalanus amphitrite (Darwin, 1854)

Figure 9; Tables 2–3

Balanus amphitrite var. *communis* Darwin, 1854: 240 (in part).
Balanus amphitrite Weltner, 1897: 264; Pilsbry, 1907: 190; 1928: 312.
Balanus amphitrite communis: Hiro, 1939: 263.
Balanus amphitrite hawaiiensis: Hiro, 1939: 260.
Amphibalanus amphitrite: Pitombo, 2004: 263.

Non-type material examined. Andaman Sea: 2 specimens, Phang-nga province, Khura Buri district, Ao Khoei beach, 30.VII.2015, A. Pochai (BUU16.BN.AA01-02). 4 specimens, Phang-nga province, Takua Thung district, Na Tai beach, 16.V.2015, A. Pochai (BUU16.BN.AA03-06). 4 specimens, Phuket province, Mueang Phuket district, Ao Yon beach, 15.VII.2015, A. Pochai (BUU16.BN.AA07-10). 3 specimens, Phuket province, Mueang Phuket district, Panwa beach, 16.VII.2015, S. Khachonpisitsak (BUU16.BN.AA11-13). 4 specimens, Phuket province, Katu district, Kalim beach, 15.VII.2015, A. Pochai (BUU16.BN.AA14-17).

Gulf of Thailand: 2 specimens, Nakhon Si Thammarat province, Sichon district, Hin Ngam beach, 09.VIII.2015, A. Pochai (BUU16.BN.AA18-19). 4 specimens, Prachuap Khiri Khan province, Bang Saphan district, Ban Krut beach, 06.IX.2015, A. Pochai (BUU16.BN.AA20-23). 2 specimens, Chon Buri province, Ko Si Chang district, Ko Kham Yai beach, 05.VII.2015, S. Khachonpisitsak (BUU16.BN.AA24-25). 4 specimens, Chon Buri province, Si Racha district, Si Racha beach, 04.VII.2015, A. Pochai (BUU16.BN.AA26-29). 3 specimens, Chon Buri province, Mueang Chon Buri district, Khao Sam Muk beach, 05.VII.2015, A. Pochai (BUU16.BN.AA30-32).

Description. Peduncle absent; base calcareous. Shell white-pale pink with 6 plates (1 carina, 2 carinal latus, 2 latus, 1 rostrum); single rows of parietal tubes (parietes single tubiferous) with transverse septa; radii solid. External surface with purple longitudinal striations from apex to base (3–4 lines per plate) without horizontal striation, transverse teeth on suture edges with denticles on lower regions, internal surface of parietes grey with black horizontal striations close to operculum. External surface of operculum brownish grey, internal surface of operculum grey-white. Scutum bigger than tergum, scutum triangular, external surface of scutum with curved striations; tergum spur board with growth lines.

Distribution. *Amphibalanus amphitrite* is a common fouling barnacle and cosmopolitan species distributed along intertidal zones of coastlines in both the Gulf of Thailand and the Andaman Sea. It was found in all stations examined. The settlement patterns are various (e.g. rocks, shells of oyster and green mussels, concrete walls of bridges and harbors, offshore vessels, dock pilling, and mooring robes). In previous records, this species distributes worldwide in both tropical and temperate regions including the Indo-West Pacific, and Western Australia (Jones 2004; Chen et al. 2014) and it has been suggested that this wide range of distribution was due to human-mediated activities during global trade expansion (Chen et al. 2014).

Remark. The morphology of *Amphibalanus amphitrite* is variable from diverse habitats worldwide. Shells exposed and eroded by heavy wave action showed no purple stripes on the external surface. The molecular analysis has confirmed its genetic differentiation which might be due to local adaptation and geographical isolation (Chen et al. 2014). Due to hypothesis on human-mediated activities as the main cause of *A. amphitrite*'s distribution across the globe, this species is considered as non-native or introduced species in these examined regions: Hawaii, California, North Carolina, and the Atlantic coast (Carlton et al. 2011), whereas it is considered as native in tropical waters (e.g. Hong Kong, Thailand, Malaysia) supported by molecular study (Chen et al. 2014). Despite the diverse morphology of *A. amphitrite*, another species in the same genus *Amphibalanus reticulatus* exhibits clear patterns of shell carrying both vertical and longitudinal striations on the external surface. The separation of settlement type is distinct between these two species; one is found mostly on rocky shores exposed to waves and the other one is found on some mollusk shells.

Amphibalanus reticulatus (Utinomi, 1967)

Figure 10; Tables 2–3

Balanus amphitrite var. *communis* Darwin, 1854: 240, pl. 5, figs. 2e, h, l [type locality: Tachitgatani, Tanabe Bay, Japan].
Balanus amphitrite communis: Hiro, 1938: 301, figs. 1a, b; Utinomi, 1956: 52, pl. 26, fig. 11.; 1960: 44, figs. 1c, d, 2c, d.
Balanus reticulatus: Utinomi, 1967: 216, figs. 9a, b, 10a, b, 11a-e, pl. 6, figs. 7–8; Henry & McLaughlin, 1975: 88, text figs. 11, 18, pl. 7, fig. d, pl. 8, pl. 9, figs. a, d, e.

Non-type material examined. Andaman Sea: 2 specimens, Phang-nga province, Takua Thung district, Na Tai beach, 16.V.2015, A. Pochai (BUU16.BN.AR01-02).

Gulf of Thailand: 3 specimens, Chon Buri province, Si Racha district, Si Racha beach, 04.VII.2015, A. Pochai (BUU16.BN.AR03-05). 3 specimens, Chon Buri

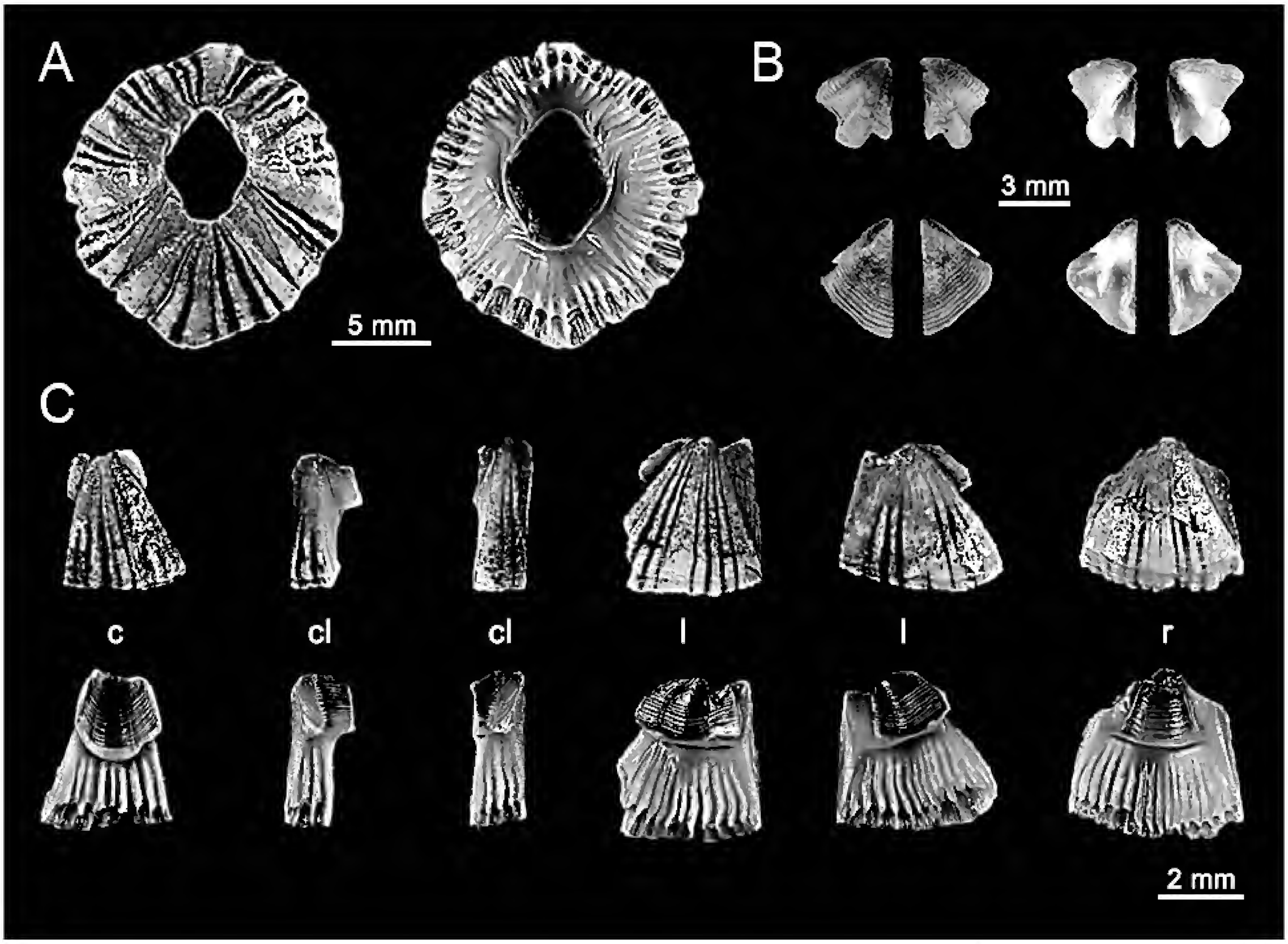

Figure 9. *Amphibalanus amphitrite* collected from Khao Sam Muk beach, Chon Buri (BUU16.BA.AA30). **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** External (upper panel) and internal (lower panel) view of shell plates. Abbreviations: c, carina; cl, carinal latus; l, latus; r, rostrum.

province, Mueang Chon Buri district, Khao Sam Muk beach, 05.VII.2015, A. Pochai (BUU16.BN.AR06-08). 3 specimens, Chon Buri province, Ko Si Chang district, Ko Kham Yai beach, 05.VII.2015, S. Khachonpisitsak (BUU16.BN.AR09-11).

Description. Peduncle absent; base calcareous. Shell white-pale pink and orange with 6 plates (1 carina, 2 carinal latus, 2 latus, 1 rostrum); single rows of parietal tubes (parietes single tubiferous) with transverse septa; radii solid. External surface with longitudinal and horizontal striations, transverse teeth on suture edges with denticles on lower regions, internal surface of parietes white. External surface of operculum white-pale pink and orange with striations in both tergum and scutum, internal surface of operculum white. Scutum bigger than tergum, scutum triangular; tergum spur sharp with growth lines.

Distribution. *Amphibalanus reticulatus* is widely distributed from Japan, the Indo-West Pacific to Australia, of which the latter is considered as an introduced species carried by ship transport (Jones 2004). In this study, *A. reticulatus* occurred in the intertidal zone along the Andaman Sea and the Gulf of Thailand. These specimens were found at Si Racha, Khao Sam Muk, Ko Kham Yai (Chon Buri) and Na Tai (Phang-nga).

Remark. *Amphibalanus reticulatus* exhibits clear vertical and horizontal striations while *Amphibalanus amphitrite* shows only vertical purple striation in all shell plates. In addition, the shapes of shell of *A. reticulatus* is more columnar than that of *A. amphitrite*, which might be due to elongation of parietes in response to crowding when growing as colonies. On all examined stations, distinct distribution and settlement between *A. amphitrite* and *A. reticulatus* can be noticed, in that *A. amphitrite* were found in almost all kinds of substrates but *A. reticulatus* preferred its attachment on shells which obviously did not live along the rocky shores and it might probably inhabit the deeper areas of the sea and were occasionally carried away into the shores by wave action.

Subfamily Megabalaninae Newman, 1979

Genus *Megabalanus* Hoek, 1913

Type species. *Megabalanus tintinnabulum* (Linnaeus, 1758)
1 genus, 1 species recorded: *Megabalanus tintinnabulum* Linnaeus, 1758.

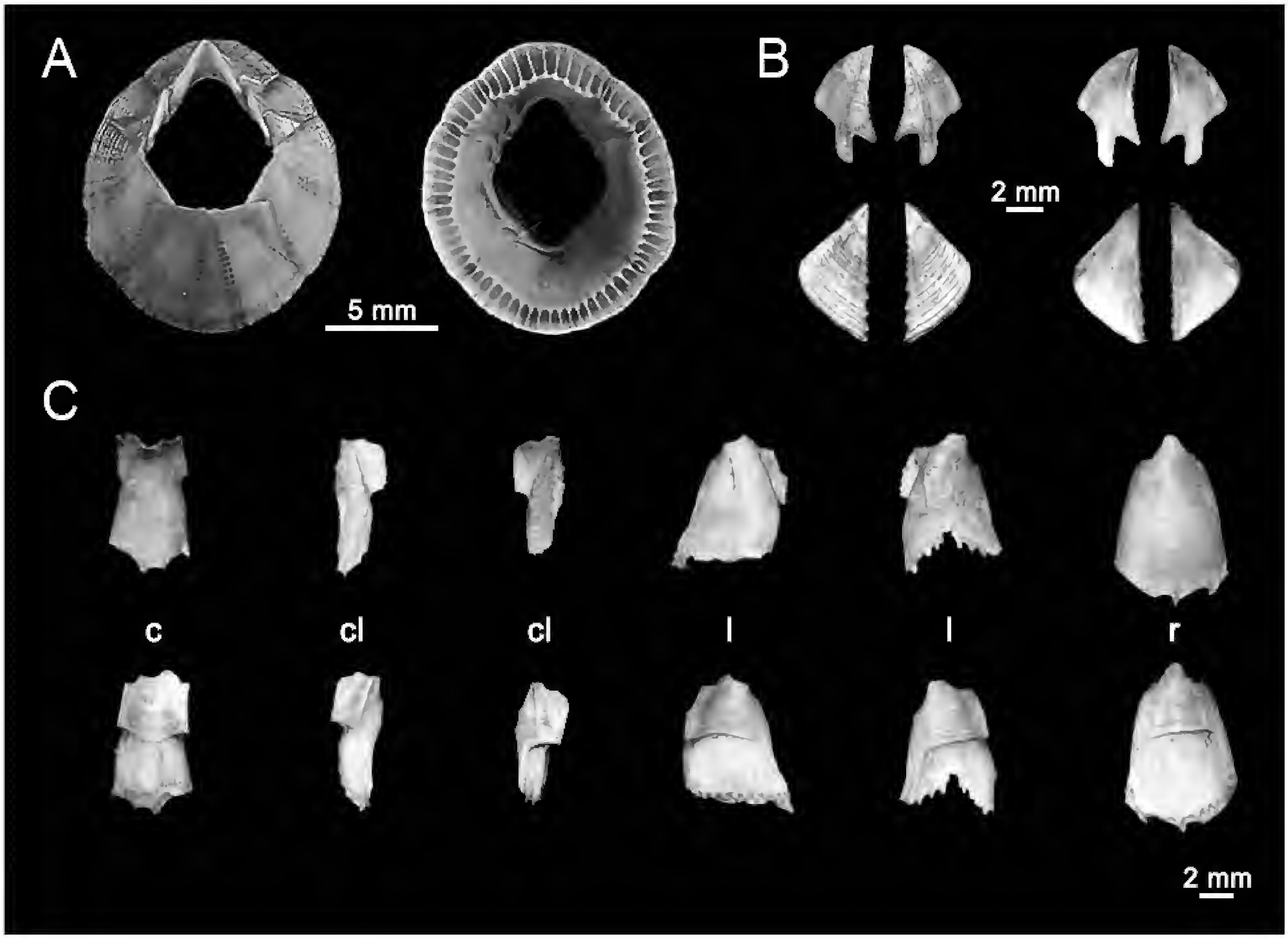

Figure 10. *Amphibalanus reticulatus* collected from Si Racha beach, Chon Buri (BUU16.BN.AR01, **A**; BUU16.BN.AR 03, **B & C**). **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** External (upper panel) and internal (lower panel) view of shell plates. Abbreviations: c, carina; cl, carinal latus; l, latus; r, rostrum.

Megabalanus tintinnabulum (Linnaeus, 1758)

Figure 11; Tables 2–3

Lepas tintinnabulum Linnaeus, 1758: 668.
Balanus tintinnabulum: Bruguiére, 1789: 165 (in part); Holthuis & Heerebout, 1972: 24, pl.1.
Lepas tintinnabulum Wood, 1815: 38, pl. 6, figs. 1, 2.
Balanus tintinnabulum tintinnabulum: Pilsbry, 1916: 55, pl. 10, fig.1–1e; Hiro, 1939: 258, figs. 7a-b; Daniel, 1956: 17, pl. 4, figs. 1–6; Davadie, 1963: 26, pl.2, fig. 4, pl. 6, figs. 1a, 2b; Zevina & Tarasov, 1963: 87, fig. 8; Stubbings, 1964: 335.
Balanus tintinnabulum var. *tintinnabulum*: Oliveira, 1941: 11, text-fig. 1, pl. 2, figs. 1, 2, pl. 4, fig. 1, pl. 5 fig. 3, pl. 8, fig. 6.
Megabalanus tintinnabulum: Newman & Ross, 1976: 68; Lacombe & Rangel, 1978: 3, fig. 4.

Non-type material examined. Andaman Sea: 3 specimens, Phang-nga province, Takua Thung district, Na Tai beach, 16.V.2015, A. Pochai (BUU16.BN.MT01-03).

Description. Peduncle absent; base calcareous. Shell cylindric or conic with 6 plates (1 carina, 2 carinal latus, 2 latus, 1 rostrum); parietes reddish to brownish red usually with longitudinal striations on external surface, parietes not prominently ribbed and rather smooth, irregular shape of parietal tubes (parietes tubiferous), sutural edges of radii with regular denticles, radii wide with horizontally striated, radii tubiferous; internal surface of parietes pale-purple with horizontal greyish violet striations around aperture. Orifice subcircular to rhombus. External surface of operculum white-pale pink and orange with prominent growth ridges in both tergums and scutums, internal surface of operculum white. Scutum bigger than tergum, scutum triangular, adductor ridge of scutum prominent; tergum with spur, spur furrow of tergum closed, scutal margin denticulate.

Distribution. *Megabalanus tintinnabulum* is widely distributed across almost all continents and is a well-known cosmopolitan fouling species. It was previously found in French Guiana, the United States, Australia, Mexico, Ecuador, Kuwait, Saudi Arabia, Sweden, France, Netherlands, Singapore, Indonesia and India (Henry and Mclaughlin 1986; Thiyagarajan et al. 1997; Jones et al. 2000; Jones 2004). Similar to *Amphibalanus*, it is considered as an introduced species in several regions and its distribution has been facilitated via shipping (Jones 2004). In Thailand, *M. tintinnabulum* specifically occurs in the low

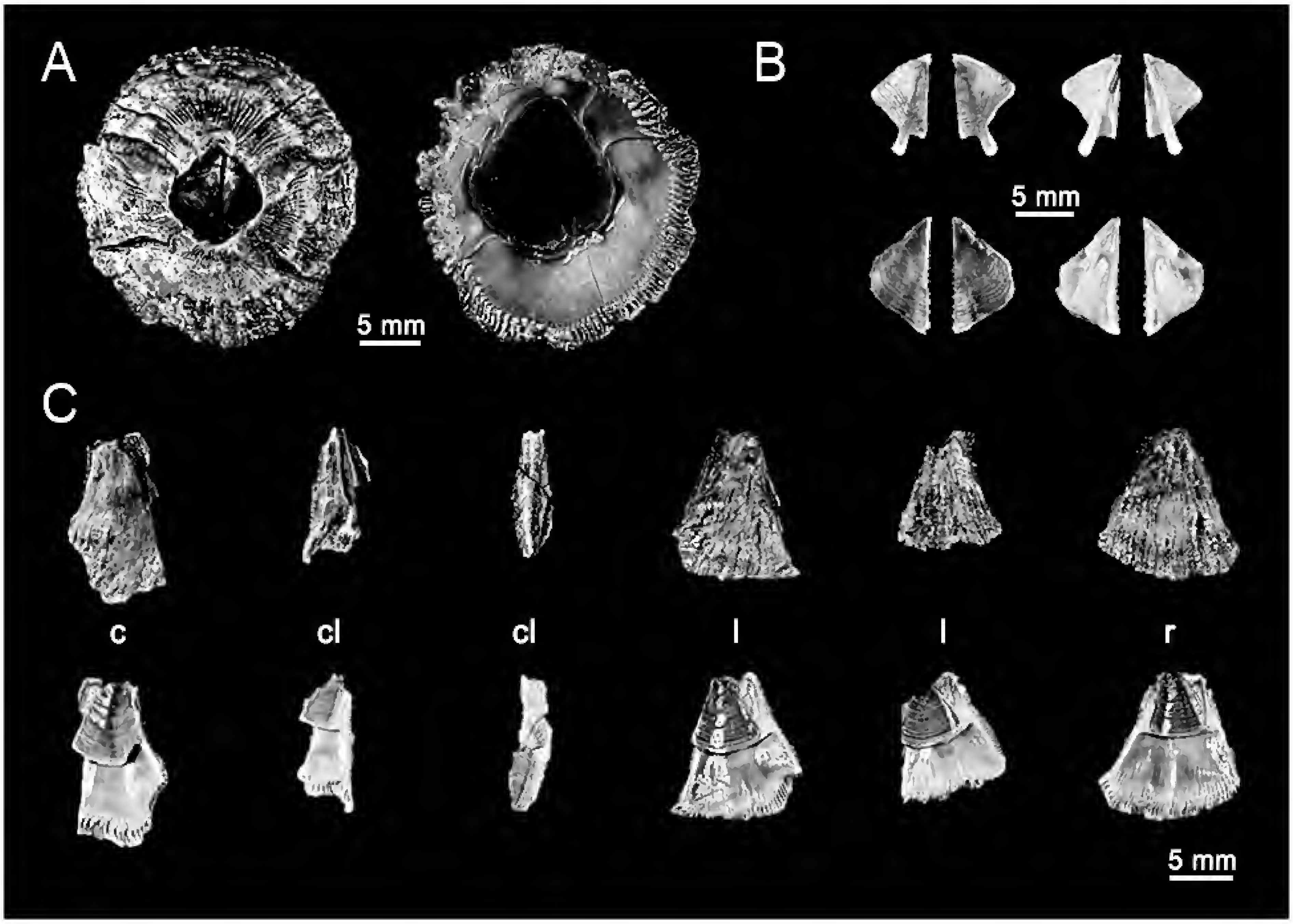

Figure 11. *Megabalanus tintinnabulum* collected from Na Tai beach, Phang-nga (BUU16.BN.MT01). **A.** Dorsal and ventral view of external shell, **B.** External (left panel) and internal (right panel) view of tergum (upper panel) and scutum (lower panel), **C.** External (upper panel) and internal (lower panel) view of shell plates. Abbreviations: c, carina; cl, carinal latus; l, latus; r, rostrum.

shores at Na Tai beach, Phang-nga province (the Andaman Sea). However, it does not appear to be a common fouling species as seen in some regions. *M. tintinnabulum* might have been introduced to Phang-nga beaches via ship transport, and the competition for habitat niche is compromised, compared to previously occupying cosmopolitan *A. amphitrite*.

Remarks. *Megabalanus tintinnabulum* has relatively larger shell plates than those of *Amphibalanus*. All three examined species (*M. tintinnabulum*, *A. amphitrite* and *A. reticulatus*) in family Balanidae have opercular valves with prominent growth ridges horizontally, and tergum with a clear spur. The coloration among these three species is easily distinguishable, in that purplish longitudinal striations presenting *A. amphitrite*, vertical and longitudinal red-orange striations with orange-pale pink background presenting *A. reticulatus* and brownish red surface with some irregular and unclear longitudinal stripes presenting *M. tintinnabulum*.

Identification key

1a	Shell conical to low conical with 4 plates with distinct parietes or shell with 4 plates with indistinct parietes or fused parietes, parietes multi-tubiferous	2
1b	Shell with 6 plates with distinct parietes	5
2a	Shell low conical, parietes discrete, summit of radii oblique, orifice pentagonal and wide, external surface of shell with deep longitudinal striations	*Newmanella spinosus* Chan & Cheang, 2016
2b	Shell conical, parietes not discrete, summit of radii horizontal, orifice circular or oval and small	3
3a	Shell green, external surface of shell with longitudinal striation, shell plates separable, tergum with obvious beak and tergum with sharp and narrow spur	*Tetraclita squamosa* (Bruguiere, 1789)
3b	Shell greyish black, external surface of shell with mosaic scale-like, plates inseparable, tergum without beak and with broad spur	4

4a Angle between basal margin and tergal margin of scutum is almost perpendicular .... *Tetraclita kuroshioensis* Chan, Tsang & Chu, 2007

4b Angle between basal margin and tergal margin of scutum is curved.... *Tetraclita singaporensis* Chan, Tsang & Chu, 2007

5a Parietes solid 6

5b Parietes tubiferous 8

6a Body length 10–30 mm, gigantic appearance .... *Euraphia hembeli* Conrad, 1837

6b Body length 3–10 mm, tergum with 3–4 lateral depressor crests 7

7a Mandible with four teeth, cirri I with conical spines, cirri II with multi-cuspidate setae and basal guard, articulation of opercular valves deep (shape of articulation similar to jigsaw-shaped), ... *Chthamalus malayensis* Pilsbry, 1916

7b Mandible with three teeth and 11 smaller setae at the lower margin, articulation of opercular valves shallow (shape of articulation from outside view similar to bird beak .... *Euraphia depressa* (Poli, 1795)

8a Parietal tubes single row and irregular shaped, shell with irregular and deep longitudinal striations, shell purplish white... .... *Megabalanus tintinnabulum* (Linnaeus, 1758)

8b Parietal tubes single row and uniform 9

9a External surface with purple longitudinal striations from apex to base against white surface.. *Amphibalanus amphitrite* (Darwin, 1854)

9b External surface with shall longitudinal and horizontal striations, shell white-pale pink and orange .... *Amphibalanus reticulatus* (Utinomi, 1967)

Discussion

In the present study, we examine geographical distribution of sessile acorn barnacles along Thai Peninsular coastal areas including the Gulf of Thailand and the Andaman Sea. So far, there has been a lack of information regarding the diversity of sessilian Thoracican barnacles in Thailand. Hence, we attempt to generate a checklist to understand the species diversification and how they distribute on intertidal rocky shores and sandy shores along the coast of Thailand. At least ten different forms of acorn barnacles were diagnosed so far that are classified into 6 genera and 3 families (Chthamalidae, Tetraclitidae and Balanidae), which can be distinguished based on their external shell morphology, including pattern of parietes, opercular plates, and arthropodal characters as described in previous literatures (Ross and Perreault 1999; Chan 2001; Chan et al. 2007a, b; Chan et al. 2009; Lozano-Cortés and Londoño-Cruz 2013; Chen et al. 2014; Hayashi and Chan 2015; Chan and Cheang 2016).

Our study also shows that the numbers of species found in the Andaman Sea (8 species) are more than those found in the Gulf of Thailand (6 species). At Na Tai station located in the Andaman Sea, up to 8 species (6 genera and 3 families) were recorded. Four of these 8 species were found only at this station including *Newmanella spinosus*, *Euraphia hembeli*, *Megabalanus tintinnabulum* and *Tetraclita singaporensis*. In other examined stations, only 2–3 species could be found, and most of them were of the genus *Amphibalanus*, *Tetraclita*, and *Chthamalus*. The differences in species abundance between two coastlines might probably due to the past history of the barnacle colonization. It has been shown in Voris (2000) that sea level was fluctuated during the Pleistocene, caused by glaciation. The spread of acorn barnacle seen in present day is possibly due to successful colonization when there were the connections between the eastern part of Indian Ocean and the Gulf of Thailand. The nature of local habitats such as the incoming oceanic current and freshwater discharge might also be another factor promoting or limiting the boundary of barnacle distribution. In addition, the spread of the barnacles found in the Gulf of Thailand was probably facilitated by the influence of the South China Sea Warm Current (SCSWC) as shown in the case of *Chthamalus malayensis* (Tsang et al. 2012). However, at this present work, we cannot clearly conclude that all of these species found in this work successfully distributed before the glaciation or influenced by nature of specific local habitats as further extensive works need to be done to include more stations along both coastlines with proper oceanographic data.

In addition, we found five new records identified as *Newmanella spinosus*, *Euraphia depressa* and *Euraphia hembeli*, *Tetraclita singaporensis*, and *Tetraclita kuroshioensis* on which the presence of these species in Thailand has not been mentioned in any literatures. *N. spinosus*, *E. hembeli* and *T. singaporensis* can only be seen at Na Tai station, Phang-nga province while *E. depressa* is specific to Khao Sam Muk, Chon Buri province. However, we cannot rule out the possibility of their presences in other places and more intensive field surveys covering all provinces along Thailand's coasts are required.

Recently, there are 26 species in the genus *Chthamalus* (Chan et al. 2009). In this study, one of them is clearly diagnosed as *Chthalamus malayensis* based on distinct shell, operculum morphology and arthropodal characters. However, we also found another Chthamalid which has shallow articulation of tergum and scutum; suggesting the possibility of a different species. Surprisingly, this Chthamalids is similar to *Chthamalus depressus* (reassigned as *Euraphia depressa*), described in Southward (1964). The presence in Thailand was not mentioned as they were thought to be found around the Mediterranean. In addition, the Chthamalids we found exhibit great variation and this has previously been reported that

Chthamalids have high intraspecific variation in external morphology (Helmuth et al. 2006; Hawkins et al. 2008) and thus using shell morphology is not ideal for taxonomic identification; thus several studies have used other measures for species diagnosis, including opercular plate geometry (Tsang et al. 2012), light microscopy and SEM of arthropodal characters (e.g. the number of conical spines and the number of setules of the basal guard setae on cirri and pattern of oral cones) (Miller and Blower 1989; Southward and Newman 2003; Yan and Chan 2004; Tsang et al. 2012) and molecular approaches (Tsang et al. 2012). In any future studies, we will use all of these measures, particularly the examination of mitochondrial COI, 12s rDNA, 16s rDNA sequences or performing DNA barcoding in order to get accurate identifications of chthamalid barnacles.

According to a field survey on water quality and metal contamination of both coastal regions of Thailand, the Andaman Sea is still in a good condition compared to the Gulf of Thailand. On the other hand, habitat degradation along the Gulf of Thailand is much more severe and the number of species of these sessile arthropods has been declining dramatically over the last 20 years due to high amount of water pollution. For example, along Chon Buri's coast around 20 years ago, at least five species were commonly seen along rocky shores of the now developing centrum area. Recently, however, only *Amphibalanus amphitrite* have been able to tolerate severe human activities and even in some sites there are no more barnacles on rocky shores. This might be because the local communities have been releasing non-treated waste water directly into the sea (personal communication and unpublished report (1996): Department of Biology, Faculty of Science, Burapha University). Hence, the richness of barnacle species can also be used to indirectly monitor the conditions of sea water.

Taken together, we demonstrate a clearer view of diversity for acorn barnacles from various localities in Thailand. This study shows at least 10 species of barnacles, in total, exist along Thai coast regions. Future works with more sampling sites and further in-depth investigations using SEM and molecular approaches with the help of phylogenetic analysis will provide a much better view especially of the history of barnacles and intraspecific variation between sessile crustaceans and that may reveal new barnacle species inhabiting Thailand.

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Supplementary material 1

Arthropodal characters of *Tetraclita kuroshioensis*

Authors: Ashitapol Pochai, Sutin Kingtong, Woranop Sukparangsi, Salinee Khachonpisitsak

Data type: species data

Explanation note: *Tetraclita kuroshioensis* collected from (BUU16.TC.TK01) from Na Tai beach, Phang-nga. A.-I. Light microscopy on arthropodal characters. A. Cirri I, B.-C. Close up on cirri I showing serrulate setae, D. Cirri II, E.-F. Close up on cirri II showing serrulate setae, G. Maxillule, H. Mandible, I. Labrum.

Supplementary material 2

Arthropodal characters of *Tetraclita singaporensis*

Authors: Ashitapol Pochai, Sutin Kingtong, Woranop Sukparangsi, Salinee Khachonpisitsak

Data type: species data

Explanation note: *Tetraclita singaporensis* collected from (BUU16.TC.TSG02) from Na Tai beach, Phang-nga. A.-I. Light microscopy on arthropodal characters. A. Cirri I, B.-C. Close up on cirri I showing serrulate setae, D. Cirri II, E.-F. Close up on cirri II showing serrulate setae, G. Maxillule, H. Mandible, I. Labrum.

Supplementary material 3

Arthropodal characters of *Tetraclita squamosa*

Authors: Ashitapol Pochai, Sutin Kingtong, Woranop Sukparangsi, Salinee Khachonpisitsak

Data type: species data

Explanation note: *Tetraclita squamosa* collected from Hin Ngam beach, Nakhon Si Thammarat (BUU16.TC.TS01). A.-I. Light microscopy on arthropodal characters. A. Cirri I, B.-C. Close up on cirri I showing serrulate setae, D. Cirri II, E.-F. Close up on cirri II showing serrulate setae, G. Maxillule, H. Mandible, I. Labrum.

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Redescription of *Nothobranchius lucius* and description of a new species from Mafia Island, eastern Tanzania (Cyprinodontiformes, Aplocheilidae)

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Abstract

Examination of specimens listed in the original description of *Nothobranchius lucius* revealed that they belong to two species. *Nothobranchius lucius* is redescribed based on the type series and other specimens collected in the type locality area, the Kibasira Swamp area, Rufiji River basin, Tanzania, at elevations between 250 and 300 m. *Nothobranchius insularis* **sp. n.** is described on the basis of specimens collected in the north part of Mafia Island, Tanzania, at about 10–15 m elevation. *Nothobranchius lucius* and *N. insularis* are considered closely related species based on the shared presence of long jaws; caudal fin, in males, with a broad dark grey to black band on its posterior margin; black dots over the whole flank, in females; metapterygoid curved, with its middle and dorsal portions separated from the sympletic by a broad interspace; and posterior process of the quadrate shorter than the ventral length of the quadrate without process. Characters useful to distinguish them include premaxillary dentition, caudal fin shape, colour pattern of flank and unpaired fins in females, fin length, and number of neuromasts of the posterior section of the anterior supraorbital series. Both species are members of a group that also includes *N. elongatus*, *N. hengstleri*, *N. interruptus*, *N. jubbi*, *N. krammeri*, and *N. melanospilus*, which are all diagnosed by the presence of two neuromasts in the anterior section of the anterior supraorbital series.

Introduction

The East Africa region comprising the coastal forests of south-eastern Kenya and eastern Tanzania is an important centre of biological diversity often known as the East Africa biodiversity hotspot (EABH), with high occurrence of endemic species (Myers et al. 2000, Azeria et al. 2007). This region exhibits the greatest species diversity of *Nothobranchius* Peters, 1868, a killifish genus that occurs in a wide geographical portion of central and eastern Africa (e.g., Parenti 1981). Among the about 60 valid species in the genus, 27 have been recorded in EABH (e.g., Costa 2009, Dorn et al. 2014). Species of *Nothobranchius* live in temporary pools formed during the rainy season, where resistant eggs undergo diapause during the dry season (e.g., Polacik et al. 2011, Pinceel et al. 2015). In EABH, there are two rainy seasons, the 'long rains' (Masika), from March to May, and the 'short rains' (Muli), from October to December, which alternate with dry periods when pools and some streams completely disappear, as described first by Fitzgerald (1898). Species of *Nothobranchius* and other African and South American aplocheiloid killifishes possessing this uncommon life cycle have been equivocally called annual fishes, reflecting the past belief that these fishes have a single generation per year (e.g., Myers 1942). Aplocheiloid killifishes with this life cycle have been alternatively known as seasonal killifishes in more recent studies (e.g., Costa 2002).

Species of *Nothobranchius* have been recently proposed as model organisms for ageing processes since they are naturally short-lived and easily bred in laboratories (e.g., Genade et al. 2005, Harel et al. 2015). However, they are mainly known as aquarium fishes due to the striking colouration exhibited by males of most species in the genus. Consequently, in the last four decades many collecting trips in EABH have been reported in the aquarium fish literature (e.g., Seegers 1997, Wildekamp 2004; Neumann 2008), which resulted in several new taxonomic records and descriptions of new species.

In a brief revision of the *N. melanospilus* species group, Wildekamp et al. (2009) described *N. lucius* Wildekamp, Shidlovskiy & Watters, 2009 on the basis of material collected in the Kilombero River drainage, Tanzania, which had been formerly identified as *N.* aff. *melanospilus* in the aquarium fish literature (e.g., Wildekamp 2004). In the original description of *N. lucius*, specimens from the Mafia Island, in Tanzania, previously identified as *N. melanospilus* (Pfeffer 1896) by Wildekamp (2004), were listed as additional non-type material belonging to *N. lucius*. The *N. melanospilus* species group was tentatively diagnosed by the presence of dark dots on the flank in females (i.e., black in *N. melanospilus*, dark brown in *N. lucius* and pale grey in *N. makondorum* Wildekamp, Shidlovskiy & Watters, 2009, according to Wildekamp et al. 2009). Subsequently, monophyly of this species group was supported in a multigene phylogeny (Dorn et al. 2014). All specimens listed by Wildekamp et al. (2009) is deposited in the Muséé Royal de l'Afrique Centrale (MRAC), Tervuren, Belgium.

While studying aplocheilid collections deposited in MRAC, discrepancies were found between data obtained by the current author from that listed by Wildekamp et al. (2009) from the same specimens. Consequently, a redescription of *N. lucius* is warranted and presented here. Comparisons also indicated that the populations from the Mafia Island, an off-shore island in the coast-line of Tanzania, belong to a distinct, new species, which is herein described.

Methods

All material examined is deposited in Musée Royal de l'Afrique Central, Tervuren (MRAC). Morphometric and meristic data were taken following Costa (1988), except for the snout length, measured between the anterior margin of the orbit and the anterior extremity of the middle portion of the upper jaw; measurements are presented as percent of standard length (SL), except for those related to head morphology, which are expressed as percent of head length. Specimens with deformed body were not measured to avoid unnecessary error. Fin-ray counts include all elements. Osteological preparations (C&S) were made according to Taylor and Van Dyke (1985). Terminology for frontal squamation follows Hoedeman (1958) and for cephalic neuromast series Costa (2001). Species were delimited using unique combinations of character states (diagnosability criterion; *e.g.*, Davis and Nixon 1992).

Results

Nothobranchius lucius Wildekamp, Shidlovskiy & Watters, 2009

Fig. 1, Table 1

Nothobranchius lucius Wildekamp, Shidlovskiy & Watters, 2009: 247 (holotype: MRAC A7-02-P-9, 49.6 mm SL; type locality: large pool on west side of road between Ifakara and the Kilombero River ferry, 2 km south of Ifakara, 1 km north of the Kilombero River, Tanzania, 8°10.30' S 36°41.54' E).

Material examined. MRAC A7-02-P-9, holotype; MRAC A7-02-P-10-25, 16 paratypes (1 C&S); Tanzania: pool on west side of the road between Ifakara and the Kilombero River ferry, 2 km south of Ifakara, 1 km north of the Kilombero River, 8°10.30'S 36°41.54'E, about 250 m asl; B. Watters *et al.*, 10 Jun. 2000. – MRAC 98-008-P-0007-0012, 6 paratypes; Tanzania: 2 km south of Ifakara, on east side of the road to Kilombero River ferry, northernmost pool between village and ferry; 8°10.04'S 36° 41.61'E, about 250 m asl; B. Watters *et al.*, 7 Jun. 1995. – MRAC A7-02-P-26-27, 2; Tanzania: 1 km south of Minepa village, large circular pool on west side of Ifakara-Lupiro road, 17 km south of Ifakara; 8°16.34'S 36°40.83'E, about 270 m asl; B. Watters *et al.*, 11 Jun. 2000. – MRAC A7-02-P-28-32, 5; Tanzania: 2 km southwest of Lupiro on road to Malinyi, 27 km south of Kilombero River ferry, ditch on southeast side of road; 8°23.45'S 36°39.45'E, about 300 m asl; B. Watters *et al.*, 11–12 Jun. 2000. – MRAC A7-02-P-37, 1; Tanzania: small pool at culvert on southeast side of Ifakara-Ruipa road, 37 km west of Ifakara, 0.5 km northeast of the junction to Narubungo village, on northern flanks of Kibasira Swamp; 8°08.88'S 36°24.91'E, about 280 m asl; B. Watters *et al.*, 9 Jun. 2002.

Diagnosis. *Nothobranchius lucius* differs from all other species of the *N. melanospilus* group, except *N. insularis*, by having snout pointed in lateral view, jaws moderately long (vs. snout blunt to weakly pointed, jaws short); caudal fin, in males, with broad dark grey to black band on the posterior margin (vs. narrow); presence, in females, of dark dots over the whole flank (dark dots when present restricted to the posterior portion of the flank). It is distinguished from *N. insularis* by having inner premaxillary teeth larger than teeth of the outer premaxillary tooth row (vs. smaller); caudal fin rounded in males (vs. subtruncate); in females, flank dark dots are rounded and arranged in horizontal rows (vs. dots vertically elongated, often arranged in oblique rows); unpaired fins, in females, with dark grey dots extending over most fin (dots restricted to the basal portion of unpaired fins); caudal, pectoral and pelvic fins longer (caudal fin length in males 31.3–34.9 % SL and 30.3–32.9 % SL in females of *N. lucius*, vs. 26.9–29.6 % SL in males and 22.8–27.4 % SL in females of *N. insularis*; pectoral-fin length 22.2–24.5 % SL in males and 20.2–24.6 % SL in females, vs. 17.1–21.8 % SL and 14.2–19.3 % SL, respectively; pelvic-fin length 11.6–13.1 % SL in males and 11.5–13.0 % SL in females,

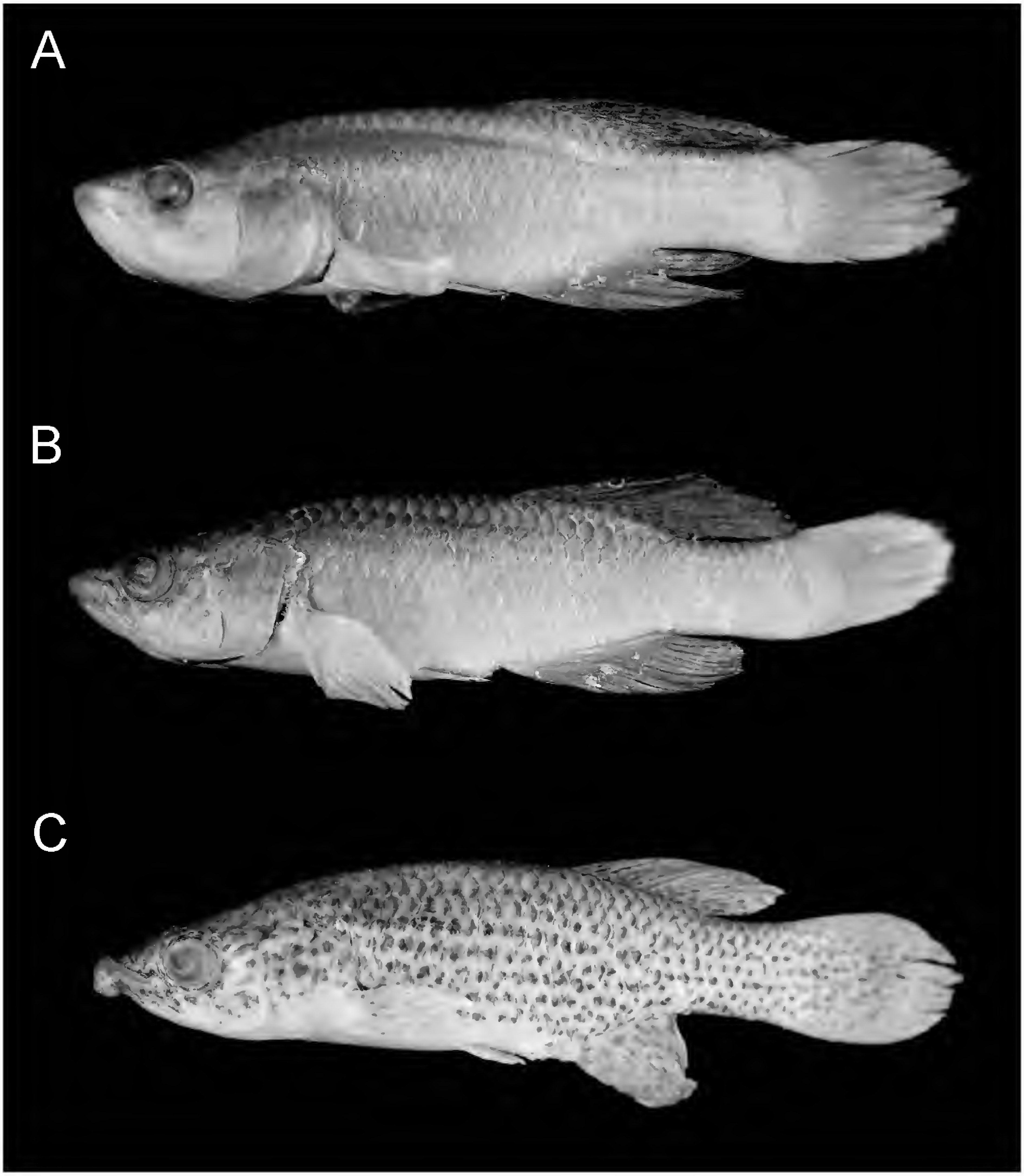

Figure 1. *Nothobranchius lucius*: **A.** MRAC A7-02-P-9, holotype, male, 49.6 mm SL; Tanzania: 2 km S of Ifakara; **B.** MRAC A7-02-P-26-27, male, 59.4 mm SL; Tanzania: 1 km S of Minepa; **C.** MRAC A7-02-P-26-27, female, 55.8 mm SL; Tanzania: 1 km S of Minepa.

vs. 8.6–11.0 % SL and 9.6–11.0 % SL, respectively); and two neuromasts in the posterior section of the anterior supraorbital series (vs. three).

Description. Morphometric data appear in Table 1. Dorsal profile slightly concave to nearly straight on head, convex from nape to posterior end of dorsal-fin base, about straight on caudal peduncle; ventral profile convex from lower jaw to anal-fin base, about straight on caudal peduncle. Body deep, compressed. Greatest body depth at vertical between bases of pectoral and pelvic fins. Jaws short, snout blunt in lateral view. Jaw teeth canine, numerous, irregularly arranged, outer teeth greater than internal teeth. Gill-rakers of first branchial arch 4 + 14–15. Six branchiostegal rays.

Dorsal and anal fins moderate in males, extremity rounded, with short filamentous rays along distal margin,

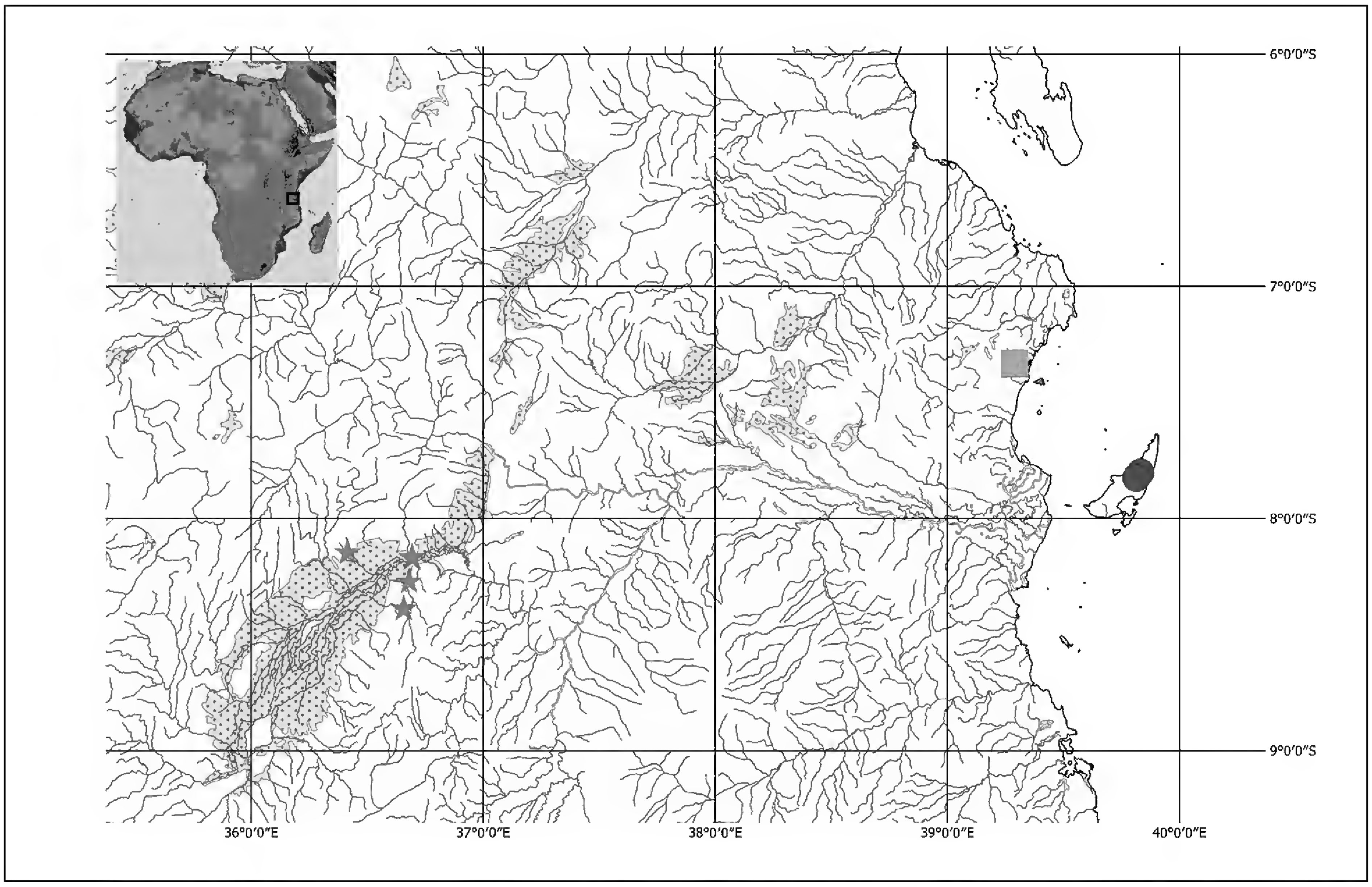

Figure 2. Geographical distribution of *Nothobranchius lucius* (stars), *Nothobranchius* cf. *lucius* (square), and *Nothobranchius insularis* sp. n. (circles); dotted areas are marshes.

Table 1. Morphometric data of *Nothobranchius lucius*.

	Holotype	paratypes	
	male	males (7)	females (9)
Standard length (mm)	49.6	40.4–53.7	35.7–52.4
Percent of standard length			
Body depth	27.4	27.0–31.8	24.6–29.6
Caudal peduncle depth	14.9	13.8–16.0	12.4–13.9
Pre-dorsal length	61.3	59.9–68.7	62.6–66.4
Pre-pelvic length	53.3	50.6–54.4	50.7–56.4
Length of dorsal-fin base	25.1	23.2–25.9	18.4–22.9
Length of anal-fin base	23.2	22.2–25.5	15.9–18.5
Caudal-fin length	31.2	31.7–34.9	30.3–32.9
Pectoral-fin length	22.3	22.2–24.5	20.2–24.6
Pelvic-fin length	12.0	11.6–13.1	11.5–13.0
Head length	33.0	31.8–34.6	31.9–34.9
Percent of head length			
Head depth	78.4	72.7–84.8	65.7–75.7
Head width	66.7	64.6–70.4	62.5–68.3
Snout length	35.0	32.5–37.1	30.7–33.9
Lower jaw length	30.9	30.2–33.6	28.2–30.4
Eye diameter	23.1	22.7–26.2	23.0–27.0

dorsal fin longer than anal fin; in females, dorsal fin rounded, anal fin sub-triangular and slightly longer than dorsal fin. Caudal fin subtruncate. Pectoral fin rounded, posterior extremity between pelvic-fin base and anus. Pelvic fin small, tip reaching urogenital papilla; pelvic-fin bases medially in contact. Dorsal-fin origin on vertical between base of first and second anal-fin rays. Dorsal-fin rays 14–16; anal-fin rays 16–18; caudal-fin rays 29–31; pectoral-fin rays 19–20; pelvic-fin rays 6. Minute contact organs on first and second pectoral-fin rays and distal portion of dorsal fin in males; rows of papillate contact organs along two distal thirds of most rays of anal fin in males.

Scales small, cycloid; body and head entirely scaled, except ventral surface of head. Minute filamentous contact organs along posterior margin of scales on middle portion of flank and latero-ventral portion of head in males. Body squamation extending over anterior 30 % of caudal-fin base; no scales on dorsal and anal-fin bases. Frontal squamation irregularly arranged in two longitudinal rows. Longitudinal series of scales 29–30; transverse series of scales 9–11; scale rows around caudal peduncle 16.

Anterior supraorbital series of neuromasts arranged in single section placed in shallow depression, with five neuromasts; in specimens above 45 mm SL, anterior series partially divided in two sections, with two larger neuromasts in each section and smaller one between them. Posterior supraorbital series with four neuromasts placed in shallow depression. Infraorbital series with 16–17 neuromasts, pre-opercular series 12–13, mandibular 10–13. One neuromast per scale of lateral line.

Colouration in alcohol (Fig. 1). ***Males.*** Flank, dorsum and head light brown, darker on posterior portion of scales of dorsal portion of flank, dorsum and opercle; venter pinkish grey; pale grey spots on suborbital region; branchiostegal membrane dark grey. Dorsal and anal fins hyaline with transverse series of grey spots, almost inconspicuous in anal fin. Caudal fin pale yellow with broad dark grey to black stripe along whole fin margin, broader on posterior margin; posterior sub-marginal area lighter. Pectoral fin hyaline, pelvic fin greyish hyaline with black tip.

Females. Flank and dorsum pale brown, side of head and venter pale yellow; rounded dark brown to black dots highly concentrated on whole trunk and head except venter, irregularly arranged in horizontal rows on flank. Whole unpaired fins hyaline with dark grey dots. Paired fins hyaline; few dark grey dots on basal portion of pectoral fin.

Distribution. *Nothobranchius lucius* occurs in localities along the Kilombero Valley, which is limited to west by the Udzungwa Mountains and to east by the Mbarika Mountains, forming the Kibasira Swamp that is part of the Rufiji River basin (Fig. 2). This region is about 300 km from the coastline and collecting localities are situated at between 250 and 300 m asl. Two specimens collected in the Luhule River floodplains, in coastal Tanzania (MRAC A7-02-P-35-36, one male and one female, 7°19.95'S 39°17.38'E, at about 20 m asl) are here tentatively identified as *N. lucius*. This species has been also recorded from the Mbezi and Ruhoi river basins, eastern Tanzanian (Wildekamp et al. 2009), but no specimen was deposited in museum collections, making identity of these records still uncertain.

Nothobranchius insularis sp. n.

http://zoobank.org/CC856CE9-244D-4642-9727-C41B819B28E7
Fig. 3, Table 2

Holotype. MRAC A7-02-P-33, 1 male, 52.9 SL; Tanzania: Mafia Island, approximately 3 km south of Kirongwe, 7°49.58'S 39°48.87'E, about 15 m asl; B. Watters et al., 31 May 2002.

Paratypes. MRAC A7-02-P-34, 1 female, 46.4 mm SL; collected with holotype. MRAC A702-P-38-44, 4 males, 43.7–55.2 mm SL (1 C&S), 3 females, 44.0–49.8 mm SL; Tanzania: Mafia Island, approximately 0.5 km east of Kirongwe, 7°48.12'S 39°49.97'E, about 10 m asl; same collectors and date as holotype.

Diagnosis. *Nothobranchius insularis* is distinguished from all species of the *N. melanospilus* group, except *N. lucius*, in possessing snout pointed in lateral view, jaws moderately long (vs. snout blunt to weakly pointed, jaws short); caudal fin, in males, with broad dark grey to black band on the posterior margin (vs. narrow); presence, in females, of dark dots over the whole flank (dark dots when present restricted to the posterior portion of the flank). The new species differs from *N. lucius* by having inner premaxillary teeth smaller than teeth of the outer premaxillary tooth row (vs. larger); caudal fin subtruncate in males (vs. rounded); in females, flank dark dots are vertically elongated and often arranged in oblique rows (vs. dots rounded, arranged in horizontal rows); unpaired fins, in females, with dark grey dots when present restricted to their basal portion (extending over most fin); caudal, pectoral and pelvic fins shorter (caudal fin length 26.9–29.6 % SL in males and 22.8–27.4 % SL in females of *N. insularis*, vs. 31.3–34.9 % SL in males and 30.3–32.9 % SL in females of *N. lucius*; pectoral-fin length 17.1–21.8 % SL in males and 14.2–19.3 % SL in females, vs. 22.2–24.5 % SL and 20.2–24.6 % SL, respectively; pelvic-fin length 8.6–11.0 % SL in males and 9.6–11.0 % SL in females, vs. 11.6–13.1 % SL and 11.5–13.0 % SL, respectively); and three neuromasts in the posterior section of the anterior supraorbital series (vs. two).

Description. Morphometric data appear in Table 2. Dorsal and ventral profiles slightly convex from snout to posterior end of dorsal and anal-fin bases, about straight on caudal peduncle. Body relatively slender, compressed. Greatest body depth at vertical just in front of pelvic-fin base. Jaws slightly elongated, snout pointed in lateral view. Jaw teeth canine, numerous, irregularly arranged, outer teeth greater than internal teeth. Gill-rakers of first branchial arch 4–5 + 14–15. Six branchiostegal rays.

Dorsal and anal fins broad in males, extremity rounded, with short filamentous rays along distal margin, dorsal fin slightly longer than anal fin; in females, dorsal fin rounded, anal fin sub-triangular and slightly longer than dorsal fin. Caudal fin subtruncate. Pectoral fin rounded, posterior extremity between pelvic-fin base and anus. Pelvic fin small, tip reaching between anus and urogenital papilla; pelvic-fin bases medially in close proximity. Dorsal-fin origin on vertical between base of first and third anal-fin rays. Dorsal-fin rays 15–16; anal-fin rays 16–18; caudal-fin rays 29–30; pectoral-fin rays 19; pelvic-fin rays 6. Minute contact organs on first and second pectoral-fin rays in males; rows of papillate contact organs along distal portion of middle dorsal-fin rays and two thirds of most rays of anal fin in males.

Scales small, cycloid; body and head entirely scaled, except ventral surface of head. Minute filamentous contact organs along posterior margin of scales on middle portion of flank and latero-ventral portion of head in males. Body squamation extending over anterior 40 % of caudal-fin base; no scales on dorsal and anal-fin bases. Frontal squamation irregularly arranged in two longitudinal rows. Longitudinal series of scales 31–32; transverse series of scales 9–10; scale rows around caudal peduncle 16.

Anterior supraorbital series of neuromasts arranged in two separate sections, each placed in shallow depression, the anterior section with two neuromasts, the posterior one with three; sometimes minute neuromast between depressions. Posterior supraorbital series with four neuromasts placed in shallow depression. Infraorbital series with 18–21 neuromasts, pre-opercular series 14–18, mandibular 17–18. One neuromast per scale of lateral line.

Colouration in alcohol (Fig. 3). ***Males.*** Flank, dorsum and head light brown, darker on posterior portion of scales of dorsal portion of flank, dorsum and opercle; venter pinkish grey; branchiostegal membrane dark grey. Dorsal and anal fins hyaline with transverse series of grey spots, almost inconspicuous in anal fin. Caudal fin pale yellow with dark grey to black stripe along whole fin

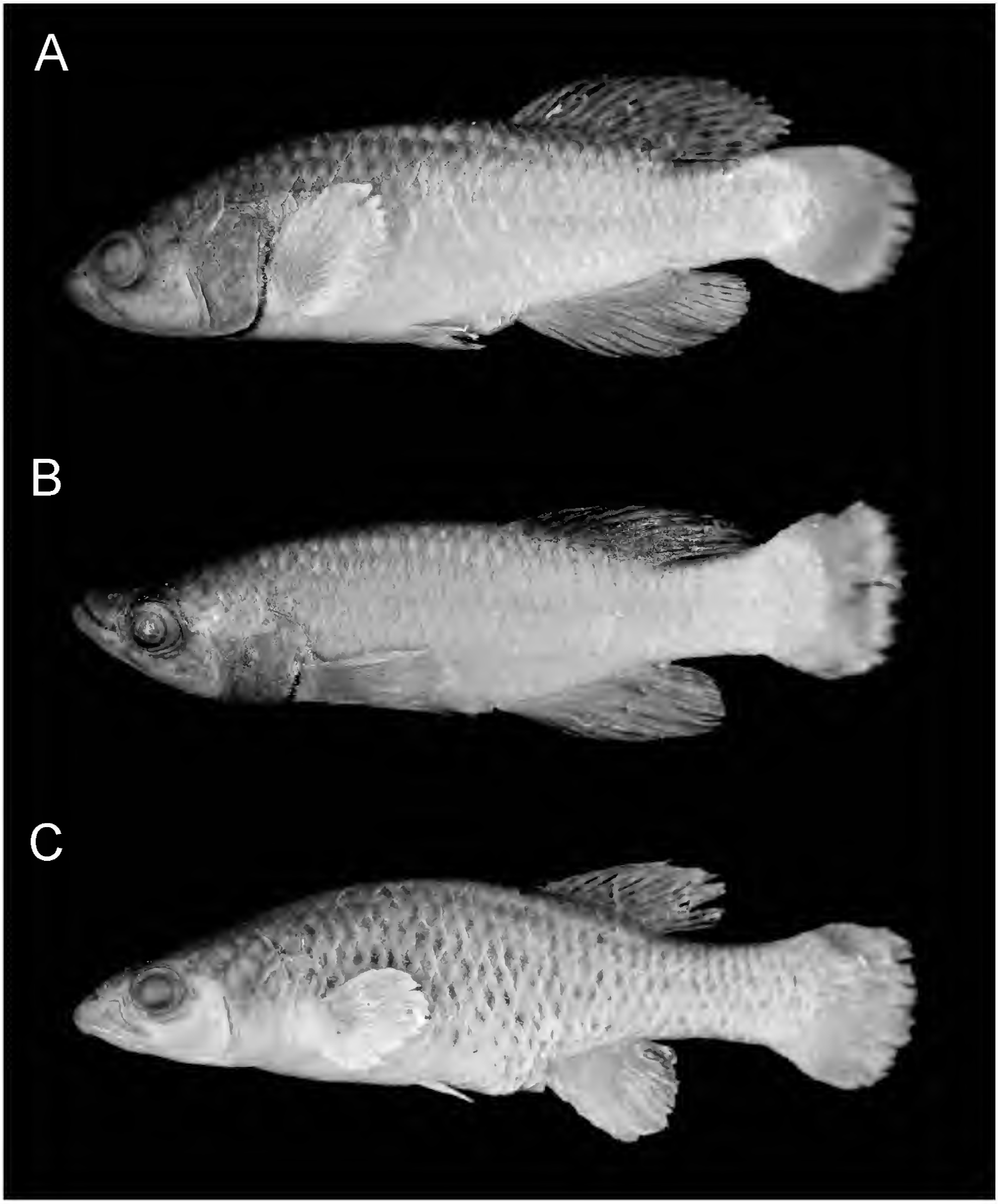

Figure 3. *Nothobranchius insularis* sp. n.: **A.** MRAC A7-02-P-33, holotype, male, 52.9 mm SL; Tanzania: 3 km S of Kirongwe, Mafia Island; **B.** MRAC A7-02-P-38-44, paratype, male, 48.3 mm SL; Tanzania: 0.5 km S of Kirongwe, Mafia Island; **C.** MRAC A7-02-P-38-44, paratype, female, 49.8 mm SL; Tanzania: 0.5 km S of Kirongwe, Mafia Island.

margin, broader on posterior margin. Pectoral fin hyaline, pelvic fin greyish hyaline with black tip.

Females. Flank and dorsum pale brown, side of head and venter pale yellow; vertically elongated dark grey to black dots irregularly arranged in oblique rows on whole flank; sometimes few pale grey dots on opercular region. Unpaired fins hyaline; elongated grey dots on basal portion of dorsal fin; anal and caudal fin often without dark marks, sometimes with almost inconspicuous pale grey dots on basal portion. Paired fins hyaline.

Table 2. Morphometric data of *Nothobranchius insularis*.

	Holotype	paratypes	
	male	males (3)	females (4)
Standard length (mm)	52.9	37.4–46.1	44.0–49.8
Percent of standard length			
Body depth	30.9	29.7–30.4	26.4–29.9
Caudal peduncle depth	15.0	13.6–14.8	13.3–14.1
Pre-dorsal length	63.5	59.9–65.2	64.7–66.7
Pre-pelvic length	51.4	48.5–51.1	50.7–52.0
Length of dorsal-fin base	24.7	20.5–25.4	19.1–21.5
Length of anal-fin base	23.0	20.1–24.0	15.1–16.9
Caudal-fin length	27.1	26.9–29.6	22.8–27.4
Pectoral-fin length	18.5	17.1–21.8	14.2–19.3
Pelvic-fin length	10.0	8.6–11.0	9.6–11.0
Head length	32.1	31.0–32.3	29.5–32.8
Percent of head length			
Head depth	85.3	79.3–82.7	77.1–81.2
Head width	67.0	65.0–65.8	64.6–70.1
Snout length	34.0	26.9–32.1	32.7–37.7
Lower jaw length	33.6	29.7–32.8	26.7–30.8
Eye diameter	26.7	26.7–27.9	26.4–28.8

Etymology. From the Latin *insularis*, meaning pertaining to an island and referring to the occurrence of the new species on Mafia Island.

Distribution. *Nothobranchius insularis* is known from two close localities in the northern part of the Mafia Island, Tanzania, at about 10–15 m asl (Fig. 2).

Discussion

Wildekamp et al. (2009) designated the type series of *N. lucius* containing the holotype and 22 paratypes that were collected in the Kilombero River drainage. An additional 18 non-type specimens were also listed. However, the table of morphometric and meristic data included in that paper indicates a total of 53 specimens of *N. lucius* examined, not 41 as indicated above. Such discrepancy supports the idea that the number of specimens used in the description was larger than that reported in the type material list, even when adding specimens listed under the non-types section that also includes material herein described as *N. insularis*. It is remarkable to notice that the type series of *N. lucius* includes some specimens that are poorly preserved (e.g. part of MRAC A7-02-P-10-25). These latter specimens have deformed body and damaged fins. Interestingly, other non-type specimens that are listed from the same drainage are well preserved (e.g. MRAC A7-02-P-26-27, 28-32).

Herein I speculate that measurements derived from poorly preserved specimens contributes to the variation presented by Wildekamp et al. (2009), which exceeds the variation reported herein based solely on the well preserved specimens reported by these authors. In addition, I have found discrepancies in what they report for some meristic characters, which are not subject to misinterpretation due to poor preservation. For example, Wildekamp et al. (2009) report the following for *N. lucius*: dorsal-fin rays 14–17, anal-fin rays 15–19, longitudinal series scales 31–35, and transverse series scales 12–14. Herein, however, I document that dorsal-fin rays range from 15–17, never 14; anal-fin rays range from 16–18, never 15 nor 19; longitudinal series scales range from 31–33, never 34 nor 35; and transverse series scales were 9–10, never 12–14. Lower fin-ray counts reported by Wildekamp et al. (2009) may be due to the first ray being often minute and embedded by thick epithelial tissue, but other differences noted above can not be explained.

Wildekamp et al. (2009: 238) distinguished *N. lucius* from other morphologically similar congeners by it having a more slender body and stronger dentition. When diagnosing *N. lucius*, Wildekamp et al. (2009: 247) distinguished this species from *N. melanospilus* and *N. makondorum* by the longer head, longer snout and more slender body in males. Morphometric values presented in that study, however, were notably overlapped among the three species, indicating that these characters are not useful to effectively distinguish species of the *N. melanospilus* group. I confirm this conclusion in the present study. The present comparison of jaw dentition in species of the *N. melanospilus* group also indicates that the dentition of *N. lucius* and *N. insularis* is not stronger than in other species, but in fact, *N. lucius* and *N. insularis* differs from other species of the group by both having more elongated jaw bones, which often yields a pike-like appearance in lateral view. In *N. lucius* and *N. insularis* the length between the anterior border of the dentary and the posterior tip of the angulo-articular is longer than the length between the anterior tip of the quadrate and the posterior margin of the preopercle (Fig. 4A; vs. shorter in the remaining species of the *N. melanospilus* group, Fig. 4B).

According to Wildekamp et al. (2009: 238), *N. lucius* may be distinguished from other species of the *N. melanospilus* group by two colouration characters: "a denser pattern of dark brown (not black) spots on the body, head and all fins of the females" (vs. black spots on the flank and base of the unpaired fins in *N. melanospilus* and grey spots on the flank in *N. makondorum*), and "a wide black margin and orange-red submargin to the caudal fin" in males (vs. caudal fin red with a narrow black margin). However, the first diagnostic character does not correspond to the figure of a live female of *N. lucius* from the type locality that is included in that same paper. The female in the figure shows that black dots, not brown, cover the whole flank, the side of the head, and the unpaired fins (Wildekamp et al. 2009: 248, fig. 9). In preserved females of *N. lucius* here examined, dots are dark brown to black, rounded, and distributed on the whole flank, side of the head, a large portion of the unpaired fins, and the basal portion of the pectoral fin; the dots of the flank are mainly arranged in horizontal rows (Fig. 1C). The colour pattern documented here for *N. lucius* greatly differs from the colour pattern exhibited by preserved females of *N. insularis*. In this species, dark grey to black dots are vertically elongated and mainly arranged in oblique rows

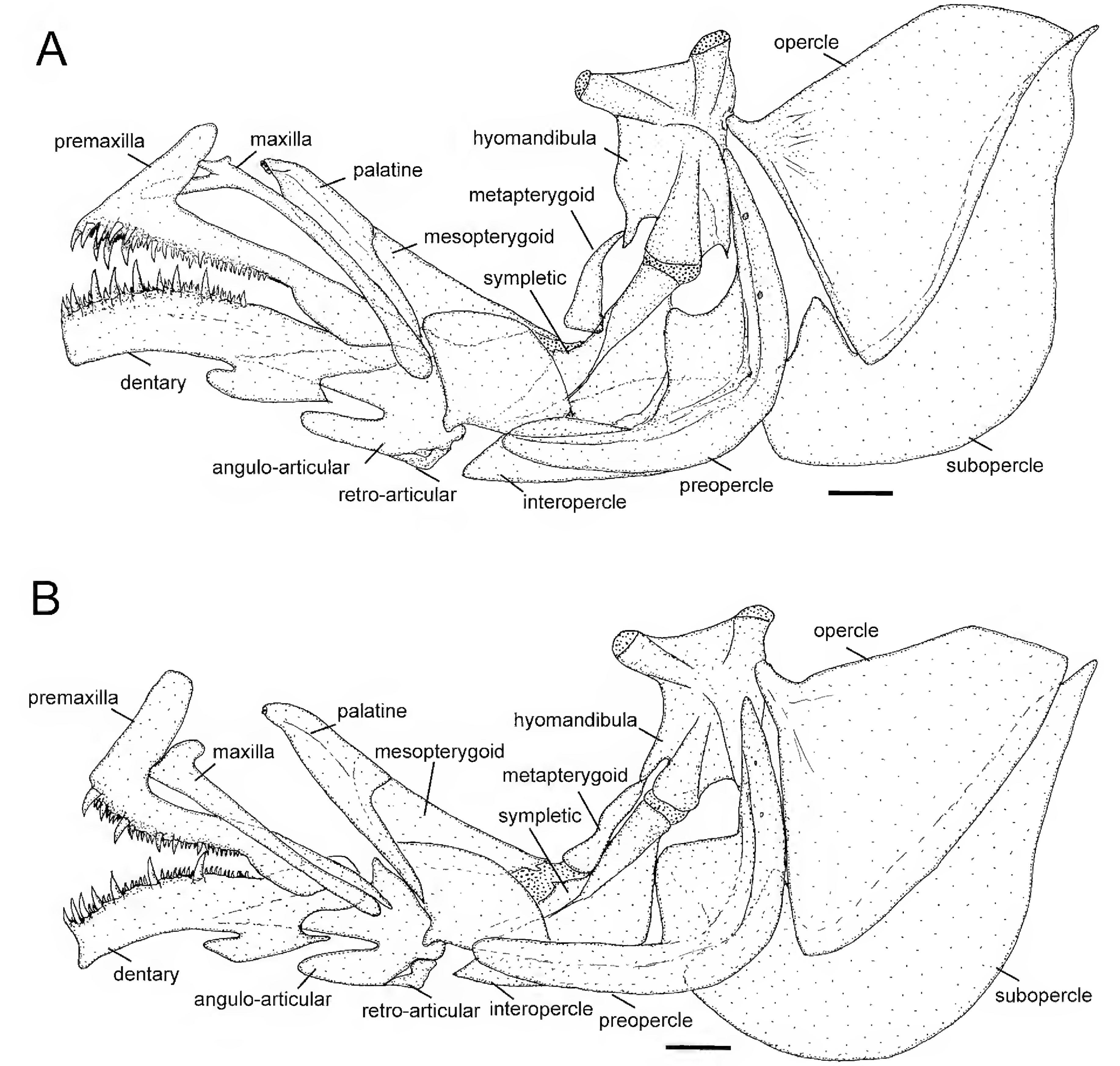

Figure 4. Jaws, jaw suspensorium and opercular apparatus, left side, lateral view, of: **A.** *Nothobranchius lucius*, paratype, male, MRAC A7-02-P-10-25, 43.0 mm SL; **B.** *N. melanospilus*, male, UFRJ 6591, 43.5 mm SL. Larger stippling indicates cartilage. Scale bar = 1 mm.

on the flank, being rare or absent on the side of the head, and are restricted to the basal portion of the unpaired fins, while being absent on the pectoral fin (Fig. 2C). The occurrence of this female colour pattern in live exemplars of *N. insularis* is confirmed in a photograph of a live female, published in an aquarium journal paper that is a report of a collecting trip in the Mafia Island (Nagy 2009: 154).

Wildekamp et al. (2009) first diagnosed the *N. melanospilus* group, comprising *N. lucius*, *N. makondorum* and *N. melanospilus*, on the basis of the presence of dark dots on the flank of females. However, examination of the material listed by Wildekamp et al. (2009) as belonging to *N. makondorum* revealed that only female specimens from the type locality area (i.e., Ruvuma River basin, southern Tanzania) have grey dots on the flank, whereas specimens from all other areas to south do not show dark pigmentation. Although this group is corroborated by molecular data (Dorn et al. 2014), no unique morphological character was found to be useful to unambiguously diagnose the *N. melanospilus* group as delimited by Wildekamp et al. (2009). On the other hand, a more inclusive clade also comprising *N. elongatus* Wildekamp, 1982, *N. hengstleri* Valdesalici, 2007, *N. insularis*, *N. interruptus* Wildekamp & Berkenkamp, 1979, *N. jubbi* Wildekamp & Berkenkamp, 1979, and *N. krammeri* Valdesalici, 2008, in adittion to *N. lucius*, *N. makondorum* and *N. melanospilus*, is here diagnosed by the presence of two neuromasts in the anterior section of the anterior supraorbital series (Fig. 5). In other nothobranchines, the anterior section contains a single neuromast. The *N. melanospilus* group as herein delimited is also supported by molecular data (Wildekamp et al. 2009, Dorn et al. 2014). Therefore, I

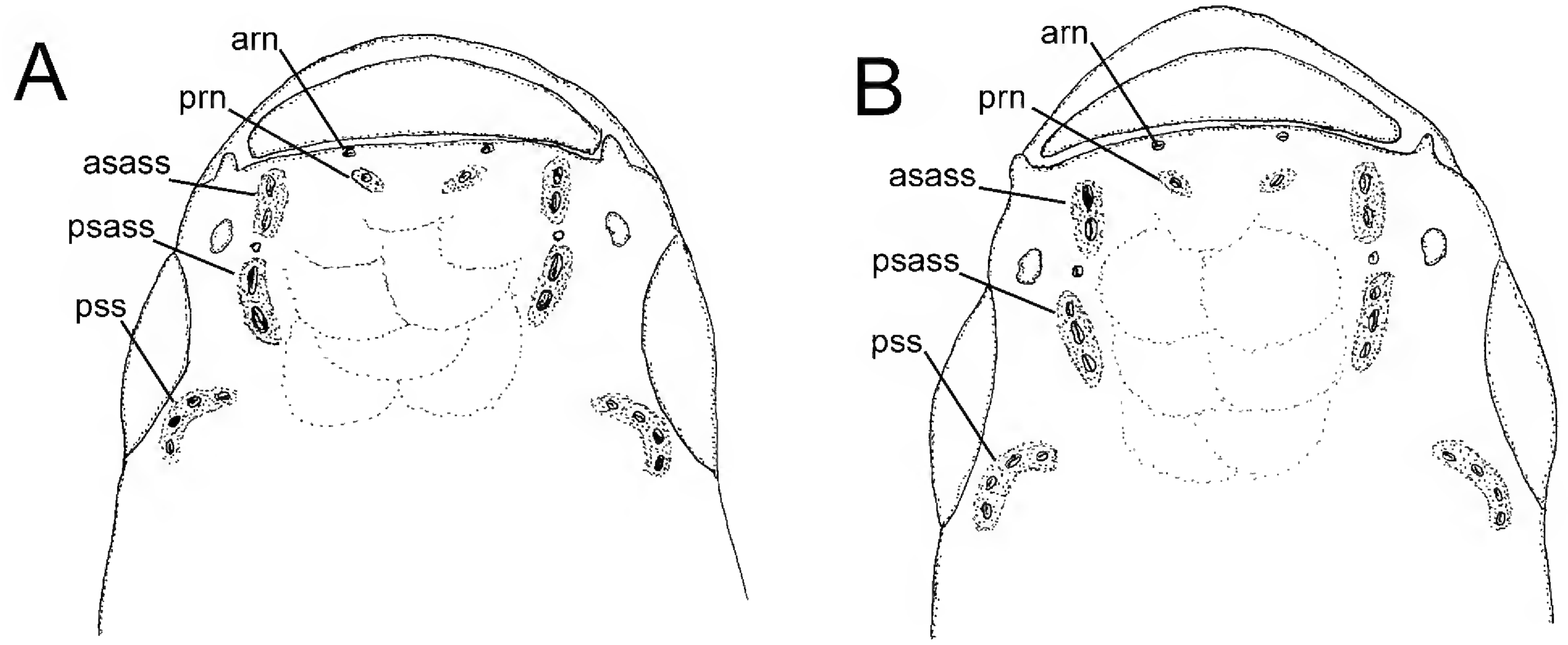

Figure 5. Diagrammatic representation of the latero-sensory system on the dorsal surface of the head in: **A.** *Nothobranchius lucius*, MRAC A7-02-P-28-32, male, 43.6 mm SL; **B.** *Nothobranchius insularis* sp. n., MRAC A702-P-38-44, paratype, male, 48.3 mm SL. **arn** – anterior rostral neuromast; **asass** – anterior section of the anterior supraorbital series; **prn** – posterior rostral neuromast; **psass** – posterior section of the anterior supraorbital series; **pss** – posterior supraorbital series.

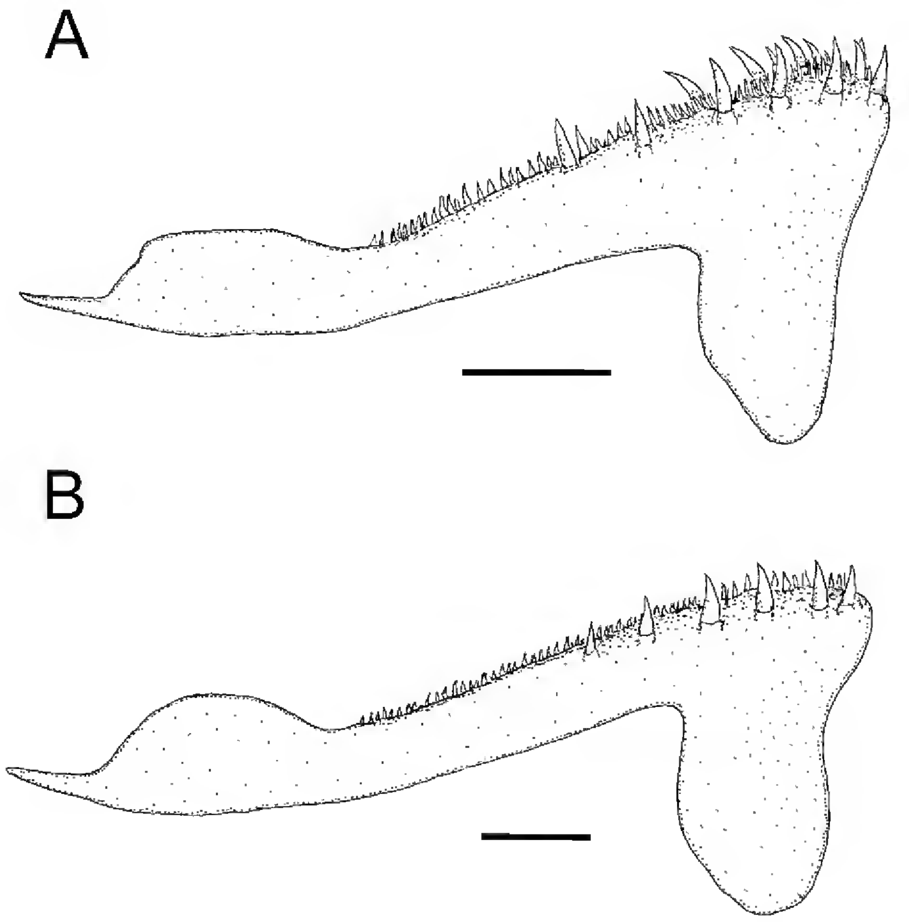

Figure 6. Left isolated premaxilla, dorsal view, ascending process inclined backwards, of: **A.** *Nothobranchius lucius*, paratype, male, MRAC A7-02-P-10-25, 43.0 mm SL. **B.** *Nothobranchius insularis* sp. n., paratype, male, MRAC A702-P-38-44, 43.7 mm SL. Scale bar = 1 mm.

propose to include all the eight species listed above in the *N. melanospilus* group.

Monophyly of the group comprising *N. lucius* and *N. insularis* is supported by derived characters states used to distinguish them from other congeners, including the presence of dark dots on the whole flank in females and the relatively long jaws, as discussed above. The present study also indicates that two character states of the jaw suspensorium are uniquely found in *N. lucius* and *N. insularis*: the metapterygoid is curved and its middle and dorsal portions are separated from the sympletic by a broad interspace (vs. nearly straight and in close proximity or in contact with sympletic) and the posterior process of the quadrate is short, its length shorter than the ventral length of the quadrate without process (vs. approximately equal or greater) (Fig. 4). Among species of the *N. melanospilus* group, *N. lucius* is unique in having an inner row of teeth directed inside the mouth on the median portion of premaxilla that are longer than the teeth of the external row (Figs 4 and 6).

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PENSOFT. museum für naturkunde

An illustrated catalogue of Rudolf Sturany's type specimens in the Naturhistorisches Museum Wien, Austria (NHMW): Red Sea gastropods

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Abstract

The Natural History Museum in Vienna hosts the samples of the late 19th century Austro-Hungarian "Pola" expeditions to the Eastern Mediterranean and the Red Sea. Rudolf Sturany studied these samples and described several new species. The type material of 35 species and forms of gastropods collected in the Red Sea is listed and illustrated. For each species, the available type material is listed, the original description and a translation into English is provided, and the current taxonomic status of the species is commented upon whenever possible. All species are illustrated in colour and with SEM imaging, with the exception of *Stylifer thielei*, whose only specimen was broken by Johannes Thiele in Berlin to study the soft parts. Finally, a table of the Pola deep and coastal stations where molluscs were collected is provided, with modern names.

Introduction

Rudolf Sturany was a malacologist who worked at the Natural History Museum (Naturhistorisches Museum Wien, NHMW) in Vienna between 1889 and 1922. He studied the samples collected by the Austro-Hungarian deep-sea expeditions to the Eastern Mediterranean Sea and the Red Sea aboard the vessel "Pola", the first to explore the deep habitats of the Red Sea (Janssen and Taviani 2015). For a detailed account of the Austro-Hungarian deep-sea expeditions see Schefbeck (1996) and, for the material collected by the "Pola" expeditions, see Stagl et al. (1996).

Sturany described several molluscan species (Sturany 1896, 1899, 1900a,b, 1903). This paper focuses on the 35 gastropod taxa described in two different works (Sturany 1900a,b and 1903). In 1900, Sturany described a first batch of deep water species (*Solariella illustris*, *Fusus bifrons*, *Nassa thaumasia*, *Nassa steindachneri*, *Nassa xesta*, *Nassa munda*, *Nassa lathraia*, *Nassa stiphra*, *Nassa sporadica*, *Columbella erythraeensis*, *Columbella nomanensis*, *Pleurotoma nannodes*, *Pleurotoma potti*, *Pleurotoma inchoata* and *Pleurotoma siebenrocki*). This paper was published in two issues of the journal *Anzeiger der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe*, and it did not have figures. The main work on Red Sea gastropods was published later in the *Denkschriften der kaiserlichen Akademie der Wissenschaften*, in 1903. It listed all the species found and illustrated all the new species, whether described in 1900 or 1903. Tables with locality data were provided. It is important to highlight that the 1903 work included a repeat of the descriptions of the species described in 1900. A line just before the description refers to the original description in the *Anzeiger*. Moreover, in some later works, this paper is cited as being published in 1904, probably because the volume of the *Denkschriften* had this date on the frontispiece. However, the first page of this work specifies that it was *vorgelegt in der Sitzung am 2 April 1903* (presented in the meeting of 2 April, 1903). In the library of the Natural History Museum of Vienna, preprints (*Besonders abgedruckt*...) with double pagination published in 1903 (date on their frontispiece) are present, and this should be considered the correct year of publication for the new names therein introduced.

Knowledge about name-bearing types is fundamental to sound taxonomic research. Indeed, the International Code of Zoological Nomenclature (ICZN 1999: 72F.4) recommends the publication of lists of types housed in institutions. Our work follows this recommendation; moreover, we tried to provide to the taxonomic community detailed illustrations of type specimens and their diagnostic characters.

A glimpse on Rudolf Sturany's life

Rudolf Sturany (13 April 1867 – 28 February 1935) was a Viennese zoologist and one of the most important Austrian malacologists. He studied at the Universities of Vienna and Leipzig and obtained his PhD in 1891 in Vienna (Adensamer 1935a, b, c; Stagl 2012). He began to work as a volunteer at the Natural History Museum of Vienna in September 1889. One year later he started his official career at the NHMW as assistant, became adjunct curator in 1901 and 6 years later curator, being responsible for the collections of molluscs, bryozoans, brachiopods and tunicates. Excursions for scientific research took him to Bosnia, Herzegovina, Dalmatia, Montenegro, Albania and Crete, where he found and described several species new to science, especially land and freshwater snails. His good contacts with zoologists and malacologists of his time enabled Sturany to work on important scientific material (the "Taurus" expedition to the Sea of Marmara, Obrutschew's expedition to the region of Pamir, the "Pola" expeditions). He obtained important collections (Obrutschew, Tschapek, Gerstenbrandt, parts of Möllendorff's, Monterosato's and Velitschowsky's collections), which led to an enormous growth and enrichment of the Museum mollusc collection. During World War I, an eye disease occurred and steadily deteriorated, forcing Sturany to retire in 1922, after 33 years dedicated to his malacological work at the NHMW.

Malacological collections at the Naturhistorisches Museum Wien

Besides the important type-material of Sturany, there are other valuable types of historical importance at the mollusc collection of the NHMW. Ignaz von Born established its oldest part with his work on the imperial collection, which was published in the 1778 "Index rerum naturalium Musei Cæsarei Vindobonensis – Pars I. Testacea" and in the superb 1780 volume "Testacea Musei Caesarei Vindobonensis, quae jusso Mariae Theresiae Augustae" (Eschner 2005). Later, parts of the Monterosato Collection were acquired in 1889 and the Draparnaud Collection was purchased probably in 1815 (Vinarski and Eschner 2016). Georg von Frauenfeld, curator of the mollusc collection at the beginning of the 19th century, collected and described many new species (Eschner 2008).

Materials and methods

This work fulfils the efforts carried out by museum curatorial staff and external researchers to segregate, label and properly store Sturany's type material. Type series of species described by Sturany were retrieved from the main collection. Only for one species, *Stylifer thielei*, no type material is available, because the only collected specimen was broken by J. Thiele of the Museum of Berlin to study the soft parts (Sturany 1903). We identified the syntypes best matching the original description but refrained from any lectotype designation following recommendation 74G of the International Code of Zoological Nomenclature.

For each species, we provide references to the original description and figure, and indicate the original localities, a list of the type and additional (i.e., collected during the "Pola" expedition but not explicitly mentioned in Sturany's original descriptions) material, the original description and its translation into English. All inventory numbers provided refer to the Mollusca collection of NHMW. Earlier attempts to update the taxonomy of Sturany's species have been undertaken by Dekker and Orlin (2000) and Janssen in Janssen and Taviani (2015). Specialist taxonomists helped us with notes on the validity of the species and other comments (D. Geiger for Fissurellidae, D. Herbert for Chilodontidae and Trochidae, A. Warén for Eulimidae, A. Kohn for Conidae s.s., A. Bonfitto for Turridae and allied families). The systematic arrangement follows Bouchet and Rocroi (2005) for most families and Bouchet et al. (2011) for Conoidea.

Photos were mostly shot with a Nikon SMZ25 microscope; large shells were photographed with a Canon 350D camera, a 50 mm lens and extension tubes. SEM images were taken with a JEOL JSM-6610LV, using low vacuum without coating. Specimen measurements have been added if substantially dissimilar from those reported in the original description or missing.

The material studied by Sturany comes from off-shore "stations" (Table 1) and coastal "localities" (Table 2); we stuck to this terminology. In the two tables, we report the collecting sites with their original orthography in German and a modern name among square brackets. The coordinates are those provided by Sturany. Type localities were established based on the information provided by Sturany. In case the type series came from several stations or

Table 1. Off-shore stations of the "Pola" expedition (from Sturany 1903).

Station number	Locality	Coordinates	Depth [m]
1	"unweit Suez" [near Suez, Egypt]	29° 37'N, 32° 29'E	–48
9	"südlich von Yenbo" [south of Yanbu' al Bahr, Saudi Arabia]	23° 21'N, 37° 37'E	–791
20	"nächst den St. Johns-Inseln" [cose to St. John's Island, Egypt]	23° 20'N, 36° 20'E	–780
44	"vor Jidda" [off Jeddah, Saudi Arabia]	21° 36'N, 38° 33'E	–902
47	"bei Yenbo" [Yanbu' al Bahr, Saudi Arabia]	23° 41'N, 38° 9'E	–610
48	"vor Yenbo" [off Yanbu' al Bahr, Saudi Arabia]	24° 5'N, 37° 45'E	–700
51	"bei Sherm Sheikh" [near Abu Ghusun, Egypt]	24° 15'N, 35° 37'E	–562
54	[Red Sea]	24° 48'N, 35° 25'E	–535
76	"südlich der Insel Senafir" [south of Sanafir Island]	27° 43'N, 34° 47'E	–900
79	"nächst der Noman-Insel" [Noman Island, Saudi Arabia]	26° 53'N, 35° 17'E	–740
81	"unweit von Ras Abu Massahrib, Noman Insel" [close to Ras Abu Massahrib, Noman Island, Saudi Arabia]	26° 34'N, 35° 33'E	–825
87	"bei Ras Mallap im Golfe von Suez" [Ra's Mal'ab in the Gulf of Suez, Egypt]	29° 7.6'N, 32° 56'E	–50
88	"bei Tor im Golfe von Suez" [El Tor, Egypte]	28° 9.3'N, 33° 35.5'E	–38
93	"bei Nawibi im Golfe von Akabah" [Nuweiba, Gulf of Aqaba, Egypt]	29° 7.5'N, 34° 49.5'E	–920
94	"bei Nawibi im Golfe von Akabah" [Nuweiba, Gulf of Aqaba, Egypt]	28° 58.6'N, 34° 43.7'E	–314
96	"nördlicher Theil des Golfes von Akabah" [northern part of the Gulf of Aqaba]	29° 13.5'N, 34° 47.8'E	–350
107	"südlich von Jidda" [south of Jeddah, Saudi Arabia]	21° 19'N, 38° 51'E	–748
109	"westlich von Jidda" [Jeddah, Saudi Arabia]	21° 19'N, 37° 39'E	–890
114	"zwischen Suakim und Lith" [between Suakin, Sudan, and Al Lith, Saudi Arabia]	19° 38'N, 37° 55'E	–535
117	"südlich von Raveya" [south of Raveya, Sudan]	20° 16.9'N, 37° 33.5'E	–638
121	"westlich von Kunfidah" [west of Al Qunfudhah, Saudi Arabia]	18° 51.9'N, 39° 5.4'E	–690
124	"bei Lith" [Al Lith, Saudi Arabia]	19° 57.3'N, 39° 29.2'E	–430
127	"südöstlich von Akik Seghir" [South-east of Akik Seghir Eritrea]	17° 42.2'N, 39° 42.3'E	–341
128	"bei Akik Seghir" [Akik Seghir, Eritrea]	18° 7.7'N, 39° 11.2'E	–457
130	"westlich von Kunfidah" [west of Al Qunfudhah, Saudi Arabia]	19° 17'N, 39° 37'E	–439
135	"südöstlich von Akik Seghir" [south-east of Akik Seghir, Eritrea]	17° 26.1'N, 39° 19'E	–332
138	"östlich von Akik Seghir" [east of Akik Seghir, Eritrea]	18° 3'N, 40° 14.7'E	–1308
143	"nächst der Insel Harmil" [near Harmil Island, Dahlak Archipelago, Eritrea]	17° 7'N, 39° 55'E	–212
145	"östlich von J. Dahalak" [east of Dahlak Island, Eritrea]	16° 2.6'N, 41° 13.5'E	–800
156	"nördlich von Jidda" [north of Jeddah, Saudi Arabia]	22° 51'N, 38° 2'E	–712
165	"nächst der Insel Senafir" [near Sanafir Island]	27° 37.4'N, 35° 3.6'E	–780
170	"bei der Insel Noman" [Noman Island, Saudi Arabia]	27° 0.2'N, 35° 17.6'E	–690
175	"bei Koseir" [El Quseir, Egypt]	26° 4'N, 34° 30'E	–690
176	"bei Koseir" [El Quseir, Egypt]	25° 57'N, 34° 36.1'E	–612
177	"bei Koseir" [El Quseir, Egypt]	26° 14'N, 34° 22.4'E	–676
178	"bei Koseir" [El Quseir, Egypt]	26° 19'N, 34° 24.5'E	–720
179	"bei Koseir" [El Quseir, Egypt]	26° 34.5'N, 34° 14.7'E	–490
184	"nächst den Brothers-Inseln" [near Brother Islands, northern Red Sea]	26° 34'N, 35° 25.5'E	–876

localities, we stated as type locality the smaller geographical area that encompasses all collecting sites.

A taxon list in alphabetical order with the page number of this paper is provided in Table 3.

Systematic list of taxa

Family Fissurellidae Fleming, 1822

Emarginula harmilensis Sturany, 1903

Figure 1
Sturany, 1903: 235, plate V, figures 12a–b.

Type locality. Station 143, "nächst der Insel Harmil" [near Harmil Island, Dahlak Archipelago, Eritrea] 17°7'N, 39°55'E, 212 m.

Type material. Holotype: NHMW 84290, length 6.8 mm.

Original description. *Von der Station 143 (212 m); 1 Exemplar.*

Die Schale ist 7 ½ mm lang, 4 mm hoch, 5 ¼ mm breit. Der stark nach rückwärts und etwas nach unten gekehrte Apex fällt fast mit dem Hinterende der Schale zusammen: die absolute Distanz des Wirbelendes zum Schalenende beträgt 2 mm, die relative (bei Projection derselben zur Basis) nur ½ mm. Die schmutzigweiße bis gelbe Grundfarbe des Gehäuses erhält durch radiär angeordnete Fleckchen, Linien und Punkte von brauner bis grünlicher Farbe ein gesprenkeltes Aussehen. Milchweiß gefärbt sind die zahlreichen Hauptradiärrippen, zwischen denen zartere Rippen liegen, die mitunter dunkler erscheinen (zwischen je 2 Hauptrippen liegt eine Nebenrippe). Die

Table 2. Coastal localities of the "Pola" expedition (from Sturany (1903)).

Locality number	Locality	Coordinates/Region
1	"Ismalia am Timsah-See" [Timsah Lake, Ismailia, Egypt]	Suez Canal
2	"Bittersee" [Great Bitter Lake, Egypt]	Suez Canal
3	"Suez" [Suez, Egypt]	Gulf of Suez
4	"Zafarana" [Zaafarana, Egypt]	Gulf of Suez
5	"Ras Mallap" [Ra's Mal'ab, Egypt]	Gulf of Suez
6	"Ras Abu Zenima (Zenihme)" [Abu Zenima, Egypt]	Gulf of Suez
7	"Ras Gharib" [Ras Ghareb, Egypt]	Gulf of Suez
8	"Tor" [El Tor, Egypt]	Gulf of Suez
9	"Akabah" [Aqaba, Jordan]	Gulf of Aqaba
10	"Nawibi" [Nuweiba, Egypt]	Gulf of Aqaba
11	"Bir al Mashiya" [Bir al Mashiya, Saudi Arabia]	Gulf of Aqaba
12	"Dahab (Mersa Dahab)" [Dahab, Egypt]	Gulf of Aqaba
13	"Senafir-Insel" [Sanafir Island, Strait of Tiran]	Northern Red Sea, 28° – 26°N
14	"Sherm Sheik" [Sharm El-Sheikh, Egypt]	Northern Red Sea, 28° – 26°N
15	"Ras Muhammed" [Ras Mohammed, Egypt]	Northern Red Sea, 28° – 26°N
16	"Shadwan-Insel" [Jazirat Shakir, Egypt]	Northern Red Sea, 28° – 26°N
17	"Noman-Insel (Ras Abu Massahrib)" [Ras Abu Massahrib, Noman Island, Saudi Arabia]	Northern Red Sea, 28° – 26°N
18	"Ras Abu Somer" [Ra's Abu Sawmah, Egypt]	Northern Red Sea, 28° – 26°N
19	"Brothers-Insel" [Brother Islands, Egypt]	Northern Red Sea, 28° – 26°N
20	"Sherm Habban (Abban)" [Sharm Habban, Saudi Arabia]	Northern Red Sea, 28° – 26°N
21	Koseir [El Quseir, Egypt]	Northern Red Sea, 28° – 26°N
22	"Mersa Dhiba" [Mersa Dhiba, Egypt]	26° – 24°N
23	"Dädalus Riff" [Daedalus Reef, Red Sea]	26° – 24°N
24	"Hassani-Insel" [Al Hasani, Saudi Arabia]	26° – 24°N
25	"Sherm Sheikh (Mersa Sheikh)" [near Abu Ghusun, Egypt]	26° – 24°N
26	"Yenbo (Jembo)" [Yanbu' al Bahr, Saudi Arabia]	26° – 24°N
27	"Port Berenice" [Berenice Troglodytica, Egypt]	24° – 22°N
28	"St. Johns-Insel" [St. John's Island, Egypt]	24° – 22°N
29	"Sherm Rabegh" [Rabigh, Saudi Arabia]	24° – 22°N
30	"Mersa Halaib" [Halayeb, Egypt]	24° – 22°N
31	"Jidda (Djeddah)" [Jeddah, Saudi Arabia]	22° – 20°N
32	"Raveiya (Mahommed Ghul)" [Gul Mohammad, Saudi Arabia]	22° – 20°N
33	"Lith" [Al Lith, Saudi Arabia]	22° – 20°N
34	"Sawakin (Suakim)" [Suakin, Sudan]	20° – 18°N
35	"Kunfidah (Kunfuda)" [Al Qunfudhah, Saudi Arabia]	20° – 18°N
36	"Akik Seghir" [Eritrea]	20° – 18°N
37	"Ras Turfa" [near Jazan, Saudi Arabia]	18° – 16°N
38	"Sarso-Insel" [Sarso Island, Saudi Arabia]	18° – 16°N
39	"Harmil-Insel" [Harmil Island, Dahlak Archipelago, Eritrea]	18° – 16°N
40	"Kadhu-Insel" [Kad-Hu, Dahlak Archipelago, Eritrea]	18° – 16°N
41	"Massawa (Massaua)" [Massawa, Eritrea]	16° – 11°N
42	"Dahalak-Insel, resp. Nakhra Khor Island" [Nakhra Khor, Dahlak Archipelago, Eritrea]	16° – 11°N
43	"Kamaran-Insel" [Kamaran Island, Yemen]	16° – 11°N
44	"Zebayir-Insel (Zebejir)" [Jabal Zubayr, Yemen]	16° – 11°N
45	"Ghuleifaka (= Landzunge Ras Mujamela)" [Ras Mujamila, Yemen]	16° – 11°N
46	"Hanfela-Insel" [island in the Bay of Anfile, Eritrea]	16° – 11°N
47	"Jebel Zukur-Insel (Djebel Zukur)" [Jazirat Jabal Zuqar, Yemen]	16° – 11°N
48	"Abayil-Insel" [Sel Abayil Deset, Eritrea]	16° – 11°N
49	"Asab" [Assab, Eritrea]	From 14°N until the end of the Bab al-Mandab Strait
50	"Perim-Insel" [Perim Island, Yemen]	From 14°N until the end of the Bab al-Mandab Strait

erwähnten Rippen werden von vielen zarten Querlinien gekreuzt, an den Kreuzungsstellen der Hauptrippen sind perlenförmige Verdickungen ausgebildet. Der Einschnitt der Schale ist etwas länger als 3 mm: die Ränder derselben sind gerade und innen mit einem verdickten Belage versehen, der sich in Form einer immer stärker werdenden weißen Schwiele bis in die Wirbelgegend fortsetzt. Die Rinne zwischen der Wirbelhöhe und dem blinden Ende des Einschnittes ist stark vertieft, weiß gefärbt und quer gestreift.

Die neue Art ist mit E. bellula *A. Ad. von den Philippinen verwandt.*

Table 3. List of treated taxa in alphabetical order, with original name, current family placement, and figure in this paper.

Taxon	Family	Page, Figure
batheon, Conus planiliratus var.	Conidae	Page 82, Figure 27
beblammena, ?Pleurotoma	Raphitomidae	Page 85, Figure 28
bifrons, Fusus	Fasciolariidae	Page 60, Figure 11
camaranensis, Capulus	Hipponicidae	Page 53, Figure 4
dichroma, Clathurella	Raphitomidae	Page 86, Figure 29
epicharis, Mangelia (Glyphostoma)	Raphitomidae	Page 88, Figure 30
erythraeensis, Columbella (Mitrella)	Columbellidae	Page 57, Figure 9
erythraeensis, Euchelus	Chilodontidae	Page 49, Figure 2
gonatophora, Mitra (?Thala)	Mitridae	Page 73, Figure 19
halaibensis, Elusa	Pyramidellidae	Page 90, Figure 31
harmilensis, Emarginula	Fissurellidae	Page 47, Figure 1
illustris, Solariella	Trochidae	Page 51, Figure 3
inchoata, Pleurotoma (?Drillia)	Drilliidae	Page 77, Figure 22
lathraia, Nassa	Nassariidae	Page 62, Figure 12
lithensis, Atys (Roxania)	Haminoeidae	Page 91, Figure 33
minor, Mitra tenuis f.	Mitridae	Page 73, Figure 20
muelleriae, Eulima	Eulimidae	Page 53, Figure 5
munda, Nassa	Nassariidae	Page 64, Figure 13
nana, Nassa thaumasia var.	Nassariidae	Page 69, Figure 17
nannodes, Pleurotoma (Surcula)	Horaiclavidae	Page 79, Figure 24
nomanensis, Columbella (Mitrella)	Columbellidae	Page 59, Figure 10
orthophyes, Eulima	Eulimidae	Page 55, Figure 6
paucicostata, Fusus bifrons f.	Fasciolariidae	Page 62, Figure 11
pertabulata, Mangelia	Clathurellidae	Page 79, Figure 25
potti, Pleurotoma (Drillia)	Drilliidae	Page 75, Figure 21
senafirensis, Triforis (?Viriola)	Triphoridae	Page 57, Figure 8
siebenrocki, Pleurotoma (Clavus)	Drilliidae	Page 78, Figure 23
sporadica, Nassa	Nassariidae	Page 65, Figure 14
steindachneri, Nassa	Nassariidae	Page 66, Figure 15
stiphra, Nassa	Nassariidae	Page 68, Figure 16
thaumasia, Nassa	Nassariidae	Page 68, Figure 17
thielei, Stylifer	Eulimidae	Page 56, Figure 7
torensis, Conus aculeiformis f.	Conidae	Page 81, Figure 26
trivittata, Syrnola	Pyramidellidae	Page 91, Figure 32
xesta, Nassa	Nassariidae	Page 69, Figure 18

Translation. From station 143 (212 m); one specimen.

The shell is 7.5 mm long, 4 mm high, 5.25 mm wide. Apex positioned strongly backward and downward almost coinciding with the end of the shell: the absolute distance from the apex to the shell margin is 2 mm, the distance between the apex projection on the base and the posterior margin is only 0.5 mm. The whitish to yellow background shell colour has a spotted appearance because of the radially arranged blotches, lines and dots of brown to greenish colour. The numerous main radial ribs are milky white, whereas the finer ribs in between are darker (between two main ribs there is one finer rib). The ribs are crossed by many delicate transverse lines, the intersections form pearl-shaped tubercles. The slit is slightly longer than 3 mm: its edges are straight showing internally a thickened coating, continuing as white callus in the spire. The groove between the apex and the slit [anal fasciole] is very deep, white and transversely ribbed.

The new species is related to *E. bellula* A. Adams from the Philippines.

Comments. [text by D. Geiger] The species is clearly a member of *Emarginula* given the overall shell outline, the height of the shell as well as the slit with parallel margins. It is not a juvenile Fissurellinae or Diodorinae, because at the size of Sturany's specimen a hole would have formed. Note that some juvenile *Diodora* have been described as distinct species, such as *Puncturella piccirida* Palazzi & Villari, 2001 from the Mediterranean. However it lacks the distinctive internal septum of *Puncturella*.

Sturany's *E. harmilensis* is characterized by a rather uncommon color pattern of tan spiral bands. Those are also found in *E. costulata* Deshayes, 1863, described from Reunion Island. Herbert (1987: figs 39–40) illustrated the by him designated lectotype, and a more typical, fully-grown specimen (figs 41–42), and discussed previous misidentifications of the species as *E. tenuicostata* Adams & Sowerby, 1863. The shared characters include overall shape, placement of the spire, length of the slit, color pattern, and number and strength of the ribs. Many species found along the coast of East Africa are also encountered in the Red Sea. Accordingly, *E. harmilensis* Sturany, 1903 is a junior synonym of *E. costulata* Deshayes, 1963.

Family Chilodontidae Wenz, 1938

Euchelus erythraeensis Sturany, 1903

Figure 2
Sturany, 1903: 266, plate V, figure 6.

Type locality. Locality 10 "Nawibi" [Nuweiba, Gulf of Aqaba, Egypt].

Additional original localities. Locality 25 (Northern Red Sea) (Table 2).

Type material. Lectotype: NHMW 37964 (station not specified, but likely locality 10, height 6.6 mm), designated by D.G. Herbert (1996), illustrated by Sturany (1903) in plate V, figure 6. Further two paralectotypes NHMW 37963 (locality 25).

Original description. *Von den Localitäten 10 und 25.*

Das abgebildete Exemplar stammt von Nawibi und weist die folgenden Dimensionen auf: Höhe der Schale 6,5 mm, Breite derselben 6 mm Höhe (Länge) der Mündung 3,6, Breite derselben 2,5 mm. Von den 6 Umgängen sind bloß die beiden ersten frei von einer Sculptur auf dem 3. Umgange sind bereits 3 Spiralrippen, auf dem 5. deren 4 bis 5 zu sehen. Diese Spiralrippen, nicht gleich in der Stärke, sondern meist etwas variabel, tragen zahlreiche Knoten von weißer oder gelbbrauner Farbe. Die Grundfarbe des Gehäuses ist weiß, Flecken von gelbbrauner oder olivengrüner Farbe finden sich ohne Re-

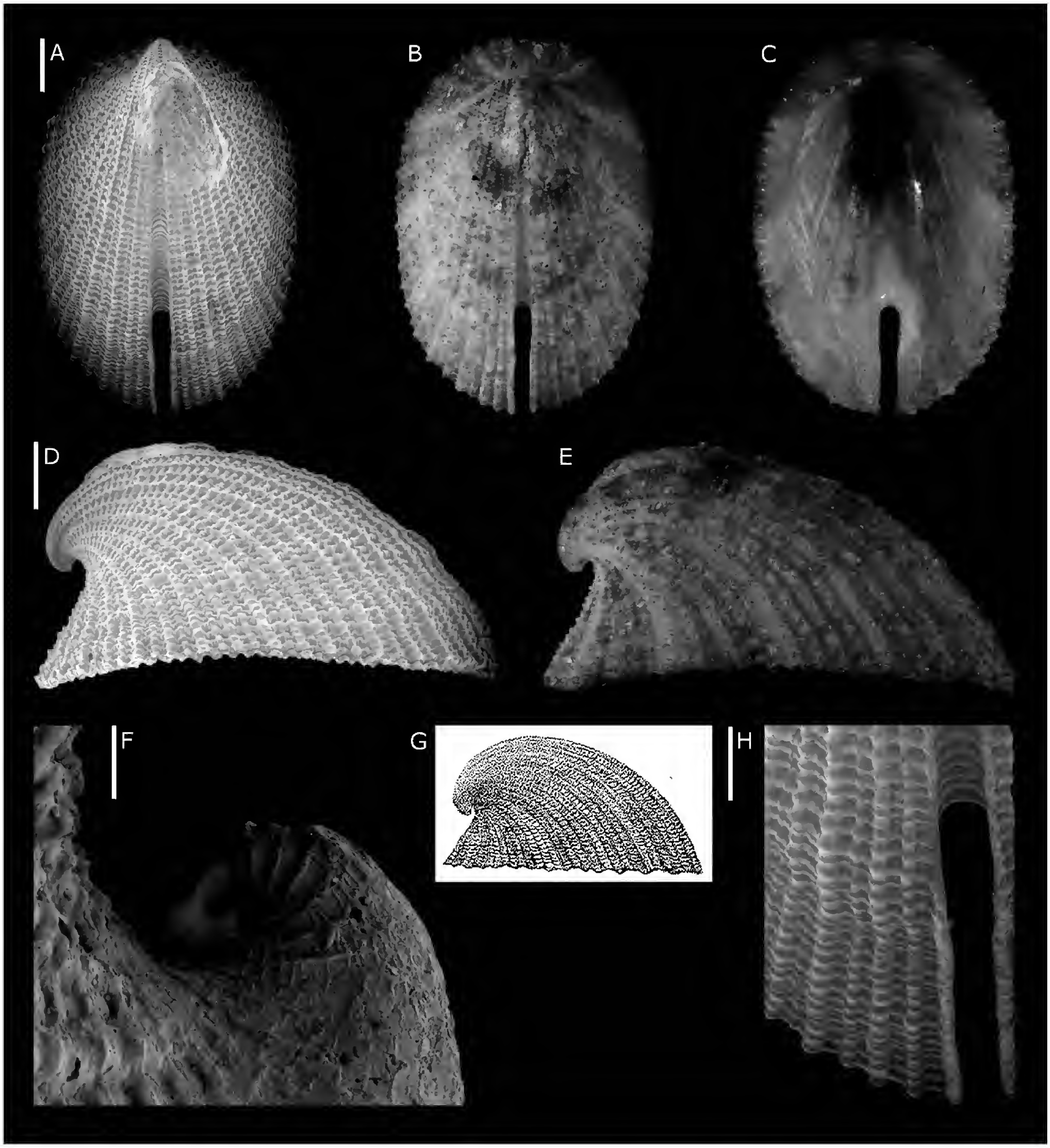


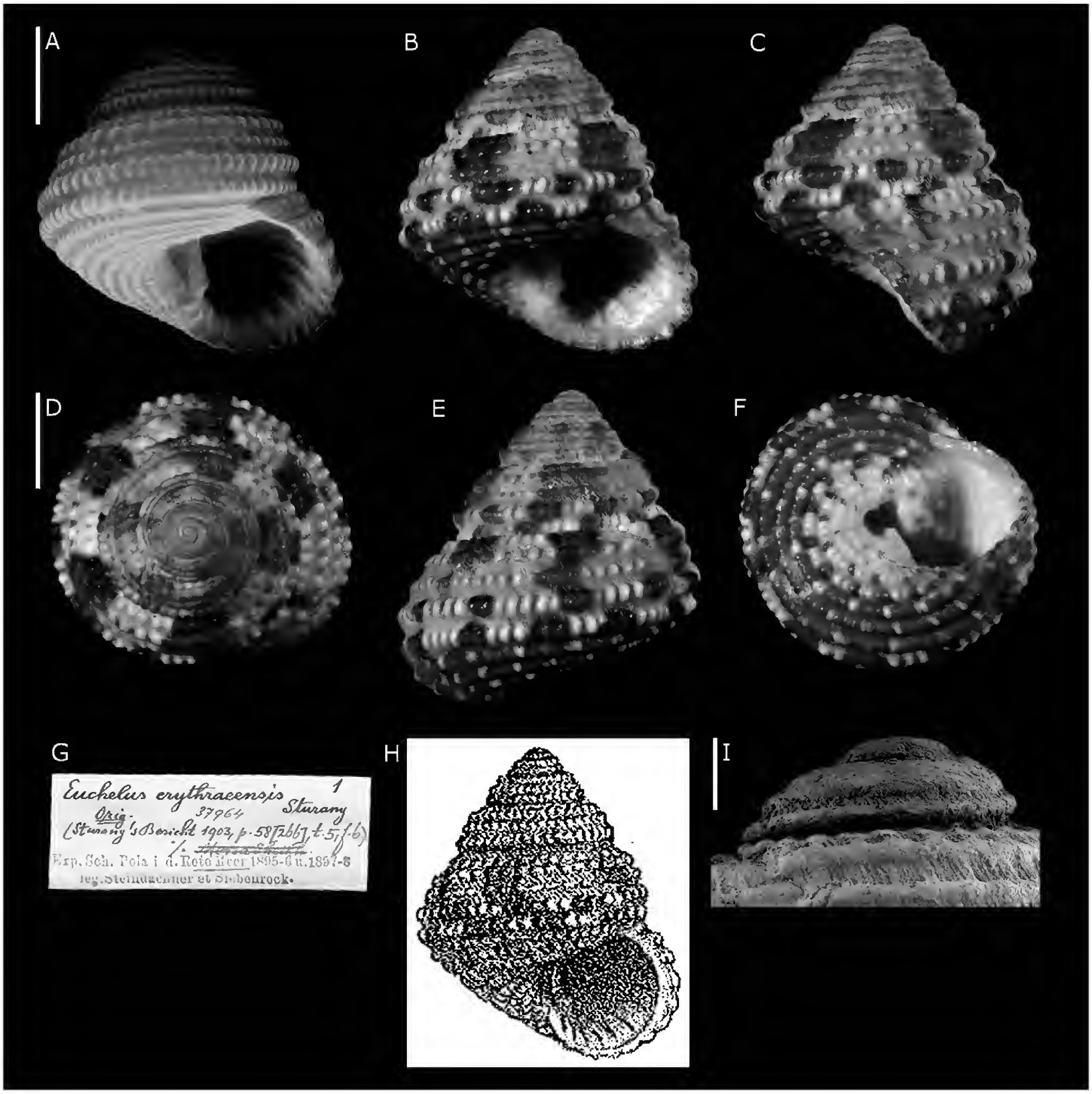
Figure 1. *Emarginula harmilensis* Sturany, 1903, Station 143 (Harmil Island, Dahlak Archipelago, Eritrea, Red Sea). **A–F, H**. Holotype, NHMW 84290: top (**A–B**), aperture (**C**), left side (**D–E**), protoconch (**F**), microsculpture (**H**). **G**. Original figure by Sturany (1903). Scale bars: **A–E**: 1 mm, **F**: 0.1 mm, **H**: 0.5 mm.

gelmäßigkeit und häufig in Zickzacklinien quer über die letzten Umgänge vertheilt. Die Basis der Schale trägt zwischen der Peripherie und dem perspectivischen Nabel 7 concentrische Knotenreihen von gemischter Farbe.

Mit E. foveolatus *A. Ad. ist diese Form nahe verwandt.*

Translation. From localities 10 and 25.

The figured specimen is from Nawibi and has the following dimensions: height of the shell 6.5 mm, width 6 mm, height (length) of the mouth 3.6, width 2.5 mm. Of the six whorls, the first two lack a sculpture. On the third whorl, three spiral ribs are visible; on the fifth whorl, four to five ribs. These spiral ribs are not of equal size and carry numerous white or yellow-brown tubercles. The background colour of the shell is white; patches of yellow-brown or olive green colour can be found without regularity and often distributed in zigzag lines across the last whorls. The base of the shell shows seven concentric



Euchelus erythraeensis 1
Orig. 37964 Sturany
(Sturany's Bericht 1903, p. 58 [266], t. 5, f. 6)
/.
Exp. Sch. Pola i. d. Rote Meer 1895-6 u. 1897-8
leg. Steindachner et Siebenrock.

Figure 2. *Euchelus erythraeensis* Sturany, 1903, Locality 10 (Nawibi, Gulf of Aqaba, Red Sea). **A–F, I**. Lectotype, NHMW 37964: front (**A–B**), right side (**C**), top (**D**), back (**E**), bottom (**F**), protoconch (**I**). **G**. Original lectotype label. **H**. Original figure by Sturany (1903). Scale bars: **A–F**: 2 mm, **I**: 0.2 mm.

series of tubercles of mixed colour between the periphery and the umbilicus.

Form closely related to *E. foveolatus* A. Adams.

Comments. This name is considered a junior synonym of *Clanculus tonnerrei* (G. Nevill & H. Nevill, 1874) (Herbert 1996).

Family Trochidae Rafinesque, 1815

Solariella illustris Sturany, 1900

Figure 3
Sturany, 1900b: 211–212; redescribed and illustrated in Sturany (1903), page 234, plate I, figures 7a–c.

Original localities. Station 48 (700 m) and Station 143 (212 m) (Central and Southern Red Sea; Table 1).

Type material. Two syntypes: NHMW 84287 (station 48), the specimen figured by Sturany (1903), plate I, figure 7a–c has been segregated, its diameter is 8.3 mm. Further seven syntypes NHMW 84288 (station 48).

Original description. *Gehäuse ziemlich festschalig, breit kegelig, weit und perspectivisch genabelt, oben weißlich mit unregelmäßig vertheilten, gelben Flecken und irisierend. Unten milchweiß mit glasig durchscheinenden Querstreifen (die allerdings nur bei frischen*

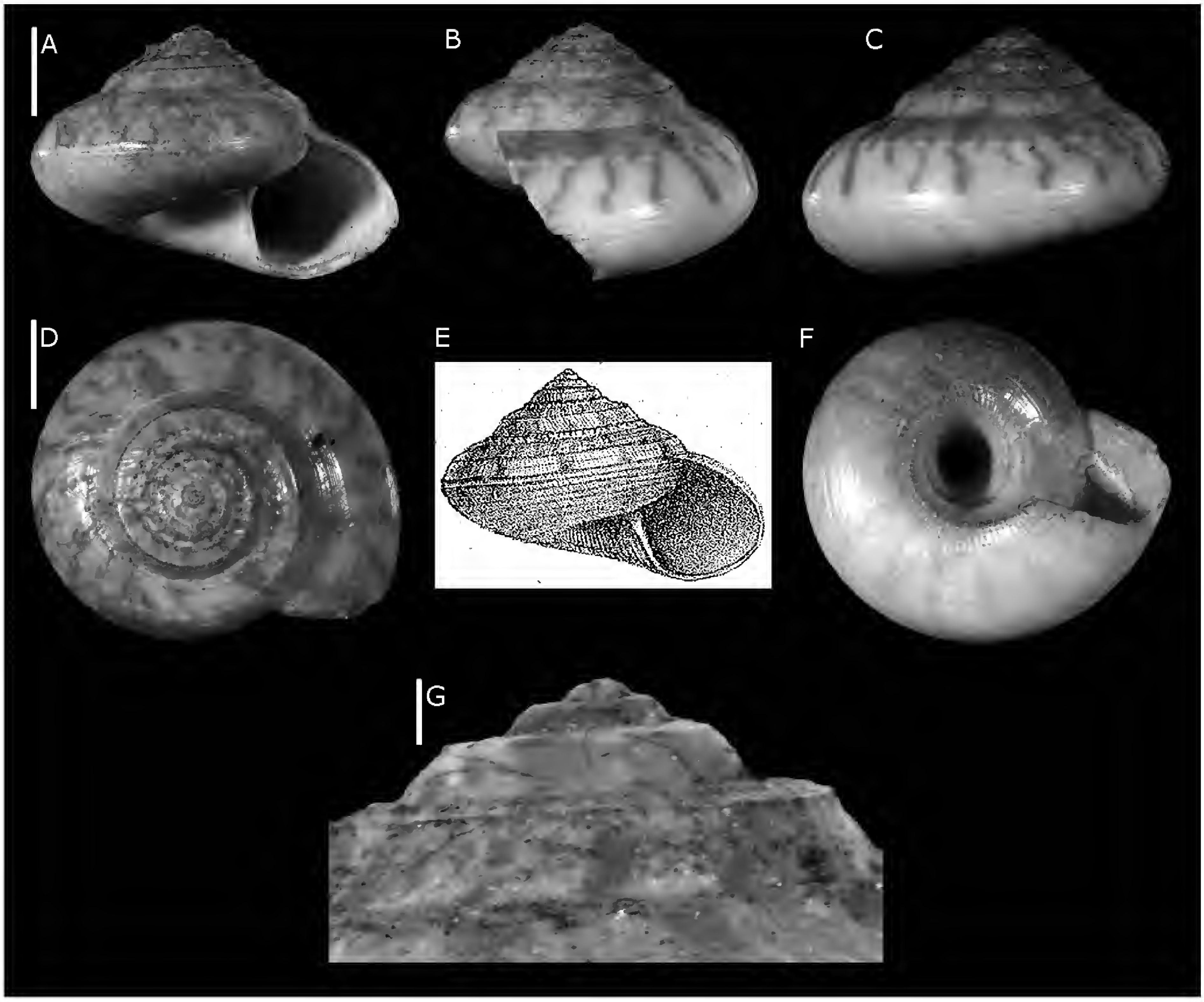


Figure 3. *Solariella illustris* Sturany, 1900, Station 48 (Yanbu' al Bahr, Saudi Arabia, Red Sea). **A–D, F–G**. Figured syntype, NHMW 84287: front (**A**), right side (**B**), back (**C**), top (**D**), bottom (**F**), apex (**G**). **E**. Original figure by Sturany (1903). Scale bars: **A–D, F**: 2 mm, **G**: 0.2 mm.

Stücken sichtbar sind und dann einen stark irisierenden Glanz besitzen), mit brauner Einfassung des Nabels. Von den mäßig gewölbten 6 – 7 Windungen ist der Apex (1 – 1 1/2 Umgänge) glatt, gelb oder mitunter rosig angehaucht; auf der folgenden Windung beginnt ein Mittelkiel, der sich bis zur Mündung verfolgen lasst, dort jedoch schon über die Mitte gerückt ist und welcher mitunter auf der vorletzten Windung von einem ganz nahe darunter entspringenden Kiel begleitet und schließlich an Stärke übertroffen wird. Auf den Schlusswindungen steht nächst der Naht eine Spiralreihe von Höckerchen, welche sich vor der Mündung wieder abschwächen, ferner ist die letzte Windung noch durch einige Spiralrippen oben und zahlreiche concentrische Spiralfurchen auf der Unterseite ausgezeichnet. Überall, und zwar am deutlichsten auf den nächst der Naht gelegenen Umgangspartien sind auch Anwachsstreifen in Form von Querriefen sichtbar. Der Nabel beträgt 1/3 der Gehäusebreite und wird von einigen Reihen dicht stehender, durch zahlreiche Quereinschnitte regelmäßig gegitterter oder geperlter Rippen umstellt, die sich tief hinein verfolgen lassen. Die oben vorgezogen Mündung ist innen perlmutterglänzend: der Deckel häutig, mit einigen concentrischen Ringen.

Großer Durchmesser der Schale 7,4 – 9,1, kleiner Durchmesser 6,1 – 8,0 mm, Höhe 4,7 – 6,4, respective 3,6 – 5,0; Längendurchmesser der Mündung 3,5 – 4,1, Breite derselben 2,9 – 3,6 mm.

Die neue Art liegt von Station 48 (700 m) in leeren Gehäusen, von Station 143 (212 m) sammt dem Thiere vor.

Translation. Fairly thick shell, broadly conical, with a wide and deep umbilicus, on top whitish with irregular yellow spots and iridescence. The bottom is milky white with glassy translucent horizontal stripes (these are only visible in fresh specimens and have a strong iridescent lustre), the umbilicus rim is brown. Of the moderately convex six to seven whorls, the apex (1 – 1.5 whorls) is smooth, yellow or pink coloured sometimes; on the next whorl, a keel in the middle of the whorl starts and can be followed down to the aperture, but here it is positioned above the centre and it is sometimes accompanied on the penultimate whorl by a keel, which arises very close below it and is finally stronger. On the final whorls, a spiral row of tubercles develops next to the suture, and is less strong close to the mouth, furthermore the last whorl is characterized by several spiral lines on top and numerous concentric spiral grooves on bottom. Everywhere, but especially close to the suture, transversal growth lines are visible. The umbilicus is one third of the shell width and is surrounded by a few dense series of transversal incisions crossed by tubercled ribs, which continue deep inside it. Mouth elongated above, inside nacreous: the operculum is membranaceus, with concentric grooves.

Larger shell diameter 7.4 to 9.1, smaller diameter 6.1 to 8.0 mm, height 4.7 to 6.4, respectively 3.6 -5.0; the mouth is 3.5 to 4.1 high, and 2.9 to 3.6 mm wide.

The new species was collected as empty shells at station 48 (700 m), while empty shells were collected at station 143 (212 m).

Comments. *Solariella illustris* is closely related to *Ethminolia nektonica* (Okutani, 1961) (Herbert 1992). Dekker and Orlin (2000: 18) and Janssen in Janssen and Taviani (2015: 525) assigned this species to *Ilanga*.

Family Hipponicidae Troschel, 1861

Capulus camaranensis Sturany, 1903

Figure 4
Sturany, 1903: 256–257, plate VII, figures 11a–c.

Original locality: Locality 43, "Kamaran-Insel" [Kamaran Island, Yemen], 16°– 11°N.

Type material. Ten syntypes: NHMW 37797 (locality 43), the specimen figured by Sturany (1903), plate I, figure 11a–c has been segregated, its width is 8.4 mm.

Original description. *Die erwachsene Schale besteht im ganzen aus 3 Umgängen; die ersten 2 glashellen Windungen bilden einen aufwärts gerichteten Apex, der jedoch nicht immer deutlich erkennbar ist, die letzte Windung den Hauptheil des Gehäuses. Die große querovale Mündung ist unten vorgezogen und hat einen breiten, verdickten Spindelrand. Die weiße Grundfarbe der Schale wird von mehreren verschieden breiten Längs- oder Spiralbändern von gelbbraunem bis orangefarbigem Ton verdrängt. An der Unterseite der Schlusswindung und gegen den Mundrand zu treten bei diesen Binden häufig Verschmelzungen zu Fleckenpartien auf.*

Junge Schalen sind einfarbig weiß und haben die Gestalt von C. hungaricus*; die Mündung ist kreisrund, der aufwärts gekehrte Apex steht noch näher zum Spindelrande, erst mit dem Anwachsen der Schale werden sie voneinander durch einen weiteren Raum getrennt.*

Die Art wurde von der Localität 43 (Kamaran-Insel) gebracht, und zwar sitzen die meisten. Exemplare auf Stacheln von Goniocidaris canaliculata *A. Ag. Einige junge Schalen haben sich auf älteren Exemplaren derselben Art angesetzt. Das Ansetzen geschieht unter Ausbildung eines festen, dicken, kalkigen Basalstückes, das genau in die Mündung der Schale passt und 2 neben einander liegende, annähernd ovale Flecken als Muskelabdrücke erkennen lässt.*

Translation. The adult shell consists of three whorls; the first two glassy whorls form an antrorse apex that is not always clearly recognizable, the last whorl is the main part of the shell. The large transversely oval mouth is elongated at the bottom and has a broad, thickened columellar lip. The white background colour of the shell is replaced by several different wide longitudinal or spiral yellow-brown to orange bands. On the basal part of the last whorl and towards the lip these bands frequently merge into dotted areas.

Young shells are plain white and have the shape of *C. hungaricus*; the aperture is circular, the antrorse apex is very close to the columellar lip; only with shell growth, they get separated by more space.

The species was brought from the locality 43 (Kamaran Island), sitting usually on spines of *Goniocidaris canaliculata* A. Ag. Some young shells are attached to older specimens of the same species. They adhere by forming a solid, thick, chalky base fitting precisely into the aperture and revealing two adjacent, almost oval dots from muscle imprints.

Comments. The identification of the echinoderm *Goniocidaris canaliculata* A. Agassiz, 1863 cannot be verified based on the available material (Figure 4 F). *Capulus camaranensis* was considered a synonym of *Malluvium lissum* (E. A. Smith, 1894) in the family Hipponicidae by Dekker and Orlin (2000: 21).

Family Eulimidae Philippi, 1853

Eulima muelleriae Sturany, 1903

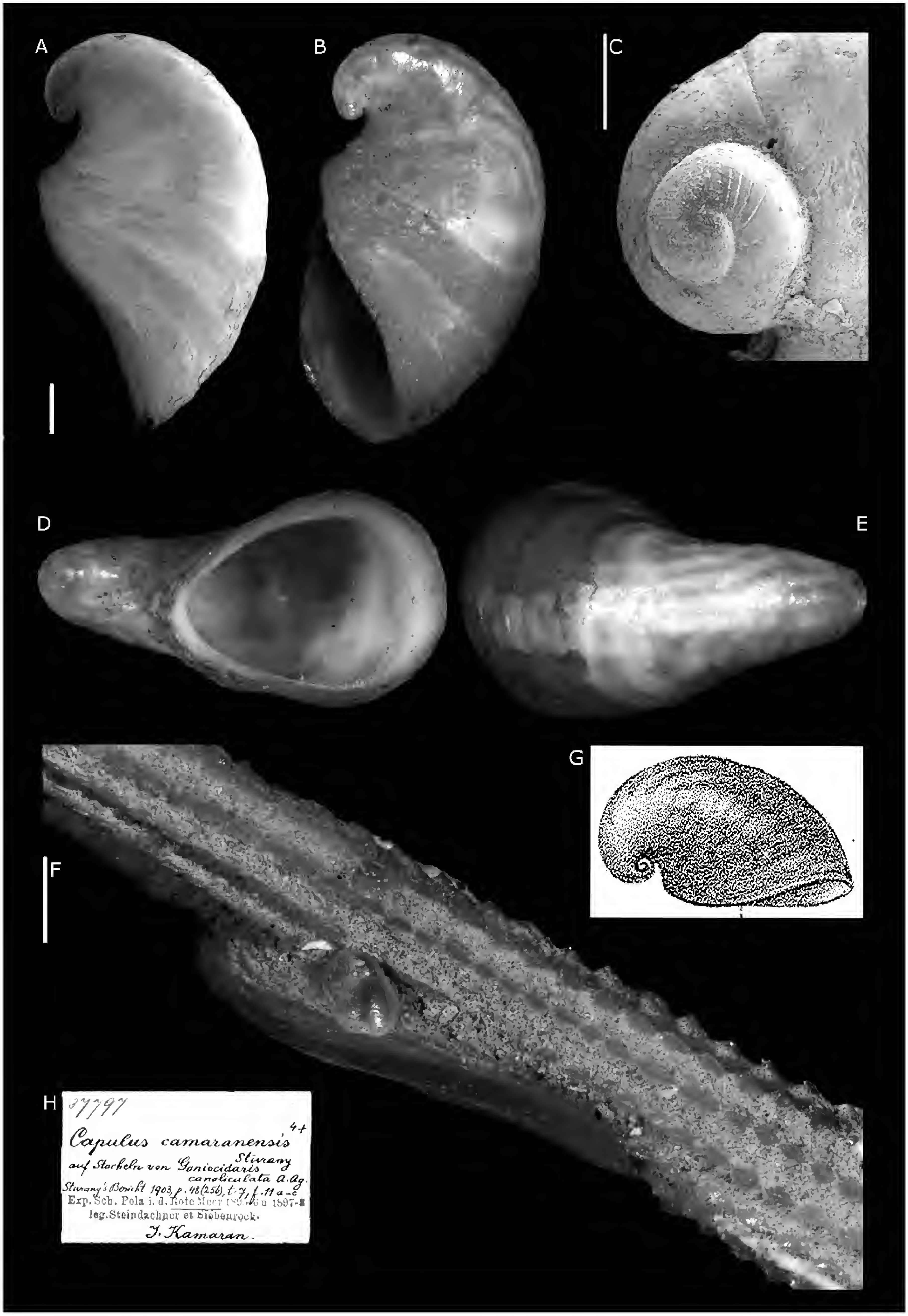
Figure 5
Sturany, 1903: 258, plate VI, figure 10.

Type locality. Locality 31, "Jidda (Djeddah)" [Jeddah, Saudi Arabia] 22°– 20°N.

Type material. Holotype: NHMW 37809, height 3.1 mm.

Original description. *Von der Localität 31.*

Die neue Art gründet sich auf ein einziges in Mülleria mauritiana *Q. & G. gefundenes Exemplar (Dr. v. Marenzeller hat die Schale bei der Bestimmung jener Holothurie entdeckt). Sie ist nahe verwandt mit* E. modicella *A. Ad. von Japan und den Philippinen, von ihr jedoch in einigen Punkten verschieden. Das Gehäuse ist stark nach rechts geneigt (mithin links concav, rechts oben convex gebaut) und besteht aus etwa 11 allmählich anwachsenden Umgängen; die Höhe der Schale beträgt 3,4, die Breite 1,2, die Höhe der Mündung circa 1 mm.*



37797

Capulus camaranensis Sturany 44

auf Stacheln von Goniocidaris canaliculata A. Ag.

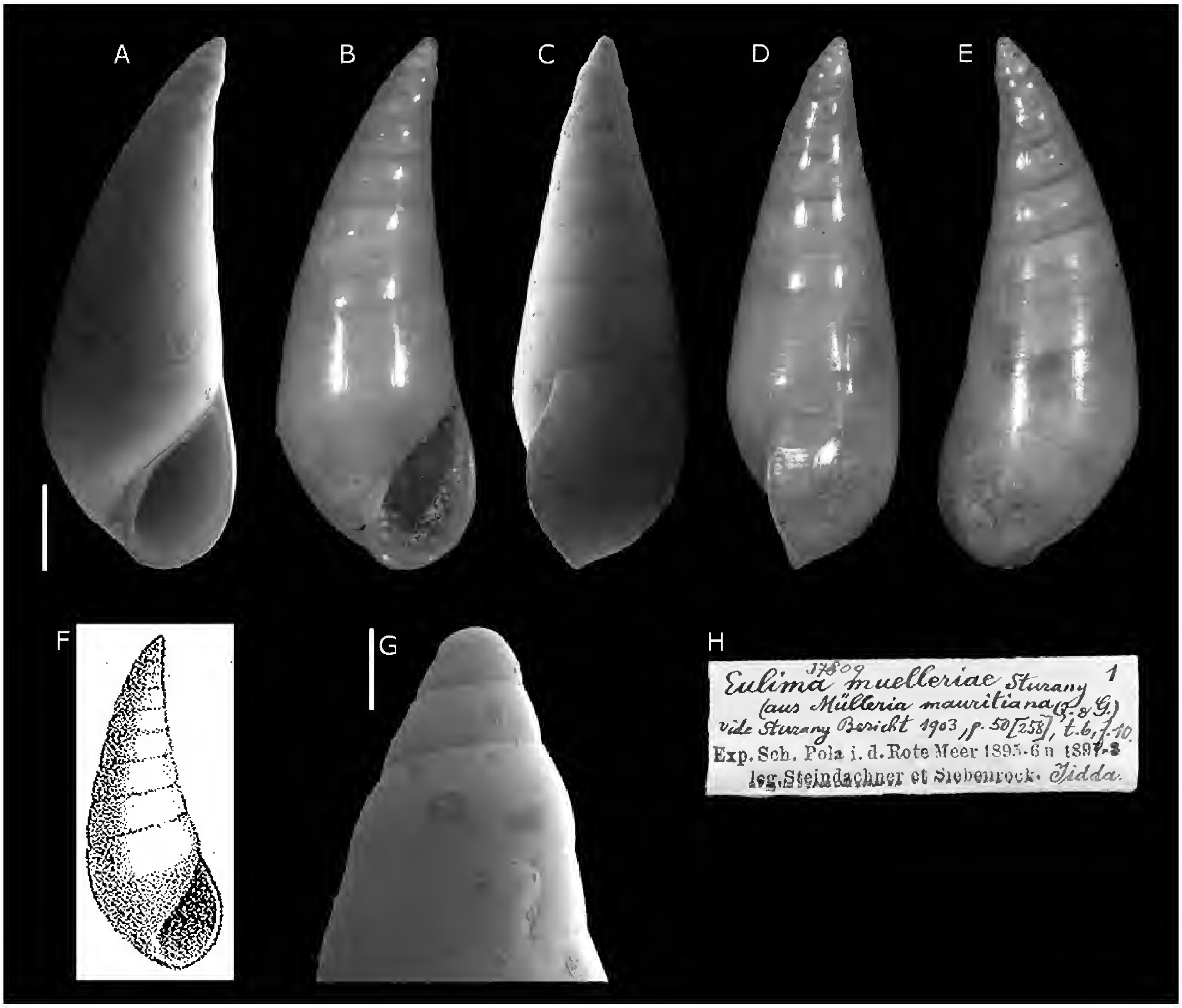
Sturany's Bericht 1903, p. 48(256), t. 7, f. 11 a–c

Exp. Sch. Pola i. d. Rote Meer [illegible] u 1897-8

leg. Steindachner et Siebenrock.

I. Kamaran.

Figure 4. *Capulus camaranensis* Sturany, 1903, Locality 43 (Kamaran Island, Yemen, Red Sea). **A–E**. Figured syntype, NHMW 37797: left side (**A–B**), protoconch (**C**), aperture (**D**), top (**E**). **F**. Post-metamorphic stage attached to *Goniocidaris canaliculata* (A. Agassiz, 1863). **G**. Original figure by Sturany (1903). **H**. Original label. Scale bars: **A–B, D–F**: 1 mm, **C**: 0.2 mm.



37809
Eulima muelleriae Sturany 1
(aus Mülleria mauritiana Q. & G.)
vide Sturany Bericht 1903, p. 50 [258], t. 6, f. 10.
Exp. Sch. Pola i. d. Rote Meer 1895-6 u 1897-8
leg. Steindachner et Siebenrock. Jidda.

Figure 5. *Eulima muelleriae* Sturany, 1903, Locality 31 (Jeddah, Saudi Arabia, Red Sea). **A–E**, **G**. Holotype, NHMW 37809: front (**A–B**), right side (**C–D**), back (**E**), protoconch (**G**). **F**. Original figure by Sturany (1903). **H**. Original holotype label. Scale bars: **A–E**: 0.5 mm, **G**: 0.1 mm.

Translation. From locality 31.

The new species is based on a single specimen found on *Mülleria mauritiana* Quoy & Gaimard [Echinodermata, Holothuriidae] (the shell was discovered by Dr. von Marenzeller when identifying this holothurian). It is closely related to *E. modicella* A. Adams from Japan and the Philippines, but differs in some respects. The shell is strongly bent to the right (therefore concave on left side, convex on top right side [it looks like a mistake because the opposite is true]) and consists of about 11 gradually increasing whorls; the height of the shell is 3.4, the width of 1.2, the height of the aperture about 1 mm.

Comments. Warén (1984) placed this species in *Melanella* and provided photos of living specimens and of sections of the snail in situ on the host.

Eulima orthophyes Sturany, 1903

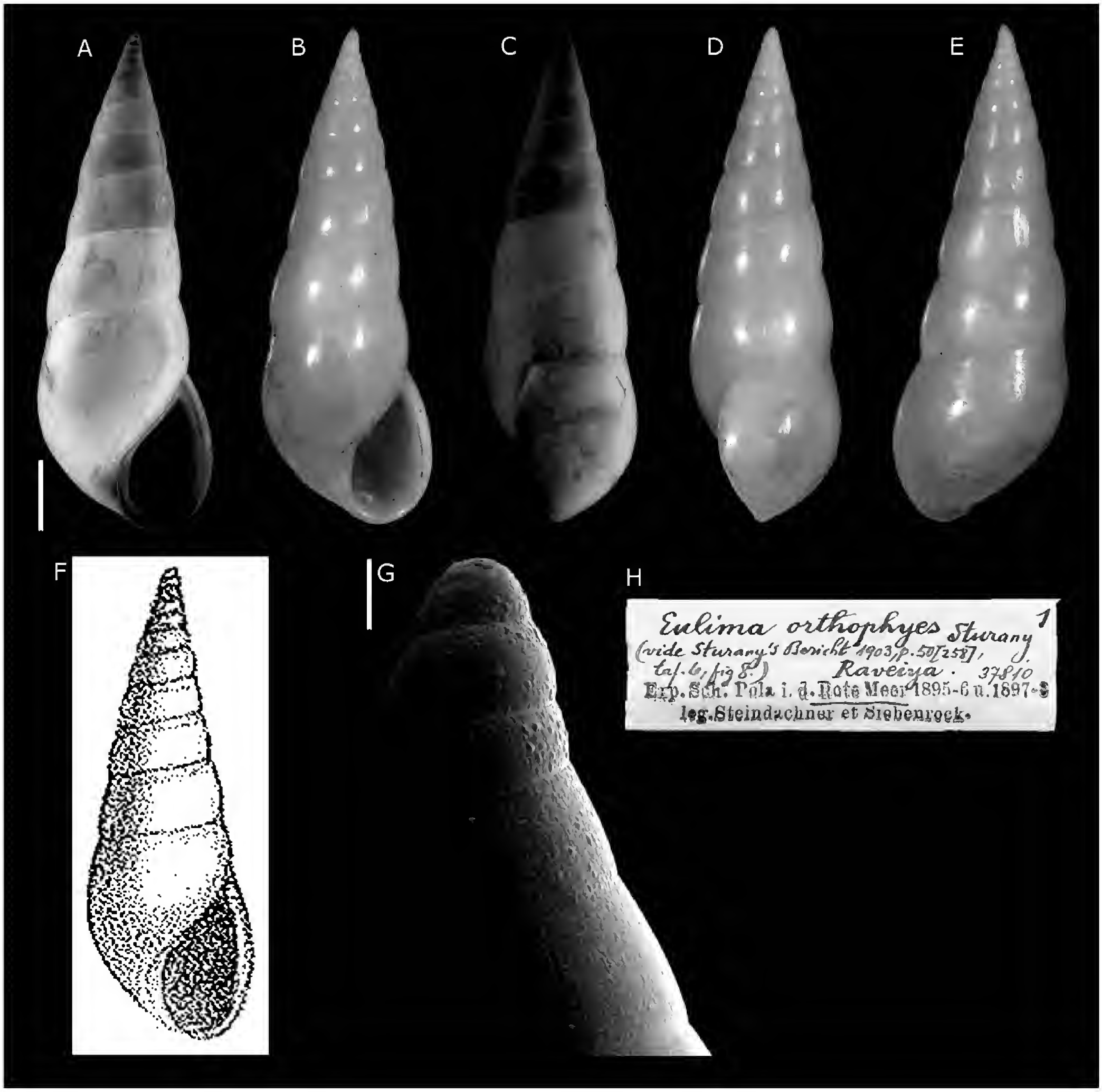
Figure 6
Sturany, 1903: 258, plate VI, figure 8.

Type locality. Locality 32, "Raveiya (Mahommed Ghul)" [Gul Mohammad, Saudi Arabia] 22°– 20°N.

Type material. Holotype: NHMW 37810, height 7 mm.

Original description. *Von der Localität 32; ein einziges Exemplar.*

Die glatte, stark glänzende, weiß gefärbte Schale ist nahezu gerade gewachsen, der Apex ist nur minimal nach rechts geneigt. Es sind 11 Umgänge vorhanden, die durch eine fadenförmige Naht voneinander getrennt werden; das Ausmaß der Schale beträgt 7,4 : 2,6 mm, die Mündung ist ungefähr 2 ½ mm hoch.



Eulima orthophyes Sturany 1
(vide Sturany's Bericht 1903, p. 50[258], J.
taf. 6, fig 8.) Raveiya. 37810
Exp. Sch. Pola i. d. Rote Meer 1895-6 u. 1897-8
leg. Steindachner et Siebenrock.

Figure 6. *Eulima orthophyes* Sturany, 1903, Locality 32 (Gul Mohammad, Saudi Arabia, Red Sea). **A–E, G**. Holotype, NHMW 37810: front (**A–B**), right side (**C–D**), back (**E**), protoconch (**G**). **F**. Original figure by Sturany (1903). **H**. Original holotype label. Scale bars: **A–E**: 1 mm, **G**: 0.1 mm.

Der Gestalt nach hat die neue Art eine gewisse Ähnlichkeit mit Stylifer acicula *Gld., im Gehäuseaufbau auch mit* E. solidula *Ad. u. Rve. von den Sandwich-Inseln (Berliner Museum!).*

Translation. From locality 32; a single specimen.

The smooth, very shiny, white-coloured shell is almost straight; the apex is minimally inclined to the right. There are 11 whorls, which are separated by a filiform suture; the size of the shell is 7.4 mm high and 2.6 mm wide, the mouth is about 2.5 mm high.

The form of the new species resembles *Stylifer acicula* Gould, the shell shape is similar to *E. solidula* Adams and Reeve from the Sandwich Islands (Berlin Museum).

Stylifer thielei Sturany, 1903

Figure 7
Sturany, 1903: 258, with text figure.

Type locality. Locality 31, "Jidda (Djeddah)" [Jeddah, Saudi Arabia] 22°– 20°N.

Type material. Destroyed.

Original description. *Von der Localität 31; ein einziges Exemplar.*

Die merkwürdig gestaltete und insbesondere auch durch den geschweiften Mundrand ausgezeichnete Schale ist aus 5 Umgängen aufgebaut und besitzt einen zitzen-

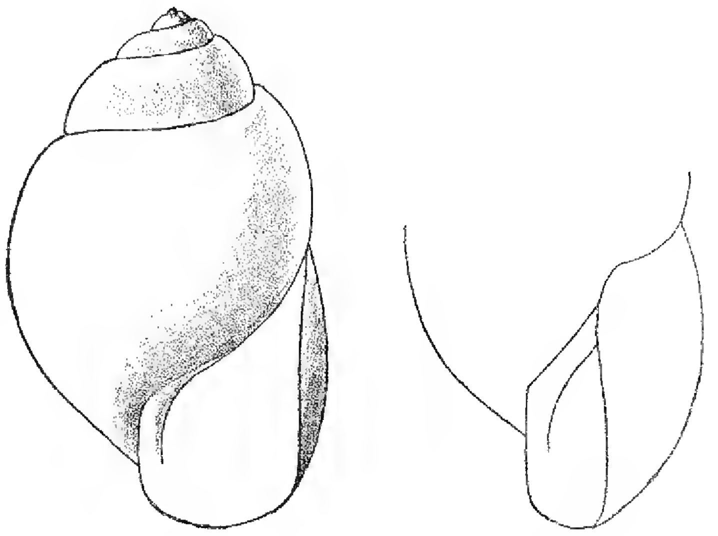


Figure 7. Original figure of *Stylifer thielei* Sturany, 1903.

förmigen Apex. Sie entbehrt jedweder Sculptur, ist matt im Glänze und weiß der Farbe nach. Höhe der Schale 5 ½, Breite 3 ½ mm. Herr Prof. Dr. Johannes Thiele in Berlin war so freundlich, die Weichtheile dieser Schnecke zu untersuchen und vor der nothwendig gewordenen Zertrümmerung der Schale die beigegebenen Zeichnungen anzufertigen. Zufolge des Fehlens einer Radula gehört das Thier zur Gattung Stylifer *Brod.*

Translation. From the locality 31; a single specimen.

The remarkably shaped shell is characterized by the curly lip, it consists of five whorls and has a teat-shaped apex. It lacks any sculpture, is dull in lustre and white in colour. Height of shell 5.5, width 3.5 mm. Prof. Dr. Johannes Thiele in Berlin was so kind to examine the soft parts of the snail and to prepare the drawings before crushing the shell. According to the lack of a radula the animal belongs to the genus *Stylifer* Broderip.

Comments. Sturany found a single specimen and sent it to Johannes Thiele in Berlin for the study of the soft parts (Sturany 1903). The shell was reported to have been crushed to extract the animal, indeed no shells were found in the Vienna and the Berlin museums (C. Zorn, pers. comm.). Warén (1981) placed it in the genus *Stylapex* and provided further figures of the shell and of living individuals. In any case, *Stilifer* is the correct spelling of the genus, *Stylifer* being an incorrect subsequent spelling by Broderip (1832).

Family Triphoridae Gray, 1847

Triforis (*?Viriola*) *senafirensis* Sturany, 1903

Figure 8
Sturany, 1903: 262–263, plate V, figures 7a–b.

Type locality. Locality 13, “Senafir-Insel” [Sanafir Island, Strait of Tiran], Northern Red Sea, 28°– 26°N.

Type material. Holotype: NHMW 37912, height 4.2 mm.

Original description. *Von der Localität 13; ein einziges Exemplar. Das 5 mm hohe und 1½ mm breite Gehäuse ist zierlich gebaut und lässt die Naht, welche einem zwischen Spiralrippen laufenden Raum gleichkommt, schwer erkennen. Es bilden ungefähr 5 feinsculptierte Umgänge das mützenförmig gestaltete, blasig aufgetriebene Embryonalgewinde, und darauf folgen die 9–10 Hauptumgänge der Schale. Auf jenem Embryonalgewinde werden zahlreiche Querlinien von 2 spiral angeordneten Rippchen gekreuzt, auf den übrigen Schalenwindungen laufen zuerst 2, dann 3 Spiralrippen von milchweißer Farbe und flachgedrückter Oberfläche, zwischen denen mikroskopisch feine Querstrichelchen erkennbar sind. Die Gesammtfarbe des Gehäuses ist dunkelrothbraun. Die Mündung ist entsprechend dem Gattungscharakter gestaltet und trägt oben am Außenrande einen kleinen Ausschnitt. Die Form ist ähnlich der als* T. hilaris *Hinds. bekannten Art von Zebu (Berliner Museum!) und dem Pacifischen Ocean (Tryon-Pilsbry).*

Translation. From location 13; a single specimen. The 5 mm high and 1.5 mm wide shell is finely built and makes the suture, which is similar to the space between spiral cords, hard to see. About five finely sculpted whorls form the cap-shaped inflated protoconch, then followed by the nine to ten teleoconch whorls. On the protoconch numerous axial ribs cross two spiral keels; on the teleoconch whorls, initially two, then three spiral milky-white flat cords run, microscopically fine horizontal lines can be seen between them. The main colour of the shell is dark reddish brown. The aperture is typical of the genus and carries on top of the outer lip of a small notch. The shape is similar to *T. hilaris* Hinds known from Cebu (Berlin Museum!) and the Pacific Ocean (Tryon-Pilsbry).

Comments. The holotype had originally a complete protoconch because Sturany described it as being formed by five whorls. Now the apex is clearly broken and only two whorls are left. Nonetheless, it can be seen that the apex is multispiral.

Family Columbellidae Swainson, 1840

Columbella (*Mitrella*) *erythraeensis* Sturany, 1900

Figure 9
Sturany, 1900b: 208–209; redescribed and illustrated in Sturany (1903), page 226, plate I, figure 5.

Type locality. Station 54, 24°48'N, 35°25'E, Central Red Sea, 535 m.

Type material. Holotype: NHMW 84221, height 13.1 mm.

Original description. *Schale spindelförmig, glänzend, weiß, mit Spuren von gelber Netzzeichnung; von den 8 Umgängen sind die ersten 2 milchweiß, glatt, zitzenförmig, die folgenden 1 1/2 mit ziemlich entfernt voneinander stehenden, deutlichen und derben Querrippchen ausgestattet, die übrigen bis auf die fadenförmige Naht und eine allerfeinste mikroskopische Spiralsculptur, sowie die mit Spiralreifen umstellte Basis des letzten Umganges glatt. Mit Ausnahme der Embryonalschale sind die Windungen nahezu flach und ungefähr stufig abgesetzt. Mündung mit 6 Zähnchen am Außenrande, mit einer Verdickung hinter demselben und mit schwachen*

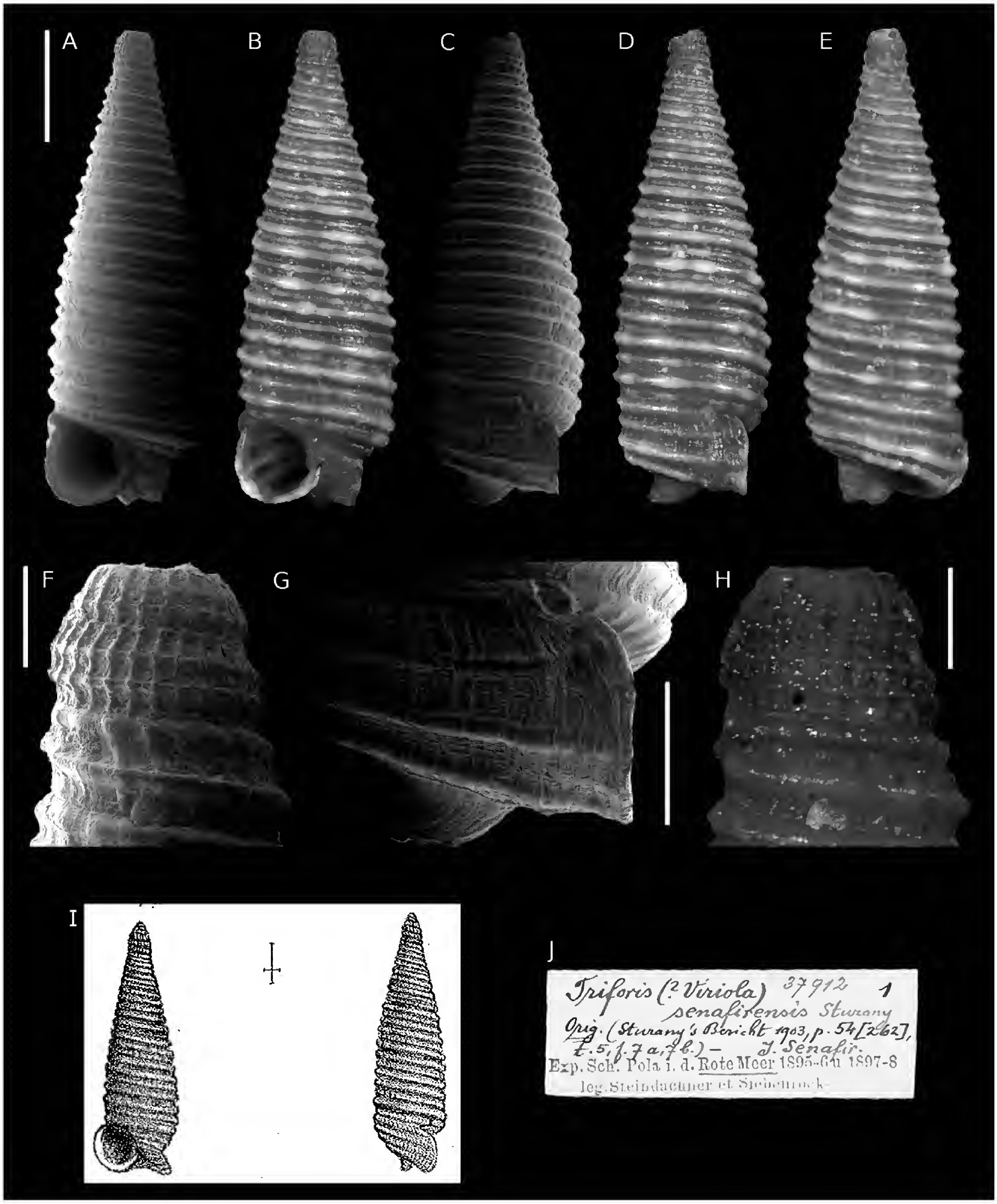
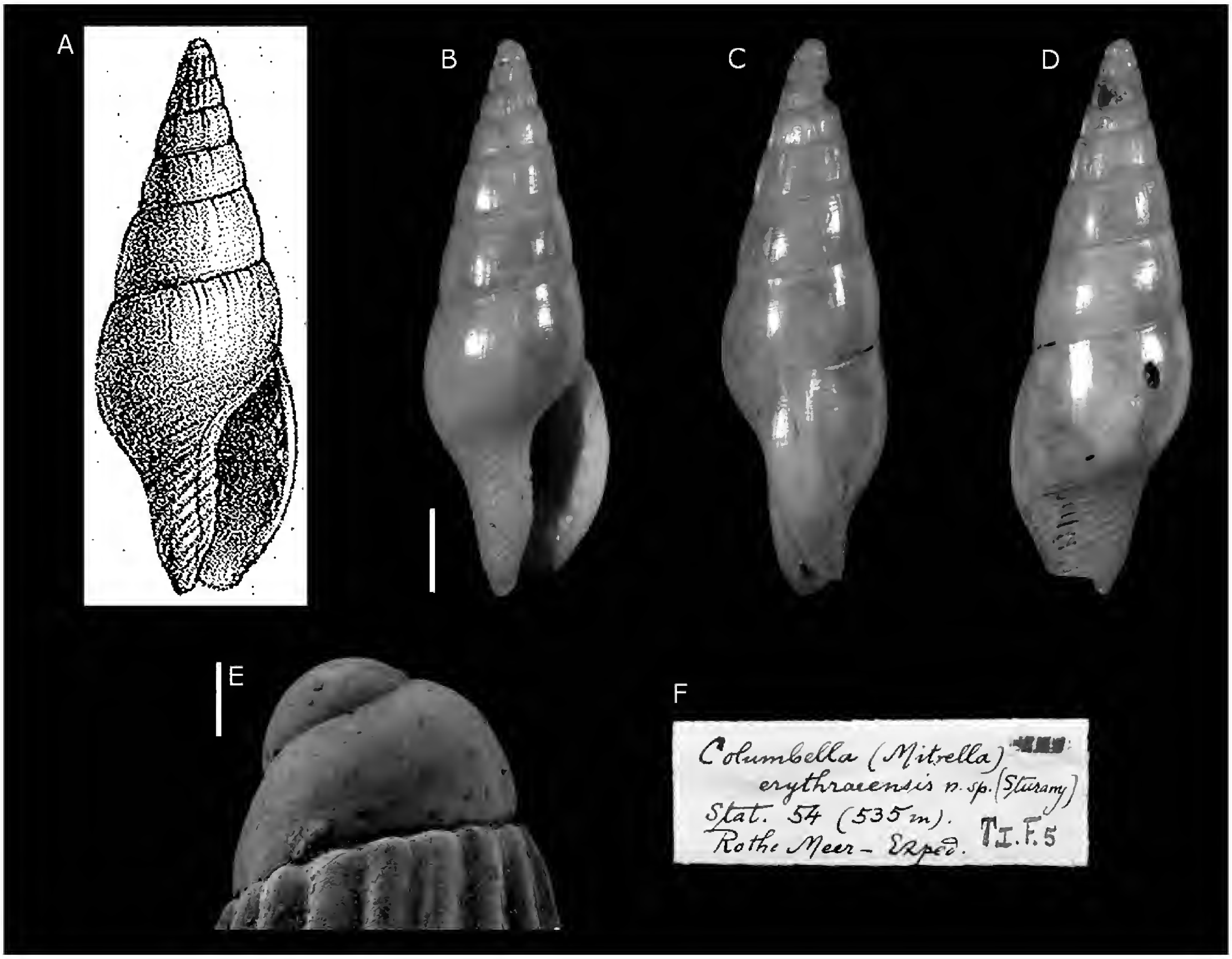


Figure 8. *Triforis senafirensis* Sturany, 1903, Locality 13 (Sanafir Island, Strait of Tiran, Northern Red Sea). **A–H**. Holotype, NHMW 37912: front (**A–B**), left side (**C–D**), back (**E**), protoconch (**F, H**), peristome (**G**). **I**. Original figure by Sturany (1903). **J**. Original holotype label. Scale bars: **A–E**: 1 mm, **F**, **H**: 0.2 mm, **G**: 0.5 mm.

Höckerchen auf der Spindel.

Höhe des Gehäuses 12,5 mm, Breite 4,0 mm, Höhe der Mündung 5,5 mm. Ein einziges Exemplar von Station 54 (535 m).

Translation. Shell fusiform, shiny, white, with traces of a yellow net pattern; of the eight whorls, the first two are milky white, smooth, teat-shaped, the following one and half has separated, pronounced and coarse axial ribs, the others almost smooth with the exception of the thread-like suture, the fine microscopic spiral sculpture, and



Columbella (Mitrella) [illegible]
erythraeensis n. sp. (Sturany)
Stat. 54 (535 m).
Rothe Meer – Exped. T.I.F.5

Figure 9. *Columbella erythraeensis* Sturany, 1900, Station 54 (Central Red Sea). **A**. Original figure by Sturany (1903). **B–E**. Holotype, NHMW 84221: front (**B**), right side (**C**), back (**D**), protoconch (**E**). **F**. Original holotype label. Scale bars: **B–D**: 2 mm, **E**: 0.2 mm.

spiral rings at base of the last whorl. With exception of the embryonic shell, the whorls are nearly flat and scalar. Aperture with six teeth on the outer lip, with a fold and weak tubercles on the columella.

Shell height 12.5 mm, width 4.0 mm, height of the mouth 5.5 mm. One specimen from station 54 (535 m).

Comments. The species has a fine spiral sculpture which is poorly visible in our figure.

Columbella (*Mitrella*) *nomanensis* Sturany, 1900

Figure 10
Sturany, 1900b: 209; redescribed and illustrated in Sturany (1903), page 226, plate I, figure 6.

Type locality. Station 170, "bei der Insel Noman" [Noman Island, Saudi Arabia] 27°0.2'N, 35°17.6'E, 690 m.

Type material. Holotype: NHMW 84222, height 7.2 mm.

Original description. *Schale spindel-bis eiförmig, matt glänzend, mit Spuren von orangegelben Flecken auf gelblich weißem Grunde; von den 8 1/2 Umgängen sind die ersten 31/2 milchweiß und glatt, die übrigen kaum gewölbt und mit ziemlich dicht stehenden Spiralstreifen ausgestattet, die an der Basis zu gröberen Spiralrippchen anwachsen.*

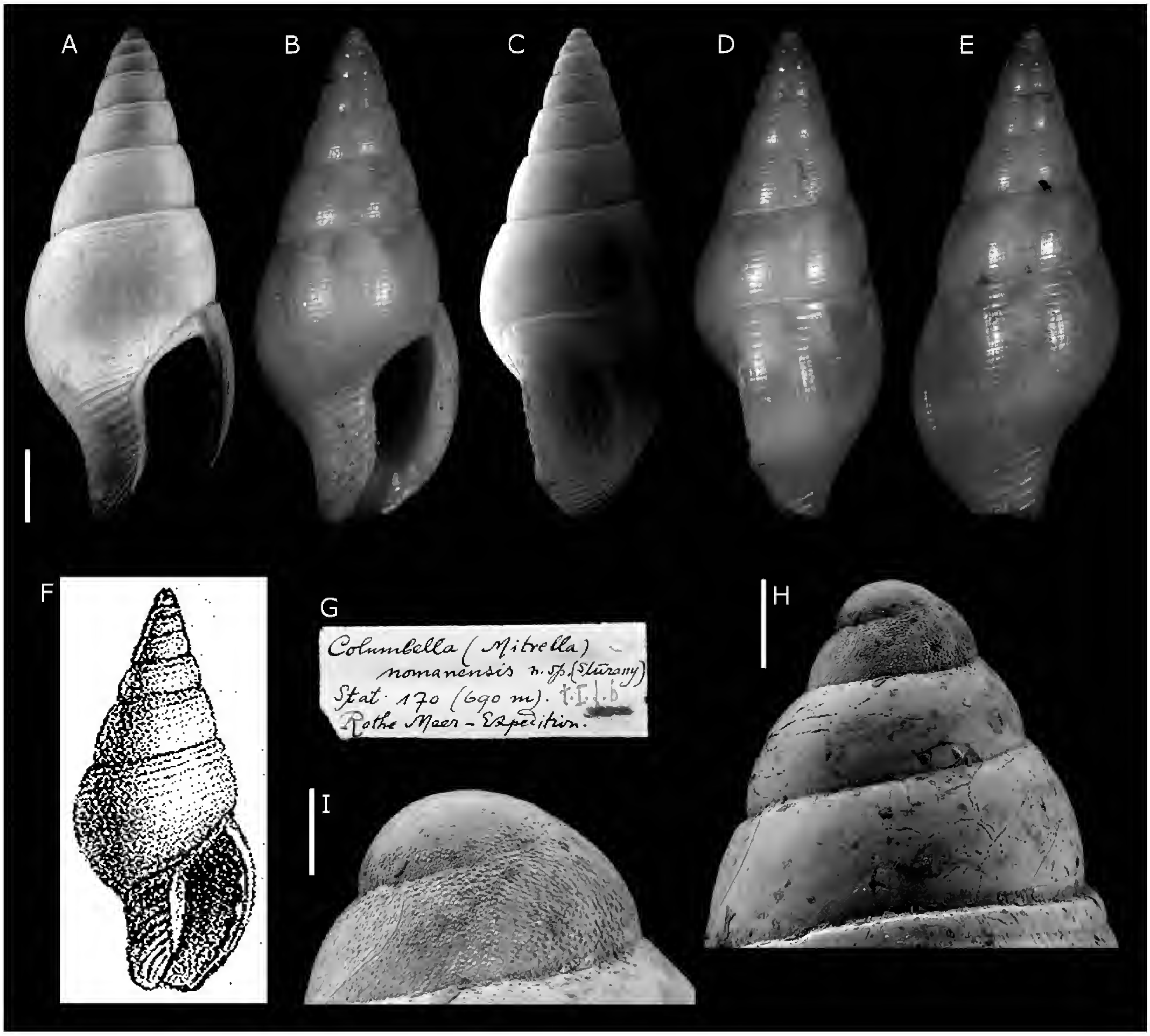
Naht fadenförmig. Am äußeren Mündungsrande sitzen 6 Zähnchen, an der Spindel schwache undeutliche Höckerchen, Mündungscanal breit und abgestutzt, zurückgebogen.

Höhe des Gehäuses 8,0 mm, Breite 3,2 mm; Höhe der Mündung 3,7 mm. Ein Exemplar von Station 170 (690 m).

Translation. Shell fusiform to ovoid, glossy, with traces of orange-yellow flammules on a yellowish-white ground; of the eight and half whorls, the first three and half are milky white and smooth, the others slightly curved and with dense spiral striae that grow into coarse spiral ridges at the base.

Suture filiform. At the outer lip six teeth, on the columella weak indistinct tubercles, siphonal canal wide and truncate, curved.

Shell height 8.0 mm, width 3.2 mm; mouth height 3.7 mm. One specimen from station 170 (690 m).



Columbella (Mitrella)
nomanensis n. sp. (Sturany)
Stat. 170 (690 m). t.I.f.6
Rothe Meer - Expedition.

Figure 10. *Columbella nomanensis* Sturany, 1900, Station 170 (Noman Island, Saudi Arabia, Red Sea). **A–E, H–I.** Holotype, NHMW 84222: front (**A–B**), right side (**C–D**), back (**E**), protoconch (**H–I**). **F**. Original figure by Sturany (1903). **G**. Original holotype label. Scale bars: **A–E**: 1 mm, **H**: 0.2 mm, **I**: 0.1 mm.

Family Fasciolariidae Gray, 1853

Fusus bifrons Sturany, 1900

Figure 11A–D, I–J
Sturany, 1900a: 197–198; redescribed and illustrated in Sturany (1903), pages 220–221, plate I, figures 1 and 3.

Original localities. Stations 9, 20, 47, 48, 76, 81, 107, 109, 121, 145, 156, 165, 170, 175, 176, 178, 179, 184 (490 – 900 m) (Red Sea; Table 1). In the original description Sturany did not refer to any particular station. Therefore, it is assumed that the whole material listed in 1903 constitutes the type material as listed below.

Type material. Figured syntypes: NHMW 84162 (locality 145), illustrated by Sturany (1903) in plate I, figure 1a, height 137.6 mm. NHMW 84147 (station 20): 1 specimen, illustrated by Sturany (1903) in plate I, figure 3a.

Further syntypes: NHMW 84148 (station 20): 1 specimen; NHMW 84150 (station 20): 1 specimen; NHMW 84152 (station 48): 1 specimen; NHMW 84153 (station 76): 1 specimen; NHMW 84157 (station 107): 1 specimen; NHMW 84158 (station 109): 1 specimen; NHMW 84159 (station 121): 1 specimen; NHMW 84163 (station 156): 5 specimens.

Additional material. NHMW 84160 (station 145): 3 specimens; NHMW 84161 (station 145): 1 specimen; NHMW 84169 (station 175): 1 specimen, form *paucicostata* written on label, but looks like the nominal species.

Original description. *Schale lang spindelförmig, ziemlich schlank, mehr oder minder festschalig, mit langem, kaum gedrehtem Canal; von den 11 stärker oder schwächer gewölbten Umgängen sind die ersten 1 1/2 als glattes, bläschenförmiges*

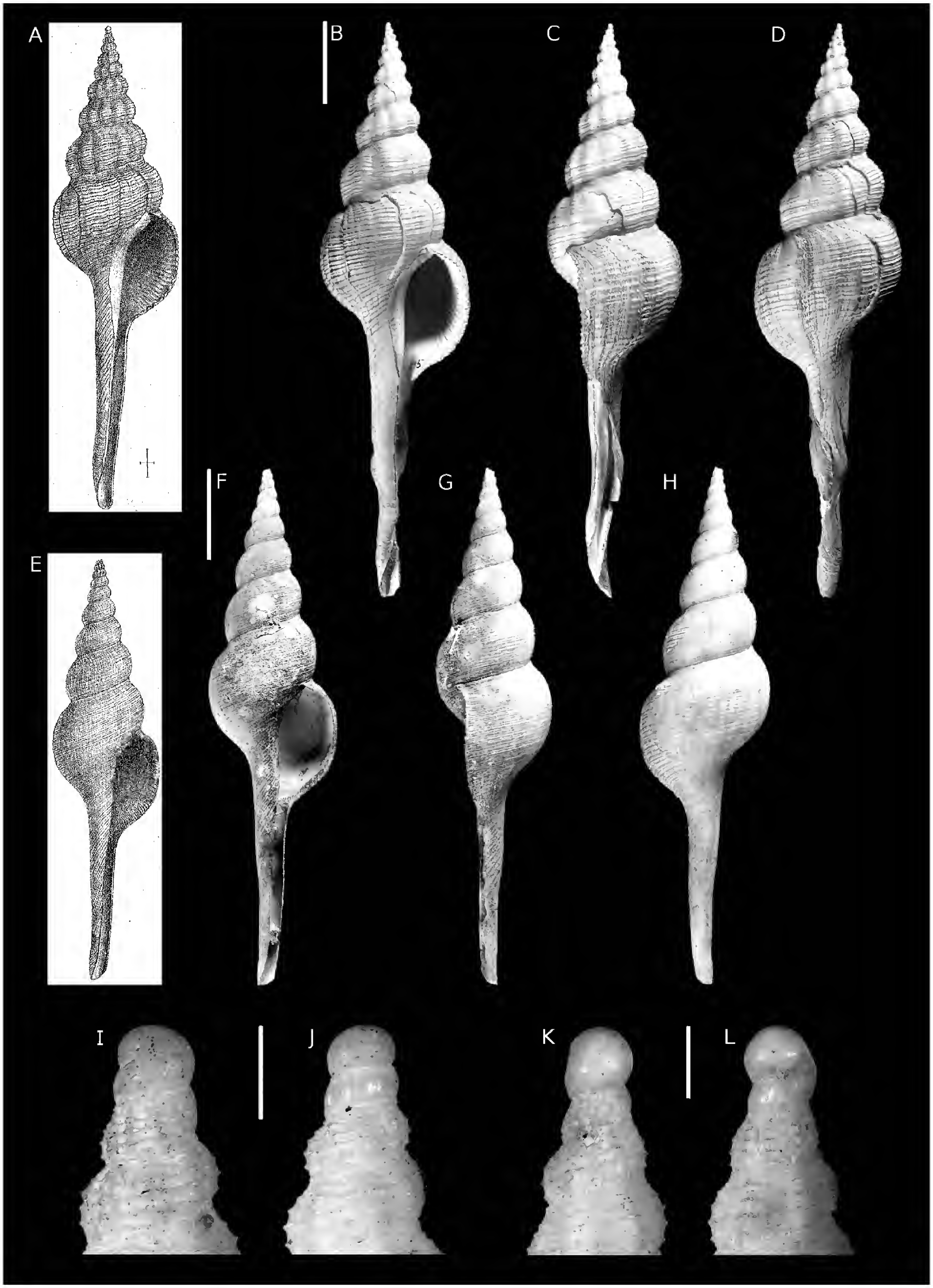


Figure 11. *Fusus bifrons* Sturany, 1900, Station 145 (east of Dahlak Island, Eritrea). **A**. Original figure of form typica by Sturany (1903). **B–D, I–J**. Figured syntype, NHMW 84147 (f. typica): front (**B**), right side (**C**), back (**D**), protoconch (**I–J**). **E**. Original figure of form *paucicostata* by Sturany (1903). **F–H, K–L**. Figured syntype, NHMW 84146 (f. *paucicostata*): front (**F**), right side (**G**), back (**H**), protoconch (**K–L**). Scale bars: **B–D, F–H**: 20 mm; **I–J, K–L**: 0.2 mm.

Embryonalgewinde abgesetzt, auf welches einige zarte Querrippen folgen, die nun aber bald zu derberen Querwülsten anwachsen und als solche entweder bis auf die letzte Windung reichen (F. typica*) oder nur drei bis vier Umgänge besetzen (F.* paucicostata*). Ferner ist eine deutliche, engstehende Spiralsculptur ausgeprägt: es wechseln stärkere und schwächere Spiralreifen ziemlich regelmäßig ab, welche entsprechend gewellt sind, wo sie über die Faltenrippen laufen. Spindel mit Belag, schwach oder gar nicht gerunzelt. Gaumen mit engen Falten besetzt. Mündung oval, nach oben etwas zugespitzt. Farbe gelblichweiß, bei frischen Exemplaren etliche Spiralreifen braun gefärbt.*

Bis 160 mm lang und 38mm breit; Mündung sammt Canal bis 92 mm lang und 19 mm breit.

Diese neue Art lässt sich weder mit F. multicarinatus *Lm., noch mit* F. turricula *Kien. (=* forceps *Perry) glatt vereinigen, doch ist sie immerhin von der letztgenannten Art abzuleiten, von der sie durch eine weniger einschneidende Naht, feinere Spiralreifen und engere Berippung des Gaumens unterschieden ist. Sie bewohnt die continentale Zone des Rothen Meeres und wurde hier zwischen 490 und 900 m Tiefe des Öfteren gedredscht. Die F.* paucicostata *ist eine charakteristische Abweichung, die sich gewöhnlich schon bei jungen Schalen durch das relativ großblasige Embryonalgewinde verräth, sowie durch das frühzeitige Aufhören der Querwülste, wodurch die folgenden Windungen flacher sich gestalten und gerade verlaufende Spiralreifen bekommen, das ganze Gehäuse auch specifisch leichter wird.*

Translation. Fusiform and elongated shell, rather slender, more or less robust, with long, slightly twisted canal; of the 11 more or less convex whorls, the first 1 1/2 are separated into a smooth, inflated protoconch after which some delicate axial ribs follow, which soon grow into coarser varices and either continue down to the last whorl (f. typica) or are present only on three to four whorls (f. *paucicostata*). Additionally, a clear, fine spiral sculpture takes form: stronger and weaker spiral rings alternate on a fairly regular basis and are undulated when they cross the ribs. Columella with a callus, weakly or not at all wrinkled. Aperture with fine teeth, oval, slightly pointed in the upper part. Colour yellowish white, with some brown spiral lines in fresh specimens.

Up to 160 mm long and 38 mm wide; aperture with canal up to 92 mm long and 19 mm wide.

This new species cannot be merged either with *F. multicarinatus* Lamarck or with *F. turricula* Kiener (=*forceps* Perry), but it can be distinguished from the latter species because of a shallower suture, finer spiral threads and narrower ribbing of the lip. It inhabits the continental zone of the Red Sea and was dredged at depths of 490-900 m. The form *paucicostata* is a characteristic deviation, usually shown in young shells by the relatively large bubbled protoconch and the early disappearance of the axial ribs, so that the following whorls appear flatter, the spiral threads straighter and the whole shell is significantly lighter.

Comments. Sturany described two forms or varieties of this species, which differ only slightly in the more or less extended development of axial ribs in respect to their strength and number. Both forms intergrade and are considered phenotypical variations of the same taxon (see also Snyder 2002).

Fusus bifrons f. *paucicostata* Sturany, 1900

Figure 11E-H, K-L

Sturany, 1900a: 197–198; redescribed and illustrated in Sturany (1903), pages 220–221, plate I, figures 2 and 4.

Original localities. Stations 9, 20, 47, 48, 76, 81, 107, 109, 121, 145, 156, 165, 170, 175, 176, 178, 179, 184 (490 – 900 m) (Red Sea; Table 1). In the original description Sturany did not refer to any particular station. Therefore, it is assumed that the whole material listed in 1903 constitutes the type material as listed below.

Type material. Figured syntypes: NHMW 84146 (station 9): 1 specimen, illustrated by Sturany (1903) in plate I, figure 4a; NHMW 84171 (station 175): 1 specimen, reported on label that this specimen is illustrated by Sturany (1903) in plate I, figure 2a, height 113 mm.

Further syntypes: NHMW 84149 (station 20): 2 specimens; NHMW 84151 (station 20): 1 specimen; NHMW 84154 (station 76): 1 specimen; NHMW 84155 (station 76): 5 specimens; NHMW 84156 (station 81): 1 specimen; NHMW 84164 (station 165): 1 specimen; NHMW 84165 (station 165): 1 specimen; NHMW 84172 (station 176): 1 specimen; NHMW 84173 (station 176): 1 specimen; NHMW 84175 (station 179): 3 specimens; NHMW 84176 (station 179): 3 specimens; NHMW 84177 (station 179): 2 specimens; NHMW 84178 (station 179): 1 specimen; NHMW 84179 (station 184): 1 specimen. Two more specimens are present without labels and inventory numbers, they probably come from stations 47 and 178.

Additional material. NHMW 84166 (station 170): 3 specimens; NHMW 84167 (station 175): 1 specimen; NHMW 84168 (station 175): 1 specimen; NHMW 84169 (station 175): 1 specimen, form *paucicostata* written on label, but looks like the nominal species; NHMW 84170 (station 175): 7 specimens.

Original description, translation and comment. See *Fusus bifrons*.

Family Nassariidae Iredale, 1916

Nassa lathraia Sturany, 1900

Figure 12

Sturany, 1900a: 200–201; redescribed and illustrated in Sturany (1903), pages 224–225, plate II, figures 2a–b.

Type locality. Station 130, "westlich von Kunfidah" [west of Al Qunfudhah, Saudi Arabia], 19°17'N, 39°37'E, 439 m.

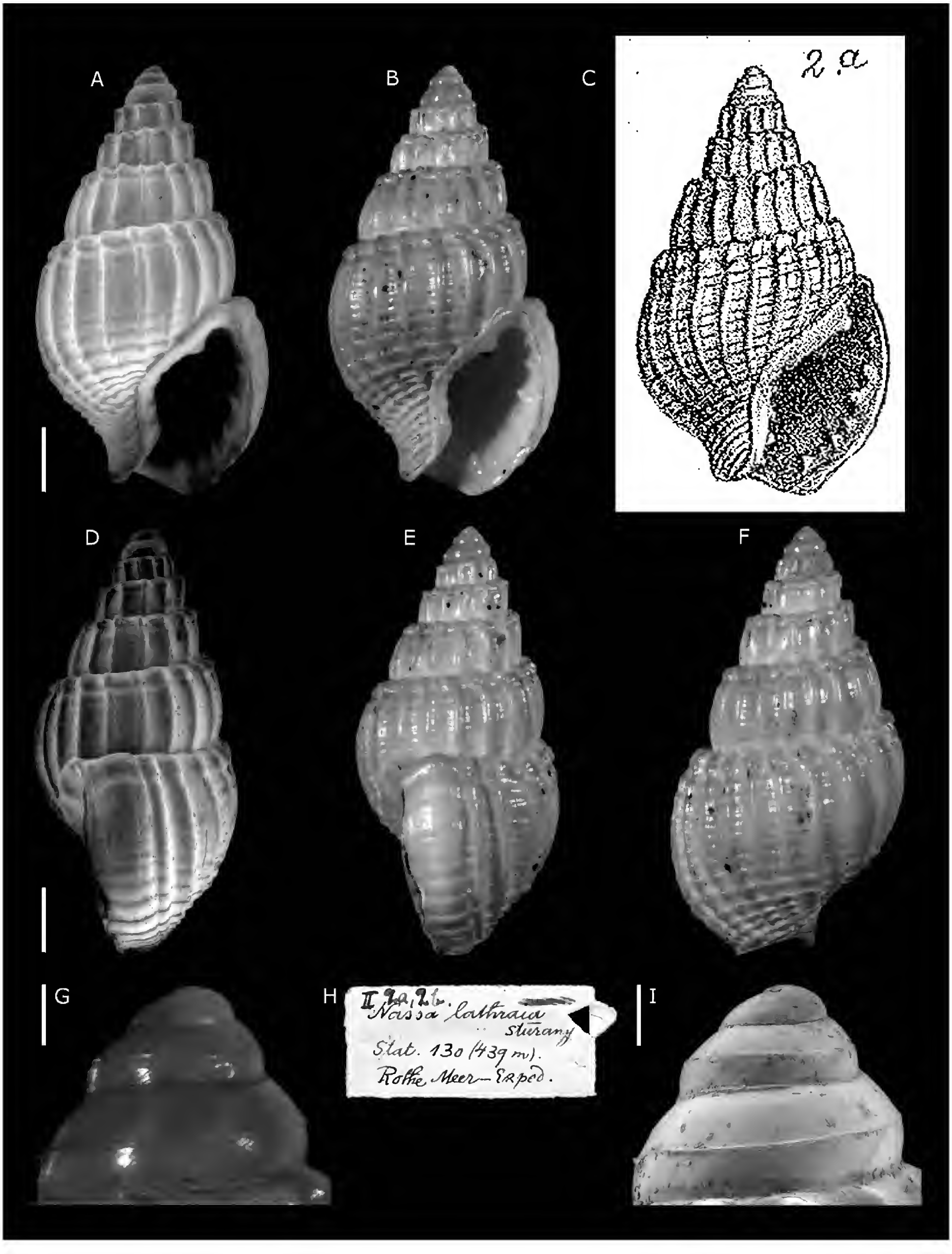


Figure 12. *Nassa lathraia* Sturany, 1900, Station 130 (Al Qunfudhah, Saudi Arabia, Red Sea). **A–B**, **D–G**, **I**. Figured syntype, NHMW 84203: front (**A–B**), right side (**D–E**), back (**F**), protoconch (**G, I**). **C**. Original figure by Sturany (1903). **H**. Original label of figured syntype. Scale bars: **A–B**, **D–F**: 1 mm, **G**, **I**: 0.2 mm.

Additional original localities. Stations 48, 51, 54, 107, 114, 121, 127, 130 (439 – 748 m) (Central and Southern Red Sea; Table 1).

Type material. Figured syntypes: NHMW 84203 (station 130; height: 6.6 mm, figured in Sturany 1903, plate II, figures 2a–b), NHMW 84205 (station 135): 1 specimen (figured in Sturany 1903, plate II, figures 1a–b). Further syntypes: NHMW 71640/O/745 (station 130): 2 specimens; NHMW 84196 (station 48): 2 specimens; NHMW 84197 (station 51): 3 specimens; NHMW 84198 (station 54): 5 specimens; NHMW 84199 (station 107): 2 specimens; NHMW 84200 (station 114): 5 specimens; NHMW 84201 (station 121): 1 specimen; NHMW 84202 (station 127): 1 specimen; NHMW 84204 (station 130): 12 specimens.

Original description. *Von den Stationen 48, 51, 54, 107, 114, 121, 127, 130 (439 – 748 m). Diese Form ist von* N. munda *durch die bedeutend spärlicher vorhandenen, jedoch schärfer ausgeprägten Querrippen unterschieden, zwischen denen die Spiralstreifung deutlich sichtbar wird. Mit Ausnahme der glatten Anfangswindungen tragen die Umgänge oben nächst der Naht eine besonders abgesetzte Körnchenreihe.*

Höhe des Gehäuses circa 7 1/2, Breite circa 3 1/2 mm; Mündung circa 3 1/2 mm hoch und 2 mm breit.

Wie N. munda *m. in der continentalen Zone gefunden, in Tiefen zwischen 439 und 748 m.*

Translation. From stations 48, 51, 54, 107, 114, 121, 127, 130 (439 – 748 m). Distinguished from *N. munda* by the much sparser, but more sharply pronounced axial ribs between which the spiral stripes are clearly visible. Except for the smooth initial whorls, the others bear a tubercled cord on their upper part next to the suture.

Shell height about 7.5, width about 3.5 mm; mouth about 3.5 mm high and 2 mm wide.

Like *N. munda*, it is found in the continental zone, at depths of 439-748 m.

Comments. For discussion of relationships and nomenclature see under *Nassa munda*.

Nassa munda Sturany, 1900

Figure 13

Sturany, 1900a: 200; redescribed and illustrated in Sturany (1903), page 223–224, plate II, figures 4a–b.

Type locality. Station 135, "südöstlich von Akik Seghir" [south-east of Akik Seghir, Eritrea], 17°26.1'N, 39°19'E, 332m.

Additional original localities. Station 135 (332 m) and 145 (800 m) (Southern Red Sea; Table 1).

Type material. Figured syntype: NHMW 84190 (station 135; height: 9.9 mm; figured in Sturany 1903, plate II, figures 4a–b). Further syntypes: NHMW 71640/O/746 (station 135): 4 specimens; NHMW 84191 (station 135): 14 specimens; NHMW 84192 (station 145): 1 specimen.

Additional material. NHMW 84193 (station 170): 1 specimen.

Original description. *Gehäuse klein und festschalig, kegelig-oval; von den acht Umgängen sind die ersten gerundet und glatt, die übrigen stufig abgesetzt und mit zahlreichen Querwülsten (etwa 26 auf der Schlusswindung) ausgestattet, die von Spiralstreifen gekreuzt und gekerbt werden. Auch ist durch eine schärfer eingegrabene Spirallinie der oberste Theil jeder Windung als eine Reihe von Höckerchen abgesetzt. Auf dem Außenrande der Mündung in der Regel sechs bis acht Zähnchen, von denen einige besonders hervortreten können. Andeutung von Bänderung nur selten zu beobachten.*

Höhe der Schale 7 1/2 bis 9 3/4, Breite 4 1/4 bis 5 mm; Höhe der Mündung 3 1/2 bis 4 1/2, Breite derselben 2 bis 2 3/4 mm.

Von Station 135 (332 m) und 145 (800 m) vorliegend.

Translation. Shell small and thick, conical-oval; of the eight whorls, the first are rounded and smooth, the other scalariform with numerous axial ribs (about 26 on the last whorl) which are crossed and notched by spiral threads. The uppermost part of each whorl bears a strongly sculptured spiral cord with a series of tubercles. On the outer edge of the mouth, there are usually six to eight teeth, some of which may be particularly prominent. Traces of colour bands can rarely be observed.

Height of the shell 7.5 to 9.75, width 4.25 to 5 mm; height of the mouth 3.5 to 4.5, width 2 to 2.75 mm.

From station 135 (332 m) and 145 (800 m).

Comments. Cernohorsky (1984: 156) listed *munda* as *nomen dubium* and possible synonym of *Nassarius* (*Zeuxis*) *idyllius* (Melvill & Standen, 1901).

Nassa lathraia as well as *N. sporadica*, *N. stiphra* and *N. munda* are published at the same date and are regarded synonymous. Examination of the type material as well as of rich material from various expeditions to the deep Red Sea (RJ) shows that the various names only denote sculptural variants which can be observed to occur together in part at the same stations and which cannot be told apart as different taxa. Whereas Janssen in Janssen and Taviani (2015) used *lathraia* as valid name, Dekker and Orlin (2000: 28) should be regarded as first revisers who selected *Nassarius mundus* (Sturany, 1900) as valid name for the taxon explicitly denoting the other names as synonyms. Cernohorsky (1984: 103) regarded *lathraia* as a possible synonym of *Nassarius* (*Niotha*) *sinusigerus* (A. Adams, 1852). Whether this is correct needs further study and comparison of many other conchologically similar species. If it proves correct, *sinusigerus* would become the valid name for this assemblage of forms denoted by Sturany with four names.

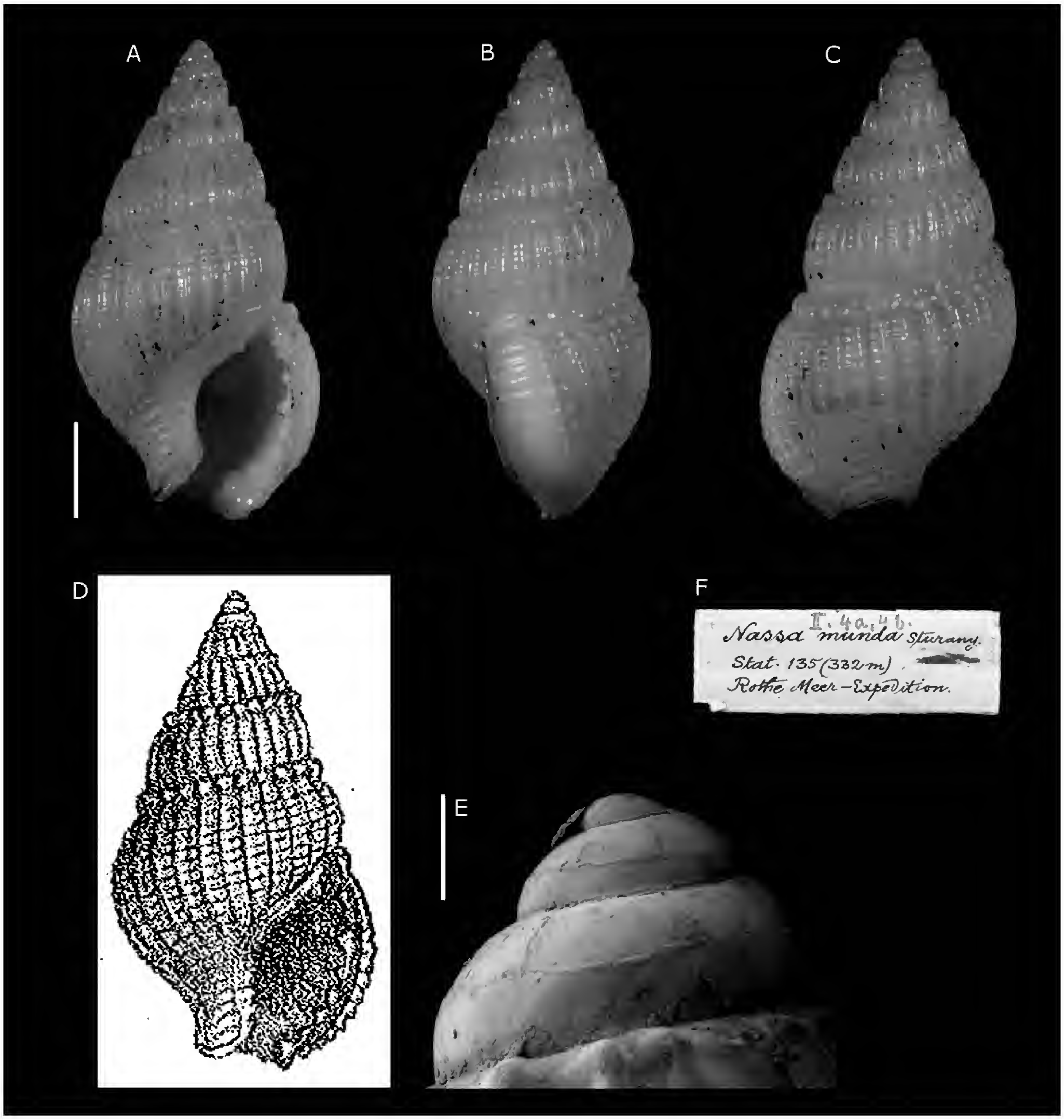


Figure 13. *Nassa munda* Sturany, 1900, Station 135 (Akik Seghir, Eritrea, Red Sea). **A–C, E**. Figured syntype, NHMW 84190: front (**A**), right side (**B**), back (**C**), protoconch (**E**). **D**. Original figure by Sturany (1903). **F**. Original label of figured syntype. Scale bars: **A–C**: 2 mm, **E**: 0.2 mm.

Nassa sporadica Sturany, 1900

Figure 14

Sturany, 1900a: 201; redescribed and illustrated in Sturany (1903), page 224, plate II, figures 5a–b.

Type material. Holotype: NHMW 84194, height 11.7 mm.

Type locality. Station 54, 24°48'N, 35°25'E, Central Red Sea, 535 m.

Original description. *Das Gewinde dieser mit* N. munda *m. verwandten Form besteht aus 8 1/2 Umgängen und ist oben stufig abgesetzt. Die Querwülste stehen bedeutend enger als bei jener Art, so dass auf der letzten Windung etwa 35 abzuzählen sind. Von einer Bänderung nur ganz geringe Spuren sichtbar. Außenrand der Mündung mehrfach und unregelmäßig gezähnt.*

Höhe der Schale 11 ½, Breite 6 1/4 mm; Mündung 6 mm hoch und 3 1/2 mm breit. — Ein einziges Exemplar von Station 54 (535 m).

Translation. The spire of this species is related to the one of *N. munda* and consists of 8.5 whorls and is sca-

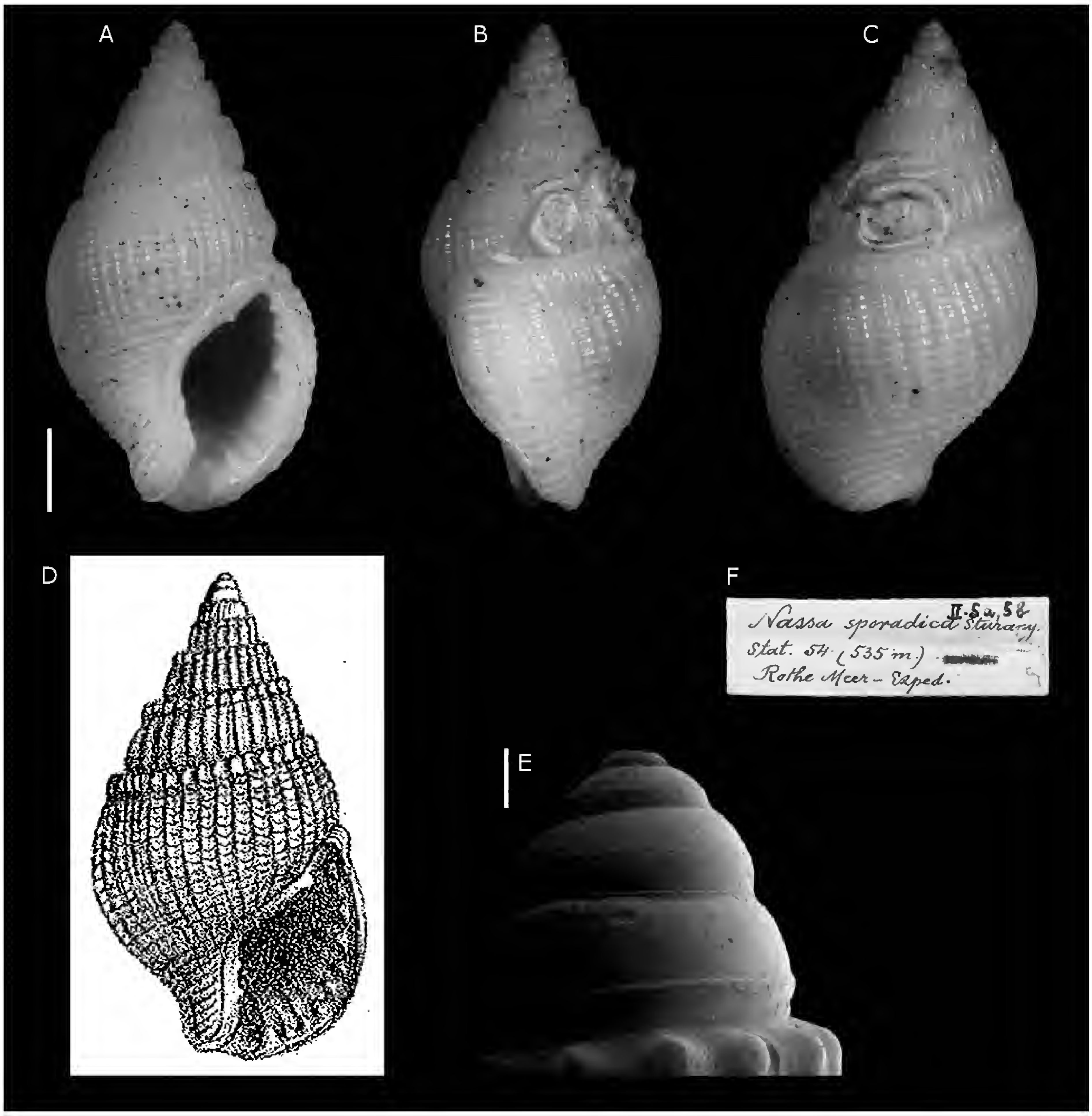


Figure 14. *Nassa sporadica* Sturany, 1900, Station 54 (Central Red Sea). **A–C**, **E.** Holotype, NHMW 84194: front (**A**), right side (**B**), back (**C**), protoconch (**E**). **D**. Original figure by Sturany (1903). **F**. Original holotype label. Scale bars: **A–C**: 2 mm, **E**: 0.2 mm.

lariform on top. The axial ribs are significantly closer compared to the mentioned species, so on the last whorl 35 can be counted. Only very small traces of colour bands are visible. Lip with numerous and irregular teeth.

Shell height 11.5, width 6.25 mm; mouth 6 mm high and 3.5 mm wide. One specimen from station 54 (535 m).

Comments. *Nassa sporadica* was regarded as *nomen dubium* and possible synonym of *Nassarius* (*Zeuxis*) *crebricostatus* (Schepman, 1911) by Cernohorsky (1984: 160). For further comments on validity of *sporadica* see under *Nassa munda*.

Nassa steindachneri Sturany, 1900

Figure 15

Sturany, 1900a: 199; redescribed and illustrated in Sturany (1903), pages 222–223, plate II, figures 9a–c.

Type locality. Station 170, "bei der Insel Noman" [Noman Island, Saudi Arabia], 27°0.2'N, 35°17.6'E, 690 m.

Additional original localities. Stations 124, 135, 170 and 179 (314 – 690 m) (Red Sea; Table 1).

Type material. Figured syntype: NHMW 84187 (station 179): 1 specimen (figured in Sturany 1903, plate II,

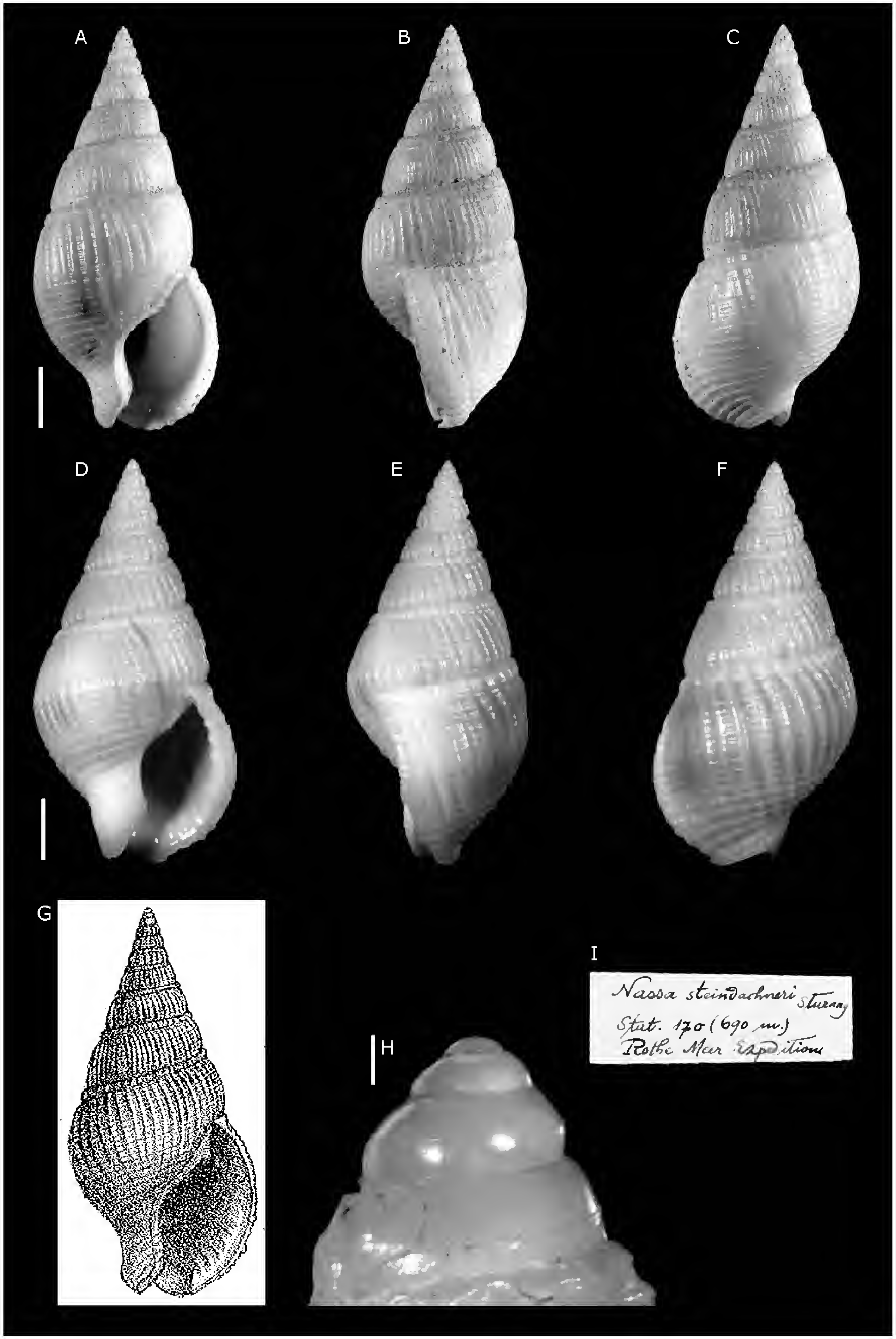


Figure 15. *Nassa steindachneri* Sturany, 1900, Station 170 (Noman Island, Saudi Arabia, Red Sea). **A–C, H**. Syntype, NHMW 84186: front (**A**), right side (**B**), back (**C**), protoconch (**H**). **D–F**. Syntype, NHMW 84185, Station 135 (Akik Seghir, Eritrea, Red Sea): front (**D**), right side (**E**), back (**F**). **G**. Original figure by Sturany (1903). **I**. Original label of syntypes NHMW 84186. Scale bars: **A–F**: 3 mm, **H**: 0.2 mm.

figures 9a–c). Further syntypes: NHMW 84186 (station 170) 3 specimens ; NHMW 84185 (station 135): 3 specimens and 1 fragment; NHMW 84188 (station 179): 5 specimens.

Additional material. NHMW 84184 (station 94): 3 specimens; NHMW 111537 (station 51): 1 specimen.

Original description. *Gehäuse in Gestalt und Windungszahl mit der vorigen Art übereinstimmend, von ihr aber durch die bis zur Mündung herabreichende Cancellierung gut unterschieden. Nur das Embryonalgewinde ist glatt, die übrigen Umgänge sind durch gröbere, etwas gekrümmte Querwülste und zarte Spirallinien regelmäßig gegittert; der oberste Theil der letzten vier Windungen ist überdies von dem übrigen Theile derselben durch eine mit der Naht parallel laufende, tiefer einschneidende Spiralfurche als wulstige Körnchenreihe getrennt. Von den Binden der verwandten Art sind nur noch Spuren sichtbar.*

Höhe der Schale 29, Breite 13 mm; Mündung 13 mm hoch und 7 mm breit. — Von den Stationen 124, 135, 170 und 179 vorliegend; in Tiefen bis 690 m gefunden.

Translation. Shell in shape and number of whorls analogue the previous species, but well differentiated by the cancellated sculpture descending to the mouth. Only the protoconch is smooth, the remaining whorls are regularly gridded by coarser, slightly curved varices and delicate spiral lines; the uppermost part of the last four whorls is also separated from the other parts by an incised spiral channel running parallel to the suture as a thick series of tubercles. Of the colour bands observed in the related species, only traces are here visible.

Shell height 29, width 13 mm; mouth 13 mm high and 7 mm wide. Found in stations 124, 135, 170 and 179; at depths up to 690 m.

Comments. When a lectotype shall be selected, a specimen should be taken which is better preserved than the specimen figured by Sturany, which has a partly eroded protoconch and early teleoconch whorls. For discussion of relationships see under *thaumasia*.

Nassa stiphra Sturany, 1900

Figure 16
Sturany, 1900a: 200–201; redescribed and illustrated in Sturany (1903), page 224, plate II, figures 3a–b.

Type locality. Station 143, "nächst der Insel Harmil" [near Harmil Island, Dahlak Archipelago, Eritrea] 17°7'N, 39°55'E, 212 m.

Type material. Holotype: NHMW 84195, height: 6.9 mm.

Original description. *Schale gedrungen, kegelförmig, aus sieben gerundeten, durch eine tiefe Naht getrennten Umgängen aufgebaut, von denen das Embryonalgewinde schwach gekielt und glatt ist, die übrigen wie bei* N. munda *mit deutlichen Querwülsten ausgestattet sind (mit 22 Wülsten auf der Schlusswindung). Auch zarte Spirallinien treten auf, jedoch nur unter der Naht und im Umkreise des Nabels deutlich. Der Außenrand der Mündung trägt sechs bis sieben Zähne, von denen ein mittlerer und der unterste kräftiger sind. Auf der letzten Windung zwei gelbe Binden auf weißem Grunde.*

Höhe der Schale 7,2, Breite 4,2 mm; Mündung 3,5 mm hoch und circa 2 mm breit. — Ein Exemplar von Station 143 (212 m).

Translation. Shell compact, cone-shaped, composed of seven rounded whorls separated by a deep suture; the protoconch is weakly keeled and smooth, the teleoconch is equipped with significant axial ribs (22 on the final whorl) as in *N. munda*. Also delicate spiral threads occur, but are distinct only under the suture and around the umbilicus. The outer lip carries internally six to seven teeth, of which the median and the lowest are the strongest. On the last whorl, there are two yellow bands on white ground.

Shell height 7.2, width 4.2 mm; mouth 3.5 mm high and about 2 mm wide. One specimen from station 143 (212 m).

Comments. This name was listed by Cernohorsky (1984: 107) as a questionable synonym of *Nassarius* (*Niotha*) *agapetus* (Watson, 1882). For further comments see under *munda*.

Nassa thaumasia Sturany, 1900

Figure 17A-E
Sturany, 1900a: 198–199; redescribed and illustrated in Sturany (1903), page 222, plate II, figure 8.

Type locality. Ras Abu Somer (not specified in the original text, but very likely locality 18, littoral; Table 2).

Additional original localities. 94 (314 m) (Northern Red Sea, Table 1).

Type material. Lectotype: NHMW 37579 (locality 18; height 27 mm), fixed by erroneous inference of "holotype" (ICZN art. 74.6) by Cernohorsky 1984: 132, pl. 25 fig. 10. Paralectotype: NHMW 111535: 1 specimen (Ras Abu Somer, likely locality 18).

Additional material. NHMW 84180 (station 87): 7 specimens.

Original description. *Gehäuse festschalig, aus 10 1/2 langsam zunehmenden, schwach stufig abgesetzten Windungen kegelig aufgebaut; das Embryonalgewinde glatt, die darauffolgenden Umgänge mit breiten Querwülsten und vier bis fünf Spiralreihen ausgestattet, die Schlusswindungen (2 1/2 oder mehr) abgeglättet bis auf* *eine zur Naht parallel ziehende Spiralfurche und eine Reihe von Spirallinien in der Nabelgegend im Umkreise des Ausschnittes der Mündungsbasis; auf gelblichweißem Grundtone sind gelbbraune Querstriemen in unregelmäßiger und spärlicher Vertheilung und auf dem letzten Umgänge zwei breite, gelbbraune Längsbinden mehr oder minder ausgeprägt; kurz vor dem äußeren Mündungsrand ein dicker Wulst, im Gaumen, sowie auf dem Wulste der Spindel und der Mündungswand eine größere Anzahl von Falten; der untere Theil des äußeren Mündungsrandes etwas ausgezackt.*

Höhe der Schale 27,2, Breite 13,0mm; Höhe der Mündung 14,0, Breite 7,5mm. Fundort: Ras Abu Somer (litoral).

Translation. Shell thick, conical, made of 10.5 slowly growing, weakly scalariform whorls; smooth protoconch, the following whorls have broad axial ribs and four to five spiral threads, the final whorls (two and half or more) smooth except for a groove parallel to the suture and a series of spiral lines in the umbilical region close to the aperture; on the yellowish-white background there are irregularly and sparsely distributed yellow-brown flecks and on the last whorl there are two wide, yellow-brown spiral bands more or less pronounced; shortly before the outer lip there is a thick varix; there is a large number of folds on the callus of the columella and the inner lip; the lower part of the lip is slightly jagged.

Shell height 27.2, width 13.0 mm; height of the mouth 14.0, width 7.5 mm. Locality: Ras Abu Somer (littoral).

Comments. *Nassa steindachneri*, *thaumasia*, *thaumasia* var. *nana* and *xesta* are regarded as synonymous. *N. thaumasia* var. *nana* and *steindachneri* occur together at station 94 and both lots show the same variability of sculpture from regularly reticulated to nearly smooth last whorls. Janssen in Janssen and Taviani (2015: 526) used *steindachneri* as valid name because this is the most common variant, but Dekker and Orlin (2000: 28) synonymised already these taxa and as first revisers selected *Nassarius thaumasius* (Sturany, 1900) as valid name. *Nassa thaumasia* was considered by Cernohorsky (1984: 130) as synonym of *Nassarius* (*Zeuxis*) *castus* (Gould, 1850). However, this is most probably wrong, because according to own observations (RJ) *thaumasia* has a much finer sculpture consisting of dense reticulation, especially on the early whorls, more numerous and finer spiral ribs on the fasciole, only weakly canaliculated sutures and a much lesser developed sutural nodules. Cernohorsky figured the alleged "holotype" of *thaumasia* on his pl. 25 fig. 10.

According to Cernohorsky (1984: 135), *Nassa steindachneri* is a synonym of *Nassarius* (*Zeuxis*) *siquijorensis* (A. Adams, 1852). If this proves to be correct, *siquijorensis* would become the valid name for the assemblage of nominal taxa described by Sturany, but this needs further study.

Nassa thaumasia f. *nana* Sturany, 1900

Figure 17H-J

Sturany, 1900a: 199; redescribed and illustrated in Sturany (1903), page 222, plate II, figure 7.

Original localities. 94 (314 m) and 96 (350 m) (Northern Red Sea, Table 1).

Type material. Syntypes: NHMW 84181 (station 94): 1 specimen; NHMW 84182 (station 94): 11 specimens; NHMW 84183 (station 96): 1 specimen.

Original description. *In der continentalen Zone (Station 94 [314 m] und Station 96 [350 m]) kommt eine kleinere Form vor (var.* nana *m.), deren Länge 20 und deren Breite 10 mm betragt bei einer Mündungsausdehnung von 10 ½: 6mm.*

Translation. In the continental zone (station 94 [314 m] and station 96 [350 m]), there is a smaller form (var. *nana*) with 20 mm length and 10 mm width, at the aperture 10.5 high and 6 mm wide.

Comments. The variety *nana* was introduced for the deep water specimens; the specimen illustrated in Figure 17 H-J is 19.8 mm high. For further comments see under *thaumasia*.

Nassa xesta Sturany, 1900

Figure 18

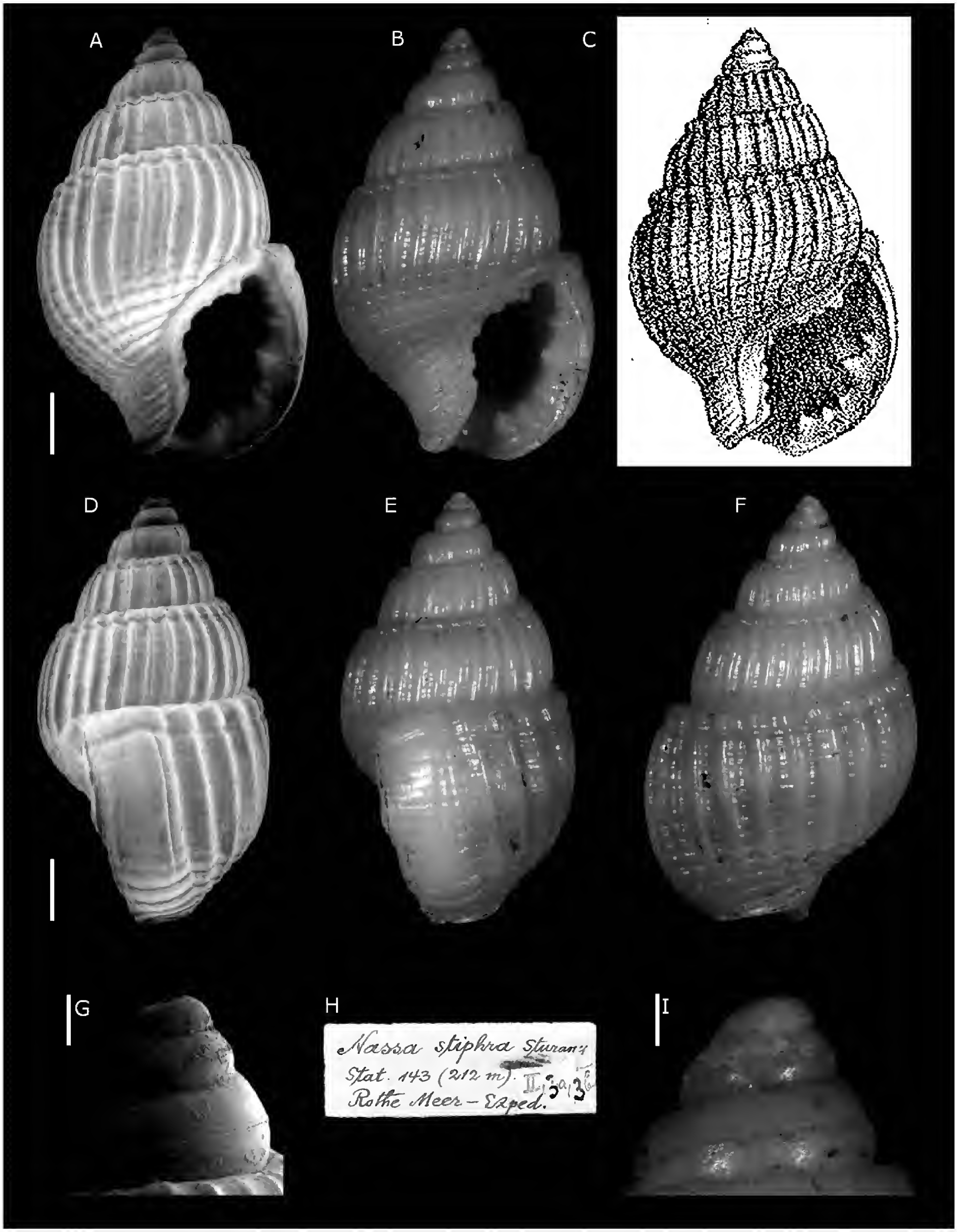
Sturany, 1900a: 199–200; redescribed and illustrated in Sturany (1903), page 223, plate II, figures 6a–b.

Type locality. Station 143, "nächst der Insel Harmil" [near Harmil Island, Dahlak Archipelago, Eritrea] 17°7'N, 39°55'E, 212 m.

Type material. Holotype: NHMW 84189, height 19.4 mm.

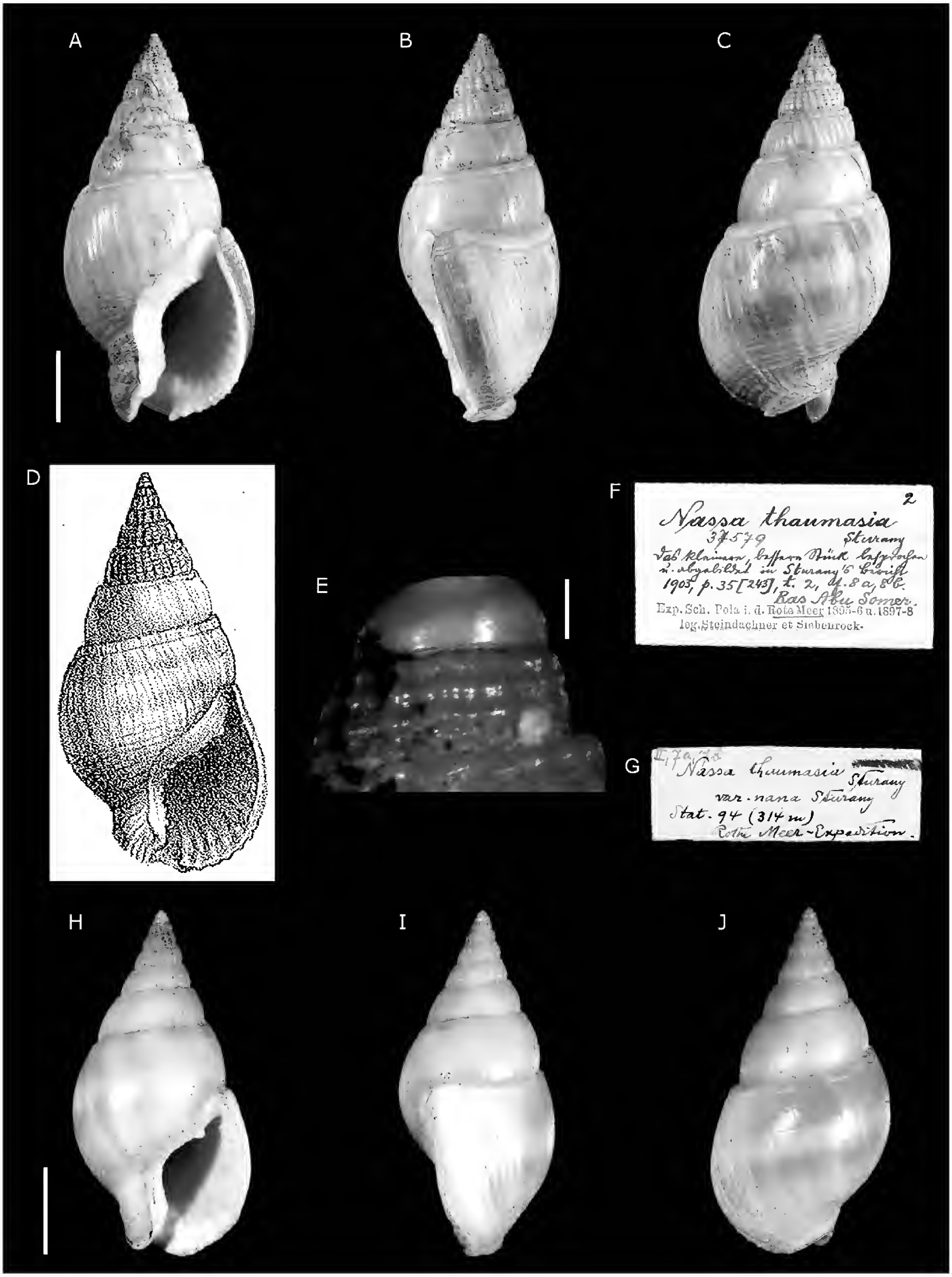
Original description. *Gehäuse kegelig aufgebaut, dickschalig, fettglänzend; von den 9 1/2 Windungen sind nur die vierte und fünfte mit Querwülsten ausgestattet, die übrigen glatt mit Ausnahme etwa noch des Basaltheiles der Schlusswindung, wo wieder concentrisch angeordnet und am Außenrande der Mündung als Kerbung endigend, fünf bis sechs Spiralreifen zu zählen sind. Eine Bänderung ist nur in Spuren vorhanden, ferner sind nächst der Naht gelbbraune Flecken sichtbar, welche von milchweißen Partien des Grundtones besonders abstechen. Vor der Mündung ein Wulst, im Gaumen zahlreiche Falten und ebenso auf den Calluspartien eine Fältelung.*

Höhe des Gehäuses 20, Breite 10mm; Mündung 9,5 mm hoch und 5,5 mm breit. — Von Station 143 (212 m) ein einziges Exemplar vorliegend.



Nassa stiphra Sturany
Stat. 143 (212 m). II/5a/3b
Rothe Meer - Exped.

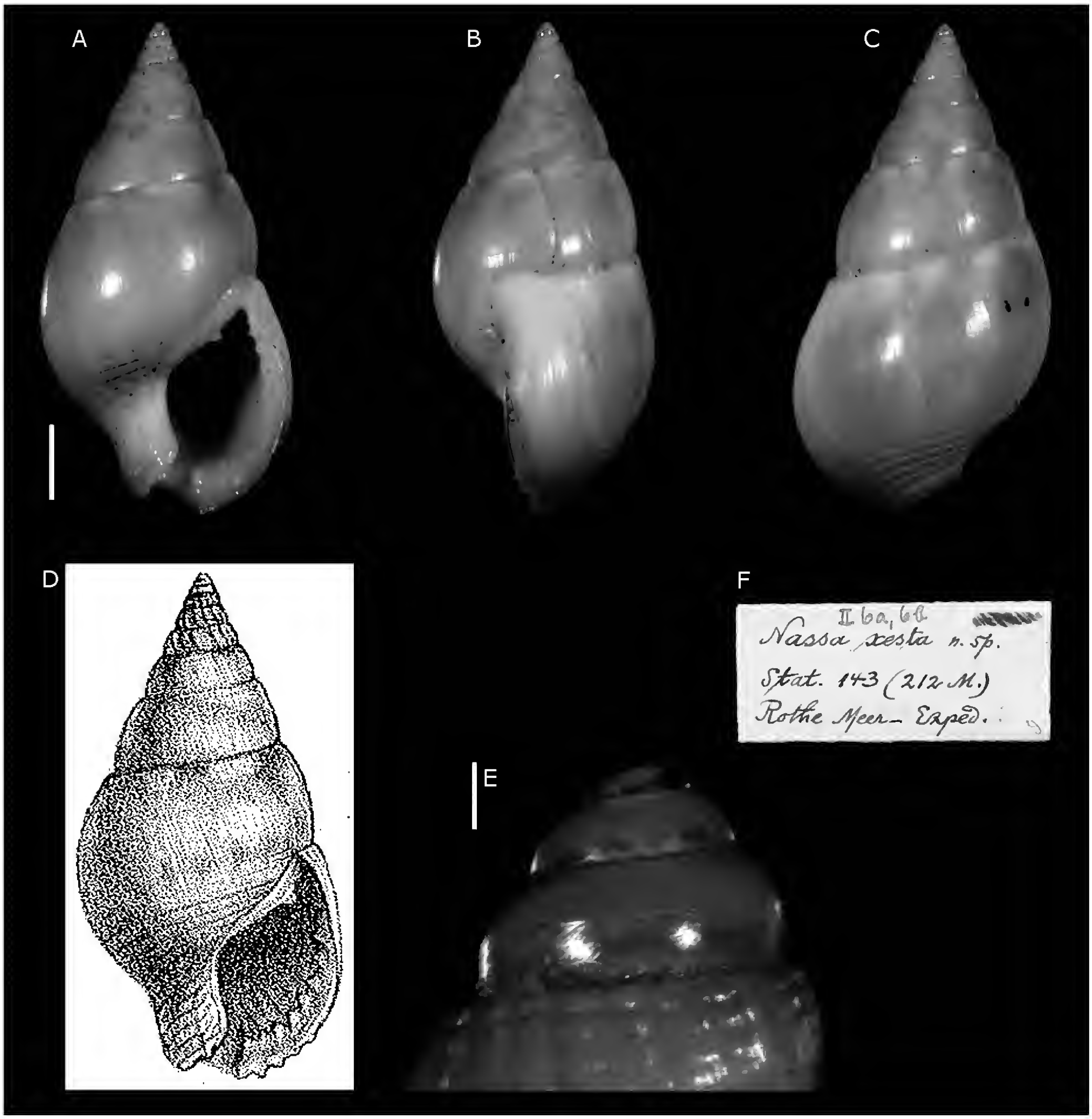
Figure 16. *Nassa stiphra* Sturany, 1900, Station 143 (Harmil Island, Dahlak Archipelago, Eritrea). **A–B**, **D–G**, **I**. Holotype, NHMW 84195: front (**A–B**), right side (**D–E**), back (**F**), protoconch (**G, I**). **C**. Original figure by Sturany (1903). **H**. Original holotype label. Scale bars: **A–B**, **D–F**: 1 mm, **G**, **I**: 0.2 mm.



2
Nassa thaumasia
37579 Sturany
Das kleinere, bessere Stück beschrieben
u. abgebildet in Sturany's Schrift
1903, p. 35[243], t. 2, f. 8 a, 8 b.
Ras Abu Somer.
Exp. Sch. Pola i. d. Rote Meer 1895-6 u. 1897-8
leg. Steindachner et Siebenrock.

II, 7a, 7b
Nassa thaumasia Sturany
var. nana Sturany
Stat. 94 (314 m)
Rothe Meer-Expedition.

Figure 17. *Nassa thaumasia* Sturany, 1900. **A–C, E**. Lectotype, NHMW 37579, Ras Abu Somer, Egypt, Red Sea (likely “locality 18”): front (**A**), right side (**B**), back (**C**), protoconch (**E**). **D**. Original figure by Sturany (1903). **F**. Original lectotype label. **G**. Original label of the form *nana*. **H–J**. Form *nana*, syntype NHMW 84181, Station 94 (Nuweiba, Gulf of Aqaba, Egypt): front (**H**), right side (**I**), back (**J**). Scale bars: **A–C, H–J**: 5 mm, **E**: 0.2 mm.



II 6a, 6b
Nassa xesta n. sp.
Stat. 143 (212 M.)
Rothe Meer-Exped.

Figure 18. *Nassa xesta* Sturany, 1900, Station 143 (Harmil Island, Dahlak Archipelago, Eritrea, Red Sea). **A–C, E**. Holotype, NHMW 84189: front (**A**), right side (**B**), back (**C**), protoconch (**E**). **D**. Original figure by Sturany (1903). **F**. Original holotype label. Scale bars: **A–C**: 3 mm, **E**: 0.2 mm.

Diese und die vorhergehenden Nassa-*Arten gehören in eine Reihe und lassen sich etwa von* N. gaudiosa *Hinds ableiten.*

Translation. Shell conical, thick, shiny; of the 9.5 whorls, only the fourth and the fifth have axial ribs, the others are smooth except at the base of the final whorl, where five to six concentric spiral grooves can be counted ending at the lip as notches. Only traces of colour bands are present, next to the suture yellow-brown flecks are visible, which contrast with the milky white ground colour. Before the aperture there is a thickened spiral rib, the lip and the callus have numerous folds.

Height of the shell 20, width 10 mm; aperture 9.5 mm high and 5.5 mm wide. From station 143 (212 m) a single specimen was found.

This and the preceding *Nassa* species belong to a series and are related to *N. gaudiosa* Hinds.

Comments. Cernohorsky (1984: 146) listed *xesta* as possible synonym of *Nassarius* (*Zeuxis*) *comptus* (A. Adams, 1852). However, closer examination of the types demonstrates that *xesta* is only an extreme form of *thaumasia* to which it agrees completely with regard to colour pattern and sculpture of the early teleoconch whorls. For further comments see under *thaumasia*.

Family Mitridae Swainson, 1831

Mitra (*?Thala*) *gonatophora* Sturany, 1903

Figure 19
Sturany, 1903: 225, plate IV, figure 2.

Original localities. Station 48 (700 m) and 51 (262 m) (Central Red Sea; Table 1).

Type material. Figured syntype: NHMW 84210 (station 48), illustrated by Sturany (1903) in plate IV, figure 2, height 7.2 mm. Further syntypes: NHMW 84211 (station 48): 1 specimen; NHMW 84212 (station 51): 2 specimens.

Original description. *Von den Stationen 48 (700 m) und 51 (562 m).*

Der zunächst folgenden Beschreibung ist ein zur Abbildung gebrachtes Exemplar von der Station 48 zu Grunde gelegt, welches bei kaum 8 Umgängen 8,2 mm hoch und 2,5 mm breit ist, während die Mündungshöhe 4,2 und die Mündungsbreite 1,5 mm beträgt. Die Schale ist spindelförmig und an der Basis etwas zurückgebogen. Die Sculptur beginnt auf der 4. Windung, kurz nach Ablauf der dritten, und zwar mit 3 Spiralreihen von Knoten. Mit dem Beginne der vorletzten Windung setzt auch eine Spaltung der beiden unteren Knotenreihen in je 2 zartere Spiralreifen ein, so dass also auf der vorletzten Windung 1 breitere obere Knotenreihe und 4 zartere, darunter gelegene Spiralreifen abzuzählen sind. Auf der Schlusswindung verlaufen unter den genannten Knotenreihen noch 9 in gleichmäßigen Entfernungen voneinander getrennte Knotenreihen, welche am äußeren Mundrande endigen, und überdies noch einige um den untersten Theil der Schale gelagerte Spiralreifen. In den Zwischenräumen der Knotenreihen liegen regelmäßige Querstriche, so dass eine Cancellierung hervorgebracht ist. Das Gehäuse ist nicht ganz einfarbig braun, in der Mündung und ebenso in der ziemlich tiefliegenden Naht ist eine weiße Färbung erkennbar. Auf der Spindel, welche weiß ausgeschlagen ist, stehen 3 stärkere Querfalten und unter diesen eine schwächere; über ihnen erscheinen einige der Spiralreifen des letzten Umganges in Form von in das Spindelfeld hereinragenden Falten fortgesetzt.

Das zweite minder gut erhaltene Exemplar von Station 48 (700 m) lässt gleichwohl einige Ergänzungen der obigen Diagnose zu. Es misst 7 ½: 2 ½ mm und lässt einen schwachen Glanz des Embryonalgewindes erkennen, sowie eine geringe Anzahl von Columellarfalten (nur 3 Hauptfalten und keine darübergelagerten Fortsetzungen der Spiralreifen bis ins Spindelfeld).

Mitra mirifica *Rve. ist wohl eine der nächststehenden Verwandten.*

Translation. From stations 48 (700 m) and 51 (562 m).

The following description is based on a figured specimen from station 48 [Figure 19 A-G], which has almost eight whorls, 8.2 mm high and 2.5 mm wide, while the height of the mouth is 4.2 and the width 1.5 mm. The shell is fusiform and at the base slightly curved. The sculpture starts on the fourth whorl, shortly after the end of the third, with three spiral rows of tubercles. At the beginning of the penultimate whorl a splitting of the two lower rows of tubercles in two delicate spiral cords begins, so that on the penultimate whorl one expanded upper row of tubercles and four more delicate, lower spiral rows can be counted. On the final whorl under the mentioned rows of tubercles, nine further rows of tubercles run at uniform distances and end at the outer lip, additionally some more spiral rows run on the lowest part of the shell. In the interstices of the spiral rows, there are regular axial riblets so that a cancellated sculpture is generated. The shell is not uniformly brown, in the mouth and on the quite deep suture a white colouration can be seen. On the columella, which has a white callus, there are three strong transverse folds, and below them a weak one; some of the spiral rows of the last whorl continue above them under the columellar callus.

The second less well-preserved specimen from Station 48 (700 m) [Figure 19 I-K] allows nevertheless some additions to the diagnosis above. It measures 7.5 mm [height] 2.5 mm [width] and reveals a weak lustre of the protoconch, and a small number of columellar folds (only three main folds, not continuing under the columella callus).

Mitra mirifica Reeve is probably one of the closest relatives.

Mitra tenuis f. *minor* Sturany, 1903

Figure 20
Sturany, 1903: 244–245, plate VII, figure 7.

Original localities. Localities 10 and 21 (Northern Red Sea; Table 2).

Type material. Figured syntype: NHMW 37613 (locality 21), illustrated by Sturany (1903) in plate IV, figure 2, height 12 mm. Further syntypes: NHMW 37612 (locality 10): 1 specimen; NHMW 37185 (locality 21): 1 specimen (preserved in ethanol).

Original description. *Von den Localitäten 10 und 21.*

Das zur Abbildung gebrachte gelbbraune Gehäuse von Koseir ist 11,5 mm hoch und 3,5 mm breit, besitzt eine Mündung von 6 mm Höhe und besteht aus 10 Umgängen. Die Anfangswindungen sind glatt, zitzenförmig, hellgelb gefärbt, die folgenden Umgänge mit einer fadenförmigen, hellfarbigen Verdickung an der oberen Naht und einigen Spirallinien ausgestattet. Auf dem letzten Umgange läuft eine mediane helle Binde, die ebenso wie die erwähnte lichte Nahtpartie sich schärfer von der sie umgebenden Färbung abheben kann (beispielsweise bei einem etwas kleineren Exemplare von Nawibi). Die Spindel ist mit einer stärkeren und einigen schwächeren Falten versehen.

Für das Rothe Meer ist M. tenuis *noch nicht bekannt gewesen. Das Berliner Museum besitzt sie von Mauritius und ebendaher stammt die nahverwandte* M. flexilabris *Sow.*

Translation. From localities 10 and 21.

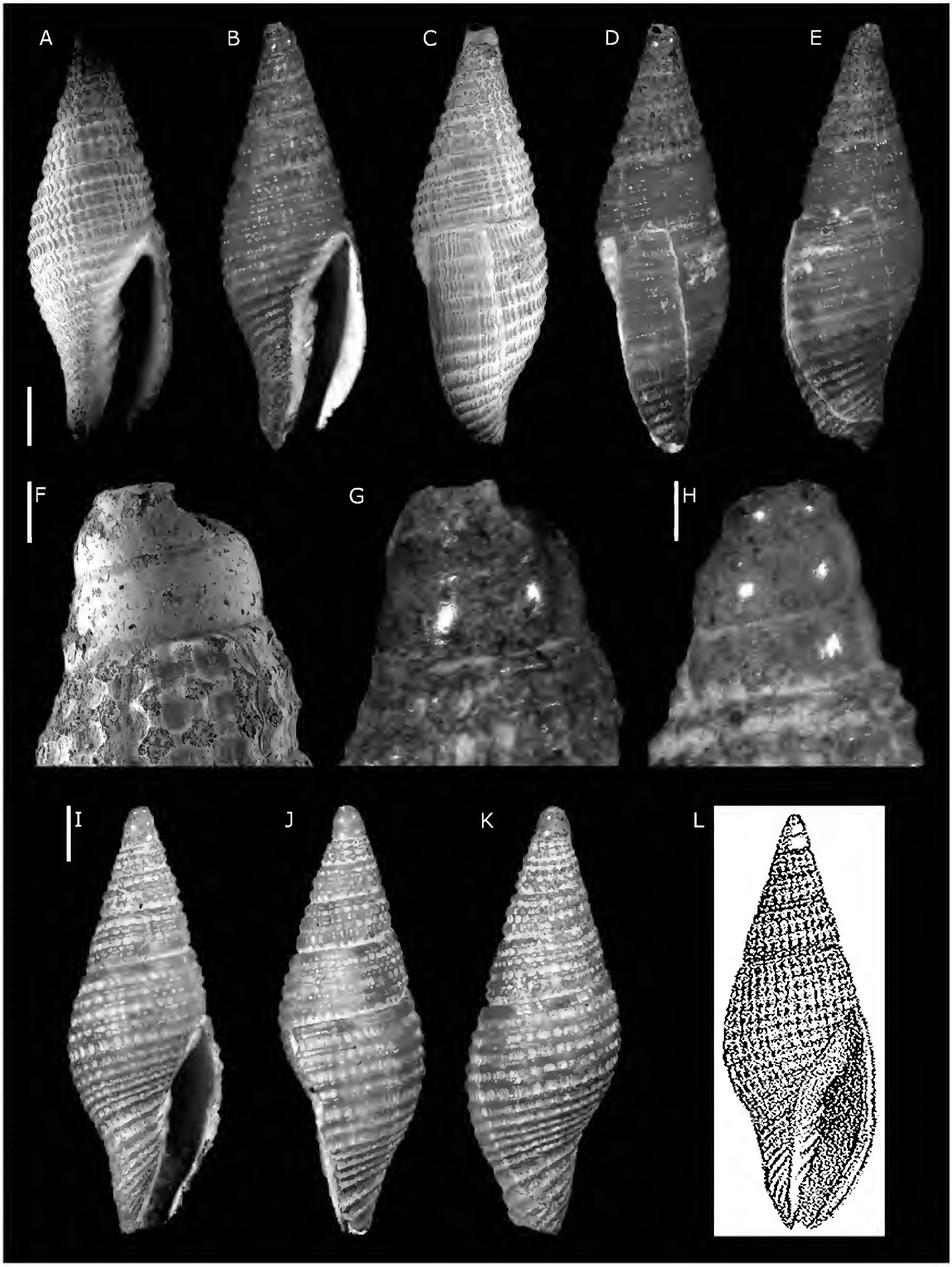
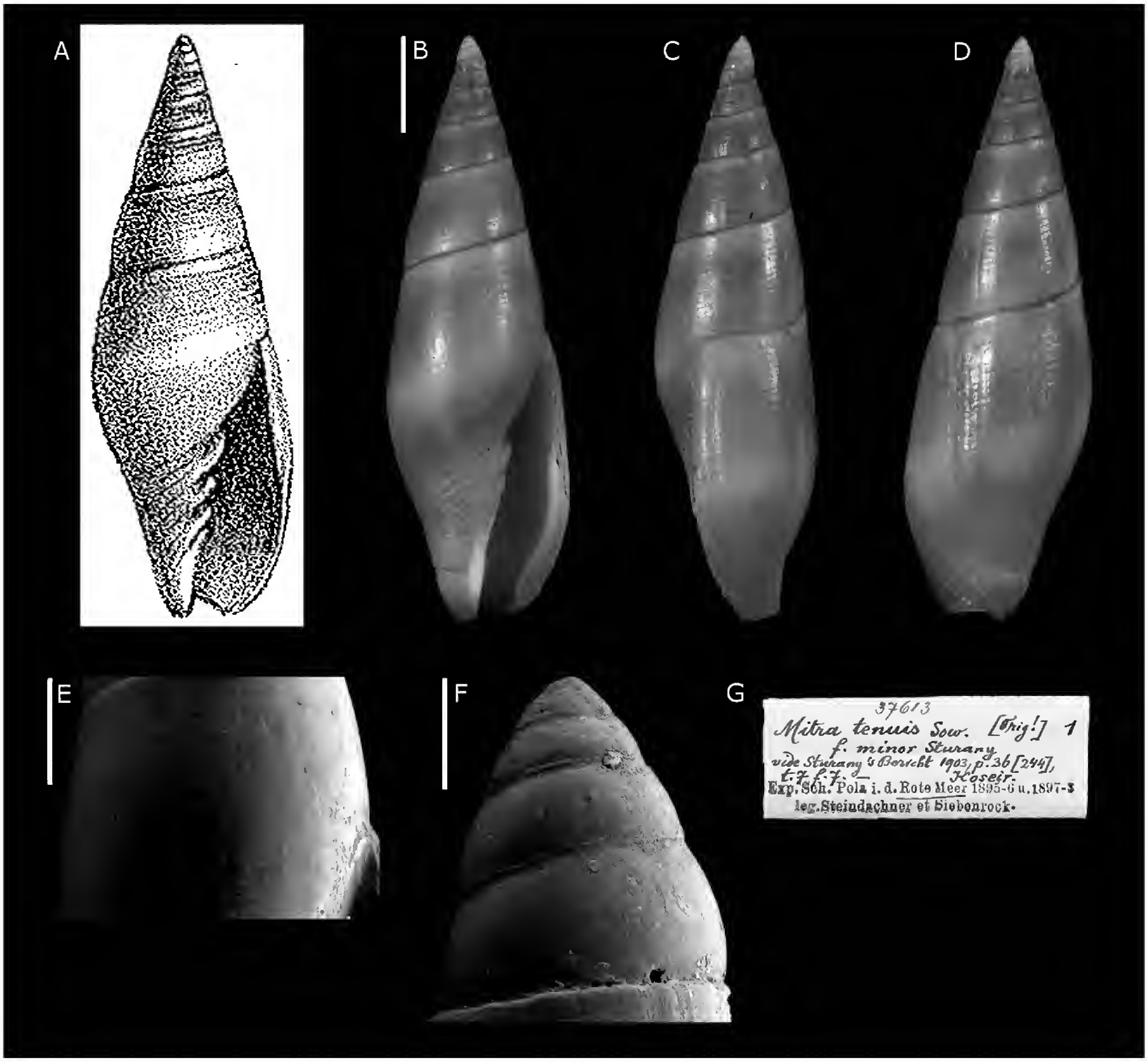


Figure 19. *Mitra gonatophora* Sturany, 1903, Station 48 (Yanbu' al Bahr, Saudi Arabia, Red Sea). **A–G**. Figured syntype, NHMW 84210: front (**A–B**), right side (**C–D**), back (**E**), protoconch (**F–G**). **H–K**. Syntype, NHMW 84211: protoconch (**H**), front (**I**), right side (**J**), back (**K**). **L**. Original figure by Sturany (1903). Scale bars: **A–E**, **I–K**: 1 mm, **F–H**: 0.2 mm.



37613
Mitra tenuis Sow. [Orig!] 1
f. minor Sturany
vide Sturany's Bericht 1903, p. 36 [244],
t. 7 f. 7. — Koseir.
Exp. Sch. Pola i. d. Rote Meer 1895-6 u. 1897-8
leg. Steindachner et Siebenrock.

Figure 20. *Mitra tenuis* f. *minor* Sturany, 1903, Locality 21 (El Quseir, Egypt, Red Sea). **A**. Original figure by Sturany (1903). **B–F**. Figured syntype, NHMW 37613: front (**B**), right side (**C**), back (**D**), microsculpture (**E**), protoconch (**F**). **G**. Original label. Scale bars: **B–D**: 2 mm, **E–F**: 0.25 mm.

The figured shell from El Quseir [locality 21] is 11.5 mm high and 3.5 mm wide, has an aperture 6 mm high and consists of 10 whorls. The protoconch is smooth, teat-shaped, light yellow, the following whorls show a filiform, brightly coloured thickening on the suture and some spiral lines. On the last whorl, there is a median light coloured band, which may show up from the surrounding colour like the mentioned bright suture (like in a slightly smaller specimen from Nawibi [locality 10]). The columella has one stronger and some weaker folds.

M. tenuis was not yet known from the Red Sea. The Berlin Museum has specimens from Mauritius and from the same locality the closely related *M. flexilabris* Sowerby.

Comments. The description of *Mitra tenuis* G.B. Sowerby III, 1874 is based on an immature specimen. Cernohorsky (1976) considered both it and Sturany's *minor* form junior synonyms of *Mitra typha* Reeve, 1845.

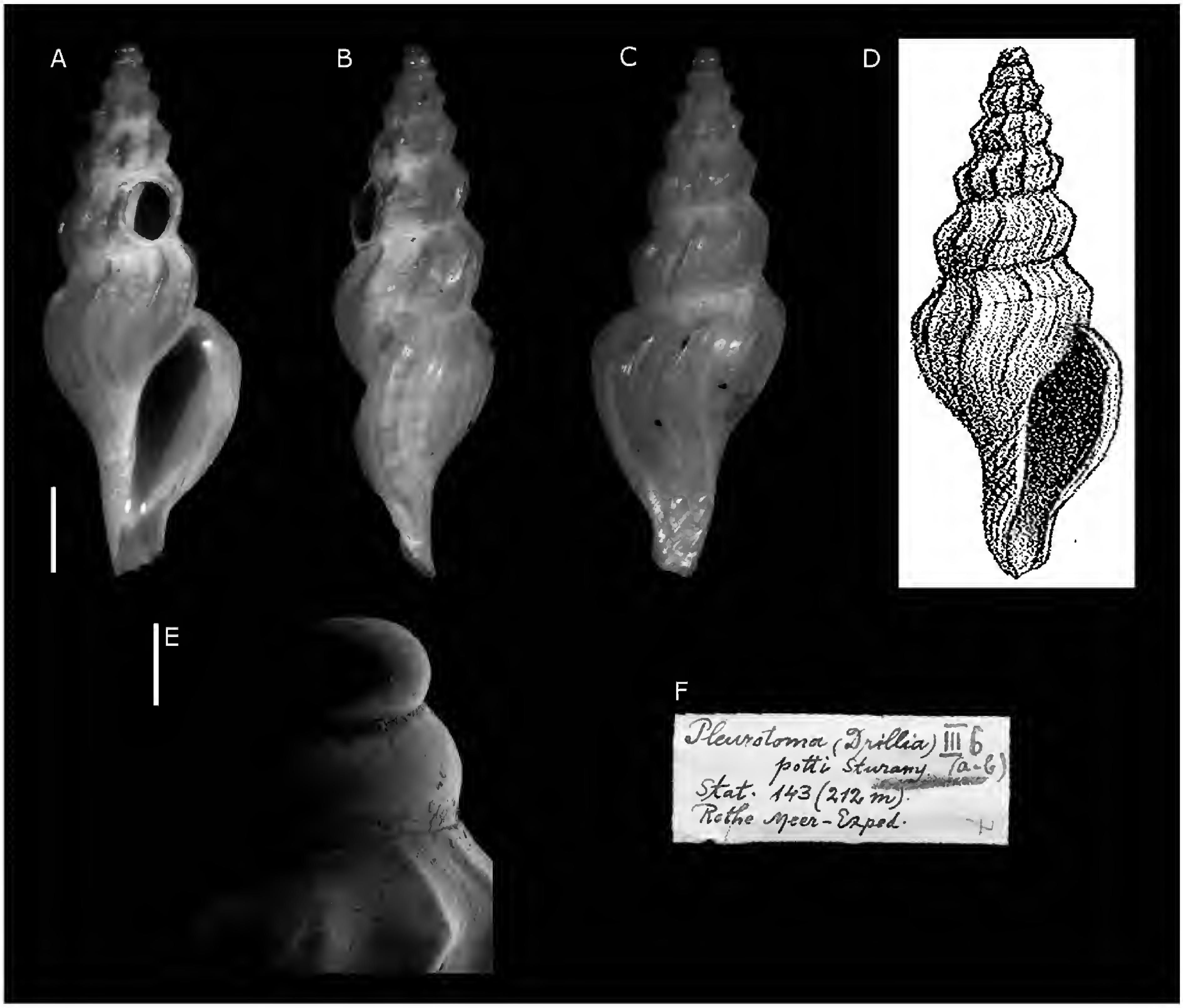
Family Drilliidae Olsson, 1964

Pleurotoma (*Drillia*) *potti* Sturany, 1900

Figure 21

Sturany, 1900b: 209–210; redescribed and illustrated in Sturany (1903), page 229, plate III, figures 6a–b.

Type locality. Station 143, "nächst der Insel Harmil" [near Harmil Island, Dahlak Archipelago, Eritrea] 17°7'N, 39°55'E, 212 m.



Pleurotoma (Drillia) III 6
potti Sturany (a-b)
Stat. 143 (212 m).
Rothe Meer-Exped.

Figure 21. *Pleurotoma potti* Sturany, 1900, Station 143 (Harmil Island, Dahlak Archipelago, Eritrea, Red Sea). **A–C, E**. Holotype, NHMW 84250: front (**A**), right side (**B**), back (**C**), protoconch (**E**). **D**. Original figure by Sturany (1903). **F**. Original holotype label. Scale bars: **A–C**: 2 mm, **E**: 0.2 mm.

Type material. Holotype: NHMW 84250, height 12.4 mm.

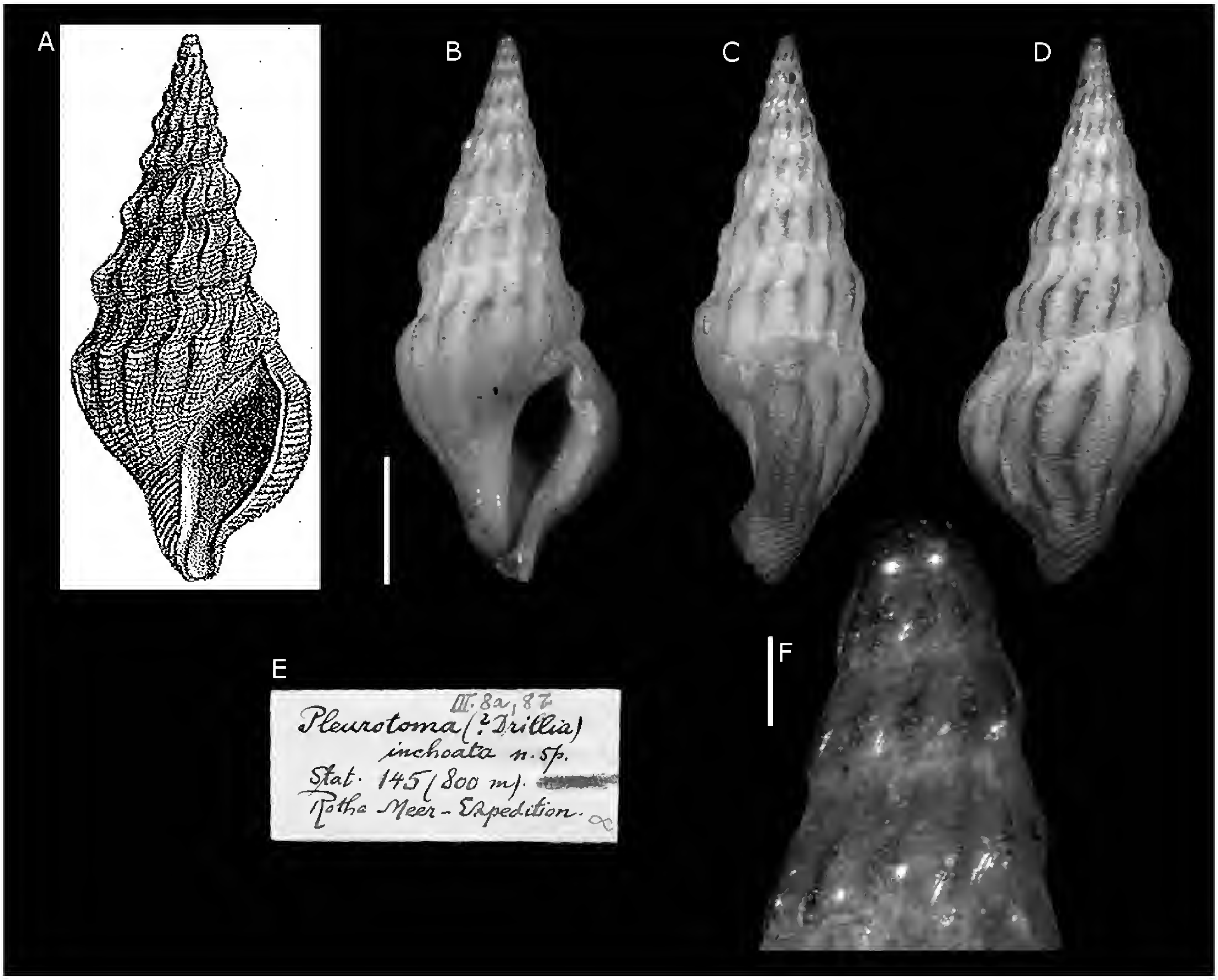
Original description. *Gehäuse spindelförmig, aus nahezu 8 Umgängen gebildet, gelbbraun mit geringen Spuren von etwa 6—7 braunen Spiralbändern, welche nur an dem Wulste vor der Mündung sichtbar sind; die Anfangswindungen glatt, glänzend und gerundet, die übrigen mit 9—10 starken, schief gestellten und gewinkelten Querfalten ausgestattet, so dass die ganzen Windungen gewinkelt erscheinen. Auf dem letzten Umgange schieben sich zwischen diese hier nur mehr in der 8-Zahl vorhandenen Querfalten einige undeutliche Nebenfalten ein und steht unmittelbar vor der Mündung eine gewaltige, von der Naht bis zur Basis verlaufende, rippenartige Verdickung. Spiralsculptur nur an der Basis der Schlusswindung angedeutet (schief über den stielförmigen Canal verlaufende Linien). Mündung langgestreckt, mit leicht zurückgebogenem Canal, scharfem, innen weiß gelippten Rande und rundem Ausschnitte.*

Höhe des Gehäuses 12,0, Breite 4,3 mm; Mündung 6,0 hoch und 2,2 mm breit.

Ein Exemplar von Station 143 (212 m).

Als verwandte Formen seien P. pudica *Hinds und* P. studeriana *Marts, genannt.*

Translation. Shell fusiform, with nearly eight whorls, light brown with fine traces of about 6 – 7 brown spiral bands, which are visible only on the lip varix; the protoconch is smooth, shiny and rounded, the other 9–10 whorls have strong, oblique and angulate axial ribs, so that the whole whorls appear angulated. On the last whorl, further indistinct axial threads are present among the last eight axial ribs and, before the aperture, there is a large axial thickening running from the suture to the base. Spiral sculpture can be recognized only at the base of the last whorl (oblique threads run on the siphonal canal). Aperture elongated, with slightly recurved canal, and a sharp, white inside, aperture border.



III. 8a, 8b
Pleurotoma (? Drillia)
inchoata n. sp.
Stat. 145 (800 m).
Rothe Meer - Expedition.

Figure 22. *Pleurotoma inchoata* Sturany, 1900, Station 145 (Dahlak Archipelago, Eritrea, Red Sea). **A**. Original figure by Sturany (1903). **B–D**, **F**. Holotype, NHMW 84251: front (**B**), right side (**C**), back (**D**), protoconch (**F**). **E**. Original holotype label. Scale bars: **B–D**: 5 mm, **F**: 0.5 mm.

Height of the shell 12.0 mm, width 4.3 mm; mouth 6.0 mm high and 2.2 mm wide.

One specimen from station 143 (212 m).

P. pudica Hinds and *P. studeriana* Martens are known as related forms.

Comments. It is considered to belong to genus *Drillia* Gray, 1838 by Tucker (2004), but it does not seem to fit well into this genus. It may belong to *Leiocithara* Hedley, 1922.

Pleurotoma (?*Drillia*) *inchoata* Sturany, 1900

Figure 22
Sturany, 1900b: 210; redescribed and illustrated in Sturany (1903), page 229–230, plate III, figures 8a–b.

Type locality. Station 145, "östlich von J. Dahalak" [east of Dahlak Island, Eritrea], 16°2.6'N, 41°13.5'E, 800 m.

Type material. Holotype: NHMW 84251, height 21.2 mm.

Original description. *Schale abgestutzt spindelförmig, hellgelb, aus 9 1/2 Umgängen bestehend, deren jeder mit Ausnahme des Embryonalgewindes in seiner oberen Hälfte concav, in seiner unteren convex gebaut ist, und welche mit zahlreichen Spiralreifen und circa 15—16 wellenförmig verlaufenden Querrippen ausgestattet sind; überdies stehen zwischen den Querrippen noch mikroskopisch feine Anwachsstreifen. Unmittelbar vor der (leider mangelhaft erhaltenen) Mündung eine knotig angeschwollene und nach rechts vorgezogene Querrippe.*

Höhe der Schale 21,3, Breite 9,0 mm; Höhe der Mündung 9,1 mm.

Ein einziges Exemplar von Station 145 (800 m).

Verwandt mit P. (Drillia) pallida *Sow.; in der Form an* Columbella angularis *Sow. gemahnend.*

Translation. Shell truncated and fusiform, pale yellow, made by 9.5 whorls, concave in their upper half and convex in the lower half, with the exception of the protoconch; with numerous spiral threads and approximately 15 – 16 undulated axial ribs among which microscopically fine growth lines stand. Immediately prior to the (unfortunately poorly preserved) aperture, there is a thick nodulose axial rib bent to the right.

Height of the shell 21.3 mm, width 9.0 mm; height of the mouth 9.1 mm.

A single specimen from station 145 (800 m).

Related to *P.* (*Drillia*) *pallida* Sowerby; shape reminding *Columbella angularis* Sowerby.

Comments. This species can be assigned to the genus *Drillia* Gray, 1838

Pleurotoma (*Clavus*) *siebenrocki* Sturany, 1900

Figure 23
Sturany, 1900b: 210–211; redescribed and illustrated in Sturany (1903), page 230, plate III, figures 9a–c.

Type locality. Station 76, "südlich der Insel Senafir" [south of Sanafir Island], 27°43'N, 34°47'E, 900 m.

Type material. Holotype: NHMW 84252, height 36.6 mm.

Original description. *Schale gethürmt, geritzt, hellgelbbraun, aus 12 Umgängen aufgebaut, die mit Ausnahme des Embryonalgewindes mit 7—8 knotenartigen Rippen besetzt sind. In der tief eingeschnürten oberen Partie der Umgänge verlaufen feine Spirallinien, im übrigen groβere, mitunter unregelmäβig geknickte oder undulierte Leistchen; die zahlreichen, feinen Anwachsstreifen sind meist nur in den concaven Partien sichtbar. Mündung mit tiefem, zungenförmigen Ausschnitt oben und sehr kurzem, zurückgebogenen Canal unten.*

Höhe des Gehäuses 36,7, Breite 14,0 mm; Mündung 16,0 mm hoch und 5,5 mm breit.

Ein Exemplar von Station 76 (900 m).

Von der nächstverwandten Art P. (Clavus) dunkeri *Wkff. durch die gestrecktere Form und die minder „strombus-artige" Mündung unterschieden.*

Translation. Shell turriculate, striated, light golden brown, composed of 12 whorls, which have 7-8 nodular ribs except on the protoconch. In the deeply constricted upper part of the whorls, there are fine spiral lines, whereas in the lower part coarser, sometimes irregularly flexed or undulated threads; the numerous, fine growth lines are usually visible in the concave part only. Mouth with deep, tongue-shaped posterior siphonal canal and a very short, recurved anterior canal at the base.

Height of the shell 36.7 mm, width 14.0 mm; mouth 16.0 mm high and 5.5 mm wide.

One specimen from station 76 (900 m).

Distinguished from the closely related species *P.* (*Clavus*) *dunkeri* Weinkauff by the more elongated shape and the less "strombus-like" aperture.

Family Horaiclavidae Bouchet, Kantor, Sysoev and Puillandre, 2011

Pleurotoma (*Surcula*) *nannodes* Sturany, 1900

Figure 24
Sturany, 1900b: 209; redescribed and illustrated in Sturany (1903), page 230, plate III, figures 2a–c.

Original localities. Stations 48 (700 m) and 143 (212 m) (Central and Southern Red Sea; Table 1).

Type material. Illustrated syntype: NHMW 84254 (station 143), illustrated by Sturany (1903) in plate III, figures 2 a–c, height 8 mm. Further one syntype NHMW 84253 (station 48).

Original description. *Schale reinweiβ, abgestutzt spindelförmig, aus 9 Umgängen bestehend. Die Embryonalwindungen glatt, die übrigen gegittert und knotig sculptiert; ein median angelegter, dominierend breiter, geperlter Spiralreifen, eine nächst der Naht verlaufende schwächere Knotenreihe und 1 bis 2 feinste Spirallinien ober und unter der Mitte (auf dem letzten Umgange sind es naturgemäβ deren mehr) werden nämlich von den zahlreichen quer und bogig über die Umgänge gestellten Längsrippen gekreuzt. Mündungsrand scharf, mit zungenförmigem Ausschnitte nächst der Naht und halbkreisförmiger Bucht an der Basis.*

Höhe der Schale 7,1 und 8,4 mm, Breite 2,7 und 3,1 mm; Mündungshöhe 2,6 und 3,0, Mündungsbreite 1,2 und 1,4 mm.

Von den Stationen 48 (700 m) und 143 (212 m) je ein Exemplar.

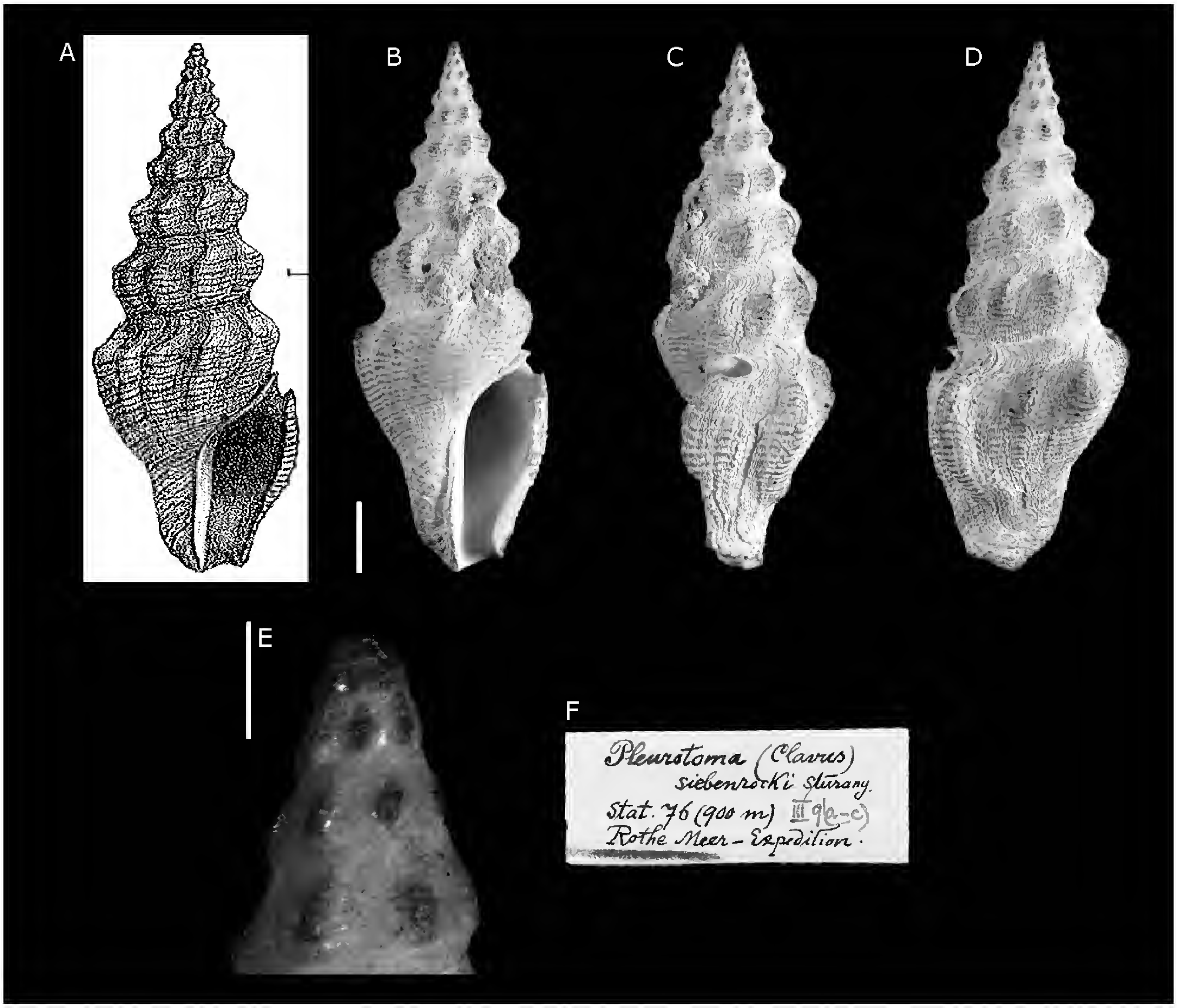
Die neue Art ist gewissermaβen eine Miniaturausgabe von P. radula *Hinds.*

Translation. Shell pure white, truncate fusiform, composed by nine whorls. Protoconch smooth, the other whorls with a reticulated and tubercled sculpture; a median, prominent, wide, tubercled spiral thread; closer to the suture, there are weaker tubercled threads and one or two fine spiral lines above and below the median prominent spiral thread (on the last whorl there are naturally more); the spiral sculpture is crossed by numerous curved axial ribs. Lip sharp, with tongue-shaped posterior siphonal canal next to the suture and a semi-circular anterior canal at the base.

Height of shells is 7.1 mm and 8.4 mm, width 2.7 mm and 3.1 mm; mouth height 2.6 mm and 3.0 mm, mouth width 1.2 mm and 1.4 mm. From each of stations 48 (700 m) and 143 (212 m) one specimen.

The new species is a kind of miniature version of *P. radula* Hinds.

Comments. This species was assigned to the genus *Paradrillia* Makiyama, 1940 by Orlin and Dekker (2000: 32) and Janssen in Janssen and Taviani (2015: 526); it looks like *Paradrillia melvilli* Powell, 1969, which could be a junior synonym.



Pleurotoma (Clavus)
siebenrockì Sturany.
Stat. 76 (900 m) III 9(a-c)
Rothe Meer-Expedition.

Figure 23. *Pleurotoma siebenrocki* Sturany, 1900, Station 76 (Sanafir Island, Strait of Tiran, Red Sea). **A**. Original figure by Sturany (1903). **B–E**. Holotype, NHMW 84252: front (**B**), right side (**C**), back (**D**), protoconch (**E**). **F**. Original holotype label. Scale bars: **B–D**: 5 mm, **E**: 1 mm.

Family Clathurellidae H. Adams & A. Adams, 1858

Mangilia pertabulata Sturany, 1903

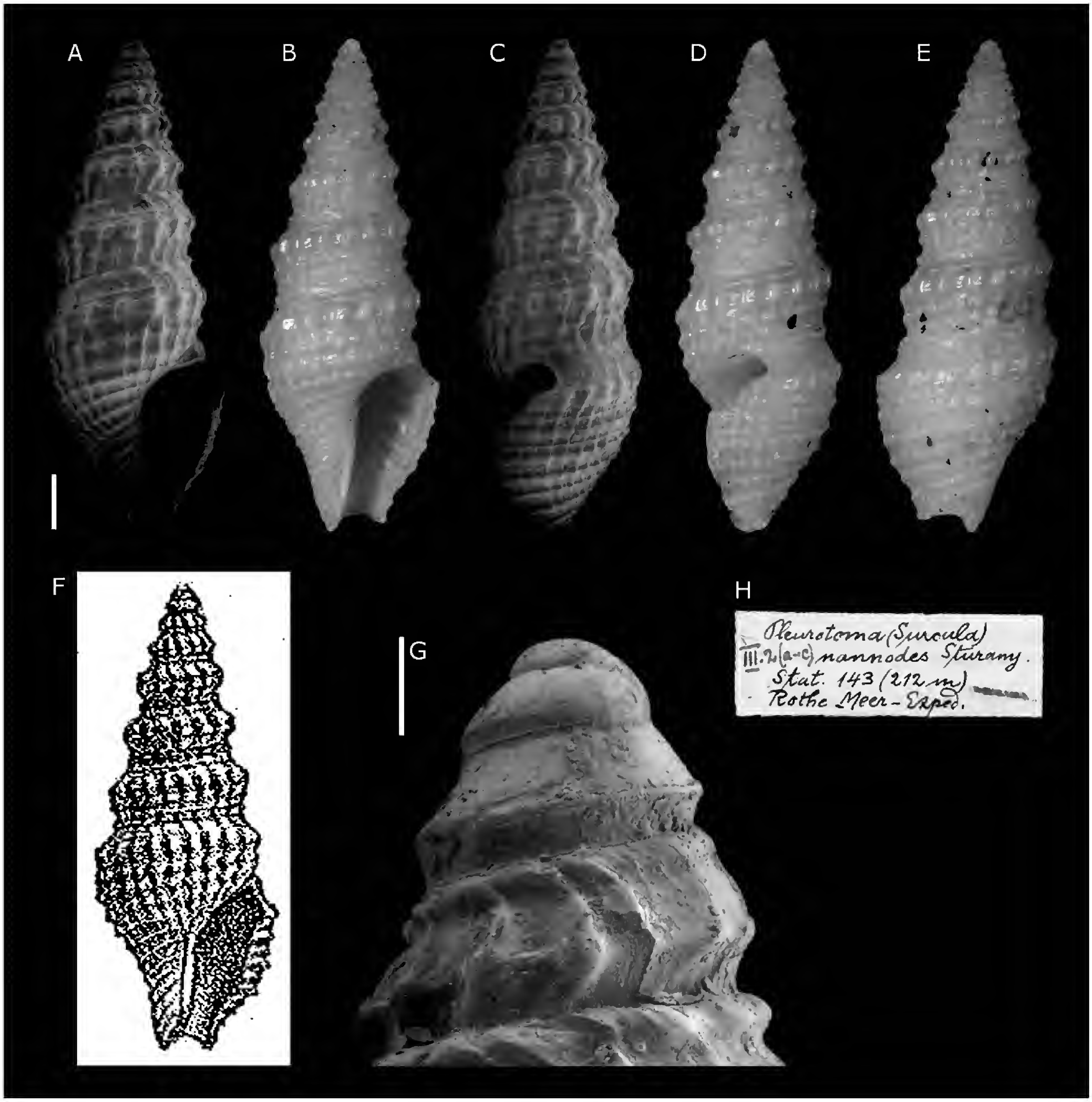
Figure 25
Sturany, 1903: 231, plate III, figures 1a–c.

Type locality. Station 145, “östlich von J. Dahalak” [east of Dahlak Island, Eritrea], 16°2.6'N, 41°13.5'E, 800 m.

Type material. Holotype: NHMW 84255, height 5.4 mm.

Original description. *Von der Station 145 (800 m); ein einziges Exemplar.*

Das spindelförmig gestaltete Gehäuse besteht aus 8 Windungen, es ist der Farbe nach weiß, nur geringe Spuren von gelbbrauner Färbung insbesondere am äußeren Mundrande und am Embryonalgewinde sind zu bemerken. Das Embryonalgewinde besteht aus einem zitzenförmigen, glatten Apex (ungefähr 1 Umgang) und 2 doppelt gekielten Umgängen (1 schnurförmiger Kiel steht in der Mitte, ein zweiter schwer auszunehmender läuft an der Naht). Die nun folgenden Umgänge haben eine mäßige Anzahl Spiralreifen, von denen regelmäßig der mittlere der stärkste und der am meisten vorgezogene ist (daher der fast rechtwinkelige Umriss jeder Windung!) und überdies Längs- und Querwülste, die in nicht allzu geringen Entfernungen von einander stehen und zwischen sich mikroskopisch feine, schief gestellte Querstrichelchen erkennen lassen. Bezüglich jener Spiralreifen sei noch bemerkt, dass 3 — 4 feine über dem stärkeren mittleren und 1 mittelstarker unter ihm liegen und dass auf der letzten Windung vom Hauptstreifen abwärts zur Basis der Schale 12 schwächere Spiralreifen vertheilt sind. Die Kreuzungsstellen der Reifen und Wülste sind naturgemäß spitzhöckerig vorgezogen. Die Mündung hat einen vorgezogenen, gewellten Mundrand, eine tiefe, halbmondförmige Bucht rechts oben und einen an



Pleurotoma (Surcula)
III.2(a-c) nannodes Sturany.
Stat. 143 (212 m)
Rothe Meer-Exped.

Figure 24. *Pleurotoma nannodes* Sturany, 1900, Station 143 (Harmil Island, Dahlak Archipelago, Eritrea, Red Sea). **A–E, G**. Figured syntype, NHMW 84254: front (**A–B**), right side (**C–D**), back (**E**), protoconch (**G**). **F**. Original figure by Sturany (1903). **H**. Original label. Scale bars: **A–E**: 1 mm, **G**: 0.2 mm.

der Basis etwas zurückgebogenen kurzen Canal; an der Mündungswand ist ein Höckerchen zu sehen.

Die Höhe der Schale beträgt 5,5, die Breite 2,5 mm die Mündung ist circa 3 mm hoch und sehr schmal.

Für die systematische Stellung der neuen Art sei ihre Verwandtschaft mit der ähnlich gestalteten, jedoch viel größeren Mangilia spurca *Hinds (Moll. Voy. Sulph. p. 17, t. 5, figure 14) und insbesondere mit* Mangilia albata *E. A. Smith aus dem Persischen Golfe (Ann. Mag. Nat. Hist. [5] X, 1882, p. 210) maßgebend.*

Translation. From station 145 (800 m); a single specimen.

The fusiform shell consists of eight whorls, it has a white colour, small traces of yellow-brown colour can be noticed especially on the outer lip and on the protoconch. The protoconch consists of a teat-shaped, smooth, apex (about one whorl) and two double-keeled whorls (one rope-like cord in the middle, a second hardly visible at the suture). The following whorls have a moderate number of spiral threads, of which regularly the median is the strongest and the most prominent (hence the almost rectangular profile of each whorl!) and also show axial and spiral cords which are not too far away one from each other and among which it is possible to recognize microscopically fine threads. On these threads, it is remarkable that three or four fine threads run above the strongest median cord and one below it, and on the last whorl from the strongest median cord

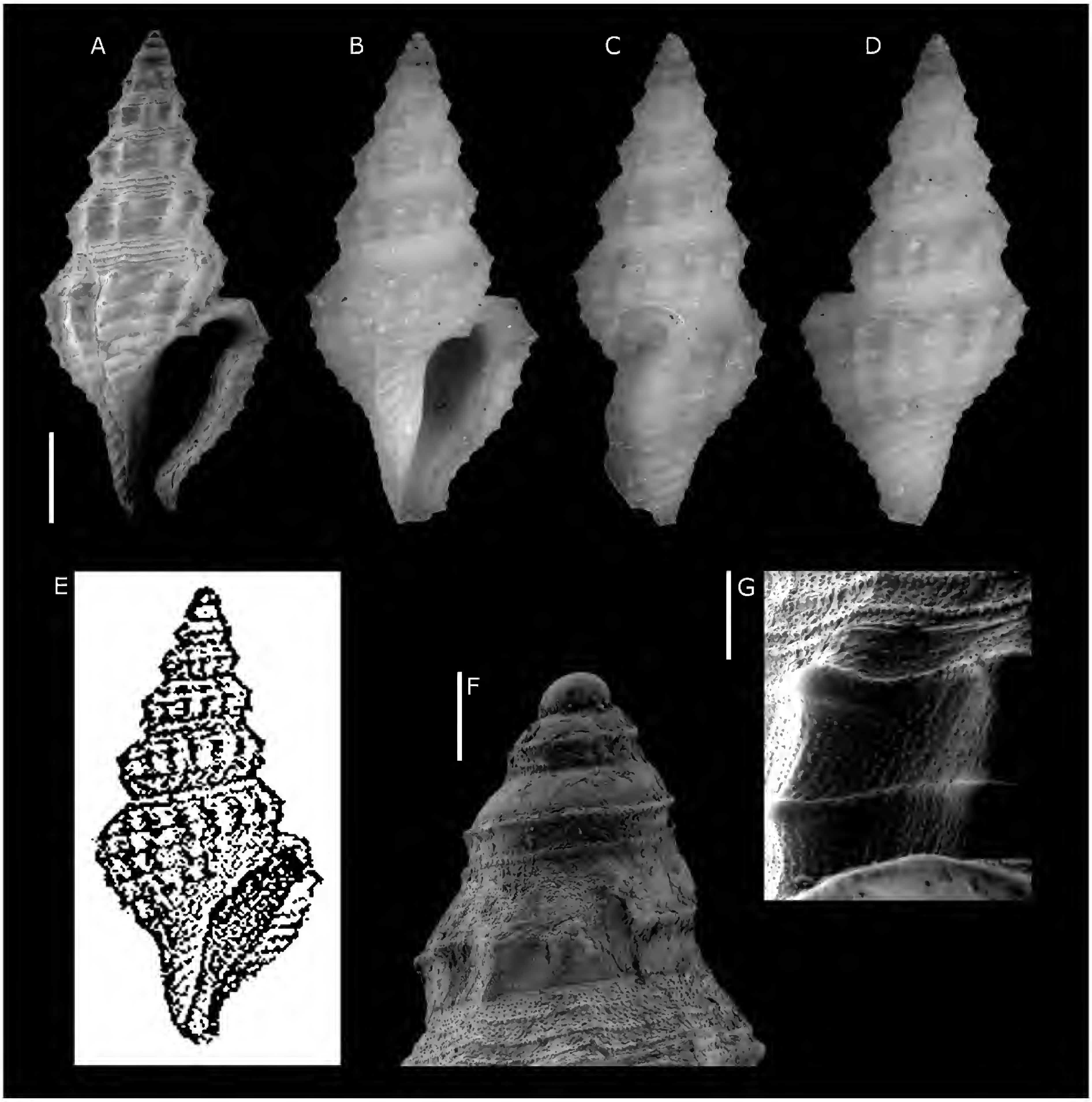


Figure 25. *Mangilia pertabulata* Sturany, 1903, Station 145 (Dahlak Archipelago, Eritrea, Red Sea). **A–D**, **F–G**. Holotype, NHMW 84255: front (**A–B**), right side (**C**), back (**D**), protoconch (**F**), microsculpture (**G**). **E**. Original figure by Sturany (1903). Scale bars: **A–D**: 1 mm, **F–G**: 0.2 mm.

to the base of the shell there are 12 weaker spiral rings. The intersections of the ribs and threads show sharp tubercles. The aperture has an elongated, undulated lip, a deep, semi-circular posterior sinus on the top right and at the base a slightly recurved short canal; a small tubercle can be seen on the inner lip.

The height of the shell is 5.5 mm, the width 2.5 mm, the aperture is about 3 mm high and very narrow.

Decisive for the systematic position of the new species is its relationship with the similar, much larger *Mangilia spurca* Hinds (Moll. Voy. Sulph. p. 17, t. 5, figure 14) and in particular with *Mangilia albata* E.A. Smith from the Persian Gulf (Ann. Mag. Nat. Hist. [5] X, 1882, p. 210).

Comments. The species was assigned to *Clathurella* Carpenter, 1857 s.l. by Janssen in Janssen and Taviani 2015: 526.

Family Conidae Fleming, 1822

Conus aculeiformis f. *torensis* Sturany, 1903

Figure 26
Sturany, 1903: 227, plate IV, figures 8a–b.

Original locality: Station 88 (58 m) (El Tor, Egypt, Red Sea; Table 1).

Type material. Figured syntype: NHMW 84223 (station 88), illustrated by Sturany (1903) in plate III, figures 2a–c, height 30.7 mm. Further five syntypes NHMW 84224 (station 88).

Original description. *Von der Station 88 (58 m); einige wenige Exemplare.*

Das langgestreckte, schlanke Gehäuse besteht aus einem Doppelkegel. Das Gewinde ist erhaben und ziemlich stufig abgesetzt; von dem glatten und glänzenden Embryonalgewinde, das sich von dem übrigen Theile des Gewindes ziemlich deutlich abhebt, fehlt in der Regel das oberste Spitzchen (ein Umgang oder mehr). Ungefähr auf der 3. Windung beginnt die Sculptur, welche aus einem unter der Mitte gegen die Naht zu gelegenen, breiten Spiralwulste und aus 2—3 über diesem in einem etwas ausgehöhlten Räume liegenden schwachen Spiralreifen besteht. Auf der Schlusswindung, die nach unten in einen langen, schmalen Kegel endigt, nimmt dann jener starke Spiralwulst den obersten Theil des Kegels ein und ist er ungefähr 1 mm von der Naht entfernt. Der letzte Umgang weist concentrische Spiralfurchen auf, und zwar stehen diese Vertiefungen an der Basis des Umganges dicht aneinander, dabei tiefer einschneidend, so dass die dazwischenliegenden Partien als Spiralrippen erscheinen, während in der Mittelpartie der Schlusswindung die Spiraleinschnitte weiter voneinander sich entfernen und seichter sind. Die Basalfurchen sind mit zahlreichen feinen Querstrichelchen ausgestattet, und ebenso ziehen über die einzelnen Umgänge des Gewindes zarte Querstriche. Die Farbe des Gehäuses ist hellgelb, auf dem Spiralwulste stehen in ziemlich regelmäßigen Entfernungen abwechselnd mit Weißfärbung dunkelgelbe oder gelbbraune Flecken, die sich oft nach oben zu ausdehnen, und auch in der Mitte der letzten Windung stehen ein paar Reihen größerer Flecken nebst den Spuren von kleineren, radialartig angeordneten. Der Außenrand der sehr engen, innen weiß gefärbten Mündung ist scharf und bildet einen stark vorgezogenen Bogen, der oben, entsprechend dem obersten vertieften Theile der Schlusswindung, einen concaven Einschnitt trägt.

Ich halte die eben beschriebene Kegelschnecke für eine Localform des C. aculeiformis *Rve. (Proc. Zool. Soc. 1843), als dessen Heimat bisher nur die indo-australischen Gewässer gegolten haben, und sehe auch in* C. sieboldi *Rve. (Jcon. f. 269),* C. australis *auct. (Tryon, Man. of Conch. VI, p. 73) und* C. *(*Leptoconus*)* saecularis *Melvill (Manch. Mem. XLII, 1898, No. 4, p. 10 des Sep., t. 1, figure 23; aus dem Persischen Golfe) nahverwandte Arten.*

Translation. From station 88 (58 m); a few specimens.

The elongated, slender shell consists of a double cone. The spire is high and fairly scalariform; from the smooth and shiny protoconch that differs quite clearly from the other parts of the spire, the upper part of the apex is missing (one whorl or more). Around the third whorl the sculpture begins, consisting of a sub-median, broad spiral cord above the suture and two or three spiral threads in the concave area above. On the last whorl, ending below in a long, narrow cone, that strong spiral cord occupies the topmost part of the cone at about 1 mm distance from the suture. The body whorl has concentric spiral grooves; these grooves are tightly arranged and deeply incised at the base of whorl, so that they seem spiral ribs, while in the middle section of the last whorl the spiral incisions are faint and shallow. The basal grooves are equipped with numerous fine spiral threads, which are also present on the spire. The colour of the shell is light yellow, on the spiral ridge dark yellow or yellow-brown flecks alternate with white colour at fairly regular distances, often expanding upwards; also in the middle of the last whorl there are a few rows of larger spots. The lip of the very narrow, inside white, mouth is sharp and forms a strong elongated curve which, seen from above, carries a concave incision at the top.

I think that the described cone snail is a local form of *C. aculeiformis* Reeve (Proc. Zool. Soc. 1843), which has been considered distributed only in the Indo-Australian waters so far; I consider also closely related species: *C. sieboldi* Reeve (Jcon. f. 269), *C. australis* auct. (Tryon, Man. of Conch. VI, p. 73) and *C.* (*Leptoconus*) *saecularis* Melvill (Manch. Mem. XLII, 1898, No. 4, p. 10 of September, t. 1, Fig. 23 from the Persian Gulf).

Comments. This form of *Conus aculeiformis* Reeve, 1844 is considered a synonym of *Conasprella elegans* (G.B. Sowerby III, 1895) (Röckel et al. 1995).

Conus planiliratus f. *batheon* Sturany, 1903

Figure 27
Sturany, 1903: 227–228, plate IV, figures 6a–c, 7a–b.

Original localities. Stations 127, 128, 143, 145 (21 – 800 m) (Eritrea, Red Sea; Table 1).

Type material. Figured syntype: NHMW 84227 (station 143), illustrated by Sturany (1903) in plate III, figures 6a–c, height 35.9 mm. Further syntypes: NHMW 84225 (station 127): 1 specimen, illustrated by Sturany (1903) in plate IV, figure 7a–b; NHMW 84226 (station 128): 1 specimen; NHMW 84228 (station 143): 5 specimens; NHMW 84229 (station 145): 2 specimens.

Original description. *Von den Stationen 127, 128, 143, 145 (212—800 m).*

Das milchglasartige Embryonalgewinde ist glatt, etwas glänzend, blasenförmig. Auf den darauffolgenden Windungen ist ein wulstförmiger Kiel wahrzunehmen, der anfangs in der Mitte liegt und einige Höcker trägt, dann aber diese letzteren verliert und, sich etwas nach unten verschiebend, nahtständig wird. Es erscheint mithin der Umriss des Gewindes stufenförmig. Zwischen dem Hauptwulste (Kiele) und der oberen Naht liegen 3 — 4 schwächere Längs- oder Spiralreifen. Auf der Schlusswindung bildet jener Hauptwulst die Kante; der Theil zwischen der Kante und der Naht ist etwas concav und es entspricht ihm am Mündungsrande oben eine einschnittartige Aushöhlung; die übrige mächtige Par-

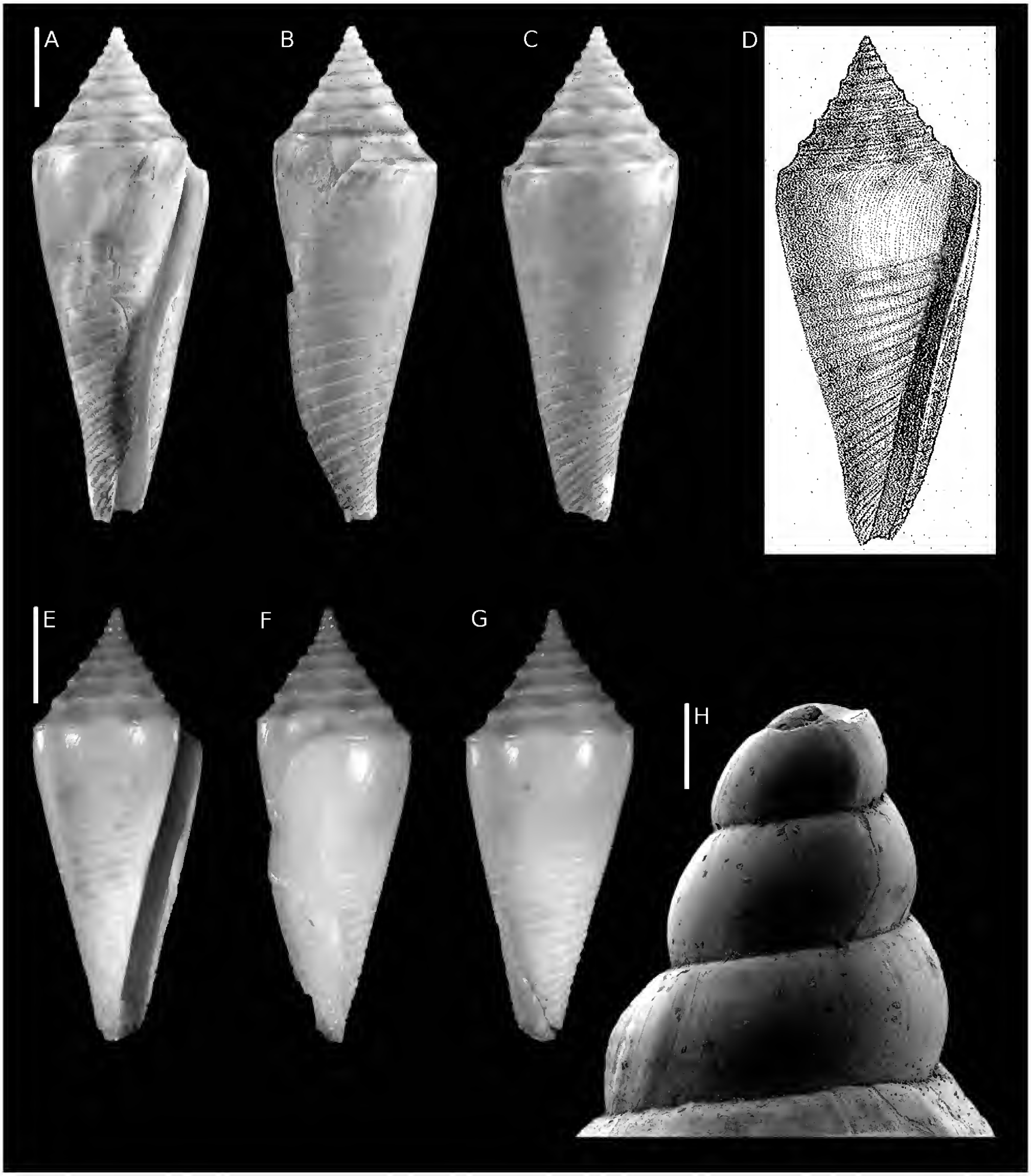


Figure 26. *Conus aculeiformis* var. *torensis* Sturany, 1903, Station 88 (El Tor, Egypt, Red Sea). **A**–**C**. Figured syntype, NHMW 84223: front (**A**), right side (**B**), back (**C**). **E**–**H**. Syntype, NHMW 84224: front (**E**), right side (**F**), back (**G**), protoconch (**H**). **D**. Original figure by Sturany (1903). Scale bars: **A**–**C**, **E**–**G**: 5 mm, **H**: 0.2 mm.

tie des letzten Umganges trägt eine größere Anzahl von rippenförmigen Spiralreifen (und zwar sind diese gleich stark in gleichen Zwischenräumen gelegen oder zwei und zwei liegen zusammengedrängt oder es wechseln stärkere und schwächere ab, ganz selten bleiben sie in der oberen Partie der Schlusswindung, ungefähr von der Kante abwärts bis zur Hälfte, aus, indem sich hier bloß seichte Spiralfurchen vorfinden). Die Zeichnung besteht aus dunkelgelben Flecken auf hellgelbem oder weißem Grunde, die hauptsächlich auf dem Hauptwulste stehen, sich aber auch quer über die Windungen lagern und auf der letzten Windung zu zahlreichen, unregelmäßig gruppierten Spiralreihen von Flecken anwachsen, von denen wieder benachbarte verschmelzen können. Bei frischen Stücken ist eine häutige Epidermis zu finden, die aus quer über

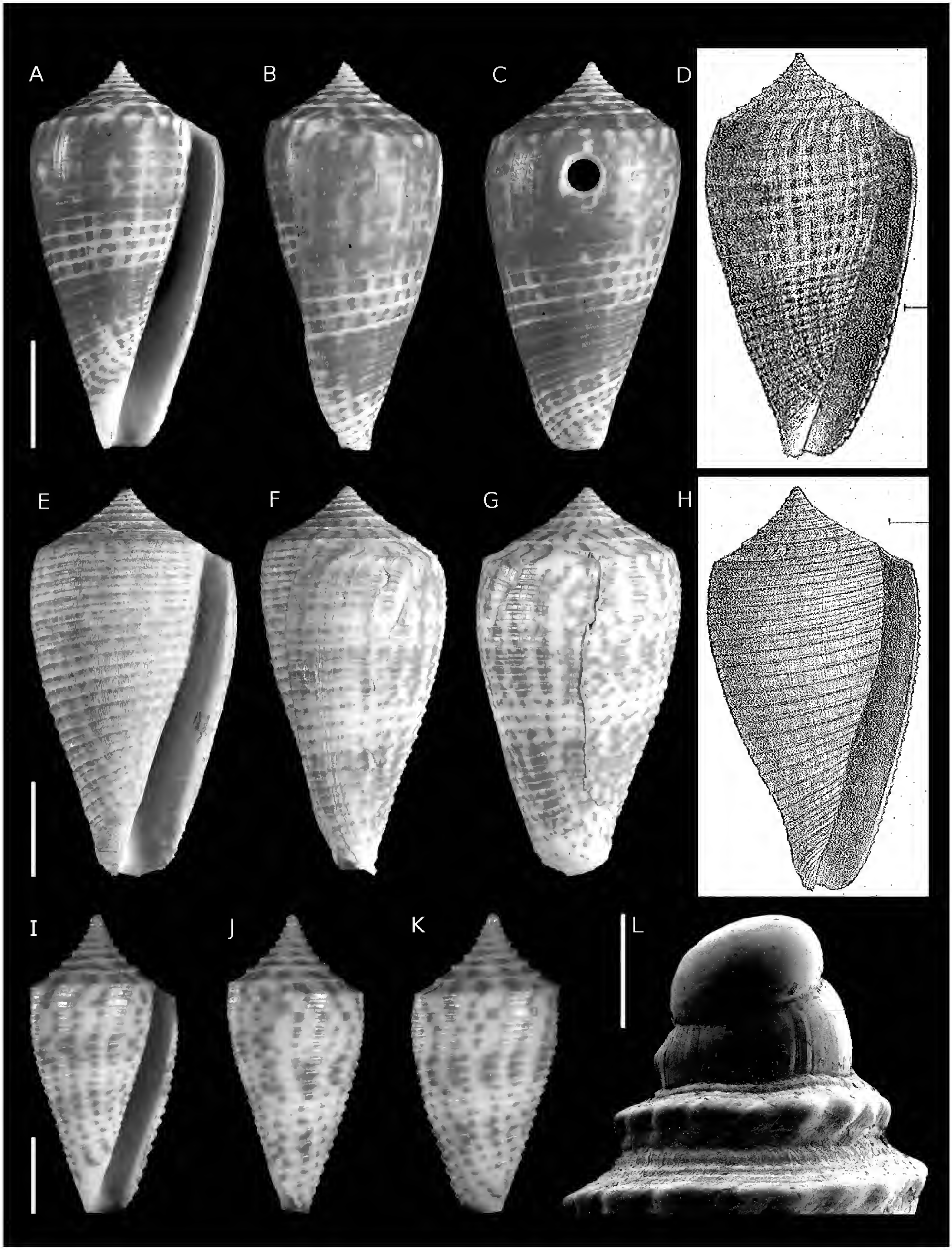


Figure 27. *Conus planiliratus* var. *batheon* Sturany, 1903. **A–C**. Figured syntype, NHMW 84227, Station 143 (Harmil Island, Dahlak Archipelago, Eritrea, Red Sea): front (**A**), right side (**B**), back (**C**). **E–G**. Figured syntype, NHMW 84225, Station 127 (Akik Seghir, Eritrea, Red Sea): front (**E**), right side (**F**), back (**G**). **I–L**. Syntype, juvenile specimen, NHMW 84228, Station 143 (Harmil Island, Dahlak Archipelago, Eritrea, Red Sea): front (**I**), right side (**J**), back (**K**), protoconch (**L**). **D**, **H**. Original figures by Sturany (1903). Scale bars: **A–C**, **E–G**: 10 mm, **I–K**: 5 mm, **L**: 0.5 mm.

die Umgänge streichenden Lamellen besteht und dem darunterliegenden Kalktheile die Querstreifung mittheilt.

Die Mündung ist eng, innen weiß, scharfrandig.

Es fällt bei dieser Zusammenstellung auf, dass die Exemplare aus größeren Tiefen schlanker sind, indem das Gewinde höher aufgebaut ist.

Conus planiliratus *wurde von Sowerby im Jahre 1870 ohne genaue Angabe eines Fundortes beschrieben (Proc. Zool. Soc. p. 255, t. XXII, figure 1); nach der Abbildung zu urtheilen, hatte sein Exemplar die Dimensionen 41 ½: 20: 34 ½,. — E. A. Smith, als Bearbeiter der »Investigator«-Mollusken, gibt für diese Art den Fundort „Off Calicut, west coast of South India, in 45 fathoms" an und erwähnt, dass das größte Exemplar ein Ausmass von 58:27 mm besitzt (Ann. Mag. Nat. Hist. (6) XIV, p. 159 [1894], pl III, fig 2).*

Mit Conus sulcatus *haben die beschriebenen Exemplare der »Pola«-Expedition die Berippung des letzten Umganges gemeinsam, während sie von ihm durch den geraden Verlauf des Kieles (Wulstes) gut unterschieden sind.*

Als nahestehende Form wäre schließlich auch noch Conus (Leptoconus) dictator *Melvill zu nennen (Manch. Mem. XLII, 1898, p. 9 des Sep., plate 1, figure 10), welche im Persischen Golfe in einer Tiefe von 10 Faden an der Sheikh Shuaib-Insel in der Größe von 47: 20 mm gefunden wurde.*

Translation. From stations 127, 128, 143, 145 (212-800 m).

The milk white protoconch is smooth, slightly glossy, bubble-shaped. On the following whorls a cord-shaped keel can be noticed, which is initially in the middle and bears some tubercules, but then loses these, and moves towards the suture. The shape of the spire appears therefore scalariform. Between the main cord (keels) and the upper suture three to four weaker longitudinal or spiral threads run. On the last whorl, that main cord forms the keel; the part between the keel and the suture is slightly concave, and it corresponds to a notch-like cavity on the upper part of the lip; the rest of this massive part carries a greater number of rib-shaped spiral cords (they are equally spaced, or they are clustered in pairs, or they are alternately strong and weak; very rarely they are absent on the upper part of the last whorl, roughly from the keel down to the middle, here fine spiral threads can be found). The pattern consists of dark yellow patches on light yellow or white ground, these patches are mainly on the main band, but also lay across the whorls and grow on the last whorl to become numerous, irregularly clustered spiral rows of spots, sometimes merging again. On fresh specimens, a membranous periostracum can be found with transverse lamellae crossing the whorls and overlaying on the transverse threads on the underlying calcareous shell.

The aperture is narrow, white inside, with a sharp lip.

It is remarkable that specimens from greater depths are slimmer with a higher spire.

Conus planiliratus was described by Sowerby in 1870 without specifying a precise locality (Proc. Soc. Zool. p. 255, t. XXII, figure 1); judging from the figure, his specimen had the dimensions 41.5 : 20 : 34.5 [mm]. In his description of the "Investigator" mollusks, E.A. Smith gives for this species the location "off Calicut, West Coast of South India, in 45 fathoms" and noted that the largest specimen had a size of 58 : 27 mm (Ann. Mag. Nat. Hist. (6) XIV, p. 159 [1894], pl. III, figure 2). The described specimens of the "Pola" expedition share with *Conus sulcatus* the ribbing of the last whorl, while they can be well distinguished by the straight direction of the keel.

Finally, the closely related form *Conus* (*Leptoconus*) *dictator* Melvill can be mentioned (Manch. Mem. XLII, 1898, p. 9 of September, plate 1, figure 10), which was found in the Persian Gulf at a depth of 10 fathoms along Sheikh Shuaib Island with the size of 47 : 20 mm.

Comments. The syntype illustrated in Figure 27E–G has a distinctly heavier and ticker shell than the one illustrated in Figure 27A–C. Recent authors do not recognize the validity of this taxon (Röckel et al. 1995; Tucker and Tenorio 2013), but disagree on to which taxon this *Conus* should be synonymized to: Röckel et al. 1995 suggested *Conus grangeri* G.B. Sowerby III, 1900, whereas Bouchet (2015) lists it as synonym of *Conus inscriptus* Reeve, 1843.

Family Raphitomidae A. Bellardi, 1875

?*Pleurotoma beblammena* Sturany, 1903

Figure 28
Sturany, 1903: 231, plate III, figures 4a–b.

Type locality. Station 143, "nächst der Insel Harmil" [near Harmil Island, Dahlak Archipelago, Eritrea] 17°7'N, 39°55'E, 212 m.

Type material. Holotype: NHMW 84256, height 9.2 mm.

Original description. *Von der Station 143 (212 m); eine unvollständige Schale.*

Die milchweiße, durchscheinende Schale ist spindelförmig gebaut und besteht aus 8 Umgängen; die Mündung ist nicht vollständig ausgebildet. Das Embryonalgewinde besteht aus kaum 2 Umgängen, die zwar glatt erscheinen, bei starker Vergrößerung jedoch eine feine Gittersculptur erkennen lassen. Die folgenden 4 — 5 Umgänge besitzen 3 starke Spiralwülste, von denen der mittlere am meisten hervortritt, und überdies in den Zwischenräumen noch je einen schwachen Spiralreifen. Durch ziemlich engstehende, etwas bogig verlaufende Querwülste wird eine Durchkreuzung der Spiralsculptur, mithin eine Cancellierung des Gehäuses hervorgerufen. Auf der vorletzten Windung treten zu den erwähnten Spiralwülsten noch 2 feinere Spiralreifen unten nächst der Naht; auf dem letzten Umgange verlaufen viele solche Spiralreifen in dem Raume zwischen der Einlenkung des Mundsaumes und der Basis des Gehäuses, ein Abwechseln von stärkeren Spiralwülsten und zarteren Spiralreifen ist hier schon weniger deutlich erkennbar. Die Spindelgegend ist abgeglättet, die Basis der Spindel ist gedreht und etwas zurückgebogen.

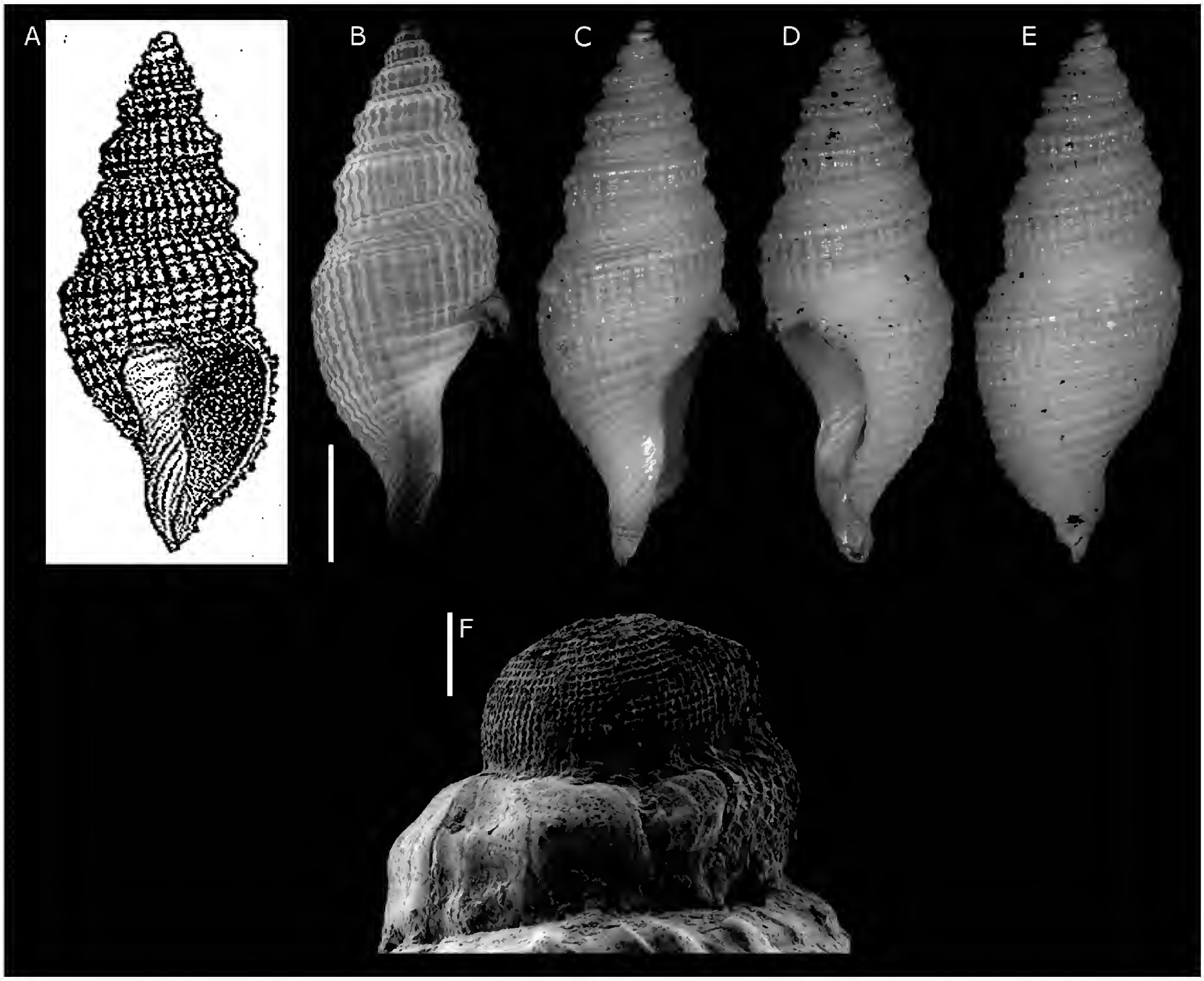


Figure 28. *Pleurotoma beblammena* Sturany, 1903, Station 143 (Harmil Island, Dahlak Archipelago, Eritrea, Red Sea). **A**. Original figure by Sturany (1903). **B–F**. Holotype, NHMW 84256: front (**B–C**), right side (**D**), back (**E**), protoconch (**F**). Scale bars: **B–E**: 2 mm, **F**: 0.1 mm.

Die Höhe der Schale beträgt 9,7, die Breite 3,6 mm.

Die systematische Stellung der beschriebenen Form ist im Hinblick auf die mangelhaft erhaltene Mündung problematisch.

Translation. From station 143 (212 m); an incomplete shell.

The milk-white, translucent shell is fusiform and consists of eight whorls; the aperture is incomplete. The protoconch consists of barely two whorls, which seem smooth, but seen under high magnification show a fine cancellated sculpture. The following four-five whorls show three strong spiral ridges with the median one most prominent, and in each interstice a weak spiral thread. The spiral sculpture is crossed by particularly narrow, slightly curved axial cords which cause a cancellated sculpture of the shell. On the last whorl, between the mentioned spiral cords two more finer spiral threads are visible below the suture; on the last whorl many spiral threads continue between the [inner] lip and the base of the shell; here, an alternation of stronger and finer spiral threads is indistinct. The columellar area is smooth, the base of the columella is twisted and slightly recurved.

The height of the shell is 9.7 mm, the width 3.6 mm.

The systematic position of the described form is problematic because of the poor condition of the aperture.

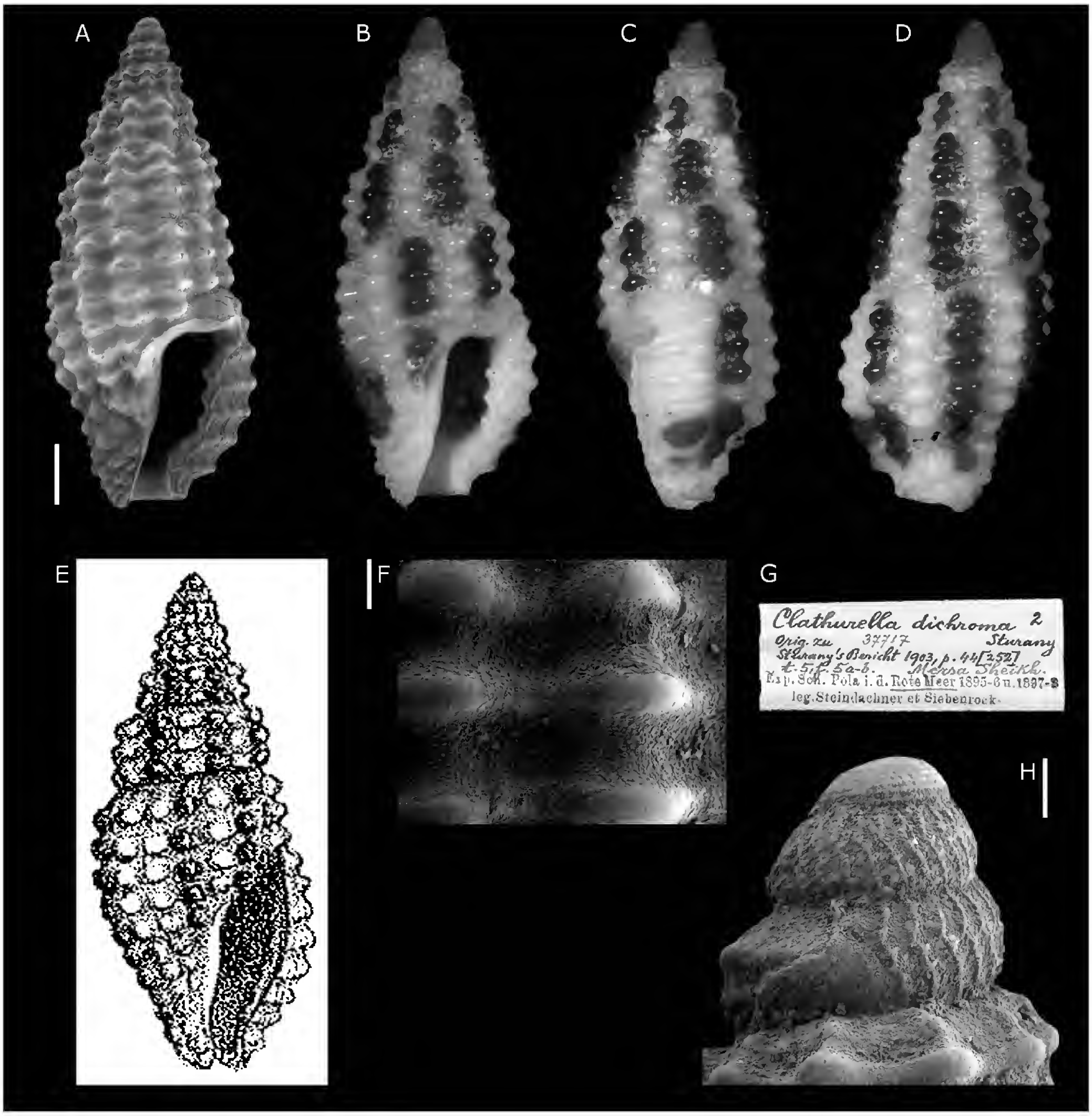
Comments. A further member of the genus *Taranidaphne* Morassi & Bonfitto, 2001.

Clathurella dichroma Sturany, 1903

Figure 29
Sturany, 1903: 252, plate V, figures 5a–b.

Original locality: Locality 25, "Sherm Sheikh (Mersa Sheikh)" [near Abu Ghusun, Egypt], 26°– 24°N.

Type material. Two syntypes: NHMW 37717 (locality 25), the specimen figured by Sturany (1903), plate V, figures 5a–b has been segregated, its height is 4 mm.



Clathurella dichroma 2
Orig. zu 37717 Sturany
Sturany's Bericht 1903, p. 44[252]
t. 5 f. 5a-b. Mersa Sheikh.
Exp. Sch. Pola i. d. Rote Meer 1895-6 u. 1897-8
leg. Steindachner et Siebenrock.

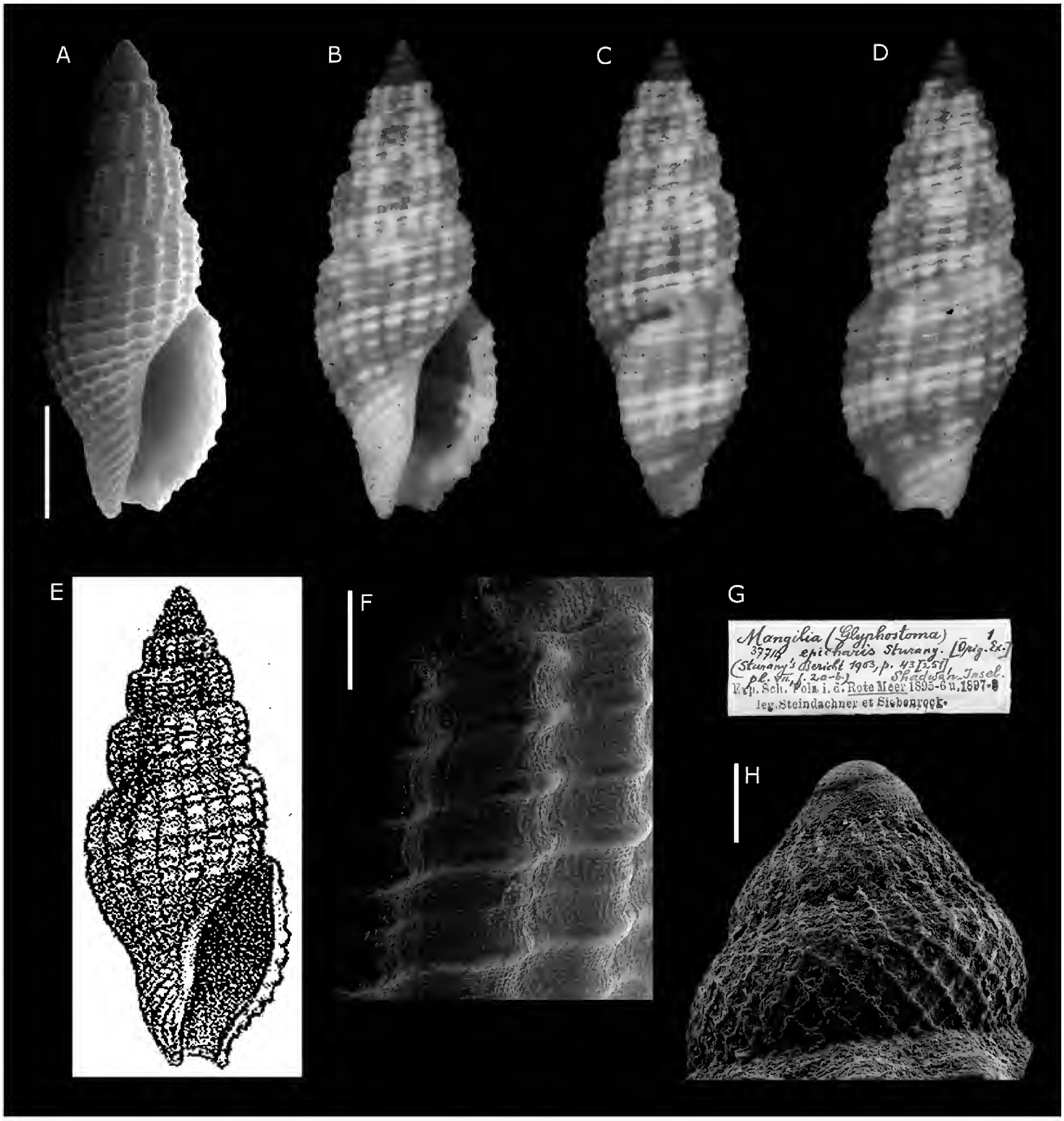
Figure 29. *Clathurella dichroma* Sturany, 1903, Locality 25 (Abu Ghusun, Egypt, Red Sea). **A–D**, **F**, **H**. Figured syntype, NHMW 37717: front (**A–B**), right side (**C**), back (**D**), microsculpture (**F**), protoconch (**H**). **E**. Original figure by Sturany (1903). **G**. Original label. Scale bars: **A–D**: 0.5 mm, **F**, **H**: 0.1 mm.

Original description. *Von der Localität 25.*

Die neue Art, bloß in 2 Exemplaren vorliegend, hat große Ähnlichkeit und Verwandtschaft mit C. rubroguttata *H. Ad. (nach Tryon einem Synonym von* tincta *Rve.). Die Schale besteht aus 8 Windungen, von denen die 3 ersten einen braunen Apex bilden; auf den Apex folgt ein Umgang in weißer Farbe, auf diesen erst die mit dunkel- oder rothbrauner Färbung gezierte Gehäusepartie. Es sind hier die Knoten, welche die 3 Längs- (Spiral-) rippen mit den Querwülsten an den Kreuzungsstellen bilden, abwechselnd weiß und rothbraun gefärbt. Der äußere Mundrand trägt oben einen Einschnitt. Die Höhe der Schale beträgt kaum 4 mm, die Breite 1,7 mm, die Mündung ist nicht halb so hoch wie das ganze Gehäuse.*

Translation. From locality 25.

The new species, present only in two specimens, has great similarity and relationship with *C. rubroguttata* H. Adams (according to Tryon a synonym of *tincta* Reeve). The shell consists of eight whorls, of which the first three form a brown apex; the apex is followed by a white coloured whorl, then the dark or reddish-brown colouring on part of the shell follows. Here there are tubercles,



Mangilia (Glyphostoma) 1
37714 epicharis Sturany. [Orig.-Ex.]
(Sturany's Bericht 1903, p. 43 [251],
pl. VII, f. 2a-b.) Shadwan-Insel.
Exp. Sch. Pola i. d. Rote Meer 1895-6 u. 1897-8
leg. Steindachner et Siebenrock.

Figure 30. *Mangelia epicharis* Sturany, 1903, Locality 16 (Jazirat Shakir, Egypt, Red Sea). **A–D**, **F**, **H**. Holotype, NHMW 37714: front (**A–B**), right side (**C**), back (**D**), microsculpture (**F**), protoconch (**H**). **E**. Original figure by Sturany (1903). **G**. Original holotype label. Scale bars: **A–D**: 0.5 mm, **F**: 0.2 mm, **H**: 0.1 mm.

formed by the intersection of three longitudinal (spiral) cords with the axial ribs, coloured alternatively white and reddish-brown. The outer lip bears an incision above. The height of the shell is barely 4 mm, width 1.7 mm, the mouth has less than half of the shell height.

Comments. This species clearly belongs to the genus *Pseudodaphnella* Boettger, 1895 (Fedosov and Puillandre 2012). It is very closely related to *Pseudodaphnella barnardi* (Brazier, 1876) and *P. phaeogranulata* Fedosov & Puillandre, 2012.

Mangilia (*Glyphostoma*) *epicharis* Sturany, 1903

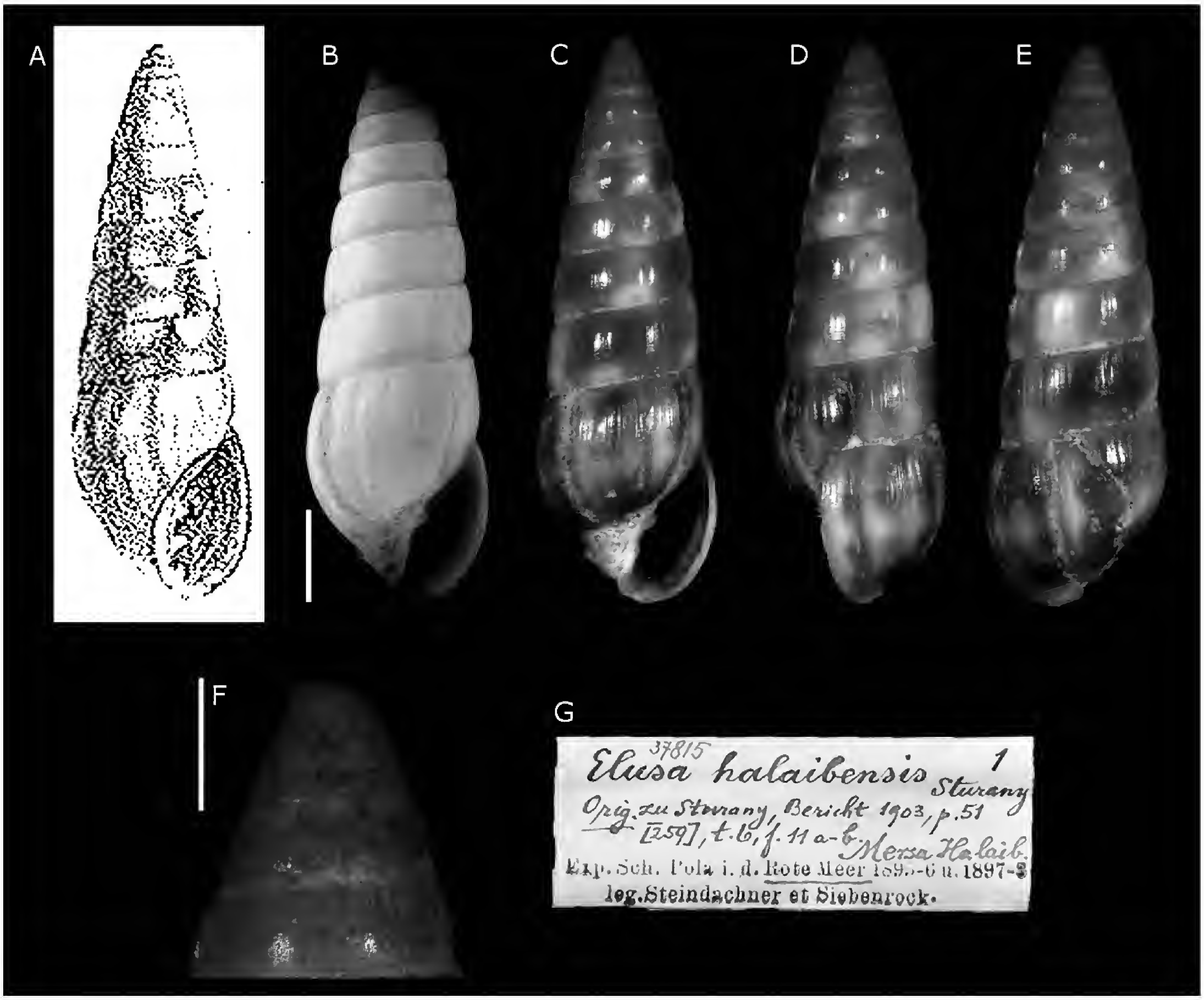
Figure 30
Sturany, 1903: 251, plate VII, figures 2a–b.

Type locality. Locality 16, "Shadwan-Insel" [Jazirat Shakir, Egypt], Northern Red Sea, 28°– 26°N.

Type material. Holotype: NHMW 37714, height 4.2 mm.

Original description. *Von der Localität 16.*

Das einzige Exemplar, welches zur Aufstellung der neuen Art Anlass gegeben hat, besitzt eine große Ähn-



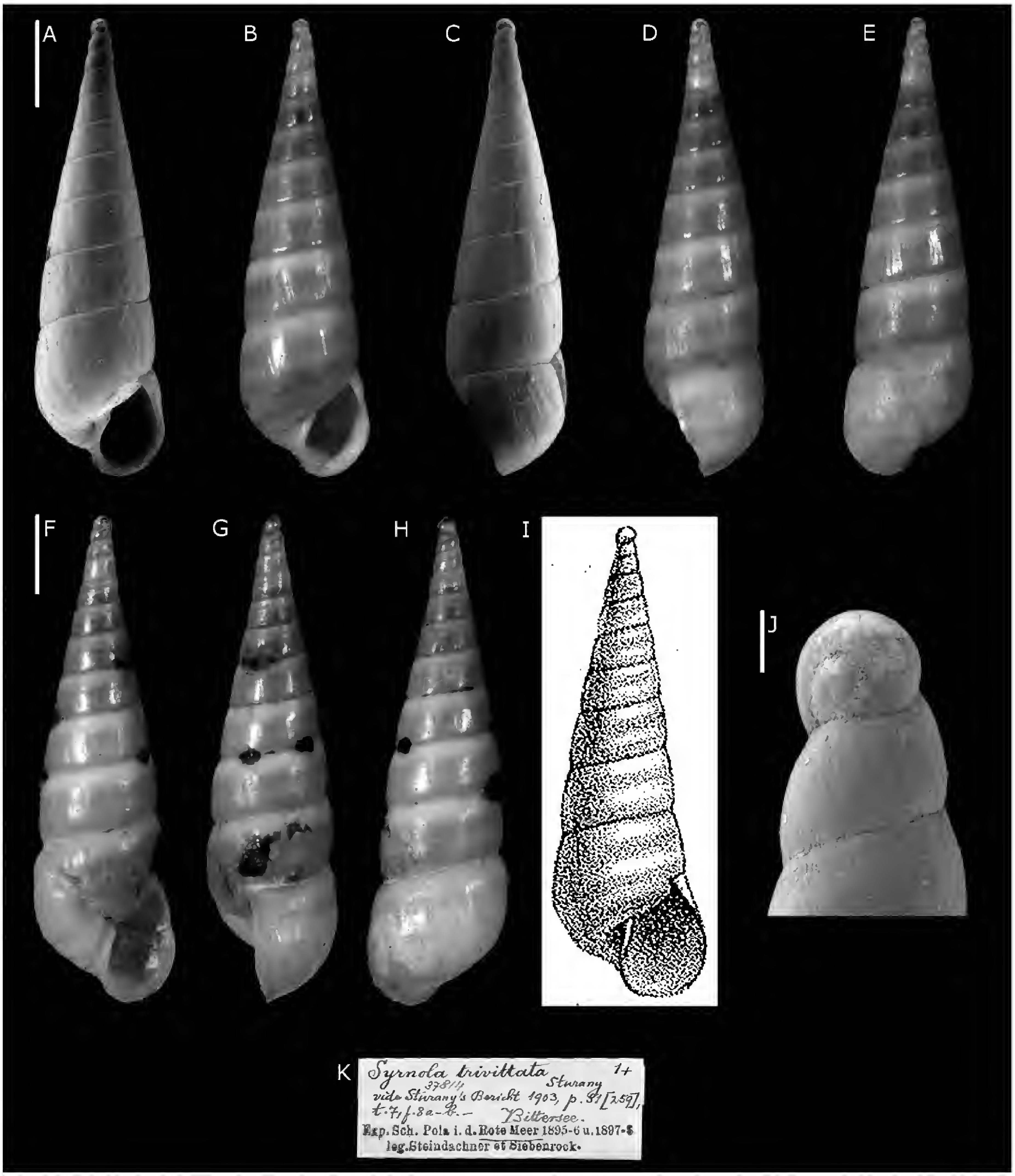
37815
Elusa halaibensis 1
Sturany
Orig. zu Sturany, Bericht 1903, p. 51
[259], t. 6, f. 11 a-b. Mersa Halaib.
Exp. Sch. Pola i. d. Rote Meer 1895-6 u. 1897-8
leg. Steindachner et Siebenrock.

Figure 31. *Elusa halaibensis* Sturany, 1903, Locality 30 (Halayeb, Egypt, Red Sea). **A**. Original figure by Sturany (1903). **B–F**. Holotype, NHMW 37815: front (**B–C**), right side (**D**), back (**E**), protoconch (**F**). **G**. Original holotype label. Scale bars: **B–E**: 2 mm, **F**: 1 mm.

lichkeit mit Glyphostoma melanoxytum *Herv. von Lifou (Journ. de Conch. XLIV, 1896, p. 78, t. 3, figure 19). Die Färbung, das Embryonalgewinde und die Größe der Hervier'schen Art stimmt, wie ich mich im Berliner Museum an einem typischen Exemplar überzeugen konnte, mit den entsprechenden Verhältnissen der neuen Art vollständig überein, hingegen bildet das tiefe Einschneiden der Windungen, also die tiefgelegene Naht bei* G. melanoxytum *ein wesentliches Unterscheidungsmerkmal. Das aus 4 Umgängen bestehende Embryonalgewinde ist eine dem übrigen Gewinde gewissermaßen aufgesetzte Mütze von gelber bis brauner Farbe. Die beiden ersten heller gefärbten Umgänge sind nur scheinbar glatt, denn sie weisen, unter dem Mikroskope betrachtet, eine feinste Punktierung auf; auf sie folgen braunfärbige Umgänge mit einer aus schief gekreuzten Linien gebildeten Gittersculptur. Die nun folgenden 4 Hauptwindungen sind stufig abgesetzt, mit Spiral- und Querwülsten ausgestattet, weiß in der Grundfarbe und mit unregelmäßig verlaufenden braunen Quer- und Spirallinien geziert. Das ganze Gehäuse ist 4,6 mm hoch und 2 mm breit.*

Translation. From locality 16.

The only specimen available from this new species has a great similarity with *Glyphostoma melanoxytum* Hervier from Lifou (Journ. de Conch. XLIV, 1896, p. 78, t. 3, Fig. 19). The colour, the protoconch and the size of Hervier's species are identical to the newly described species, as I was able to study type specimens in the Museum in Berlin, but the deep incision of the whorls and therefore the deep suture of *G. melanoxytum* is a significant distinguishing feature. The protoconch, consisting of four whorls, is put like a yellow to brown cap on the spire. The first two lighter coloured whorls are only apparently smooth: viewed under the microscope, they show a fine dotting; then brown coloured whorls follow with obliquely crossed lines forming a cancellated sculpture. The following four main whorls are scalariform with spiral ridges and varices, white in colour and decorated with irregularly brown transverse and spiral lines. The entire shell is 4.6 mm high and 2 mm wide.



Syrnola trivittata 1+
37814 Sturany
vide Sturany's Bericht 1903, p. 81 [259],
t. 7, f. 8 a–b. — Bittersee.
Exp. Sch. Pola i. d. Rote Meer 1895-6 u. 1897-8
leg. Steindachner et Siebenrock.

Figure 32. *Syrnola trivittata* Sturany, 1903 (Bitter Lakes, Suez Canal). **A–E, J**. Figured syntype, NHMW 37814: front (**A–B**), right side (**C–D**), back (**E**), protoconch (**J**). **F–H**. Syntype, NHMW 37814: front (**F**), right side (**G**), back (**H**). **I**. Original figure by Sturany (1903). **K**. Original label. Scale bars: **A–H**: 1 mm, **J**: 0.1 mm.

Family Pyramidellidae A. Adams, 1860

Elusa halaibensis Sturany, 1903

Figure 31
Sturany, 1903: 259, plate VI, figures 11a–b.

Type locality. Locality 30, "Mersa Halaib" [Halayeb, Egypt], 24°– 22°N.

Type material. Holotype: NHMW 37815, height 12.2 mm.

Original description. *Von der Localität 30: eine einzige Schale.*

Von der langgestreckten Schale sind 11 langsam anwachsende Umgänge erhalten, das Spitzchen fehlt. Unregelmäßig angeordnete Flecken von brauner bis violetter Farbe, welche wohl aus aufgelösten Spiralbinden *hervorgegangen sind, finden sich über das Gehäuse verbreitet, die violette Farbe ist besonders auf dem letzten Umgange ausgeprägt. Das ganze Gehäuse misst 12 mm in der Höhe, 3,7 mm in der Breite, die Mündung ist sehr schmal und 3,5 mm hoch; die Spindel ist mit einer größeren Falte und 2 ganz kleinen unter dieser gelegenen Falten besetzt.*

Die neue Art ist mit E. brunneo-maculata *Melv. (Mem. Proc. Manch. Lit. et Philos. Soc. 1896/97, p. 13, plate 6, figure 5) nahe verwandt.*

Translation. From location 30: a single shell.

Elongated shell, with 11 slowly growing whorls, the apex is missing. Irregularly arranged flammules of brown to violet in colour are found spread throughout the whole shell and probably derive from a dissolved spiral band, the purple colour is particularly prominent on the last whorl. The whole shell measures 12 mm in height, 3.7 mm in width, the mouth is very narrow and 3.5 mm high; the columella has one larger fold and two smaller ones below it.

The new species is closely related to *E. brunneo-maculata* Melvill (Mem. Proc. Manch. Lit. et Philos. Soc. 1896-97, p. 13, plate 6, figure 5.

Syrnola trivittata Sturany, 1903

Figure 32
Sturany, 1903: 259, plate VII, figures 8a–b.

Original locality: Bitter Lakes in the Suez Canal.

Type material. Two syntypes: NHMW 37814 (Bitter Lakes), the specimen figured by Sturany (1903), plate VII, figures 8a–b has been segregated, its height is 5.2 mm.

Original description. *2 Exemplare aus dem Bittersee im Suezcanale.*

Das abgebildete Gehäuse ist 5 ½ mm hoch und 1 ½ mm breit und besteht aus 10 flachen Umgängen. Die Anfangswindungen sind glashell und geben dem Gehäuse einen kugeligen Abschluss nach oben; die darauffolgenden Umgänge haben eine gelblichgrüne Binde auf weißem Grunde, der besonders oben gegen die Naht zu bindenförmig hervortritt (die Naht sieht hier fadenförmig aus); noch weiter nach unten treten 2, auf der Schlusswindung sogar 3 Spiralbinden von der genannten Färbung auf. Die Mündung ist ungefähr 1 mm hoch und trägt eine schwache Falte auf der Spindel.

Das zweite Exemplar misst 6.2 mm hat 11 Umgänge und undeutliche Spiralbinden.

Die besprochene Form ist am ehesten mit S. tincta *Ang. (Australien) zu vergleichen, die ich am Berliner Museum zu sehen Gelegenheit hatte.*

Translation. Two specimens from the Bitter Lake in the Suez Canal.

The figured shell is 5.5 mm high and 1.5 mm wide and consists of 10 flat whorls. The protoconch is crystal clear and give the shell a globular completion on top; the subsequent whorls have a yellowish green band on white background, such white background is particularly visible as a band close to the suture (the suture seems filiform); further down the shell, two, on the last whorl even three, spiral bands of the mentioned colour appear. The aperture is approximately 1 mm high and has a light fold on the columella.

The second specimen is 6.2 mm and it has 11 whorls and indistinct spiral bands.

The described form is compared best with *S. tincta* Angus (Australia), which I had the opportunity to see at the Berlin Museum.

Family Haminoeidae Pilsbry, 1895

Atys (*Roxania*) *lithensis* Sturany, 1903

Figure 33
Sturany, 1903: 235, plate VI, figures 2a–b.

Type locality. Station 114, “zwischen Suakim und Lith” [between Suakin, Sudan, and Al Lith, Saudi Arabia], 19°38'N, 37°55'E, 535 m.

Type material. Holotype: NHMW 84291, height 12.2 mm.

Original description. *Von der Station 114 (535m); ein einziges Exemplar.*

Das kleine, weiße Gehäuse, dessen Gewinde eingesenkt ist, so dass eigentlich nur der letzte Umgang frei bleibt, ist stichförmig genabelt und besitzt zahlreiche, spiral angeordnete Reihen von Pünktchen. Die Mündung überragt oben ein wenig die Ebene des Gewindes und hat eine Höhe von 3 ½ mm die Breite der Schale beträgt 2 ½ mm.

In Gestalt und Sculptur erinnert diese Conchylie lebhaft an die mediterrane Atys *(*Roxania*)* utriculus *Brocchi einerseits und an die japanische* A. *(*Roxania*)* punctulata *A. Ad. anderseits, aber auch mit* Cylichna noronyensis *Watson könnte sie verwandt sein.*

Translation. From station 114 (535m); a single specimen.

Small white shell, the spire is sunk so that only the last whorl is visible, the umbilicus is stitch-shaped and has numerous, spirally arranged rows of dots. The aperture reaches slightly above the spire and has a height of 3.5 mm, the width of the shell is 2.5 mm.

In shape and sculpture this shell vividly resembles on one hand the mediterranean *Atys* (*Roxania*) *utriculus* Brocchi, on the other hand the japanese *A.* (*Roxania*) *punctulata* A. Adams, but may also be related to *Cylichna noronyensis* Watson.

Comments. This species was assigned to *Roxania* by Dekker and Orlin (2000: 34) and Janssen in Janssen and Taviani (2015: 527).

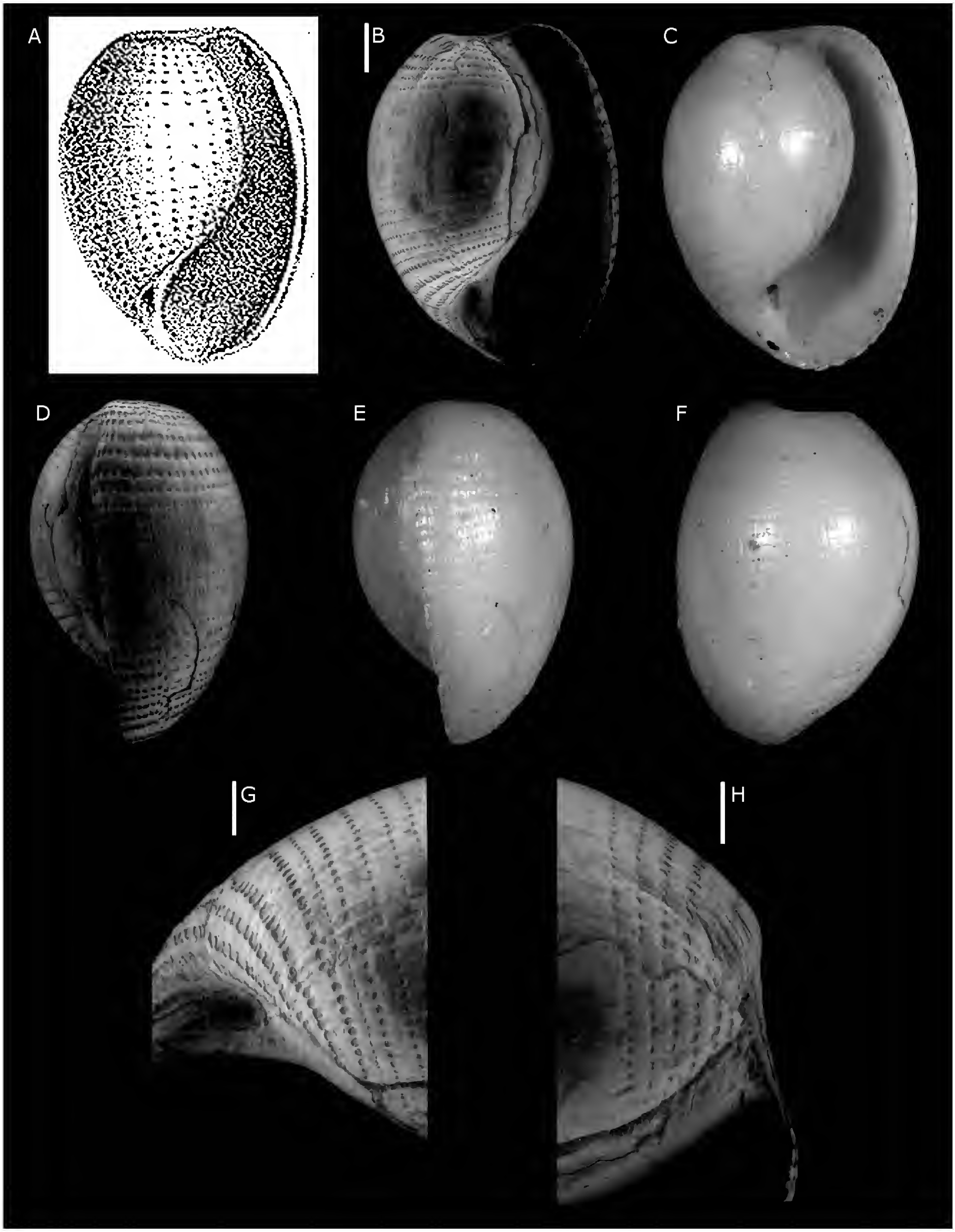


Figure 33. *Atys lithensis* Sturany, 1903, Station 144 (between Suakin, Sudan, Al Lith, Saudi Arabia, Red Sea). **A**. Original figure by Sturany (1903). **B–H**. Holotype, NHMW 84291: front (**B–C**), right side (**D–E**), back (**F**), microsculpture (**G–H**). Scale bars: **B–F**: 0.5 mm, **G–H**: 0.25 mm.

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Diversity and taxonomy of Vietnamese *Pollicaria* (Gastropoda, Pupinidae)

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Abstract

Species in the genus *Pollicaria* (Gastropoda: Pupinidae) are conspicuous members of the southeast Asian land snail fauna. Originally erected in 1856, both the genus and its constituent species have been reorganized multiple times with the most recent treatment published in 2013. Collections of Vietnamese *Pollicaria* during 2014 and 2015 raised questions of the utility of currently used diagnostic shell characters and identification keys in species identification. An examination of the authors' collections, combined with museum specimens, suggested that at least three species of *Pollicaria* occur or have historically occurred in Vietnam. It is suggested that *P. rochebruni* is a senior synonym of *P. crossei* and treat both taxa as conspecific. A second species, *P. mouhoti*, was believed to only occur in Cambodia, Laos, and Thailand. A possible third species, based only on previous karyotypic work, is discussed. Our data further suggest that shell features such as color and size lack consistent utility in species-level identifications in *Pollicaria*.

Key Words

Pollicaria rochebruni
Pollicaria crossei
Pollicaria mouhoti
Vietnam
pupinid

Introduction

The genus *Pollicaria* was erected by Gould (1856) to include large pupinid snails of southeastern Asia possessing the following characters: a thick ovate shell, distorted and flattened in the adult; a circular aperture; and an internal shoulder or groove inside the palatal edge of the peristome (Pain 1974). The taxonomy and systematics of *Pollicaria* have remained in flux for many years. At the same time he erected the genus, Gould (1856) described *Cyclostoma pollex* Gould, 1856 and made it the type species of *Pollicaria*. Benson (1859) erected the genus *Hybocystis* with *Megalomastoma gravidum* Benson, 1856 from Burma as the type species, recognizing that *C. pollex* was synonymous with the previously described *M. gravidum*. Haines described *C. myersii* Haines, 1858 from Siam, and three more species were described in *Hybocystis*: *H. mouhoti* Pfeiffer, 1862 from the Lao Mountains of Cambodia; and *H. elephas* de Morgan, 1885 and *H. jousseaumi* de Morgan, 1885 from the Perak region of Malaysia. Benson (1860) recognized that *Hybocystis* was a junior synonym of *Pollicaria*, but the former name remained in use until Pain's (1974) revision. Crosse (1885) revised *Hybocystis* into two sections, one with *H. elephas* and its junior synonym *H. jousseaumi* and the other with *H. gravida*, *H. mouhoti*, and *H. myersii*. In 1887, two species of *Hybocystis* were described from Tonkin (northern Vietnam), *H. rochebruni* Mabille, 1887 and *H. crossei* Dautzenberg & d'Hammonville, 1887. Dautzenberg and Fischer (1905) equated *H. rochebruni* and *H. crossei* with *H. gravida*, indicating that any shell differences between species were not consistent but rather existed in a continuum between extremes.

Pain (1974) revised the then six nominal *Pollicaria* species into three based on shell morphology: *P. gravida*, including *P. rochebruni* and *P. crossei*; *P. elephas*; and *P. myersii*, including its junior synonym *P. mouhoti*. Kongim et al. (2010) provided karyotype analyses for *P. gravida*, *P. elephas*, and *P. myersii*, along with

P. mouhoti as a separate species. They found karyotype differences between all four species and found two distinct karyotypes in Vietnamese *P. gravida*; their "big brown shell" and "small orange shell" samples differed in the centromere position of one chromosome pair (Kongim et al. 2010:127). However, they did not karyotype any topotypic *P. gravida* from Burma. Most recently, Kongim et al. (2013) reassessed *Pollicaria* using a combination of shell, radula, and reproductive characters and recognized six separate species: *P. gravida*, *P. myersii*, *P. mouhoti*, *P. elephas*, *P. rochebruni*, and *P. crossei*. They correctly recognized that not all *Pollicaria* possess the shouldering inside the peristome, and assigned the different karyotypes of Vietnamese *P. gravida* (Kongim et al. 2010) to *P. rochebruni* ("big brown shell") and *P. crossei* ("small orange shell"). The two species were diagnosed in their key based on shell size and color; *P. rochebruni* is large (>40 mm) with a brownish shell, while *P. crossei* is small (<35 mm) with a bright orange shell (Kongim et al. 2013). Both species are thus separate from the small yellow-shelled *P. gravida* from Burma. Kongim et al. (2013) also provided revised distributions for all species and figured type and additional material.

While identifying Vietnamese land snails collected in 2015 by PMH and DVT, we found Kongim et al. (2013) to be problematic in identifying specimens of *P. rochebruni* and *P. crossei*. We noted specifically that smaller (30-35 mm) reddish-brown shells and larger (35-40 mm) orange shells were left unidentifiable by the key, and that species-specific characters of the key conflicted with the comparative characters listed by Kongim et al. (2013:28). Of additional interest were records of putative *P. mouhoti* from Lào Cai, Vietnam (Solem 1966), a species that Kongim et al. (2013) had restricted to Cambodia, Laos, and Thailand, and internet references to additional species in northeast Vietnam and southern China. In an effort to resolve the taxonomic and distribution issues presented by Kongim et al. (2013), we undertook a morphological and molecular examination of Vietnamese *Pollicaria* specimens, along with original descriptions and other literature relevant to the genus, to address two research questions. First, are *P. rochebruni* and *P. crossei* separate valid species? Second, beyond those specimens listed in Solem (1966), is there evidence of additional *Pollicaria* species in Vietnam?

Materials and methods

Specimens collected by the authors were vouchered at the Carnegie Museum of Natural History (CM), Philadelphia, Pennsylvania. Collection data for Vietnamese *Pollicaria* came from the following museums: Chulalongkorn University, Museum of Zoology, Bangkok, Thailand (CUMZ); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Florida Museum of Natural History, University of Florida, Gainesville, Florida (FLMNH); Museum National d'Histoire Naturelle, Paris, France (MNHN), Royal Belgian Institute of Natural Sciences (RBINS), and National Museum of Natural History, Smithsonian Institute, Washington D.C. (USNM). Specimens from MNHN, CUMZ, and RBINS were not made available, so we treated the identifications and locality data given in Kongim et al. (2013) as correct. All Vietnamese *Pollicaria* holdings from FLMNH, MCZ, and USNM were borrowed, identified by the authors based on Kongim et al. (2013), latitude and longitude coordinates estimated, and mapped with DIVA-GIS (Hijmans et al. 2008).

We also searched the Internet for shell dealers selling *Pollicaria* specimens from Vietnam and surrounding areas. While we lacked the funding to purchase specimens outright, we examined shell images and locality information from the dealer websites. Requests to formally include images and additional information in this manuscript went unanswered. We accepted that this information was not equivalent to that of vouchered specimens, but could be important in determining the diversity and distribution (Turney et al. 2015) of *Pollicaria* species.

Live *Pollicaria* specimens were collected in Vietnam by PMH, DVT, and local farmers in 2015, preserved in ethanol, and DNA was successfully sequenced from two of them. One individual collected south of Hoàng Liên National Park had a reddish-brown shell we identified as *P. rochebruni*; the other was collected from Cúc Phương National Park and had an orange shell that was consistent with *P. crossei sensu* Kongim et al. (2013). Using foot tissue we followed a standard CTAB and phenol/chloroform DNA extraction method (Saghai-Maroof et al. 1984), then amplified one mitochondrial (16S) and two nuclear (18S and 28S) gene fragments by PCR. Amplification conditions were the same for all fragments and included an initial denaturing step (94°C for 120 s), 30 cycles (94°C for 60 s, 50°C for 60 s, 72°C for 120 s), and a final extension step (72°C for 10 minutes). We employed the following primer pairs: 16Sar and 16Sbr (Palumbi et al. 1991), 18S1F and 18S4R (Giribet et al. 1996), and 28SD1F and 28SD6R (Park and Ó Foighil 2000). Sequences were generated with the Sanger method on an ABI 3730xl by Genewiz (South Plainsfield, New Jersey, USA). Contigs were assembled in Geneious (BioMatters Ltd.) and combined with Cyclophoroidea data taken from GenBank (Table 1). Each gene fragment was aligned separately using MUSCLE (Edgar 2004) and the appropriate substitution model selected by Bayesian information criterion in IQTREE (Nguyen et al. 2015). The models chosen were HKY+G4 (Hasegawa et al. 1985) for 16S, JC+I+G4 (Jukes and Cantor 1969) for 18S, and TN+I+G4 (Tamura and Nei 1993) for 28S. The combined three gene dataset was analyzed under maximum likelihood in IQTREE allowing each gene partition to be optimized under its own model. Branch support was estimated using 10,000 ultra-fast bootstrap replicates (Minh et al. 2013) in IQTREE.

Results

A review of the original descriptions of both *P. rochebruni* and *P. crossei* suggested that Mabille (1887a) and

Table 1. GenBank accession numbers for all taxa included in the phylogenetic analysis.

Species	16S	18S	28S
Acroptychia bathiei	HM753491	HM753437	HM753380
Acroptychia milloti	HM753492	HM753438	HM753381
Adelopoma tucma	HM753534	HM753450	HM753393
Aperostoma palmeri	DQ093479	DQ093435	DQ093458
Arinia paricostata	HM753500	HM753441	HM753384
Bellamya bengalensis	FJ405724	FJ405678	FJ405623
Cochlostoma elegans	HM753489	HM753435	HM753378
Cochlostoma roseoli	HM753490	HM753436	HM753379
Cochlostoma septemspirale	HM753497	HM753423	HM753367
Cyclophorus aurantiacus	JX474723	KJ407088	KF319206
Cyclophorus bensoni	JX474670	KJ407082	KF319138
Cyclophorus cantori	JX474718	KJ407089	KF319193
Cyclophorus hirasei	AY010505	AF055644	HM003647
Cyclophorus latus	HM753484	HM753430	HM753374
Cyclotus taivanus	HM753485	HM753431	HM753375
Diplommatina canaliculata	HM753504	HM753445	HM753388
Diplommatina gomantongensis	HM753509	HM753451	HM753394
Diplommatina rubicunda	HM753520	HM753477	HM753417
Diplommatina rubra	HM753514	HM753456	HM753399
Japonia sp.	HM753486	HM753432	HM753376
Leptopoma vitreum	JX474741	KJ407147	KF319214
Opisthostoma austeni	KC250904	KC250930	KC250955
Opisthostoma hailei	KC250897	KC250923	KC250948
Opisthostoma mirabile	HM753529	HM753466	HM753406
Opisthostoma obliquedentatum	HM753530	HM753467	HM753407
Opisthostoma platycephalum	KC250905	KC250931	KC250956
Opisthostoma tenerum	KC250902	KC250928	KC250953
Palaina albata	HM753531	HM753469	HM753409
Palaina striolata	HM753533	HM753470	HM753410
Pollicaria cf. *crossei*	KY359073	KY359075	KY359077
Pollicaria rochebruni	KY359072	KY359074	KY359076
Pseudopomatias eos	KP271244	n/a	n/a
Pseudopomatias maasseni	KM103252	n/a	n/a
Pupina hosei	HM753493	HM753439	HM753382
Pupinella swinhoei	HM753494	HM753440	HM753383

Dautzenberg and d'Hamonville (1887) described shells of the same species from Tonkin (Figure 1). Authors of both species provided nearly identical data for the size and shape of the shell, aperture, apex, and sutures, and the number of whorls (Table 2). Mabille (1887a) did not provide information on the color of *P. rochebruni*, but did note the interior shoulder of the peristome. Dautzenberg and d'Hamonville (1887a) gave the color of *P. crossei* as reddish-brown, did not mention the shouldered peristome, but did note the triangular breathing device. The illustration of *P. rochebruni* in Mabille (1887b) clearly shows the breathing triangle, though the shouldered peristome is not immediately apparent in the illustrated *P. crossei* shell (Dautzenberg and d'Hamonville 1887). No mention is made in either description of any small orange shells.

Table 2. Morphological character comparison taken from the original descriptions of *Pollicaria rochebruni* and *P. crossei*.

	P. rochebruni	***P. crossei***
Height	39 mm	39 mm
Diameter	21 mm	20 mm
Color	n/a	Reddish-brown
Peristome	Thick, upturned, with a channel in the upper portion of the lip	White, circular, thickened, with a triangular air space at the lip.
Whorls	6.5 to 7 convex, flattened	7 convex, flattened on the upper part
Aperture	Circular	Circular
Shell	Ovate-pupiform, striate, and distorted	Pupiform, striate, and distorted
Sutures	Impressed	Linear and impressed
Apex	Obtuse	Obtuse

A total of 87 museum specimens (Figure 2) was examined and an additional 44 specimens were collected by PMH and DVT. Many shells were weathered and slightly pitted, and most were light tan to medium brown in color. Of the 131 total specimens, 124 possessed a shoulder inside the peristome and seven did not. Using the key to *Pollicaria* in Kongim et al. (2013:25) we were able to identify 12 specimens to species level: three *P. rochebruni*, two *P. crossei*, and seven *P. mouhoti*. Seventeen specimens had a peristome with the interior shoulder, but were between 35 and 40 mm in height and excluded by the key. The remaining 119 specimens also had an interiorly shouldered peristome, but had shell size and coloration combinations different than those given in the key. Using the table of comparative characters given later in Kongim et al. (2013:28), we identified 43 *P. rochebruni*, two *P. crossei*, and seven *P. mouhoti* from the same set of 131 specimens. The remaining shells did not fit any combination of characters given in the table. The seven putative *P. mouhoti* specimens more closely resembled the specimens of *P. myersii* figured in Kongim et al. (2013:27) than the lectotype of *P. mouhoti* figured therein.

Pollicaria specimens are advertised for sale at five websites: eBay.com, yhshells.com, femorale.com, conchology.be, and topseashells.com. Taken together, these specimens suggest that the known distribution of *Pollicaria* species should be expanded to include Guangxi autonomous region and Yunnan province in southern China. These two regions are adjacent to the northern borders of Vietnam, Laos, and Myanmar. Shells from these two regions were identified by their sellers as *P. crossei*, *P. gravida*, and *P. rochebruni*. All but two Chinese specimens possessed the interiorly shouldered perisotome; the other two possessed the flared lip and no shoulder seen in *P. mouhoti* and *P. myersii*. Shell sizes varied up to 45 mm in length, and shell colors varied from light tan through orange, reddish brown, dark brown, and dark purple. Vietnamese *Pollicaria* specimens varied similarly in color and size to the Chinese samples, and all possessed the interior shoulder in the peristome. These specimens were labelled as *P. crossei* and *P. rochebruni*.

DNA sequences from our putative *P. rochebruni* and *P. crossei* specimens (Figure 3) were identical for all three genes. Alignment lengths for each gene were 566 positions for 16S, 430 for 18S, and 838 for 28S. Our phylogenetic analysis produced a single tree (log-likelihood -17304.7519)

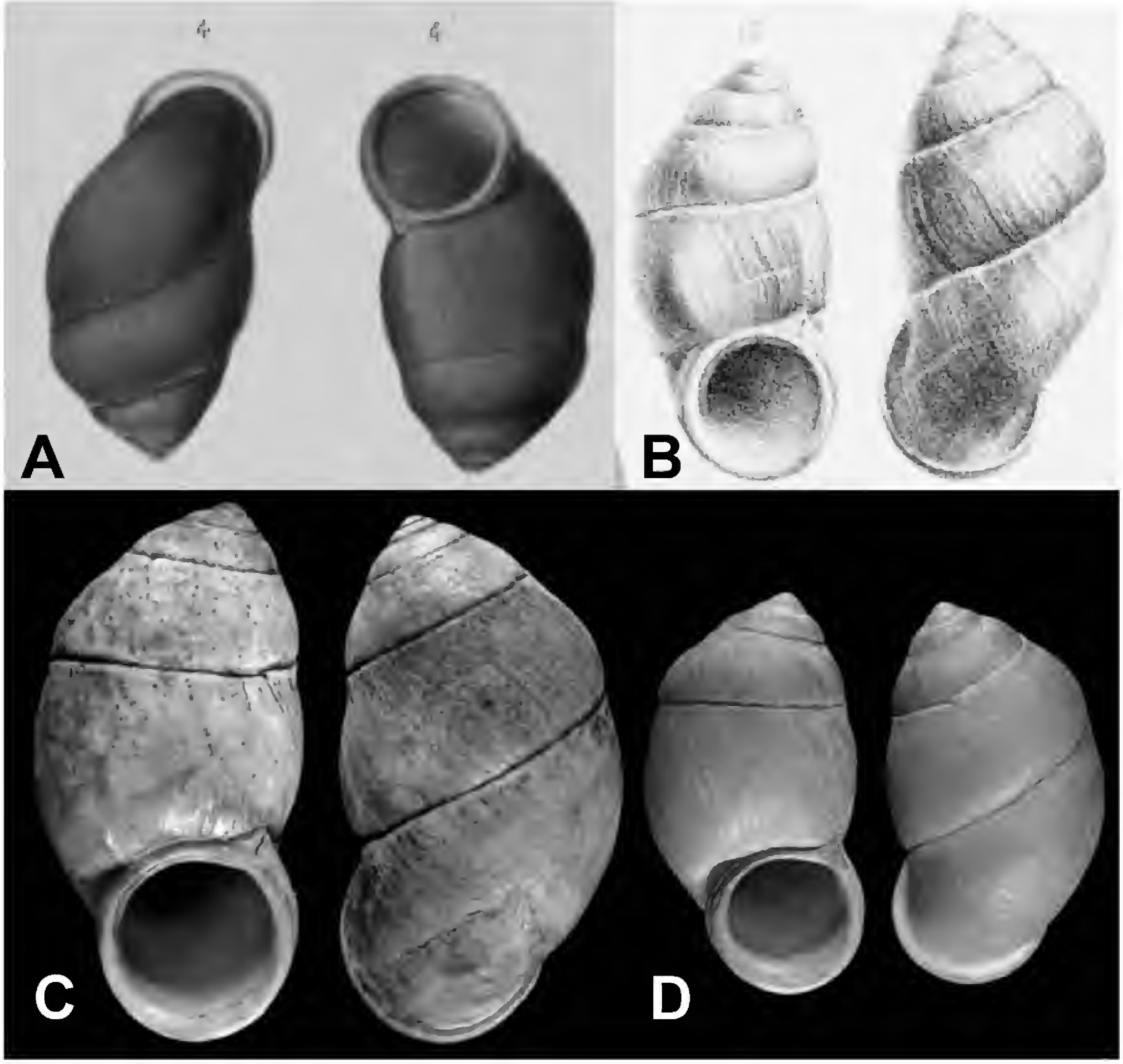

Figure 1. Original illustrations and type material of Vietnamese *Pollicaria*. **A**. *Pollicaria crossei* from Dautzenberg and d'Hamonville (1887). **B**. *P. rochebruni* from Mabille (1887b). No figure was provided in Mabille (1887a). **C**. *P. rochebruni*, lectotype MNHN 21305. **D**. *P. crossei*, lectotype MNHN 21304. Lectotype images from Kongim et al. (2013).

that recovered a monophyletic, well-supported Pupinidae sister to Cochlostomatidae. *Pollicaria* was resolved as sister to a clade of all other pupinids (Figure 4).

Discussion

Based on museum, online, and our own data, we believe that at least two, and possibly three, species of *Pollicaria* occur or have historically occurred in Vietnam. We consider the first, *P. rochebruni*, to comprise both *P. rochebruni sensu stricto* and *P. crossei* pre-Kongin et al. (2013). We treat *P. rochebruni* and *P. crossei* as synonyms based on the similarity of their original descriptions, the natural variation seen among shells of both species, and preliminary molecular evidence. The name *P. rochebruni* (publication date 14 May 1887) has priority over *P. crossei* (1 July 1887) and should be applied from hereon. We follow Kongim et al. (2013) in keeping *P. rochebruni* separate from *P. gravida*, given the lack of specimens of *Pollicaria* with an internally shouldered peristome from between Burma and Vietnam. This implies that the two species are geographically separate; based on the underlying geology, those regions separated approximately 40 million years ago (Yin 2010). However, since museum records only document presence not absence, future collections may suggest a continuous distribution. Additional karyotype and sequence analysis is needed to confirm or refute the separation between topotypic *P. gravida* and *P. rochebruni*. The revised distribution of *P. rochebruni* now includes Vietnam south to Đà Nẵng, with a possibility of stretching northeast into southern China (Figure 5).

We identified the second Vietnamese *Pollicaria* species as *P. mouhoti*, based on Solem's (1966) identifying collections of shells with peristomes lacking an internal shoulder and possessing a flared and partially reflexed lip to that species. We identified seven museum specimens which keyed out to *P. mouhoti* based on Kongim et al.

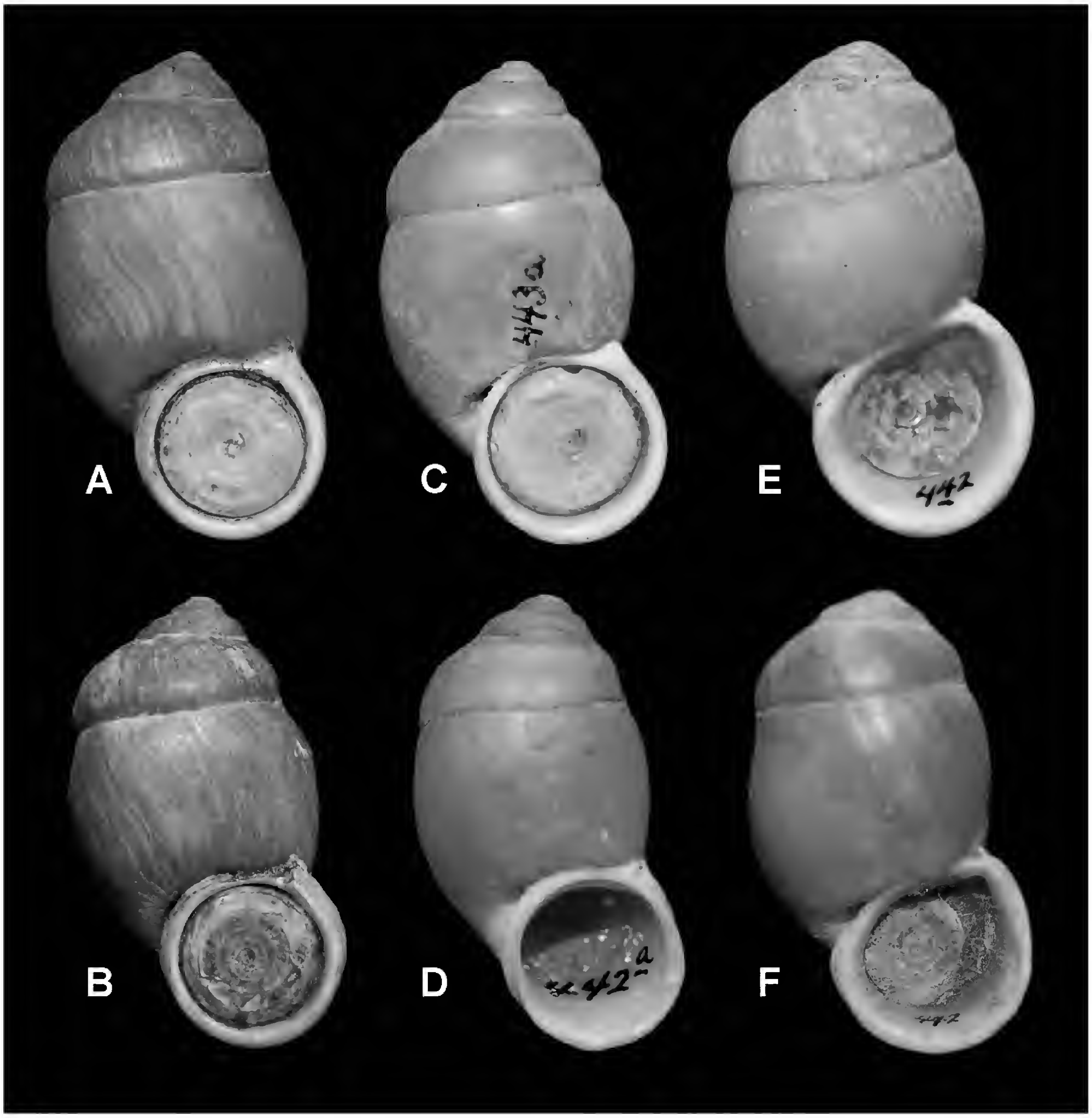

Figure 2. Vietnamese *Pollicaria* from museum collections. **A** and **B**. FLMNH 130267, *Pollicaria rochebruni*, Tonkin Province, 36.9 mm and 34.4 mm respectively. **C**. FLMNH 164622 (in part), *P.* cf. *crossei sensu* Kongim et al. (2013), Thất Khê, Tonkin Province. 28.5 mm. Labeled as *P. rochebruni*. **D**. FLMNH 164621 (in part), *P.* cf. *crossei sensu* Kongim et al. (2013), Pak-Kha, Tonkin Province, 24.6 mm. Labeled as *P. mouhoti*. **E** and **F**. FLMNH 164620, *P. mouhoti*, Gia Phu, Tonkin Province, 32.5 mm and 30.9 mm respectively.

(2013). Shells of *P. mouhoti* were collected by Solem (1966) in Vat Son, and we found additional museum specimens from Thái Nguyên, Gia Phu, Muong, and Bắc Kạn. Internet records suggest similar shells can be found in southern China, but it is unknown if they are the same species. The distribution of *P. mouhoti* in Vietnam appears restricted to isolated areas in the north.

A possible third Vietnamese *Pollicaria* species is based on karyotype differences that Kongim et al. (2010) uncovered in nominal *P. gravida* from Vietnam. Kongim et al. (2013) assigned their two *P. gravida* karyoptyes to *P. rochebruni* and *P. crossei*, the former having a large brown shell and the latter a small orange shell. We did not generate chromosome spreads for any individuals, but based on the figures in Kongim et al. (2010) we find the karyotypes between the brown and orange individuals to be equivocal. We also feel the radula differences listed in Kongim et al. (2013) are non-diagnostic characters. Kongim et al. (2010) believed that their small, orange-shelled snail was the result of sympatric speciation due to chromosomal evolution as outlined in King (1993). This hypothesis is consistent with studies of similar patterns of intra- and interspecific karyotype variation seen elsewhere (e.g. Ayala and Coluzzi 2005). Whereas authors have provided possible selective pressures that may accompany the karyotypic divergence (e.g. elevation and temperature), there is insufficient data available to pose any similar hypothesis for this *Pollicaria* species. Given

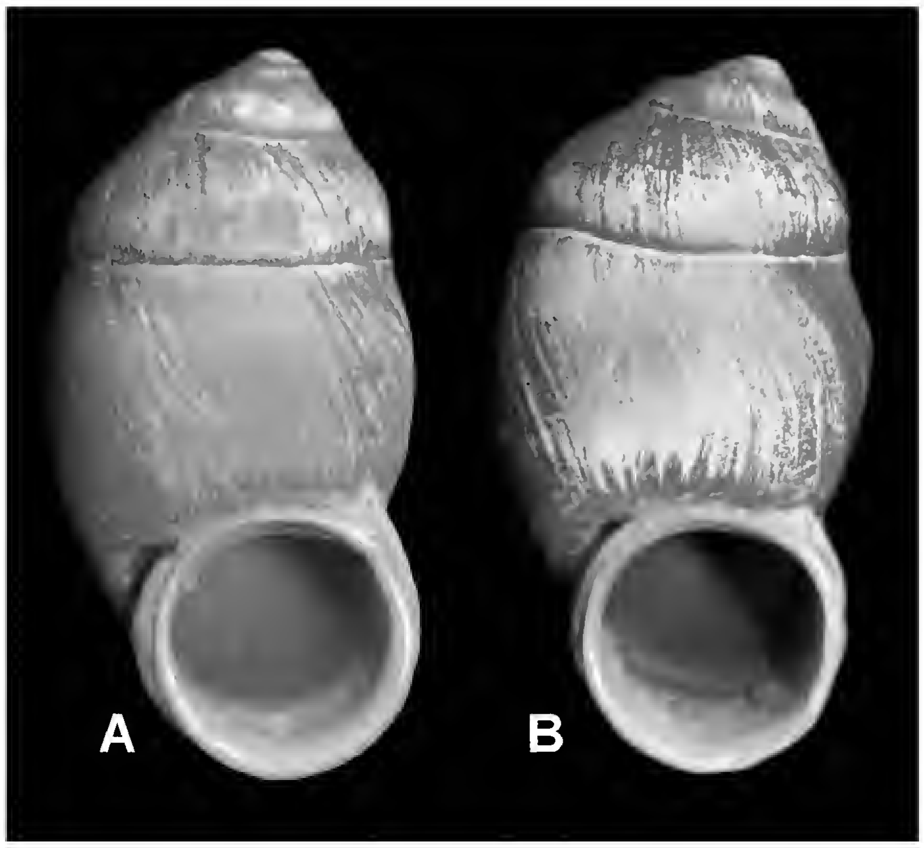

Figure 3. *Pollicaria* specimens sequenced in this study. **A**. CM 155302, orange phenotype (cf. *P. crossei sensu* Kongim et al. [2013]), 38.6 mm. **B**. CM 155307, red-brown phenotype (cf. *P. rochebruni*), 24.7 mm.

our synonymizing of *P. crossei* with *P. rochebruni*, if the individuals with the unique karyotype represent a new species it will require a new name. The known distribution of this possible taxon is limited to Cúc Phương National Park and Hữu Liên nature preserve (Kongim et al. 2013).

Our preliminary molecular evidence suggests that shell color and size may not be reliable for consistent species identification in Vietnamese *Pollicaria*. Sequences from one small, reddish-brown shelled snail (cf. *P. rochebruni*) and one large, orange-shelled snail (cf. *P. crossei*) were identical at three genetic loci. Our orange-shelled snail was larger than the nominal *P. crossei* in Kongim et al. (2013), and was collected alongside similarly-sized individuals with brownish and reddish shells. We feel both of our sequenced specimens represent *P. rochebruni*, supporting our belief that shell color in *Pollicaria* species can vary greatly. This contrasts with Kongim et al. (2013), who felt that shell color was diagnostic for many species.

Despite our best efforts and those of Kongim et al. (2013) to untangle the taxonomy of *Pollicaria*, we recognize the need for more work on the genus. Karyotypes of topotypic *P. gravida* remain unknown so no comparisons to the Vietnamese and other taxa can be made. Additional field work in southeastern Asia and southern China is needed to determine the true ranges of each species.

Systematic accounts

Family Pupinidae

Genus *Pollicaria* Gould, 1856

Type species. *Megalostoma gravidum* Benson, 1856 (=*Cyclostoma pollex* Gould, 1856), designated by Pain (1974).

Pollicaria rochebruni (Mabille, 1887)

Hybocystis rochebruni Mabille 1887a:12; Mabille 1887b: 138, pl. 2, figs 12 and 13; Dautzenberg and Fischer 1905:171

Pollicaria rochebruni – Kobelt 1902: 290; Kongim et al. 2013: 35, figs 5D and 5E

Hybocystis crossei Dautzenberg and d'Hamonville 1887: 220, pl. 8, fig. 4; Kobelt and Möllendorf 1899: 137; Kobelt 1902: 290; Dautzenberg and Fischer 1905:171

Pollicaria crossei – Kongim et al. 2013: 37, fig. 5F

Hybocystis gravida – Pain 1974: 174.

Pollicaria gravida – Kongim et al. 2010: 127 ("big brown shell")

Type Designation and locality. Lectotype MNHN 21305, Tonkin. Paralectotypes MNHN 25855, Tonkin (Kongim et al. 2013).

Material examined. All material from Vietnam / Tonkin Province. The number in parentheses is the number of shells from each lot assigned to the species. Locality names have been corrected wherever possible. – CM 155301, south of QL279, Thẩm Dương, Văn Bàn District, Lao Cai (7); CM 155302, Vườn quốc gia Cúc Phương, Lạc Sơn District, Hòa Bình (3); CM 155303, south of QL279, Thẩm Dương, Văn Bàn District, Lao Cai (7); CM 155304, limestone mountain at bridge into Tan Moui, near intersection of QL279 and DT234B, southwest of Chi Lăng, Lạng Sơn (6); CM 155305, ca. 60 m north of the intersection of QL1A and DT234B, Chi Lăng, Lạng Sơn (6); CM 155306, limestone mountain off QL279 at H9/155 road marker, ca. 1.1 km southwest of Dong Mo and 0.9 km southwest of Chi Lăng, Lạng Sơn (1); CM 155307, Công An huyện Cao Phong at QL6, Cao Phong, Hòa Bình (15); FLMNH 130259, Thất Khê (4); FLMNH 130265, Phu Ly (3); FLMNH 130623, Thái Nguyên (1); FLMNH 130258, Bắc Kạn (3); FLMNH 130261, Thái Nguyên (3); FLMNH 130262, Thái Nguyên (3); FLMNH 130624, Phi Mi (1); FLMNH 130260, Thái Nguyên (2); FLMNH 130268 (1); FLMNH 243794, Thái Nguyên (2); FLMNH 271764, Ninh Bình Province, Cúc Phương National Park, path to fairy cave, primary forest (1); FLMNH 164619, Thái Nguyên (2); FLMNH 164620, Gia Phu (2); FLMNH 164621, Pak-Kha (2); FLMNH 164622, Thất Khê (3); FLMNH 164623, Chợ Rã (4); FLMNH 130267 (2); FLMNH 242525 (2); FLMNH 192609, Thất Khê (6); FLMNH 130266 (1); MCZ 180001, vicinity of Lake Ba Bể (2); MCZ 180002 (2); MCZ 180003, Thất Khê (2); MCZ 180004, vicinity of Lake Ba Bể (3); MCZ 180005, Thái Nguyên (1); MCZ 180006, Thái Nguyên (4); MCZ 180007, Pak-Kha (4); MCZ 180008, Bảo Lạc (2); MCZ 180009, Pak-Kha (1); MCZ 197272, Pak-Kha (4); MCZ 380546 (1); USNM 207972, Lào Cai (1); USNM 207973, Lào Cai (1); USNM 207974, Chợ Rã (1); USNM 207975, Bắc Kạn (1); USNM 207976, Chợ Rã (1); USNM 207977, Chợ Rã (1); USNM 207978, Muong (1); USNM 207979, Muong (1); USNM 207980, Vân Sơn (1); USNM 207981, Vân Sơn (1); USNM 220045, Ba Bể (3); USNM 335963, Bắc Kạn (2).

Literature records (not examined). All from Vietnam, taken from Kongim et al. (2013). CUMZ 1523, Phong Na

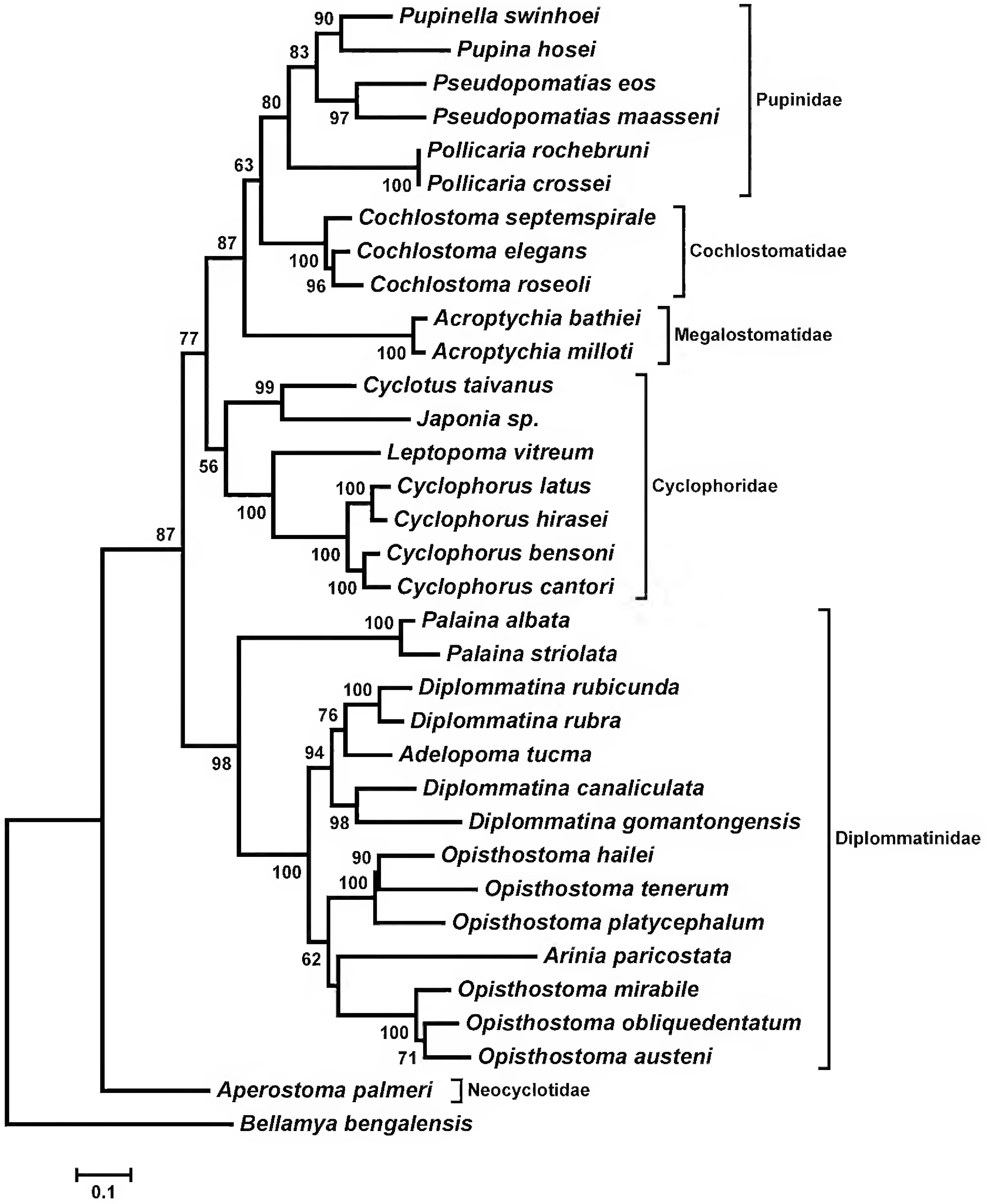

Figure 4. Phylogenetic tree (log likelihood= -17304.7519) based on three ribosomal genes (mt 16S, nuclear 18S and 28S) showing *Pollicaria* as sister to all other pupinid taxa. Values at branches are bootstrap values based on 10,000 ultrafast replicates.

National Park, Quảng Bình; CUMZ 1532, Cúc Phương National Park, Ninh Bình; CUMZ 1539, Phong Na National Park, Quảng Bình; CUMZ 1552, Phong Na National Park, Quảng Bình; CUMZ 1556, Bạch Mã National Park; CUMZ 1568, Phong Na National Park, Quảng Bình; CUMZ 1568, Cúc Phương National Park, Ninh Bình; CUMZ 1573, Cúc Phương National Park, Ninh Bình; CUMZ 1587, Cúc Phương National Park, Ninh Bình; CUMZ 1589, Khe Sen, Đà Nẵng; CUMZ 1594, Hữu Liên Nature preserve; MNHN 21304, Than Moi, Tonkin; RBINS 525390, Than Moi, Tonkin.

Description. Pupoid shell, to 45 mm length and 20 mm diameter, color varying from tan to orange, reddish-brown, and dark brown, possibly dark purple. Old specimens are often finely pitted. Whorls 5-7, transverse growth lines present, sutures linear and slightly impressed, apex obtuse and occasionally distorted to the left (assuming standard

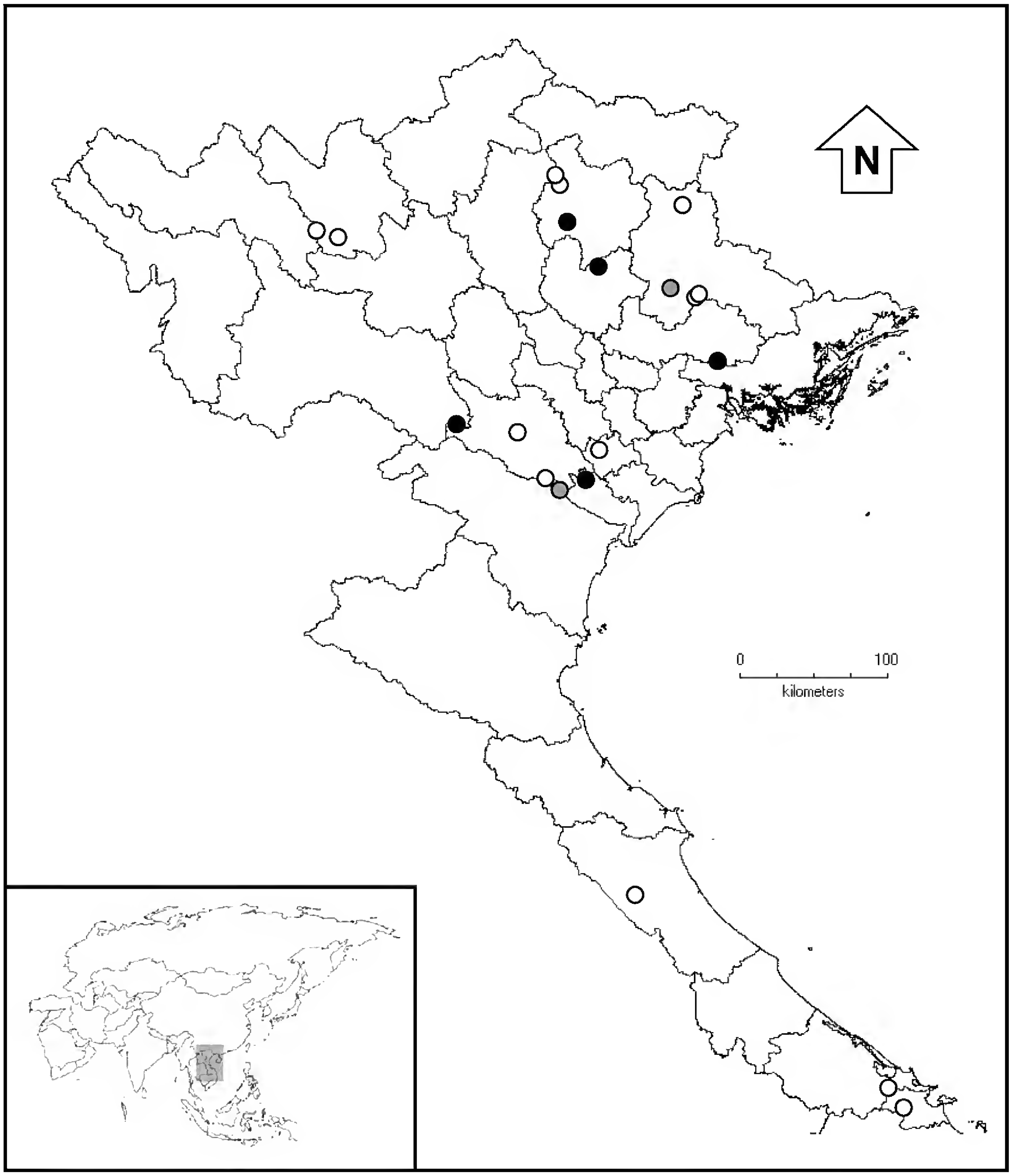

Figure 5. Revised distribution map for North Vietnamese *Pollicaria* species. *Pollicaria rochebruni* is present at all sites shown. Black dots indicate the presence of *P. mouhoti*, while gray dots indicate the presence of the putative new species of Kongim et al. (2013). Coordinates for localities taken from museum data were estimated from historical sources.

anatomical position), spire short. Penultimate body whorl may appear inflated relative to whorls on either side. Aperture circular with a right posterior triangular breathing structure. Peristome thickened, white to shell colored, with a thin parietal declining shoulder inside; umbilicus narrow. Operculum concentric, thick, and calcareous.

Radula with teeth in a 2-1-1-1-2 arrangement, based on the figure in Kongim et al. (2013: Figure 6E). Central tooth with three cusps, the middle one longer that the others. Lateral teeth with one large cusp and one smaller cusp on the central side. Marginals with one large central cusp flanked by one smaller cusp on each time. Kongim et al. (2013) described the radula as having more cusps per tooth than illustrated.

Distribution. Northern Vietnam south to Đà Nẵng (Figure 5). Possibly in Guangxi autonomous region and Yunnan Province, China.

Discussion. By synonymizing *P. rochebruni* and *P. crossei*, we suggest that all *Pollicaria* specimens from Vietnam that possess an interiorly shouldered peristome are a single species, excluding some smaller (< 35 mm) individuals with bright orange shells. We found live specimens of *P. rochebruni* at the bases of and in the valleys between karst outcrops in northern Vietnam. Reports from local farmers indicated that snails are more abundant during the spring rains, when native residents eat them as a delicacy. Some Chinese shells found for sale on the Internet are consistent morphologically with *P. rochebruni* but may represent a separate species.

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A review of the reproductive biology of the only known matrotrophic viviparous anuran, the West African Nimba toad, *Nimbaphrynoides occidentalis*

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Abstract

Amphibians, and anurans in particular, show the highest diversity of reproductive modes among tetrapods. Nevertheless, viviparity is scarce in anurans and its occurrence is even more often assumed rather than confirmed. Probably the best studied viviparous amphibian is the Nimba toad, *Nimbaphrynoides occidentalis*. During more than 40 years of research, the Nimba toad's reproductive morphology, endocrine activity of the ovary as well as the pituitary gland, and to some extent the ecological impact (seasonality, humidity, food availability) on reproduction was examined. Due to the Nimba toad's unique reproductive mode, summaries are usually included in reviews discussing amphibian reproduction and articles on reproductive biology often discuss the exceptional reproductive system of Nimba toads. However, to our knowledge a detailed synthesis, summarising all the different original studies on the toad's reproduction, is so far missing. In this paper we review and summarise all available initial publications, which often have been published in French and/or are difficult to access. A short overview is given of the climatic and environmental conditions experienced by Nimba toads and the key findings supporting a "true" viviparous reproduction with matrotrophy (maternal provision of nutrition during the gestation) and pueriparity (birth of juveniles). Then foetal development (morphological, gonad and pituitary development), and the female (ovary, oviduct, pituitary and their endocrine interactions) and the male reproductive system (testes and pituitary) are reviewed. Finally, the reproductive cycle and its link to the Nimba mountains' seasonality and ecological/ conservation implications are discussed.

Introduction

Viviparity, in the sense of retaining developing eggs or foetuses within the female genital tract, evolved numerous times in vertebrates and within tetrapods especially in squamates (Blackburn 1999, 2015, Pyron and Burbrink 2014, van Dyke et al. 2014). Internal fertilisation is necessary to allow oviductal egg retention and viviparity (Wake 2015b). As most caudates (90%, Wake 2015a) and all caecilians are internally fertilising (Gomes et al. 2012, Wake 2015a) they show the first requirement for viviparity (Wake 2015a, 2015b). Nineteen (2.7%, Buckley 2012) of the ca 700 caudate species (695 AmphibiaWeb 2017, 703 Frost 2017, both accesses 11.01.2017) and about one fourth of the ca 200 caecilian species (205 AmphibiaWeb 2017, 205 Frost 2017, both accessed 11.01.2017) are known or assumed to be viviparous (Buckley 2012, San Mauro et al. 2014, Wake 2015a, 2015b). Anurans (frogs and toads), on the other hand, show a very high diversity in reproductive modes (at least 42 modes, Haddad and Prado 2005, Iskandar et al. 2014), but internal fertilisation and viviparity are very rare. Of the ca 6,700 recognised anuran species (6,714 AmphibiaWeb 2017, 6,678 Frost 2017, both accessed 11.01.2017), viviparity is only known or assumed in 17 species (0.3%) of five genera: *Craugastor* (1 species), *Eleutherodactylus* (1), *Limnonectes* (1), *Necto-*

phrynoides (13) and *Nimbaphrynoides* (1). Hence, within the Amphibia, viviparity is common in caecilians, rare in caudates and exceptional in anurans.

Viviparous reproductive modes may differ in two fundamental traits: i) at which developmental stage offspring are born and ii) in the way foetuses receive the nutritional energy for their development. During amphibian development the adult anuran body plan is only achieved after metamorphosis is completed (Duellman and Trueb 1986, Wells 2010). In larviparous species, offspring are born at any larval stage before metamorphosis (Greven 2003) and newborn larvae are dependent on open water. In pueriparous species offspring are born after metamorphosis (Greven 2003) and water independent juveniles are born. Within caudates 14 (64%) of the viviparous species and some subspecies of *Salamandra salamandra* (Buckley et al. 2007, Wake 2015a, 2015b) and *Salamandra algira* (Beukema et al. 2010, Escoriza and Ben Hasssine 2014) are pueriparous. In anurans only one of the known 17 viviparous species is larviparous (*Limnonectes larvaepartus*; Iskandar et al. 2014, Kusrini et al. 2015), all others (94%) are pueriparous. Within caecilians no larviparous species are known, nevertheless oviparous species may lay eggs in the neurula stage (Sarasin and Sarasin 1887, Kupfer et al. 2006, Gomes et al. 2012). Hence, pueriparity is the only known viviparous mode in caecilians and more common in anurans than in caudates.

Foetal development and growth needs energy. This energy can be provided by the mother via yolk rich (lecithotrophic) eggs, or by unfertilised eggs and smaller siblings (oophagy and embryophagy, sometimes called adelphophagy), or the mother continuously nourishes the foetus during gestation (matrotrophy). A good example for lecithotrophy is direct development: large, yolk rich eggs are deposited at humid locations, outside of water, and the entire development takes place within the egg, exclusively powered by yolk (Guibé and Lamotte 1958, Hanken 2003). The best-known example for matrotrophy are mammals, in which yolk poor eggs are fertilised and very early within the development the nutritional needs of the foetus are provided for by the mother via a placenta. Nutrition through unfertilised eggs and/ or intra-oviductal cannibalism of the offspring, is known for example from *Salamandra salamandra* subspecies (Buckley et al. 2007, Buckley 2012). Matrotrophy in amphibians may be achieved through the development of a particular intra-oviductal epithelium (e.g. “zona trophica” in *Salamandra atra*) with increased mitoses, cell growth and apoptosis (Vilter 1986, Wake 2015a, 2015b). This epithelium is consumed by the foetuses, for which they developed special dentition in salamanders and caecilians (Wake 1993, 2015a, Gomes et al. 2012). In some oviparous caecilians with maternal care, special epidermal cells are produced by the mother and eaten by the offspring (skin feeding, Kupfer et al. 2006, Wake 2015a). The distinction between lecitotrophy, oophagy and matrotrophy is not as sharp as between pueriparous and larviparous species and the different types are not mutually exclusive (Wake 2015a, 2015b). All eggs contain some amount of yolk which is consumed before other nutrition is used (Wake 2015a). The best studied viviparous salamander, *Salamandra atra*, for example combines lecitotrophy, with oophagy and matrotrophy (Vilter 1986, Wake 2015a). Within this species, only two eggs, one per oviduct, receive all egg layers necessary for fertilisation. In each oviduct one foetus develops, first dependent on its own yolk, after hatching by feeding on the unfertilised eggs within the oviduct and last by matrotrophy where foetuses feed of the epithelium cells in a “zona trophica” (Vilter 1986, Wake 2015a). Within caecilians and caudates matrotrophy is known from several species (San Mauro et al. 2014, Wake 2015b). In anurans, only a single species is known in which most energy for foetal development derives from matrotrophy (Xavier 1971, Wake 1993, 2015a, 2015b). This species is *Nimbaphrynoides occidentalis* (Xavier 1977, 1986, Wake 2015b).

This unique matrotrophic (and pueriparous) anuran is a small (snout vent length (SVL) 15–27 mm, Lamotte 1959, Xavier 1971) West African bufonid, endemic to a few square kilometres (4 km², Lamotte 1959) of the high altitude grasslands of the Nimba mountains (Lamotte 1959, Lamotte and Sanchez-Lamotte 1999, Hillers et al. 2008, Sandberger-Loua et al. 2016a), a small mountain chain in the tri-border area of Guinea, Ivory Coast and Liberia (Figure 1). Shortly after its description as *Nectophrynoides occidentalis* Angel, 1943, its unique viviparous reproductive mode was recognised (Angel and Lamotte 1944a, 1944b) and led to numerous, partly very detailed studies. After the internal fertilisation of very tiny (~500 µm) yolk-poor eggs (Angel and Lamotte 1944b, Lamotte and Rey 1957, Vilter and Lugand 1959a, Xavier 1971), the eggs are retained within the lower part of the oviduct (Angel and Lamotte 1944a, Vilter and Lamotte 1956, Xavier 1971), the oviductal epithelium secrets liquid mucoproteins to nourish the foetuses (Vilter and Lugand 1959b, Xavier 1971, 1977, 1986), which are born after nine months as fully developed juveniles (e.g. Angel and Lamotte 1947, Lamotte et al. 1956, Lamotte 1959, Xavier 1971). Françoise Xavier summarised her own large body of work in two book chapters (Xavier 1977, 1986) and summaries are included e.g. in reviews by M. Wake (e.g.: Wake 1993, 2015a, 2015b) and in K.D. Wells’ book (2010). Within this review we synthesise all the extensive work by F. Xavier, but as well the studies of M. Zuber-Vogeli, M. Lamotte, J. Gavaud, V. Vilter and others.

A short history of the taxonomy of *Nimbaphrynoides occidentalis*

The Nimba toad was described as *Nectophrynoides occidentalis* Angel, 1943, due to its similarity to the then two known East African *Nectophrynoides* Noble, 1926 species, *N. viviparous* (Tornier, 1905) and *N. tornieri* (Roux, 1906). For the same reason the new species was assumed to be pueriparous and lecitotrophic (Angel 1943). Later it was even hypothesised to be parthenogenetic, as during the first field survey M. Lamotte had not recorded any males (Angel and Lamotte 1944a, 1944b). During a second field period males and matings were observed and subsequently matrotrophy assumed (Angel and Lamotte 1944b). Dubois (1986) revised the genus *Nectophrynoides*, which at that time comprised oviparous, lecitotrophic viviparous and matrotrophic viviparous species and placed them, according to their reproductive mode, into four different genera: *Spinophrynoides* (for the oviparous Ethiopian *S. osgoodi*, now placed in *Altiphrynoides* and feared to be extinct; Gower et al. 2013), *Altiphrynoides* (for the direct developing *A. malcolmi* from Ethiopia), *Nectophrynoides* (now 13 lecitotrophic pueriparous species all from Tanzania, one extinct in the wild), and *Nimbaphrynoides* (now one species from the Nimba mountains in Guinea, Ivory Coast and Liberia). The *Nimbaphrynoides* population from Liberia was described as a separate species (Xavier 1978), but because of high genetic and acoustic similarity is now considered to be a sub-species of *N. occidentalis* (Sandberger et al. 2010). Based on morphological data it was assumed that *N. occidentalis* is more closely related to *Altiphrynoides* than to *Nectophrynoides* (Wake 1980b, Grandison 1981), and most closely related to *Didynamipus sjostedti* (Grandison 1981, Graybeal and Cannatella 1995), a small, probably direct developing forest toad from Cameroon (Gonwouo et al. 2013). A recent, comprehensive phylogenetic study by Liedtke et al. (2016) confirmed *Didynamipus* as sistergroup to Nimba toads. Interestingly, while *Altiphrynoides*, *Nectophrynoides* and *Nimbaphrynoides* are part of the same clade, none of these form a sistergroup relationship with each other. This suggests that direct development and viviparity seen in these taxa possibly evolved independently of each other (Liedtke et al. 2016).

The habitat of the Nimba toad

Nimba toads are endemic to the Nimba mountains, which are a south-west, north-east oriented mountain chain in Liberia, Ivory Coast and Guinea (see Figure 1). This steep-sided mountain chain is about 40 km long and in parts up to 12 km wide (Schnell 1952). The surrounding lowlands are at about 500 m asl, whereas the highest peak, Richard-Molard, reaches 1,762 m asl (Schnell 1952, Leclerc et al. 1955, Lamotte 1959, Lamotte et al. 2003). In its southern, Liberian part the mountain ridge is lower (Lamotte et al. 2003), and after mining activities now only rarely exceeds 1,200 m asl. In the northern, Guinean part the main ridge undulates between 1,200 m asl and 1,762 m asl (Leclerc et al. 1955). It consists of banded iron formations (Billa et al. 1999), which are of high global economic importance (Berge 1974, Lamotte 1983, Schnell 1987). The presence of Nimba toads and chimpanzees as part of a rich and endemic fauna and flora led to the declaration of the Nimba mountains as a World Heritage Site in Guinea in 1981 and Ivory Coast in 1982 (UNESCO July 22, 2015/2015). Due to increasing mining exploration activities, the WHS has been listed as in danger since 1992 (Poilecot and Loua 2009, UNESCO July 22, 2015/2015). In 2014 its outlook was considered to be "critical" (IUCN January 11, 2017/2014).

The climate of the area is characterised by first rains in March/ April, a rainy season from May to October and a dry season from November to February/ March. Mean yearly temperature is 25°C in the lowlands (550 m asl) and 19°C at high altitudes (Leclerc et al. 1955, Lamotte 1958, Lamotte and Roy 1962, Lamotte et al. 2003). Mean annual precipitation is 2,093 mm, but is estimated to range from 1,500 mm in the lowlands to 3,000 mm on the ridges (Lamotte 1959, Lamotte et al. 2003). The rainy season at high altitude is characterised by nearly constant fog and rather continuous, but not very heavy, rain (Lamotte 1959). The dry season is characterised by larger temperature fluctuations, low humidity, little rain and dry season fires (see Figure 2, Schnell 1952, Lamotte 1958, 1959). The change from one season to the other is characterised by tornadoes and thunderstorms (Schnell 1952, Leclerc et al. 1955, Lamotte 1959). The first rains after the dry season may arrive between the end of February and April, whereas the very humid rainy season does not

Figure 1. The Nimba mountains. Left: elevation map of the Nimba mountains, with an inset map showing the position of the Nimba mountains within West Africa. Right: a large part of the Nimba mountains showing the steep slopes, the high altitude grasslands, the forests in the lowlands and the ravines.

Figure 2. Rainy and dry season at Nimba. The rainy season (top) is characterised by persistent fog and rain, whereas the dry season (middle) is characterised by little rain, high temperature fluctuations and dry season fires. After dry season fires the grasses sprout very fast (bottom, © Nèma Soua Loua).

start before June (Schnell 1952, Leclerc et al. 1955, Lamotte 1959). The transition between the rainy and the dry season is much faster and happens during a few weeks between October and November (Lamotte 1959). High elevations receive more rain than the lowlands during the rainy season, but less rain during the intermittent and dry seasons (Lamotte 1959, Lamotte and Roy 1962).

The areas outside the World Heritage Site are almost exclusively anthropogenically altered landscapes (Schnell 1952, 1987, Fournier 1987, Lamotte et al. 2003). Within the reserve the lower flanks and lowlands of the Nimba mountains are mainly covered in evergreen forests. In the South forests naturally grow as well on the mountain ridges, whereas in the North they are restricted to ravines (Lamotte et al. 1962, Fournier 1987). The lowland forests are a mosaic of primary and secondary forests (Lamotte 1947b, Schnell 1952, 1987, Fournier 1987). At higher altitudes the lowland forests transition into a montane forest characterised by lower tree diversity, the presence of *Parinari excelsa,* many epiphytes and less lianas (Schnell 1952). Savannas are mostly found in the lowlands on the eastern sides of the mountain chain, growing on thinner top-soils than forests (Schnell 1952, 1987, Fournier 1987, Lamotte et al. 2003). Within Guinea the largest parts of the high altitudes are covered in montane grasslands (Lamotte 1947a, 1947b, 1958, 1959, Schnell 1952, 1987, Lamotte and Roy 1961a, 1962, Lamotte et al. 1962, 2003a, Fournier 1987). These grasslands are characterised by the high abundance of the grass *Loudetia kagerensis* (Schnell 1952, 1987, Fournier 1987), fast regrowth after fires and despite their thin layer of top soil a large herbaceous biomass (Fournier 1987). Depending on the soil characteristics and anthropogenic impacts (e.g.: mining roads) slightly differing plant assemblages can be recognised (Fournier 1987, Schnell 1987). Standing open water is present only at two locations on the mountain top and only for some months during the rainy season (June/ July-September). These ponds are very shallow (< 5 cm). Due to the rarity of open water, the harsh climatic conditions and the isolation of the mountain a high percentage of the species in the high altitude grasslands is endemic (Lamotte and Roy 1961a), such as the Nimba toad, which occurs exclusively in the high altitude grasslands above 1,200 m asl (Lamotte 1959, Hillers et al. 2008, Sandberger-Loua et al. 2016a).

Annual seasonality and activity patterns

The very pronounced differences between the rainy and the dry season has strong effects on the toad's activity patterns (Lamotte 1959, Sandberger-Loua et al. 2016a) and their reproductive cycle (Xavier 1971, Gavaud 1977). Nimba

Figure 3. Nimba toad females. Left: a young female towards the end of the rainy season. Right: a large gestating female in June, shortly before parturition.

toads are only active during the rainy season (Lamotte 1959, Sandberger-Loua et al. 2016a). With the first rains gestating females emerge from the aestivation sites, later joined by virgin females and males (Lamotte 1959, Xavier 1971, Lamotte and Sanchez-Lamotte 1999). When rains become more permanent and humidity rarely drops below saturation, juveniles are born (compare Figure 3, Angel and Lamotte 1947, Lamotte 1959). Nimba toads mate at the end of the rainy season, in September/ October, rarely November (Angel and Lamotte 1947, Lamotte 1959, Xavier 1971, Lamotte and Xavier 1976b, Lamotte and Sanchez-Lamotte 1999). Mated females go underground, whereas unmated females and males may stay as long above ground as the rains continue (Lamotte 1959, Xavier 1971). During the dry season toads are dormant underground (Angel and Lamotte 1947, Vilter 1955, Lamotte and Xavier 1976a), hiding under rocks and within crevices (Vilter 1955), where humidity is higher and temperature less variable (Lamotte 1959). Nimba toads have a gestation period of nine months (October-June, e.g. Angel and Lamotte 1947, Lamotte et al. 1956, Lamotte 1959, Xavier 1971), of which they spend about the first six months (may vary between 4–7 months, October/ November to February/ March/ April) dormant underground and only the last 3 months (2–5 months, February/ March/ April to June) active above ground (e.g.: Angel and Lamotte 1947, Lamotte 1959).

Nimba toad females have a life expectancy of three to four, rarely five years; males reach even only up to three years (Castanet et al. 2000). On average, females give birth to nine young per gestation (range 4–20, Angel 1943, Angel and Lamotte 1944a, 1944b, Vilter 1956a, Lamotte and Xavier 1976a). However, the number of offspring born per gestation increases with age and hence, with size (Lamotte 1959, Xavier 1971). The average number of offspring per female in their first year is four, in the second 6.5, in their third 9.4 and in their fourth year 12 young (Xavier 1971). Assuming a life expectancy of three years, each female may give birth to about 20 offspring during her lifetime (32 if females survive four years). For a toad this is a very small number (Liedtke et al. 2014). This even assumes that females are mature three months after their birth and mate at the end of the rainy season of the same year. Depending on the length of the rainy season, between 30% and 70% of the respective year's newborn females become mature, nevertheless, the range indicates that an equal number of females become mature only the following year (Angel and Lamotte 1947, Lamotte and Rey 1957, Lamotte 1959). Average female lifetime reproductive output may thus even be much smaller.

In summary: Nimba toads are endemic to the high altitude grasslands above 1,200 m asl of the Nimba mountains in West Africa. Their sexual cycle and their activity are strongly linked to the local seasonality. They spend the dry season underground (4–7, on average 6 months) and they are active only during the rainy season. The active time covers the last three months (range 2–5 months) of the gestation and about three months between gestations. All Nimba toad males and 30–70% of females become mature within three months, the remaining females within 15 months. The female life-time reproductive output is very low with a maximum of 20–32 offspring.

Mating

Generally females are larger than males (females: SVL: 15–27 mm, Xavier 1971, 1986, 2009, Lamotte and Xavier 1976b, males: SVL: 15–23 mm, Lamotte and Xavier 1976b, Xavier 1986, 2009). Males have a darker back (Le Quang Trong 1967) and during most of their active above ground life recognisable nuptial pads (Angel and Lamotte 1947, 1948). Nuptial pad development is linked to spermatogenesis (Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966), and can be observed in males with an SVL of

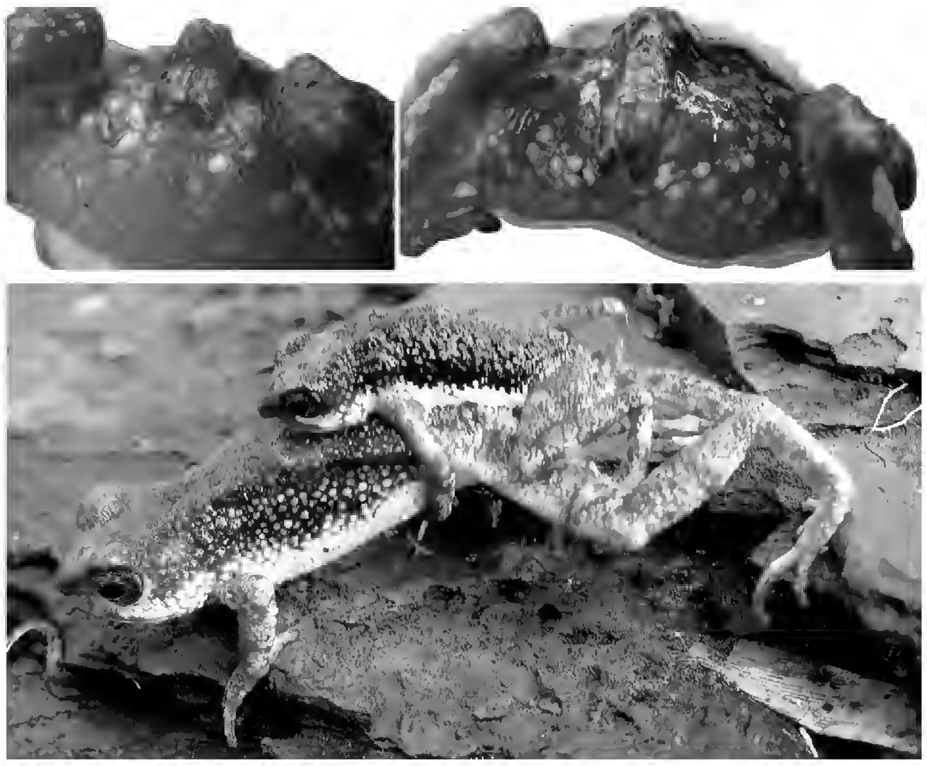

Figure 4. Female and male cloaca of Nimba toads and a pair in amplexus. The female cloaca (top left) is close to the urostyle, whereas the male cloaca (top right) is ventrally oriented. During mating it swells and encloses the female cloaca. During the amplexus lumbalis the female is constantly horizontally swaying (bottom).

only 13 to 14 mm (Angel and Lamotte 1948). The most important secondary sex difference, however, is the position of the cloaca (Angel and Lamotte 1947, Xavier 1971, 1986). The female cloaca is very close to the urostyle, whereas the male cloaca is more ventrally positioned and the distance to the urostyle is larger (Figure 4; Angel and Lamotte 1947, 1948, Xavier 1971).

Mating occurs without a copulatory organ (Angel and Lamotte 1947, Xavier 1971, 1986). Sperm transfer is ascertained by cloacal apposition (Xavier 1971), in which the male cloaca swells and encloses the female cloaca (Angel and Lamotte 1948, Xavier 1971). In contrast to all other bufonids amplexus is lumbal and is accompanied by a particular behavioural repertoire, described by Xavier (1971): males crouch on their front legs and as soon as the female moves, follow her and grab her tightly in the groin. This is supported by the spines of the nuptial pads on the males' thumbs and first fingers. Females are often injured by these nuptial pads during mating. As soon as the female is grabbed she starts swaying from one side to the other without cease. Mating occurs mainly during the day and may take several hours to more than one day (Xavier 1971). If mating occurs during the night it is interrupted by torch light (Angel and Lamotte 1948).

Due to the long duration of mating, it was assumed that Nimba toads may ovulate during this time (Lamotte et al. 1956). However, it was later shown that females, if kept without males, also ovulate (Xavier 1974). The unfertilised eggs are kept within the enlarged distal end of the oviduct and a pseudo-gestation develops (Xavier 1969, 1971, 1974). In some other amphibians with internal fertilisation, a receptaculum seminis (spermatheca) can be found (Wake 2015a). In Nimba toads fertilisation quite likely occurs within the upper part of the oviduct, but no receptaculum seminis nor any other accumulation of sperm in any part of the oviducts was found (Xavier 1971). Nevertheless, in 25% of Nimba toad litters more than one sire is needed to explain the genotypes found (Sandberger-Loua et al. 2016b).

In summary: mating occurs without specialised copulatory organs and sperm transfer is achieved through direct contact of the morphologically differently positioned male and female cloacae. Mating position is an amplexus lumbalis, being exceptional within Bufonidae. No receptaculum was found, nor any other accumulation of sperm, nor indication of ovulation induced by mating. Mating takes several hours and polyandry occurs.

Matrotrophy

Nimba toad eggs are very yolk poor and with a diameter of 500–600 μm (on average 540 μm, Vilter and Lamotte 1956, Vilter and Lugand 1959b, Lamotte et al. 1964, Xavier 1971, 1986) and a weight of 220 μg (Xavier 1971), particularly small. Newborn toadlets on the other hand, have an average SVL of 7.5 mm (Lamotte and Xavier 1976a, Xavier 1977, range: 6–10 mm, Angel and Lamotte 1944b, Lamotte and Rey 1957, Xavier 1971), this is one third of the mother's SVL (Lamotte et al. 1956, Xavier 1971), and an average weight of 45 mg (range: 30–60 mg, Xavier 1971, 1977, Lamotte and Xavier 1976a, 1976b). In a family-wide analysis of African bufonid egg sizes, Nimba toad eggs were described as being exceptionally small and well below the average egg size for other species of comparable adult size (Liedtke et al. 2014). Two anurans of similar adult size are, for example, the direct developing *Arthroleptis crusculum* (SVL < 20 mm, Guibé and Lamotte 1958) and the lecitotrophic *Nectophrynoides tornieri* (SVL: 25–27 mm, Angel and Lamotte 1948). In *Arthroleptis crusculum,* eggs are 3.5 mm in diameter (Guibé and Lamotte 1958, 7× the size of a Nimba toad egg) and newly hatched juveniles have a SVL of 5 mm (0.67× the size of Nimba toad toadlets). In *Nectophrynoides tornieri,* eggs measure 2 mm in diameter (4× the size of a Nimba toad egg) and newborn juveniles 5.4 mm (Lamotte and Xavier 1972a, 0.72 × of Nimba toad toadlets). Hence, metamorphs in the direct developing species are 1.4 times larger than the egg, in the viviparous, lecitotrophic toad 2.7 times larger and in the matrotrophic Nimba toad 15 times larger than the egg. This huge increase in size from egg to juvenile and particularly in weight (Nimba toad juveniles are > 200 times heavier than the eggs, Vilter and Lugand 1959b, Xavier 1971), requires energy, which has to be provided by the mother.

Matrotrophy is characterized by the transport of (nutritional) energy from the mother to the foetus. It is challenging to prove this process, nevertheless matrotrophy was very early (Vilter and Lugand 1959b) assumed in Nimba toads. No placentation occurs (Xavier 1971, Lamotte and Xavier 1976b), but matrotrophy was first linked to the observation that within the oviductal liquid microscopic whitish droplets were observed ("uterine milk", Vilter and Lugand 1959b). These were likewise found in the vacuoles within oviductal epithelium cells (Vilter and

Figure 5. Foetal labial papillae. Labial papillae are forming during stage Ia (left) and are well developed at stage Ib (right). See foetal development for more information on developmental stages. Redrawn after Lamotte and Xavier (1972b).

Lugand 1959b). Additionally it was observed that very early during the foetal development labial papillae appear (Figure 5) and foetuses have well developed intestines and livers very similar to adults early on (Angel and Lamotte 1944b). The hypothesis thus was that foetuses feed on the liquid "uterine milk" via the labial papillae (Vilter and Lugand 1959b, Xavier 1971, Lamotte and Xavier 1976b). To prove the nutritional transfer from mother to foetus, Xavier (1971) injected radioactively marked amino acids into gestating females. Six percent of these radioactively marked amino acids could be detected within 30 hours in the foetuses. They first were detectable in the digestive system, then in the very large liver and after 48 hours, in foetal muscle and brain tissue (Xavier 1971, 1977, 1986). This indicates that amino acids from the mother are transferred to the foetus and that they enter the foetus through the digestive system. This supports the hypothesis that mucoproteins are synthesised and released by the distal oviduct epithelium cells that form nutrients that are being fed upon by the foetuses with their labial papillae. The exact function of the papillae is unknown. Nevertheless, temporally they are linked to the presence of white droplets and it can be speculated that they are used to mechanically induce the mucoprotein secretion. It was also shown that well-nourished females gave birth to larger juveniles than under-nourished females (Xavier 1971), which provides additional supporting evidence for the importance of maternal nutrient transfer to the developing foetuses.

Another possibility to transfer nutrients from the mother to the foetuses is the ovulation of unfertilised eggs, or intra-oviductal cannibalism of other foetuses (Wake 2015a). Nimba toad follicles develop into corpora lutea after ovulation and persist for the time of gestation (Lamotte and Rey 1954, Lamotte et al. 1956, 1964, Xavier 1970b) and hence, the number of ovulated eggs can be compared with the number of foetuses in the oviduct (Lamotte et al. 1964). Usually all of the ovulated eggs develop into foetuses, but up to three more corpora lutea than foetuses were observed (Lamotte et al. 1964). While cannibalism or feeding on unfertilised eggs and other foetuses cannot be completely ruled out, it is unlikely to constitute a major source of nutrients to the developing foetuses.

In summary: newborn Nimba toads are 15 times larger and > 200 times heavier than the egg. It was shown that marked amino acids injected into mothers are detectable within 30 hours in the foetal digestive system and liver. This supports the hypothesis that foetuses take up their nutrition through the very early developed digestive system and nutrition is provided by oviductal epithelial mucous cells. Additionally, matrotrophy is supported as foetal size at birth is linked to environmental conditions during the last third of the gestation period, during which females are active and most of the foetal growth occurs.

Parturition

Parturition may take several hours to over two days, depending on the number of offspring (Xavier 1971, Lamotte 1982). Juveniles are either born legs or head first, on their venter or on their back, depending on the position they had within the distal end of the oviduct (Xavier 1971, 1986). At the end of gestation nearly all of the body cavity of the female is occupied by the oviducts (compare Figures 3 and 6a), severely restricting all other organs (Angel and Lamotte 1944a, Vilter 1956a, Xavier 1971). At this stage, the distal end of the oviduct becomes very stretched and the wall, especially the muscle layer, is very thin and supposedly too thin and weak to induce labour (Angel and Lamotte 1944a, Vilter 1956a, Xavier 1971). In any case, the injection of labour inducing pharmaceuticals had no effect on gravid *N. occidentalis* (Vilter 1956a). V. Vilter (1956a) was the first to observe females giving birth and developed a scenario on how birthing is achieved. Females press their thighs to their flanks, the feet are further away from the body, the two legs building a double W and are in that way supporting the pressure on the flanks (Figure 6b, c). V. Vilter (1956a) hypothesised that with their lungs (possibly too small and simple, Angel and Lamotte 1944b, compare Figure 7) and with some muscle support they are at the same time increasing the intraperitoneal pressure on the distal end of the oviduct from the cranial direction. The whole body is pressed to the ground, barring oviductal extension towards the ground. Vilter's (1956a) hypothesis is that with this posture the female is restricting the space within the oviduct and forces the juveniles to take the "only possible way out", through the cloaca. As support for his idea he claims that females just before or after giving birth are more sensitive to light (smaller pupils when exposed to light than females several weeks before giving birth). This would make them seek out shelters offering suitable support for the "birthing posture" and protecting them during birthing (Vilter 1956b).

There is indication that first all juveniles from one and only thereafter from the other oviduct are born (Xavier 1971). The passage through the cloaca is very fast (a few seconds), but if parturition is interrupted at this stage the juvenile dies, if juveniles already die within the oviduct they will stay there until the mother dies of sepsis (Xavier 1971). These latter observations indicate an active part of the juveniles during parturition.

In summary: Nimba toad females have not enough muscle power in their oviducts to induce labour. Hence, they induce birth through a unique "birthing posture". If foetuses die within the oviduct or during parturition, they may not be evacuated, hinting at necessary juvenile activity during parturition.

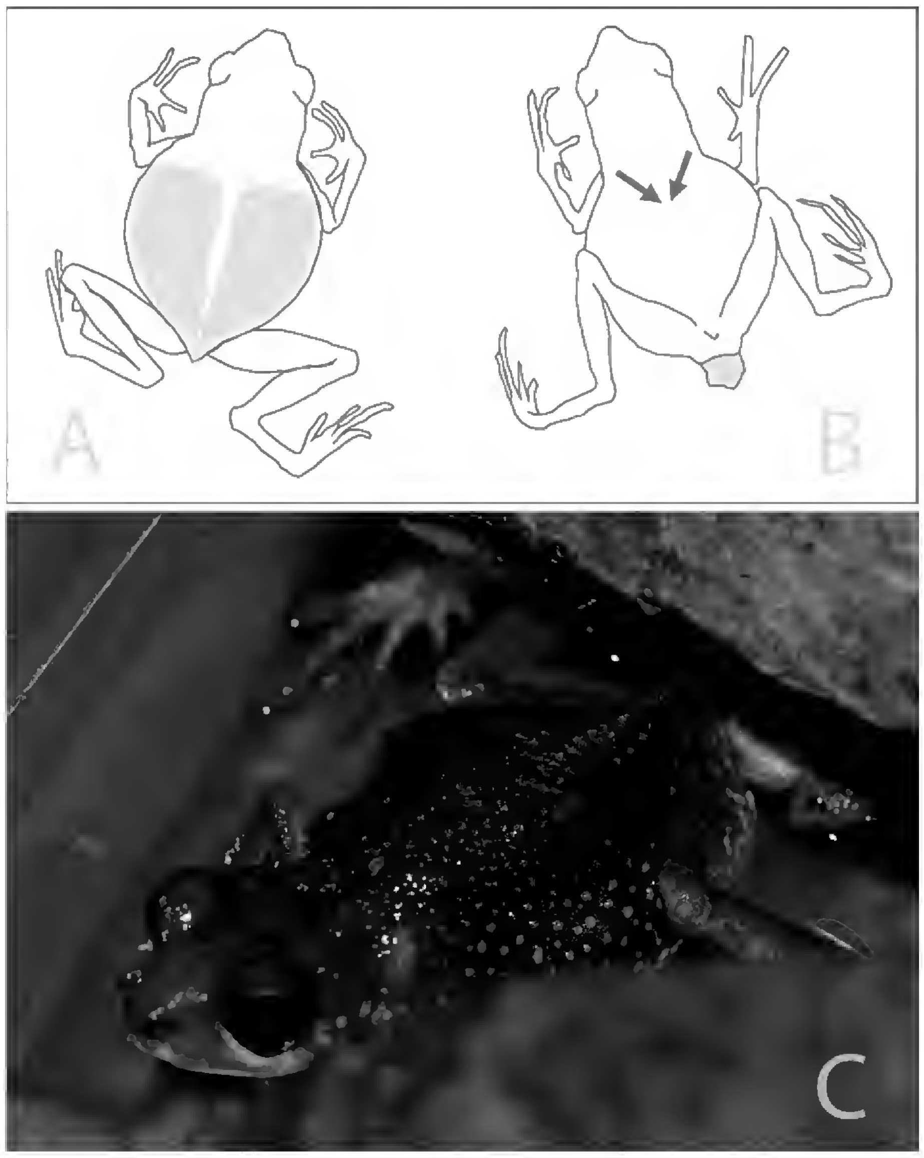

Figure 6. “Birthing posture” in Nimba toads. **A**: gestating Nimba toad; the grey shading indicates the size and position of the enlarged distal parts of the oviduct (uterus), **B**: shows the “birthing posture”, in which females build a double W with their legs and increase pressure on their uteri. Compare the position of legs on the photograph on the right (**C**) of a female giving birth, showing likewise the double W, of the legs. **A** and **B** are redrawn after Vilter (1956a).

Foetal development

Aquatic tadpoles of other anurans generally have a tail, with more or less pronounced fins, first external and later internal gills, a coiled gut, a spiracle, and mouth parts (i.e. horny beaks, labial teeth (keratodonts) and labial papillae, Altig and McDiarmid 1999, Channing et al. 2012). Nimba toad foetuses have a large square head and large eyes (Angel and Lamotte 1944a). They have neither internal nor external gills, nor spiracle, nor coiled gut and neither keratodonts nor horny beaks at any time during their development (Angel and Lamotte 1944a, 1944b, Xavier 1971, 1986, Lamotte and Xavier 1976a, 1976b). Their tails have very narrow fins and for most of the time they possess labial papillae (Angel and Lamotte 1944a, 1944b, Xavier 1971, 1977, 1986). The gut and the large and well developed liver are already adult-like relatively early during development (Figure 7, Angel and Lamotte 1944b). These peculiarities of the foetal morphology preclude the application of Gosner stages (Gosner 1960) usually used to describe early anuran development (Xavier 1971). Therefore, we use herein the eight stages for the foetal development defined and used by Zuber-Vogeli and Bihouès-Louis (1971), Lamotte and Xavier (1972b) and Lamotte et al. (1973). For the different stages see Figure 8.

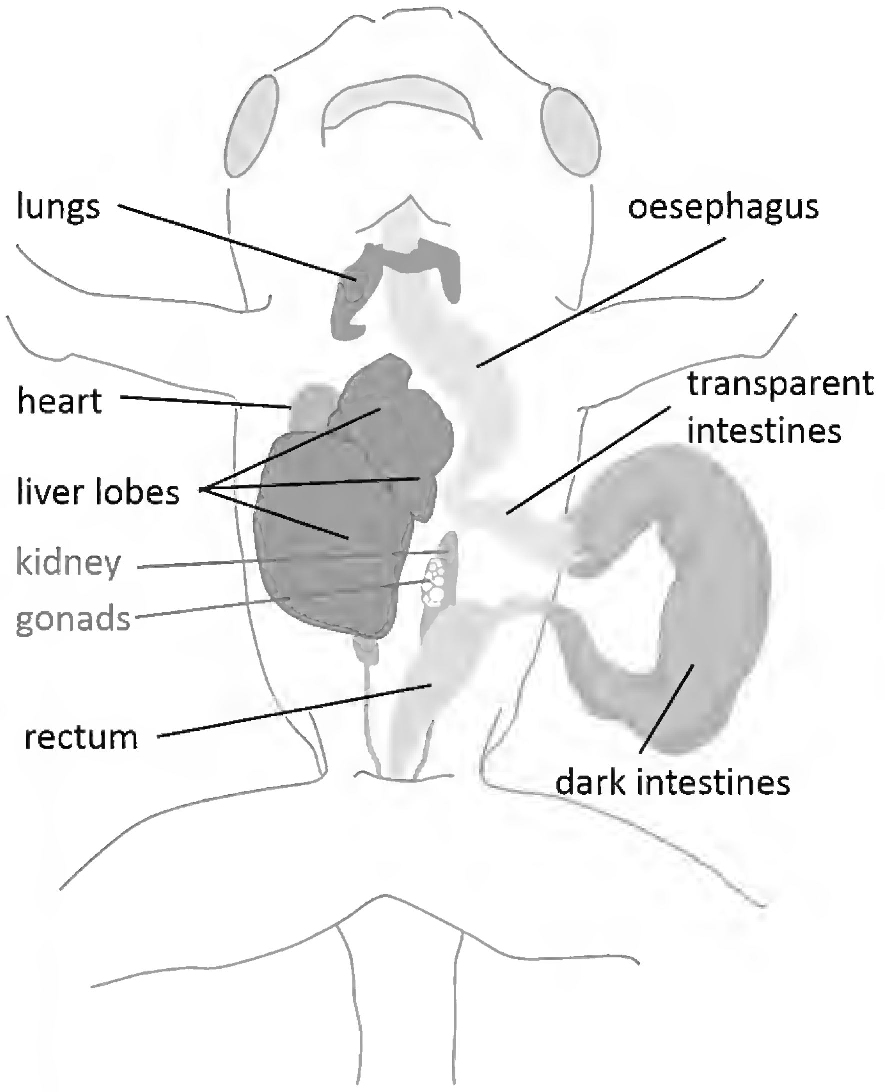

Figure 7. Foetal digestive system. Exceptional for an anuran foetus is the straight and differentiated gut, with an oesophagus, the transparent and the dark intestines (stomach) and a rectum, as well as the large liver lobes. Additionally, shown are small lungs (as well small in adults), the heart, kidney and gonads. Redrawn after Angel and Lamotte (1944a).

Stage 0

Stage 0 is the earliest described stage; it has a duration of less than two months. At stage 0 foetuses have a tail, some yolk is still visible, no eyes, no pigmentation and no cloacal opening. During this stage the intestines are forming. Foetus size varies between 1.0–2.7 mm (body: 0.6–1.4 mm, tail: 0.4–1.3 mm, Lamotte and Prum 1957, Lamotte and Xavier 1972b). Gonocytes (foetal germ cells) are already identifiable and large (range 25–55 µm, most 30–40 µm), and they assemble in a line between the aorta and the Wolffian ducts (Lamotte et al. 1973).

Stage Ia

Stage Ia has a duration of less than two months. Some yolk is still visible in early stage Ia foetuses but completely resorbed in older specimens. During this stage the head develops fast, the eyes appear and become pigmented, the mouth, first visible as a depression, develops into a slit and connects to the oesophagus, and papillae appear on the lower and upper lip (Lamotte and Xavier 1972b). The lobes of the liver become visible and the first pigmentation appears, hind limb buds are still absent (Lamotte and Xavier 1972b). Body size is on average 1.6 mm, tail length 1.9 mm. All gonocytes migrate into the periphery of the primordial gonads. Gonads are longer than wide and built stalks. A renal stalk protrudes into the gonad. At the end of stage Ia sex differentiation occurs, and all intracellular vitelline flakes

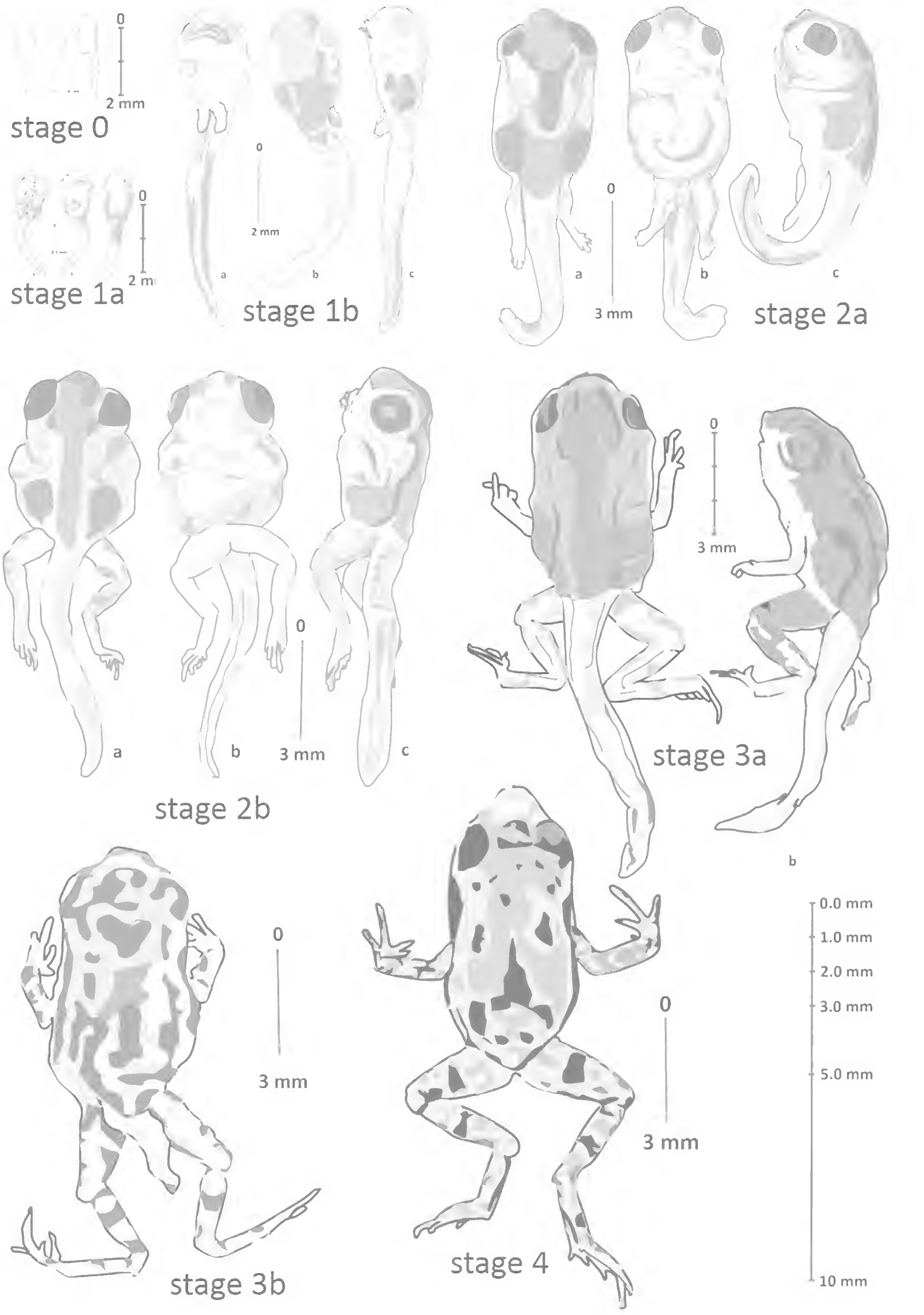

Figure 8. Embryonic development. Shown are the eight stages as found in the literature. Redrawn after Lamotte and Xavier (1972b).

are resorbed (Lamotte et al. 1973). Within the pituitary gland the pars distalis, pars intermedia, pars tuberalis and the nervous lobe are differentiated (Zuber-Vogeli and Bihouès-Louis 1971).

Stage Ib

Stage Ib has the longest duration (about two months). It is characterised by the appearance of the hind limb buds and their separation into thigh and lower leg. Front limbs develop under the transparent opercular skin fold. Pigment cells start to appear on the flanks. The digestive system and large liver-lobes are well developed (Lamotte and Xavier 1972b). Total length of foetuses varies between 3.8–6.2 mm (body: 1.8–2.4 mm, tail: 2–4 mm, Lamotte and Xavier 1972b). The small ovaries (200–300 µm) are pear-shaped and stalked, sometimes with a central cavity. They contain oocytes and oogonia in pre-meiosis, which are arranged in the periphery of the ovary. During this stage the first follicle cells appear and some oogonia start growing. The testes have a compact appearance, are small (300 × 70 µm) and become more elongated. The cells within the testes show no apparent order, but large spermatogonia can be observed (Lamotte et al. 1973). Within the pituitary gland the first glycoprotein type 1, 2 and 3 cells, and protein type 1 cells appear (Zuber-Vogeli and Bihouès-Louis 1971, Zuber-Vogeli and Doerr-Schott 1984). The latter are distributed in all areas of the pars distalis (Zuber-Vogeli and Doerr-Schott 1984). For cell type descriptions see the section on the (female) pituitary gland below.

Stage IIa

This stage has a duration of about one month and its beginning coincides with the emergence of females from their underground aestivation sites. It is characterised by the further differentiation of the hind limbs into thigh, lower leg and foot. The limbs are still short, and at the end of this stage the toes appear but are not separated. Foetuses of this stage have a large liver and the cloacal tail piece (sensu Gosner 1960) is still present. A clear boundary between body and tail becomes apparent; the eyes protrude and increase in size. Pigment cells increase in number; the pigmentation starts intensifying at the head and the darker colour arrives in the middle of the back at the end of this stage, the dark circles at the flanks persist. The hind limbs begin to be dorsally pigmented (Lamotte and Xavier 1972b). Foetus size varies between 6.4 and 12.5 mm (body 2.4–5.3 mm, tail 4–7.5 mm, hind limbs: 0.9–3.4 mm, Lamotte and Xavier 1972b). The ovary continues increasing in size, oocytes increase in number and their cytoplasm increases in volume (Lamotte et al. 1973). During this stage glycoprotein type 2 cells (corticotropic cells) and melanotropic cells are present in the pars distalis and pars intermedia. Protein type 2 cells (somatotropic cells) were rare before but appear in this stage in the dorso-caudal region of the pars distalis (Zuber-Vogeli and Bihouès-Louis 1971).

Stage IIb

This stage has a duration of less than one month. It is characterised by the elongation of the limb and to a lesser extent by their differentiation. The metatarsal tubercle appears, toes become separated and the front limbs continue developing beneath the opercular skin fold and start distending the thin membrane. The eyes grow quickly and the pupil appears. The mouth is still surrounded by papillae (Lamotte and Xavier 1972b). At this stage the pituitary gland changes, becomes spherical, the sinus of the pars distalis becomes extended; the position of the pars intermedia is modified as the median protuberance is thickening. Mitoses of the glycoprotein type 1 cells are observed (Zuber-Vogeli and Bihouès-Louis 1971). About 1/10 of the surface of the thyroid gland becomes vascularised (Lamotte and Prum 1957).

Stage IIIa

This stage has a duration of a few weeks. It is characterised by the start of the tail resorption, the rupture of the opercular skin fold and the breaking through of the front limbs. Front and hind limbs are coloured dorsally with the species-specific stripes. The head elongates, nares are visible, the pupils are further developed and the labial papillae start to decrease in size (Lamotte and Xavier 1972b). Some of the oogonia continue growing until the first ovulation. Within testes spermatocytes start maturing, conjunctive tissue appears which builds the basis of the future seminiferous lobules. The intra-testicular oocytes, present in low numbers until that stage, start decreasing in size (Lamotte et al. 1973). Protein type 1 cells and glycoprotein type 1 cells are still visible and distributed in all areas of the pars distalis, but for the latter secretory activity is reduced (Zuber-Vogeli and Doerr-Schott 1984).

Stage IIIb

This stage has a duration of a few weeks. It is characterised by the resorption of the tail and the labial papillae. The head becomes more elongated; the pupils are fully developed. Foetuses already show the characteristic juvenile colouration (Lamotte and Xavier 1972b). The ovaries are large (300–600 µm, Lamotte et al. 1973). The activity of the glycoprotein type 1 cells is reduced, glycoprotein type 3 cells are very active and protein type 1 cells, melanotropic and protein type 2 cells still present (Lamotte et al. 1973, Zuber-Vogeli and Doerr-Schott 1984). The thyroid is highly vascularised (1/3 of the surface) and the colloid amount reduced drastically (Lamotte and Prum 1957).

Stage IV

This stage has a duration of just a few days. At this stage foetal development is completed, the juvenile toads are a bit stockier and have slightly longer extremities and proportionately larger eyes compared to adults. Labial papillae are absent, the nares moved lateral. SVL ranges between 6–10 mm, hind legs ca. 9 mm, front legs, 5.6 mm and on the feet all tubercles are visible (Lamotte and Prum 1957, Lamotte and Xavier 1972b). Large oocytes grow particularly fast before birth. Some lobes are present in testes; the first vascularised interstitial tissue appears; Sertoli cells appear at the beginning of the second cycle of meiosis. Most often spermatocyte maturation begins with birth, nevertheless spermatogenesis was observed even before birth (Lamotte and Prum 1957, Lamotte et al. 1973). Thyroid activity increases again within this stage (Lamotte and Prum 1957). The pituitary gland of newborn toads does not differ from the pituitary gland of adults (Zuber-Vogeli and Bihouès-Louis 1971).

In summary: Nimba toad foetuses are characterised by the absence of a coiled gut, internal and external gills, spiracle, horny bill and labial teeth, and the presence of a gut similar to those of adults, large livers, a large head with large eyes, a mouth with papillae and the early development of the reproductive, locomotor, digestive, and respiratory systems. The foetal development is linked to the different seasons experienced by the adults. During the first 5–6 months, the time mothers spend underground during the dry season, development is slow (stages 0-IIa, Xavier 1971, 1986, Lamotte et al. 1973, Lamotte and Xavier 1976b). Foetal development and growth is accelerated from the moment of emergence and the start of the active life of females (Xavier 1971, 1986, Lamotte et al. 1973, Lamotte and Xavier 1976a).

Female reproductive system

Within this section the morphology and temporary changes of the oviduct, ovary and the pituitary gland are described and their possible interactions are discussed. The most complete description of the female reproductive system is given in the doctoral thesis of Xavier (1971).

Oviduct

The oviduct is rather simple, it consists of two parallel strings (Figure 9, Lamotte and Tuchmann-Dubplessis 1948, Xavier 1971, 1986), which can be separated into three parts: each string in the tube or oviduct sensu stricto, the uterus, which is the lower enlarged part, in which the foetuses develop (non-homologous to the mammalian uterus) and the common tube, a short tube which unites the lower-most part of both uteri (Xavier 1971, 1976).

Tube or oviduct sensu stricto. The tube consists of an inner epithelium, a connective tissue, a thin muscle layer and is surrounded by a thin envelop (Xavier 1971). The epithelium is ragged and two cell types can be distinguished, ciliated cells and mucous cells. Based on histology and the epithelial secretions produced, the tube can be separated into four parts (from anterior to posterior): i) a ciliated part, ii) a part in which mainly acidic secretions occur, iii) an acidic and neutral part, in which acidic and neutral secretions are observed and iv) a neutral part with exclusively neutral secretions (Xavier 1971, 1973).

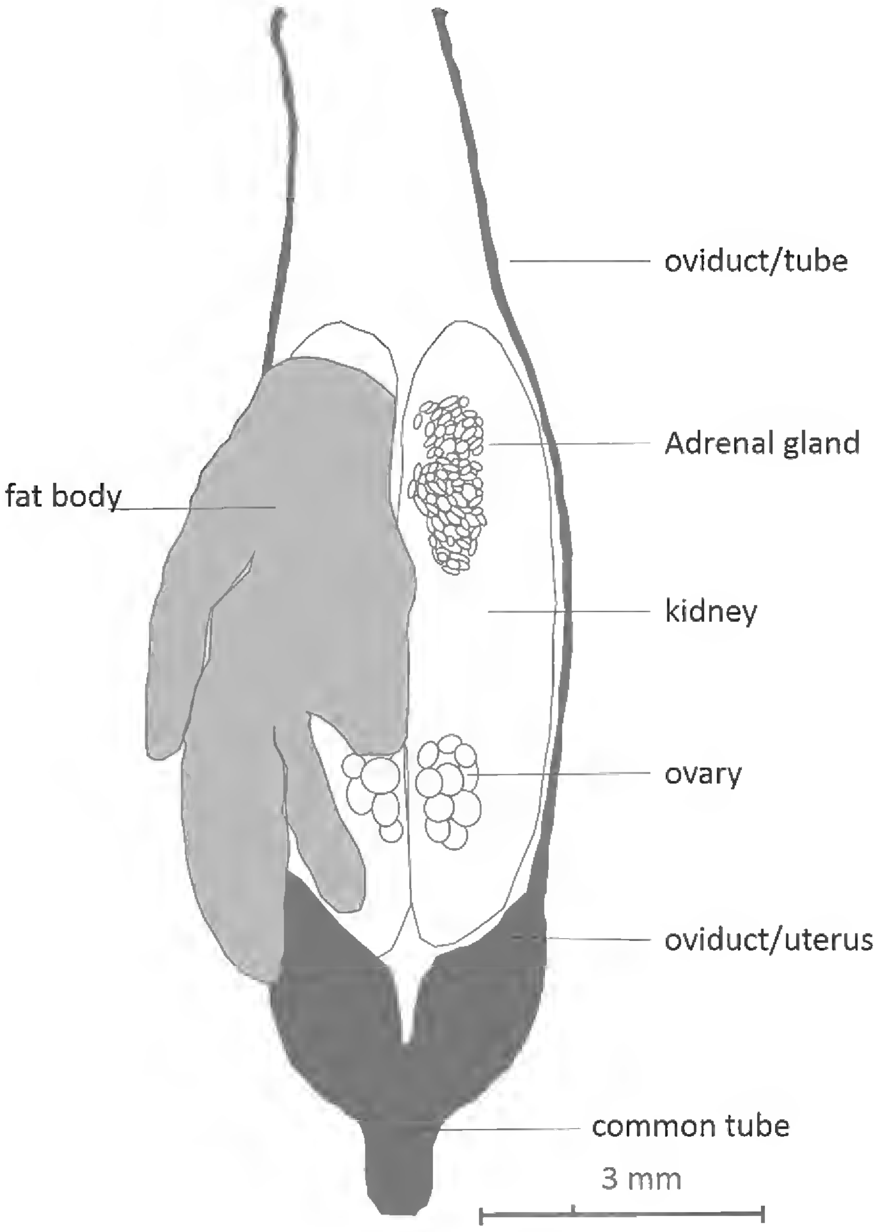

Figure 9. The female reproductive system. Redrawn after Lamotte et al. (1964).

Within a reproductive cycle the tube changes little. It is hypertrophic and active only before and during ovulation (diameter between 350–450 µm, Vilter 1957) at the end of the rainy season (Vilter 1957, Xavier 1971, 1973, 1974, 1976, 1986, Lamotte and Xavier 1976a). After ovulation activity stops and the tube diameter decreases in size until it reaches its thinnest diameter during dormancy (Vilter 1957, Xavier 1971). Some weeks after emergence, activity is slowly taken up again, but only speeds up some weeks after parturition (diameter at parturition: 100–110 µm) for the preparation of the new ovulation (Vilter 1957, Xavier 1971, 1974). During gestation the tube does not change much (Lamotte and Tuchmann-Dubplessis 1948, Xavier 1971).

Uterus. As a modification of the tubular oviduct sensu stricto, the uterus also consists of an epithelium, connective tissue, a thin muscle layer and an envelope (Lamotte and Tuchmann-Dubplessis 1948, Xavier 1971). Depending on the season only mucous cells or mucous and ciliated cells can be recognised (Angel and Lamotte 1948, Lamotte and Tuchmann-Dubplessis 1948, Xavier 1971, 1973, 1986). Some weeks after birthing the uterus is 2–3 mm long, 0.5–1 mm wide and 0.5 mm high (Xavier 1971), just before ovulation it already increased in size to 3–4 mm length, 1–2 mm width and 0.5–2 mm height (Angel and Lamotte 1948, Lamotte and Tuchmann-Dubplessis 1948, Xavier 1971). During the last months of gestation the uterus is very large, filling most of the abdomen and squeezing all other organs (Lamotte and Tuchmann-Dubplessis 1948, Xavier 1971). Within one reproductive cycle three phases can be distinguished: a proliferation phase, starting 12 days after parturition and lasting until ovulation, a secretion phase, starting with ovulation and ending with parturition and an apoptosis phase during the first 12 days after parturition (Xavier 1971, 1973, 1977, 1986).

The proliferation phase starts in July/ August when the new epithelium is built from the connective tissue (Xavier et al. 1970, Xavier 1971), at first ciliated and mucous cells are present and within mucous cells mitoses can be observed (Xavier 1971, 1973, 1986). At the same time blood vessels appear during the first gestation and increase in number in the following gestations (Xavier 1971, 1986). In September, shortly before ovulation, the ciliated cells disappear, the epithelium is folded into longitudinal ridges, blood vessels form within the ridges of the epithelium, between the connective tissue and epithelium (Xavier 1971).

The secretion phase lasts the entire gestation period and is characterised by the secretion of mucoproteins by all mucous cells. Nevertheless, the importance of various factors changes over the duration of the gestation. During the first part of the gestation, mainly within the first part of dormancy, the muscle layer increases, the vascularisation of the connective tissue increases and mitoses can be observed (Angel and Lamotte 1948, Xavier 1971, 1977, 1986, Lamotte and Xavier 1976a). At the end of the gestation, when foetuses are at stages III and IV (the time the labial papillae start being resorbed, Xavier 1971, Lamotte and Xavier 1972b) the secretion of mucoproteins decreases and glycoproteins are secreted and the blood vessels open into the uterine cavity (Xavier 1971, 1973, 1986).

The apoptosis phase is the shortest and lasts only for about 12 days (Xavier 1971, 1973, 1986), nevertheless it has the largest impact on the uterus. After parturition the uterus collapses, the muscle layer and the connective tissue are arranged in lateral folds, but the epithelium shows no structure after collapse (Vilter and Lamotte 1956). The reason for the different reactions is that the epithelium detaches from the connective tissue and is finally phagocytised within the uterine cavity (Xavier 1971, 1973, 1976, 1977, 1986). The secretion of glycoproteins, starting already at the end of the secretion phase, is intensified and this leads to the disconnection of the epithelium (Xavier 1971, 1973, 1977, 1986). At the same time, the blood vessels are surrounded and phagocytised by many mast cells, and from the connective tissue a new epithelium is building (Xavier 1971, 1973, 1977, 1986). After 12 days the uterus has the same appearance as that of virgin females, the epithelium is ragged, contains mucous and ciliated cells, and some mitoses can be observed.

Common tube. The common tube consists of an epithelium, connective tissue, a muscle layer and an envelope. The muscle layer is thicker than in the oviduct sensu stricto. It follows the cyclic changes of the uterus, with the only exception that the apoptosis phase and the glycoprotein secretion are missing. The transition from the secretion to the proliferation phase is achieved as ciliated cells appear (Xavier 1971).

In summary: the oviduct is separated into the tube, the uterus (distal end of the oviduct) and the common tube. The tube is only active before ovulation and hence, changes the least of the three parts. The uterus supports the foetuses during gestation, undergoes the largest size changes, and rebuilds its epithelium after every gestation. The common tube follows a similar development as the uterus, but is missing the apoptosis phase, in which the epithelium is completely exchanged.

Ovary

The ovaries are situated in the posterior third of the body (Xavier 1971). They are small, of irregular shape (1–2.5 mm wide and 0.5–1 mm large, Xavier 1971, 1974) and have a weight of 0.15–0.75 mg (Xavier and Ozon 1971). They contain oogonia and follicles of different sizes, the total number rarely exceeding 60 (Angel and Lamotte 1944b, Lamotte and Rey 1954, 1957, Lamotte et al. 1964, Xavier et al. 1970, Xavier 1974). Not all eggs are ovulated at the same time; 4–20 eggs, most often 8–9 eggs, per ovulation were observed (Angel and Lamotte 1944b, Lamotte et al. 1964, Xavier 1971, 1977, 1986). The number of ovulated eggs depends on the female's size (age), with larger females ovulating more eggs. First-gestating females may ovulate 1–8 eggs, whereas older females may ovulate between 14–18, and the largest females up to 20 eggs (Lamotte et al. 1964, Xavier 1971, 1986).

Follicles consist of a theca layer and granulosa cells (Xavier 1971, 1977, 1986). Most follicles in an ovary have a size between 150–200 µm diameter (Angel and Lamotte 1944a, 1944b); mature follicles on the other hand are larger with a diameter of 500–650 µm (Lamotte and Rey 1954, Lamotte et al. 1956, Xavier 1971). At birth oocytes all have the same size (< 220 µm) but within fast-developing females during mating season two types of follicles can be observed, the majority is < 300 µm and a few are mature with a size between 500–620 µm (Lamotte and Rey 1957).

After ovulation, follicles decrease slightly in size (280–320 µm diameter, Lamotte and Rey 1954) and develop into corpora lutea (Lamotte and Rey 1954, Lamotte et al. 1956, Vilter and Lugand 1959a, Xavier et al. 1970, Xavier 1971, 1974, Lamotte and Xavier 1976a). A corpus luteum develops when granulosa cells invade the follicle cavity and the theca thickens (Lamotte and Rey 1954, Xavier 1971, 1974). The corpora lutea persist during the entire gestation (Lamotte and Rey 1954, Lamotte et al. 1956, Vilter and Lugand 1959a, Xavier et al. 1970, Xavier 1971), nevertheless they decrease in size after emergence (Lamotte and Rey 1954, Lamotte et al. 1956, Xavier 1971, 1977, 1986). Large follicles that did not reach maturity in time, and did not ovulate their ova, undergo atresia (Xavier et al. 1970, Xavier 1971).

Hence, within the ovary two phases can be observed, a follicular phase, which is characterised by follicle growth, and a luteal phase, during which the corpora lutea are present (Xavier and Ozon 1971, Xavier 1971, 1986, Lamotte and Xavier 1976a). The follicular phase starts slowly with emergence, vitellogenesis takes place after parturition, and the phase ends with ovulation (Lamotte et al. 1964, Xavier 1971, 1977, 1986). This phase is characterised by the growth of the follicles involved in the next ovulation and vitellogenesis (Xavier and Ozon 1971, Xavier 1971, 1977, 1986). The presence and activity of 17α-hydroxylase and 3β-hydroxy-steroid dehydrogenase (3β-HSD) was observed within the follicles, particularly before ovulation (Ozon and Xavier 1968, Xavier et al. 1970, Xavier 1971). Only before ovulation the theca cells of the follicles show enzymatic activity (Xavier et al. 1970), during which oestrogens are produced until ovulation (Xavier 1971, 1986). During the same time granulosa cells of the follicles produce progesterone (Xavier and Ozon 1971, Xavier 1971, 1986). Pre-ovulation oestrogen, progesterone, as well as 4-adrostenedione and testosterone are produced within the granulosa or theca cells of mature follicles (Xavier 1976).

The luteal phase starts with the gestation. Corpora lutea decrease in size during the active life of females after emergence, and are rapidly disappearing after parturition (Vilter and Lugand 1959a, Lamotte et al. 1964, Xavier 1970a, 1970b, 1971, 1976, 1977, 1986, Xavier et al. 1970, Xavier and Ozon 1971). During the luteal phase progesterone, but no oestrogen is produced (Ozon and Xavier 1968, Xavier et al. 1970, Xavier and Ozon 1971, Xavier 1971, 1986). Progesterone levels are linked to number and size of corpora lutea and hence, decrease after emergence (Xavier et al. 1970, Xavier and Ozon 1971, Xavier 1971, Lamotte and Xavier 1976a). Larger females with more corpora lutea have higher progesterone levels (Xavier and Ozon 1971, Xavier 1971). During the dry season corpora lutea are larger and progesterone levels are high and this time coincides with the time of slow foetal growth and the absence of follicle growth. The two ovarian phases are non-exclusive as both are overlapping from emergence until parturition. Nevertheless, during this overlapping time corpora lutea decrease in size, and follicle growth is slow (Ozon and Xavier 1968, Xavier 1970a, 1970b, 1971, 1986, Xavier et al. 1970, Xavier and Ozon 1971).

In summary: Nimba toads have small ovaries, which contain only few follicles (< 60), of which a small proportion (4–20) reaches maturity every year. After ovulation follicles develop into corpora lutea, which are present during the entire gestation period. Within follicles androgens (oestrogen and testosterone) are produced within the theca cells, whereas the granulosa cells produce progesterone. During the luteal phase, exclusively progesterone is produced by the granulosa cells. Progesterone levels are highest during the dry season, when foetal and follicle development is slow or absent.

Pituitary gland

The pituitary gland is comparatively small (Vilter et al. 1959), and does not differ between virgin females and males after emergence (Zuber-Vogeli 1968). After parturition the volume of the pituitary decreases dramatically, but increases again after emergence and is maximal just before birthing (Vilter et al. 1959). Three types of glycoprotein cells (in some publications called basophilic, amphophilic or cyanophilic cells) and two types of protein cells (sometimes termed acidic cells) were determined (Zuber-Vogeli 1968). Different names were used for the same pituitary cell types, between different as well as within the same publications. To avoid confusion and standardise usage, we use the following names: glycoprotein type 1 cells (other names: gonadotropic cells, basophilic PAS purple cells, gonadotropic type I and FSH-cells), glycoprotein type 2 cells (corticotropic cells, basophilic PAS red cells, gamma cells, gonadotropic cells II), glycoprotein type 3 cells (thyrotropic cells), protein type 1 cells (prolactin-like cells, somatotropic cells, orangeophilic cells, alpha cells), protein type 2 cells (prolactin-like cells, somatotropic cells, erythrosonophilic cells). Within the two protein cell types, the challenge is that it was first assumed that the protein type 2 cells are the prolactin-like cells, but it was later demonstrated that they produce somatotropin (STH, Zuber-Vogeli et al. 1975).

The glycoprotein type 1 cells are widely distributed within the pituitary gland (Zuber-Vogeli 1968, Xavier 1971), these cells and their mitochondria are large (Zuber-Vogeli and Doerr-Schott 1976). During dormancy glycoprotein type 1 cells are small or even absent (Zuber-Vogeli 1968, Xavier 1971, Zuber-Vogeli and Xavier 1973, Zuber-Vogeli et al. 1975). They increase in size and activity after emergence and are most active between parturition and ovulation (Zuber-Vogeli and Herlant 1964, Zuber-Vogeli 1968, Zuber-Vogeli and Xavier 1973, Zuber-Vogeli et al. 1975). In females they are active during the follicular phase (Xavier 1971) and in males during spermatogenesis (Zuber-Vogeli et al. 1975). Hence, it was assumed that they are equivalent to the gonadotropic cells. The glycoprotein type 2 cells are scarcely found within the rostro-ventral part of the pituitary (Zuber-Vogeli and Herlant 1964, Zuber-Vogeli and Doerr-Schott 1976), have a well-developed Golgi apparatus and endoplasmic reticulum (Zuber-Vogeli and Doerr-Schott 1976). These cells are not visible during dormancy, are few and small at emergence, and most prominent in July/ August (Zuber-Vogeli 1966, 1968). In females it was assumed either that they may have no function (Zuber-Vogeli and Xavier 1973), or that they are corticotropic cells (Zuber-Vogeli et al. 1975, Zuber-Vogeli and Doerr-Schott 1976). The least is known about the glycoprotein type 3 cells. They are scarce and had to be excluded from many studies due to this fact (e.g. Zuber-Vogeli and Doerr-Schott 1976), the only thing known is that they are distributed throughout the gland (Zuber-Vogeli and Herlant 1964).

Protein type 1 cells are large, widely distributed cells within the pituitary gland (Zuber-Vogeli and Herlant 1964, Zuber-Vogeli et al. 1975) and are often ciliated (Zuber-Vogeli et al. 1975, Zuber-Vogeli 1978), their cytoplasm contains many granules (Zuber-Vogeli 1978) and their Golgi apparatus shows activity (Zuber-Vogeli and Doerr-Schott 1976). In the presence of artificially injected bromocriptine, the cells are smaller, have smaller nuclei and the present granules increase homogeneously within the cytoplasm, and M. Zuber-Vogeli (1978) assumed that bromocriptine is hindering the exocytosis of prolactin. Within non-gestating females protein type 1 cells increase in number after emergence (Zuber-Vogeli 1968). In gestating females protein type 1 cells are abundant during dormancy and abundant at emergence (Zuber-Vogeli 1968). After birth they increase in number and have a large nucleus, large Golgi apparatus, many mitochondria, a well-developed endoplasmic reticulum and exocytose was observed 16 days after parturition (Zuber-Vogeli 1978). One month after parturition they are abundant and well developed (Zuber-Vogeli 1978). Protein type 2 cells are more localised at the dorsal and caudal poles of the pituitary gland (Zuber-Vogeli and Herlant 1964, Zuber-Vogeli 1968, Zuber-Vogeli and Doerr-Schott 1976). At the beginning of gestation the Golgi apparatus is well visible (Zuber-Vogeli and Doerr-Schott 1976). Protein type 2 cells are abundant during dormancy, decrease in number with emergence and disappear with parturition (Zuber-Vogeli and Xavier 1973, Zuber-Vogeli 1978). Hence, it was assumed that their presence is linked to the presence of corpora lutea and it was wrongly assumed that they are prolactin-like cells (Zuber-Vogeli 1968, Xavier 1971, Zuber-Vogeli and Xavier 1973). Later it was found that they are somatotropic cells (Zuber-Vogeli et al. 1975, Zuber-Vogeli and Doerr-Schott 1976).

Within one sexual cycle this means that at the beginning of the gestation glycoprotein and protein type 1 cells are present and protein type 2 cells are appearing. Glycoprotein type 2 cells are less abundant but easily and brightly stainable (Zuber-Vogeli and Xavier 1973). At emergence of the females from their dormancy sites protein type 1 cells are present, protein type 2 cells disappear, glycoprotein type 1 cells restart activity, glycoprotein type 2 cells are present, and glycoprotein type 3 cells are scarce (Zuber-Vogeli and Xavier 1973). Twenty days after parturition protein type 1 cells increase in number and glycoprotein type 1 cells are secreting (Zuber-Vogeli and Xavier 1973). One month after parturition protein type 1 cells are abundant and the glycoprotein type 1 cells are large and well granulated (Zuber-Vogeli and Xavier 1973). It was concluded that the pituitary is controlling the follicle growth, ovulation and corpora lutea development and maintenance (Vilter and Lugand 1959a, Xavier 1986).

In summary: five different cell types can be distinguished within the pituitary gland, three glycoprotein cell types and two protein cell types. The glycoprotein type 1 cells are visible and active during the toad's active life, follicle development and vitellogenesis. This indicates a connection between the glycoprotein type 1 cells and the ovarian follicular phase, which makes them gonadotropic cells. The protein type 1 cells are well visible and active during most of the time, with a slight decrease in activity for some time after emergence. They had been shown to secret prolactin.

Interaction between different organs

Within the female reproductive cycle three time periods lead to changes within the reproductive system: i) before toads become dormant ovulation and mating occur and gestation starts. Within the oviduct this leads to the cease of activity within the tube, the start of the secretion phase within the uterus and within the ovary to the start of the luteal phase, in the pituitary glycoprotein type 1 cells become scarcer and protein type 2 cells appear; ii) With emergence at the beginning of the rainy season, the uterus starts to increase considerably in size as foetal growth and development takes up speed, within the ovaries the corpora lutea start decreasing in size, the follicles slowly start development and within the pituitary the glycoprotein type 1 cells start to appear, protein type 1 and 2 cells become less abundant; iii) With the birth of juveniles in June the tube increases developmental speed, the uterus collapses and rebuilds a new epithelium, within the ovary the corpora lutea disappear and follicle growth intensifies, within the pituitary the glycoprotein type 1 cells show very high activity, the protein type 1 cells increase their activity as well and protein type 2 cells are absent. Hence, the question arises, whether these changes in the different organs are coincidences or one change is triggering the change in another organ. To answer this question several experiments were carried out. If not stated otherwise studies are described in Xavier (1971).

Ovary and foetus development. During the dry season corpora lutea are present, large and active, and it was shown that they produce progesterone. Foetal development is slow during dormancy (Xavier 1976). Ovariectomy (the surgical removal of ovaries) of females early during gestation leads in 50% of females to parturition of normally developed foetuses three months earlier than in non-ovariectomised females (Xavier et al. 1970, Xavier and Ozon 1971, Xavier 1971). In the other 50%, which are assumed to be first-gestating females, ovariectomy leads to abortion (see below). Implantation of progesterone into gestating females after emergence leads to normally developed foetuses, but parturition occurs 2–3 months later than in non-progesterone treated females. This indicates that progesterone produced by the corpora lutea slows down developmental speed of foetuses naturally during dormancy and experimentally during the active life of gestating females (Xavier 1970a, 1970b, 1971, 1976, 1986).

If females are separated from males during the mating season, ovulation occurs and a "pseudo-gestation" develops (Xavier 1969, 1974). Within the first four months the uteri are long bags (5 × 3 mm) containing separated eggs and within the ovary corpora lutea develop normally (stage 1, summarised from: Vilter and Lugand 1959a, Xavier 1969, 1971, 1974). Within the next 1 to $1^1/_2$ months the eggs are still separated but the corpora lutea decrease and follicles increase in size (stage 2). After emergence uteri are thinner (epithelium, connective tissue and muscle layer), less transparent and the mucous cells reduce production and later ciliated cells appear, and the unfertilised eggs start accumulating (stage 3). The accumulated eggs are then lysed, the mucous cells stop secreting and the uterus changes into the same stage as for virgin females (stage 4). In general, the mucous layer is less thick and less ragged than in gestating females and the uterus does not substantially change. The pseudo-gestation is shorter than a gestation and leads to ovulation 3–4 months earlier (June) than in gestating females (September/ October). If no fertilisation occurs a new pseudo-gestation is established (Xavier 1974). Hence, the absence of fertilisation and with that of foetuses leads at first to normal developments within the ovary and the uterus, but particularly after emergence the pseudo-gestation cycle is faster and shorter. This may indicate that the presence of foetuses is needed for normal uterus and ovary cycles during that period.

Ovary and oviduct. The tube's endocrine cycle is synchronised with the follicular phase of the ovary. Follicles and tube start slowly developing after emergence and are most active before and during ovulation, and are not active during dormancy. In females ovariectomised after parturition the tube does not show any activity towards the end of the rainy season, usually the time of highest activity. In females ovariectomised at about the time of ovulation, the tube maintains high activity for the next 6 months and activity is terminated only after two years. This indicates that the ovary is controlling tube activity (Xavier 1971). At the time of ovulation within the follicles oestrogen is secreted by the theca cells and progesterone by the granulosa cells. One year after ovariectomy Xavier (1971) injected oestrogen, testosterone and progesterone at the time of ovulation. She made the following observations: oestrogen (oestradiol) and testosterone initiated hypertrophy and development of the epithelial cells within the tube, the injection of progesterone initiated the thickening of the muscle layer. Only if oestrogen and progesterone were injected simultaneously the tube did show normal development during ovulation. If first oestrogen and three weeks later progesterone was injected this triggered the secretion of the mucous cells within the tube. If first oestrogen and after one-month progesterone was injected this triggered the decrease in tube activity. Hence, oestrogen and progesterone together are needed for normal tube development during ovulation and progesterone is needed to stop tube activity (Xavier 1971, 1986).

Another connection between ovary and tube became apparent by an observation of Lamotte et al. (1964). The number of ovulated eggs in one ovary corresponds very closely to the number of foetuses developing within the uterus of the same side. In unilaterally ovariectomised females, most eggs developed into foetuses in the uterus of that side on which the ovary was still present (Figure 10A, Xavier 1971). If one tube was closed (bound) of the same side as the ovary was still present, most eggs developed into foetuses in the uterus of the non-manipulated side, and very few ended up in the bound oviduct or within the body cavity (Figure 10B). If one uterus was removed and females were unilaterally ovariectomised (Figure 10C) or kept both ovaries (Figure 10D), most eggs were found in the remaining uterus (Xavier 1971). This indicates a preference of eggs to be present in the uterus of the same side than the ovary they came from. Additionally, one uterus may host all eggs ovulated from two ovaries, and that foetuses are not able to pass from one uterus into the other passing the common tube, as in that case eggs should have been present in both uteri in the experiment shown in 10B (Xavier 1971, 1977, 1986).

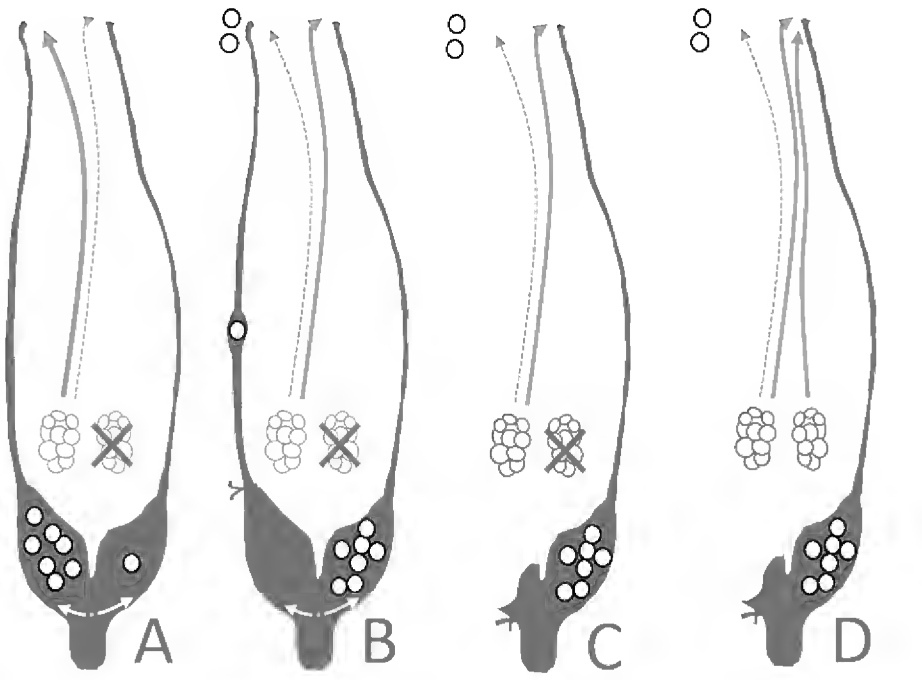

Figure 10. Experiments on female ovary, oviduct and uterus removal. Shown are the positions of eggs in the uteri after unilateral ovariectomy (**A**), after unilateral ovariectomy and the connection between oviduct and uteri bound at the side with the still present ovary (**B**), unilateral ovariectomy and the oviduct and uterus at the side of the still present ovary removed (**C**) and the unilateral removal of the oviduct and the uterus without ovariectomy (**D**). The red cross indicates the ovary removed, the red lines indicate positions where either oviduct (**B**) or the uterus (**C** and **D**) were bound. The two-headed arrow with the two red lines indicates that eggs apparently do not wander from one uterus to the other passing the common tube. Redrawn after Xavier (1971).

The uterus does not follow the same cycle as the follicles and the tube. The largest change of the uterus is during gestation. Nevertheless, during the follicular phase after parturition in ovariectomised females the injection of oestrogen initiated the development of the mucous layer and some blood vessels, the injection of testosterone the development of the connective tissue and some blood vessels, and the injection of progesterone the development of the muscle layer and an epithelium without ciliated cells. Only if oestrogen and three weeks later progesterone were injected together, did the uterus develop as in non-ovariectomised females (Xavier 1971, 1986). This indicates that the hormones produced by the ovary are controlling uterus development between gestations.

The removal of ovaries at the beginning of gestation leads to abortion 3–4 months after the operation in 50% of gestating females. Whether ovariectomy leads to abortion depends on the female's age. In all females 3–4 months old (hence, born the same year) and within 50% of females 15–16 months old, ovariectomy resulted in abortion. In all older females the gestation continued. As females may either get mature within 3–4 months, or one year later, females 15–16 months of age may be gestating for the first or the second time. Françoise Xavier (1971) concludes that ovariectomy leads to abortion only in females gestating for the first time. She links this to the progesterone levels produced by the ovaries, before ovariectomy. Older females show 4× higher progesterone levels than females gestating for the first time. Françoise Xavier assumes that a progesterone threshold needs to be reached to trigger uterus development. Additionally, within the uterus structures needed for gestation are in part still present (e.g.: blood vessels) in older females, but need to build in first-gestating females. Françoise Xavier assumed that foetuses develop faster as progesterone is missing and on the other hand the uterus development is hindered. This leads to asynchrony between foetuses and uterus in females gestating for the first time and finally to abortion (Xavier 1970a, 1971, 1977, 1986).

After emergence, ovariectomy of gestating females never results in abortion, irrespective of the female's age. This indicates that at this stage of the gestation the ovary has no longer an important effect on gestation (Xavier 1971, 1986, Zuber-Vogeli and Xavier 1973).

Hysterectomy (the removal of uteri) at the beginning of the gestation leads to atresia of small follicles and the corpora lutea disappear faster. After ovulation in non-hysterectomised females only nearly mature follicles are destroyed by atresia. Hence, ovary and uterus are influencing each other. To examine whether this connection is linked to the uterus, or to the developing foetuses, foetuses were removed by caesarean section (Xavier 1971). During early gestation the same modifications of the ovary are observed, but caesarean section after emergence leads to a collapse and apoptosis of the uterus, similar to that after birth, but does not change the ovaries (Xavier 1971). Considering that hysterectomy and caesarean section lead to atresia of small follicles, but pseudo-gestation (see above) does not, this raises the question whether atresia of small follicles is triggered by the traumata of the operations, or if mating (which is missing in pseudo-gestating females) triggers some other development which is similarly changed.

Ovary and pituitary gland. After ovariectomy at the beginning of gestation the glycoprotein type 1 cells are contracted and de-granulated. The protein type 2 cells, which are normally appearing with the corpora lutea, are absent, but protein type 1 cells are very abundant. Ovariectomy after emergence does not lead to large changes within the pituitary gland. Ovariectomy one month after parturition leads to the degranulation of the glycoprotein type 1 cells and they develop into "castration cells". Hence, the absence of the ovary has the largest effect on the pituitary at the beginning of the gestation and after parturition during vitellogenesis (Zuber-Vogeli and Xavier 1973).

Examining the effect of the pituitary on the ovary is much more problematic, as females die within the next 15–25 days after the flattening (destruction) of the pituitary, indicating that the pituitary has other vital functions in Nimba toads (Xavier 1971). Destruction of the pituitary at the beginning of the gestation, leads to atresia of small follicles > 180 µm and smaller corpora lutea develop, but does not lead to abortion within 15–25 days. Destruction of the pituitary gland after emergence leads to abortion within the next six days. As the destruction of the pituitary obviously has lethal effects on the female, F. Xavier hypothesised that abortion might be linked to the large energy demands of foetuses during that period, which cannot be supplied by the injured female. Destruction of the pituitary just before parturition has no negative impacts on parturition or foetuses (Xavier 1971).

Summary of interactions. The ovary seems to have the largest effect on the other reproductive organs from June to emergence at the beginning of the rainy season. Nevertheless, the ovary has different functions between parturition and ovulation (vitellogenesis) and during the first six months of the gestation females rest underground (dormancy). During vitellogenesis follicles grow and develop quickly and they synthesise oestrogen, testosterone and progesterone. Ovariectomy at the beginning of this period hinders the development of the oviduct – tube and uterus. This non-development can be circumvented with the injection of oestrogen and progesterone, indicating, that these hormones are vital for oviduct development during vitellogenesis. As well within the pituitary gland, glycoprotein type 1 cells (gonadotropic cells) develop into "castration cells" if the ovaries are removed at the beginning of vitellogenesis. During dormancy the corpora lutea are large, numerous and active and synthesise progesterone. Progesterone slows foetal development during dormancy and if experimentally applied as well after emergence. Ovariectomy of first-gestating females leads to abortion, which was as well linked to lower progesterone levels in first-gestating, than in older females. Within the pituitary protein type 2 cells appear with the development of corpora lutea. In neutered females they are absent during the whole dry season. Hence, most of the year the ovary influences the development of the pituitary gland, the tube and the uterus and during dormancy as well foetus development.

Between emergence and parturition foetuses develop quickly, stretching the uterus and restricting the other organs within the female. This development is only stopped by the destruction of the pituitary gland, which is lethal to females. Development can be slowed down by the injection of progesterone. On the other hand, the absence of foetuses in pseudo-gestating females leads to faster development of the ovary (decrease of corpora lutea and development of follicles), but has no effect on the pituitary gland. If foetuses are removed through caesarean section after emergence, with the apoptosis phase the uterus starts a new cycle, earlier than in normally gestating females. These results are in accordance with the hypothesis that the presence and development of foetuses are important for normal development of ovaries, and through them on the oviduct and the pituitary gland. On the other hand, change of the females from the inactive, low nutrition life underground to an active high nutrition life above ground and external factors might be important too.

Male reproductive system

The reproductive system of Nimba toad males received less attention than that of females. Respective research focused more on the environmental and cyclic dependencies of the reproductive cycle than on morphology and physiology of the reproductive system. Primary publications are by M. Zuber-Vogeli (Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966) and J. Gavaud (Gavaud 1976a, 1977).

Nimba toad males lose at 13 mm SVL their juvenile colouration (Angel and Lamotte 1948) and become mature already about 3 months after they are born. They are much more active than females, mainly calling, fighting with other males and harassing females (Sandberger-Loua et al. 2016b). This more active behaviour of males could increase their predation risk and lead to higher energetic costs. Males have a positive energy budget only between emergence and July. During the mating season and particularly the dry season, males lose up to 30% of their body weight, attributed to lower food intake rates (Lamotte 1972).

In summary: males have been studies less than females; are smaller, darker and at least during the mating season more active than females. Due to their more active life-style they may suffer from higher predation pressure and possibly as well higher energy demands.

Testes

Nimba toad testes are small (< 2 mm) ovoid masses (Gavaud 1976a), situated in the dorsal body cavity and connected to the kidneys (Gavaud 1976a) by the mesentery (Angel and Lamotte 1948). Testes are attached to the fat-body and the kidneys; they contain numerous efferent canals at all times, but the space they occupy within the testes varies with the annual cycle (Gavaud 1976a). The seminiferous tubes are filled with gonad cells, and all but primary spermatogonia are grouped in pyramidal cysts (Gavaud 1976a). Cysts surround Sertoli cells and within each cyst the mitoses and meioses are synchronised (Angel and Lamotte 1948, Gavaud 1976a). Gonad cells are attached by the Sertoli cells to the cysts (Gavaud 1976a). Only a fraction of the primary spermatogonia develop into spermatozoa (Gavaud 1976a). Endocrine activity through the presence of 5α-dehydrotestosterone (5α-DHT) was observed (Gavaud 1976b) within Sertoli cells and some cells of the connective tissue (Gavaud 1976a). This tissue is pigmented during the dry season and unpigmented during the rainy season (Angel and Lamotte 1948), giving the testes a dark appearance during the dry and a whitish appearance during the rainy season (Gavaud 1976a).

Most bufonids have a Bidder's organ, a part of the testes that contains oocytes, and which is separated from the testes by a separate envelope. During Nimba toad foetal development testes usually contain 1 or 2 (rarely 5 or 6) oocytes per male (Lamotte et al. 1973). Oocytes are always positioned at the periphery and often grouped at one of the poles of the testes, but always within the testes and not separated by an envelope (Lamotte et al. 1973). Intra-testicular oocytes are small. They are not well developed at foetal stage Ia and Ib, and grow slowly until stage IIb. Stage III is the time of accelerated spermatogenesis and during this stage intra-testicular oocytes decrease rapidly in size and have disappeared by stage IV (Lamotte et al. 1973). Hence, in contrast to other bufonids, the presence of oocytes in male Nimba toads is only transitory during foetal development.

The spermatozoa show no apparent modification compared to those of other bufonids. The only differences are that the perforatorium ends slightly posterior to the acrosome vesicle, the distal centriole is penetrated throughout its length by the central singlets of the axoneme and no mitochondrial collar is present, but mitochondria are located around the anterior axoneme (Scheltinga and Jamieson 2003). It is assumed that due to the viviparous reproduction (and the absence of spermatheca in females and hence presumably low levels of sperm competition) testes are small, cysts are few and only a few spermatozoa are produced during each mating season (Angel and Lamotte 1948, Lamotte et al. 1973, Gavaud 1976a).

In summary: Nimba toad testes are ovoid masses, which are white during the rainy and dark during the dry season. During embryonic development the testes may contain a few oocytes, which disappear before birth and are never surrounded by an envelope. The seminiferous tubes are always numerous, but vary their size during the reproductive cycle. Most gonad cells are grouped around Sertoli cells and within each group development is synchronised. The spermatozoon is a typical bufonid spermatozoon with little modification.

Annual reproductive cycle

Male adaptations to the viviparous reproductive mode are less distinct than in female Nimba toads; however, the male reproductive cycle is likewise tightly linked to the climatic cycle of the environment. Nimba toad males have a discontinuous reproductive cycle, (Zuber-Vogeli and Xavier 1965, Gavaud 1976a, 1976b). In contrast to temperate anurans spermatogenesis is not triggered by temperature, but by humidity (Zuber-Vogeli and Xavier 1965, Gavaud 1976a).

The dry season dormancy is characterised by low metabolism (Gavaud 1976a), invisible colourless nuptial pads without spines (Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966, Gavaud 1976a), testes and seminiferous ducts decrease in size during the first half of dormancy and stay the same in the second half (testes weight 0.1–0.4 mg, Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966, Gavaud 1976a). Some primary spermatogonia are present (Zuber-Vogeli 1966, Gavaud 1976a, 1977) and are with their Sertoli cells attached to the walls of the seminiferous tubes (Gavaud 1976a). Primary spermatogonia increase in number during the first few months of dormancy until in mid-January when they fill 20–35%, and Sertoli cells 15–32% of the testes volume until the end of the dry season (Gavaud 1976a). As Sertoli cells increase in number they detach from the walls of the testes and migrate into the centre of the seminiferous tubes (Gavaud 1976a). During this time secondary spermatogonia were rarely observed (Gavaud 1976a).

In April, when males emerge, one month after females, testes are still black and nuptial pads are not yet visible and their fat bodies are very small (Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966). Most of the primary spermatogonia are still attached to the walls with their Sertoli cells, so that the seminiferous tubes are hollow (Zuber-Vogeli and Xavier 1965). Larger (SVL ca.19 mm) males may be advanced in their reproductive development compared to smaller males (SVL: 17–18 mm, Zuber-Vogeli and Xavier 1965). With emergence, the secondary spermatogonia appear (Zuber-Vogeli 1966, Gavaud 1976a, 1977), which continue to divide until they fill the whole testes in June (Gavaud 1977). In May testes start increasing in size (Zuber-Vogeli and Xavier 1965, Gavaud 1976a), and primary spermatocytes (45%), secondary spermatocytes (25%), and spermatids (15%) fill most of the testes volume (Gavaud 1976a). Pyknosis of some cells can be observed (Gavaud 1976a).

In June nuptial pads start to turn black, testes increase further in size (Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966) and secondary spermatogonia occupy 35–55% of the testes (Gavaud 1976a), meiosis occurs and all stages can be observed, but no secondary spermatocytes nor spermatids (Zuber-Vogeli 1966, Gavaud 1976a). July/ August is the time of spermatogenesis (Zuber-Vogeli and Xavier 1965, Gavaud 1976a, 1976b), testes continue to increase in size (Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966, Gavaud 1976a) and nuptial pads become more pronounced (darker and larger spines, Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966). At around this time recently born males reach 13–15 mm SVL and spermatogenesis is accelerated (Angel and Lamotte 1948). The quantity of secondary spermatogonia decreases dramatically from about 50% to 7% of the testes volume (Gavaud 1976a). At the same time spermatozoids mature and detach themselves from Sertoli cells (Gavaud 1976a).

During the mating season the nuptial pads are blackest and spiniest (Figure 11, Zuber-Vogeli and Xavier 1965, Zuber-Vogeli 1966). Within the testes, mobile spermatozoa are abundant (Zuber-Vogeli and Xavier 1965, Gavaud 1976a) whereas cysts of spermatids and some spermatogonia are only rarely observed (Zuber-Vogeli and Xavier 1965, Gavaud 1976a). During the mating season only some spermatogonia divide, but spermatogenesis does not continue (Gavaud 1976a). After the mating season spermatozoids degenerate, nuptial pads become transparent, testes darken and decrease in size (Zuber-Vogeli and Xavier 1965, Gavaud 1976a) and only divisions of primary spermatogonia can be observed at the beginning of the dry season (Gavaud 1976a).

Figure 11. Male during the mating season, showing pronounced nuptial pads on the thumbs. © Joseph Doumbia

Similarly to females, the male reproductive cycle is linked to three important seasonal points, the mating season and the subsequent dormancy underground (slow or no development), emergence during the next rainy season (beginning of spermatogenesis with the appearance of secondary spermatogonia), and in June/ July when rain becomes permanent spermatogenesis intensifies (appearance of spermatocytes). Despite this strong link individual males may finish their spermatogenesis at different times due to individual differences in developmental speed (Zuber-Vogeli and Xavier 1965, Gavaud 1976a). Larger males mate earlier than smaller males older than one year (Zuber-Vogeli and Xavier 1965). As spermatogenesis speed is individual, this may indicate that the reproductive cycle is influenced by several environmental variables and/ or internally determined. Experimentally, Gavaud (1977) could show that spermatogenesis and particularly its developmental speed is strongly linked to the annual environmental cycle. Jaqueline Gavaud conducted two experiments, one to determine important environmental variables for the slowed or stopped spermatogenesis during the dry season (Gavaud 1976a), and a second one determining the environmental variables important for the correct timing of spermatogenesis during the rainy season (Gavaud 1977). In these studies, she could show that spermatogenesis depends mainly on prey availability and humidity levels, of which negative effects could be intensified by reversed light intensity (1000 lux during the dry season, or 10 lux during the rainy season). She compared the reproductive development of males within the experiments to wild caught males. During the dry season, comparable testes development was achieved with nutrition once per month (50 mg), an aerial humidity of 35% and a 12h light regime at 10 lux. During the wet season comparable development to wild males was observed with nutrition every second day (25 mg), 90% humidity and a light regime of 12h with 1000 lux. Generally, little food, low humidity and less light lead to slower or no gonad development than much food, high humidity and much light (Gavaud 1977). The endocrine activity of testes is highest in July. She assumes that the beginning of spermatogenesis after emergence and the slowing down or stopping of spermatogenesis after the mating season is mainly influenced by external factors (nutrition and humidity, Gavaud 1976b, 1977), whereas the onset of mitoses of primary and secondary spermatogonia towards the end of the dry season is triggered by endogenous factors (Gavaud 1976b, 1977).

In summary: the male reproductive cycle is interrupted during the dry season, when only divisions of primary spermatogonia are observed. Only after emergence, which is later in males than in females, spermatogenesis starts and is accelerated after June, when rain is more permanent, and results in the presence of spermatozoids during the mating season. During the mating season only primary spermatogonia divide. Spermatogenesis is accelerated through the availability of prey and high humidity. Nevertheless, individual males differ in the quantity and speed of the different gonad cell stages and larger males develop faster and mate earlier than smaller (but nevertheless, sufficiently old) males.

Male pituitary gland

Monique Zuber-Vogeli examined the male pituitary gland and focused on the annual reproductive cycle (Zuber-Vogeli 1966). The male pituitary gland contains the same five cell types as in females. Following the same terminology as for the female pituitary, the protein type 1 cells are the most abundant during the entire year. She assumed that they are somatotropic cells as in most vertebrates. As in females the glycoprotein type 3 cells are very rare and difficult to find. Three cell types undergo seasonal changes: the glycoprotein type 1 and 2 cells and the protein type 2 cells. The glycoprotein type 1 cells show the largest variability and are changing in accordance to the male reproductive cycle. They are less abundant or absent during the dry season, they are abundant and contain filled vacuoles in July (the time of most intensive spermatogenesis) and during the mating season (Zuber-Vogeli 1966). The glycoprotein type 2 cells are surrounding the anterior pole of the pituitary and are rare at emergence, but increase in number and activity until July/ August, when nuptial pad colouration and spermatogenesis is the strongest. Monique Zuber-Vogeli (1966) links the glycoprotein type 1 and 2 cells to the gonadotropic and the luteinising cells, respectively, described in *Rana temporaria* (van Oort 1961). The protein type 2 cells are present only in June/ July when spermatogenesis is the most active, and function is unclear. Nevertheless, it seems that within the male pituitary gland the cell types which show the largest changes within one year are linked to the reproductive cycle.

In summary: in the male pituitary, all five cell types were present, but only three of these five showed temporal modification. The glycoprotein type 1 cells are linked in males and females to gonad development and are rare during the dry season and most abundant during spermatogenesis/ vitellogenesis in July/ August and during the mating season. The protein type 1 cells are always the most abundant in males and females and show some, but little variability. The glycoprotein type 3 cells, which are assumed to be the thyrotropic cells, are always rare in both sexes. The glycoprotein type 2 cells and the protein type 2 cells differ in their annual activity between the sexes. Glycoprotein type 2 cells show no variability in females, but in males they are absent during the dry season and increase in number after emergence until they reach their maximum in July/ August and they were linked to nuptial pad development. The largest discrepancy is between female and male protein type 2 cells. In females they are abundant and active during the dry season, whereas in males they are only present in July/ August.

Summary and discussion

Viviparity in Nimba toads

Within anurans, Nimba toads have a highly derived and unique reproductive mode. They retain eggs and foetuses within their oviducts and are pueriparous and matrotrophic. As in other viviparous amphibian species, they have internal fertilisation, a reduction in number of developing eggs, and a prolonged developmental period (Wake 1992, 2015a). Several morphological and physiological adaptations are present in females, foetuses and, to a lesser extent, in males of *N. occidentalis*. The reproductive systems are small. This seems to be a trend in viviparous amphibians (Wake 2015a, 2015b). Oviducts are straight; the lower end of the oviduct is enlarged. From toads of the East African genera *Altiphrynoides* and *Nectophrynoides* it is known that the oviducts can be divided into a thinner anterior part (tube) and a sometimes dilated lower part, uterus (Wake 1980, Xavier 1986). This is not surprising for the pueriparous, lecitotrophic *Nectophrynoides tornieri*, but more puzzling for the direct developing *Altiphrynoides malcolmi* (Wake 1980). In Nimba toads, the uterine mucous layer first secrets mucoproteins, later glycogen. That the oviductal mucous layer is providing nutrition is also known from *Salamandra atra* and several caecilians (Vilter 1986, Gomes et al. 2012, Wake 2015b). In *S. atra* a "zona trophica" in the (apical) pole of the oviduct is providing epithelial cells that detach from the connective tissue by apoptosis (Vilter 1986). Within studied caecilians and Nimba toads the whole oviduct wall may provide nutrition (Xavier 1971, Gomes et al. 2012). In *S. atra* and caecilians, foetuses develop a "foetal dentition" to scrape off the epithelial cells (Vilter 1986, Gomes et al. 2012, Wake 2015a, 2015b), whereas Nimba toad foetuses develop labial papillae, and feed on liquids secreted by the epithelial cells ("uterine milk"). That epithelial cells secret mucoproteins is also known for *Rhinoderma darwinii* (Goicoechea et al. 1986). In this species males keep their offspring within their vocal sacs from the moment young show muscular movement until metamorphosis (Garrido et al. 1975, Jorquera et al. 1982, Goicoechea et al. 1986). The epithelial cells of the male vocal sac secret mucoproteins (Garrido et al. 1975), which are first absorbed by the foetal skin, later presumably ingested (Goicoechea et al. 1986). Recently was shown that the pouch prooding *Gastroteca excubitor* transfers nutrients from the mother to the devoping embryos (Warne and

Catenazzi 2016). After parturition, the uterus of *N. occidentalis* collapses, the existing mucous layer disconnects from the connective tissue and is lysed within the uterine lumen, while a completely new mucous layer is built from the connective tissue. An apoptotic phase exchanging the uterine mucous layer after parturition/ spawning is absent in *N. tornieri* (Xavier 1986) and has not been described for *S. atra* (Vilter 1986) nor for any of the viviparous caecilians (Gomes et al. 2012, Wake 2015a, 2015b). Hence, at present Nimba toads are the only viviparous (in the sense of oviductal egg retention) amphibian known to provide liquid foetal nutrition and whose uterus has an apoptotic phase.

In Nimba toads the ovaries are small and contain small follicles, of which only very few mature within each reproductive cycle. For example, in *A. malcolmi* and *N. tornieri* ovaries are considerably larger and contain more follicles at very different developmental stages (Wake 1980b, Xavier 1986). In *Didynamipus sjostedti* 18 mature and ten very small ova were observed (Grandison 1981). In *Nimbaphrynoides, A. malcolmi and Nectophrynoides*, follicles develop into corpora lutea, but they are smaller, less persistent and less active in the East African species than in Nimba toads (Wake 1980b, Xavier 1986). No corpora lutea were reported for the pueriparous, lecitotrophic *Eleutherodactylus jasperi* (Wake 1978), but are present in oviparous, as well as pueriparous caecilians (Wake 1993, Gomes et al. 2012). Corpora lutea are hypothesised to be important to determine birthing stage (larviparous/ pueriparous) in subspecies of *S. salamandra* and to maintain gestation (Wake 2015a, 2015b). In Nimba toads it was shown that the ovaries and possibly the progesterone produced by the corpora lutea are important in the first weeks of first-gestating females to maintain the gestation. In older females, the observed effect of progesterone is not to maintain the gestation, but to decrease foetal developmental speed. In Nimba toads and *S. atra* ovariectomy, and hence the removal of corpora lutea in later stages of the gestation (after emergence and after the first year, respectively), has no effect on gestation duration and maintenance (Xavier 1971, Vilter 1986). At this stage the presence of foetuses in the uteri seems to be more important in Nimba toads than the presence of ovaries. Hence, at least in these two species, corpora lutea are not important for the maintenance of gestation and timing of parturition. Nevertheless, the hormones produced within the follicles (namely oestrogen and progesterone, possibly testosterone) are important for the preparative development of the oviduct and uterus. In the marsupial frog *Gastrotheca riobambae,* oestrogen, progesterone and the presence of foetuses are as well important for pouch development and the maintenance of the gestation at least for the first weeks (del Pino 1983). In summary, the Nimba toad female reproductive system is characterised by several adaptations to viviparity, including the endocrine function of the ovary. Characteristics of the ovary seem to be similar to other viviparous or back-brooding anurans.

Nimba toad foetuses have no internal, nor external gills, no spiracle, no coiled gut and neither labial teeth nor horny beaks at any time during their development, but they possess labial papillae, a gut similar in structure to that of adults, well developed livers, and their development takes nine months. It was hypothesised that within viviparous amphibians metamorphosis is prolonged (Wake 2015a). As Nimba toads lack many tadpole specific characteristics, metamorphosis is restricted to the development of the front limbs under the opercular skin fold and the rupture of the latter in stage IIIa, the resorption of the tail and the labial papillae during stage IIIb. Poorly developed mouthparts are generally found in species without a free swimming tadpole stage and within direct developers gills and spiracle are only present for a short time (Wake 1978). In *N. tornieri*, *N. viviparus* and *A. malcolmi* neither beak, nor labial teeth, nor papillae are present (Lamotte and Xavier 1972a, Wake 1980b). The free-swimming tadpoles of *Schismaderma* have jaw-sheaths, labial teeth, marginal papillae, a sinistral spiracle midway along the body and a characteristic, half-moon shaped flap on the head (Channing et al. 2012). *Nectophrynoides tornieri* are known to have a sinistral spiracle (Grandison 1978, Wake 1980b). The publications on Nimba toad foetal development state that the development of the gut and livers is very early (e.g. Lamotte et al. 1973). Hence, it seems that the most obvious morphological differences of Nimba toads, the several rows of labial papillae and early development of the gastrointestinal system in the foetus and the uterine secretion and apoptosis in females, are linked to matrotrophy.

Based on morphology Grandison (1981) and Graybeal and Cannatella (1995) postulated that the two viviparous lineages, *Nimbaphrynoides* and *Nectophrynoides*, might not be sister taxa. This was recently confirmed by Liedtke et al. (2016), who showed that while the two viviparous lineages are part of the same clade, they do not appear to be very closely related, which suggests that viviparity may have evolved independently in each of them. Here, we have identified six characteristics linked to viviparity specific of Nimba toads, which provide strong evidence that viviparity evolved indeed independently in this species. These characteristics comprise three traits which are common in other amphibians, but not usually found in other viviparous species (small and yolk poor eggs, prolonged mucoprotein secretion of the oviduct/ uterus epithelium after fertilisation, labial papillae of the foetuses), two behavioural or ecologically important traits (“behavioural birthing” and the developmental break during the dry season) and one characteristic which to our knowledge is not known of any other amphibian, but of mammals (complete apoptosis and rebuilding of the uterine epithelium after parturition). First, small yolk-poor eggs are common in oviparous amphibians with free swimming tadpoles, but are not known from other viviparous anurans. Second, in amphibians the oviduct secrets mucoproteins to produce the egg layers prior to oviposition and/ or fertilisation (Shivers and James 1970). In Nimba toads the upper part of the oviduct has the same function, but the lower enlarged part (uterus) secrets mucoproteins to nourish the foetuses. Hence the temporal shift of the mucoprotein secretion within the uterus after fertilisation and during gestation (Xavier 1986) is exceptional. Third, foetal labial papillae are not uncommon in anurans and several functions of the papillae were hypothesised (hormonal secretion, enhancing the sucking capabilities of lotic tadpoles etc., McDiarmid and Altig 1999). In direct developers and lecitotrophic viviparous species foetuses have no or only very reduced labial appendices present for a limited duration (papillae, labial teeth etc.). Only in matrotrophic caecilians and adelphophagous salamanders, foetuses have special foetal teeth (Wake 2015a). Hence, the uniqueness is, that Nimba toad foetuses have labial appendices even so they are viviparous and no other labial feature than these papillae. The papillae are certainly linked to feeding as they appear and disappear with the mucoprotein secretion activity of the endometrium (Lamotte and Xavier 1972b), but the exact function is not known. Apart from the mucoprotein secretion of the oviduct/ uterus, which is found in all amphibians (Shivers and James 1970), these traits are more likely present in oviparous species with free-swimming tadpoles than in direct developing and ovoviviparous species. *Didynamipus sjostedti* and one *Altiphrynoides* species (*A. malcolmi*) have large yolk-rich eggs; *A. osgoodi* and *Schismaderma* have small eggs and are oviparous (Liedtke et al. 2016). This shows that within this clade egg sizes and reproductive modes vary greatly.

The other three unique traits of the Nimba toad reproduction can be regarded as adaptations to an unpredictable environment and time constraints due to the seasonality. First, the developmental break during the dry season coincides with an inactive life with presumably a low energy budget (Xavier and Ozon 1971, Lamotte 1972). The duration of this inactivity is synchronised with the duration of the dry season and its duration varies between 3–6 months depending on the onset of the monsoon (Lamotte 1959). Irrespective of the month with first rains (February – April), Nimba toad females emerge with these first rains, and the earlier they emerge, the larger are the juveniles born in June (Lamotte 1959, Xavier 1971). The larger the newborns, the higher is their survival probability. Hence, the dry season duration is unpredictable and Nimba toads are flexible in responding to this unpredictability. Second, after parturition the endometrium is exchanged and rebuilt. We speculate that this is due to the temporal constraint, that a functional endometrium needs to be present within three months after parturition to allow the new foetuses to develop. It might be more effective and faster to rebuild the endometrium, than to re-arrange the old one within a collapsed uterus, additionally this may decrease the mother offspring conflict. Whether this alone is a sufficient explanation for the evolution of a unique trait not described of other viviparous amphibians needs further consideration. Additionally, determination whether it does not occur in other viviparous amphibians is necessary. In Nimba toads the apoptosis phase lasts for 12 days only (Xavier and Ozon 1971) and probably might not have been recorded in less well studied amphibian species. Third, female Nimba toads are not able to expel juveniles at the end of the gestation and hence, induce parturition by behaviourally restricting the space for juveniles (Vilter 1956a) and young are involved in the birthing process (Xavier and Ozon 1971). Other than in mammals, no female mechanism has evolved to end a gestation and no morphological or physiological traits evolved to enhance parturition. Changes in progesterone levels (e.g. produced by the corpora lutea) are often discussed as triggers for parturition. As in Nimba toads ovariectomy has no effect on parturition and gestation duration, no indication exists that corpora lutea produced progesterone is important for parturition. Nevertheless, the glycogen secretion of the uterine endometrium could set a time frame for parturition. The inducing mechanism for the glycogen secretion is unknown. The absence of known parturition inducing mechanisms could be due to a lack of opportunity or necessity. The Nimba toad uterus has a thin muscle layer (Xavier 1971), and it should not be very challenging to increase it, giving it the power to expel juveniles from the uterus. On the other hand, the "birthing posture" allows for parturition, and might be easier to be controlled and if necessary interrupted by females. This may allow them to give birth to single or few offspring and interrupt birthing, if predators or other unpredictable threats are approaching. The behavioural induced parturition does not allow to give birth to dead juveniles, ending in the death by sepsis of the mother (Xavier 1971). This may indicate that intra-uterine death of juveniles is rare and the evolutionary advantages of behavioural parturition (temporal flexibility) might be greater than the necessity to induce labour by muscle power. The three traits mentioned here have a strong temporal link with the environmental unpredictability or with the Nimba mountains seasonality. This may indicate that the Nimba mountains environment and seasonality had a strong influence on the evolution and/ or maintenance of viviparity.

Ecology of Nimba toads

Within one year two important periods mainly determine the reproductive cycle of a female: one, at the end of the rainy season with ovulation, mating and the beginning gestation, the second in June with the birth of juveniles. These seasonal periods are important for males as well, as during mating season spermatozoids are present, but disappear afterwards, in June at the time juveniles are born, spermatogenesis is intensified. Nevertheless, one further important period in the season is the emergence at the beginning of the rainy season, which results as well in changes within the reproductive system. Hence, within one year three periods lead to important changes within the Nimba toad reproductive system, one might be triggered by reproductive and/ or environmental clues (late rainy season), one is characterised by environment – the beginning of the rainy season (emergence), and one is

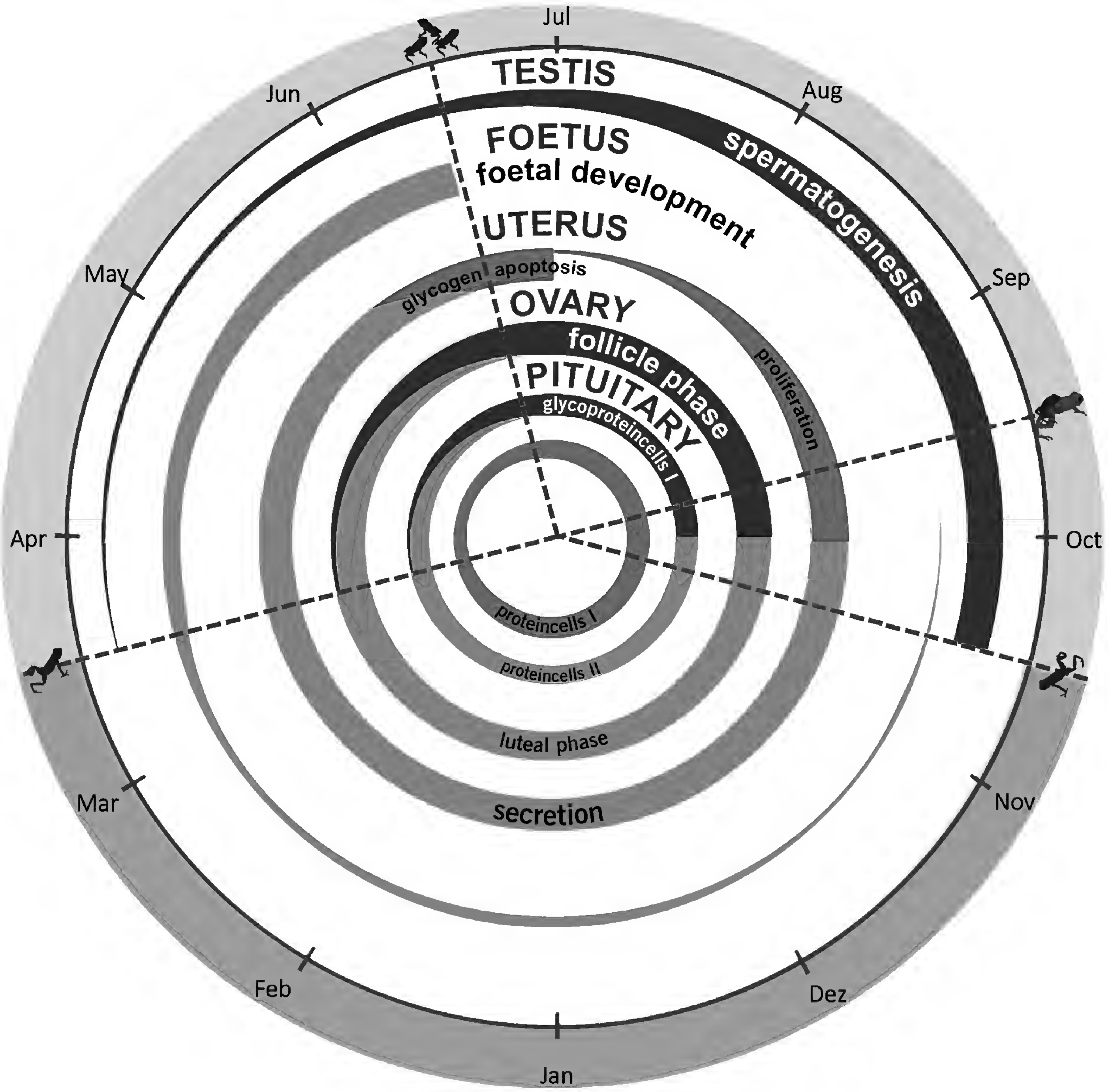

Figure 12. Summary of the temporal development of the foetus and male and female reproductive system. The outer layer gives the months as abbreviations and the seasons by colour (yellow: dry season, blue: rainy season). Toads mate between mid-September and mid-October on average, are going underground mid-October and emerge in mid-March from their dormancy sites. Juveniles are born in mid-June (pictograms). Spermatogenesis shows the development within the male reproductive system. Foetal growth gives the speed of development and growth. The uterus shows three phases: a proliferation phase in which the uterine epithelium develops, a secretion phase during the gestation and an apoptosis phase during which the uterine epithelium is completely exchanged (old one removed and new one built). The ovary has two phases: the follicles phase, characterised by follicle growth and the luteal phase characterised by the presence of corpora lutea. Within the female pituitary three cell types show variation within the annual cycle, the glycoprotein type 1 cells and the protein type 1 and type 2 cells. Within the male pituitary as well three cell types show variation (not shown), glycoprotein type 1 cells and glycoprotein type 2 cells in the same way as those of females, whereas protein type 2 cells are only present in July/ August.

characterised by reproduction at least in females - the end of gestation and intensification of spermatogenesis and intensification of rains (June). In Figure 12 we summarise the temporal changes of the male and female reproductive and foetal development. Most developments can be placed in either of two categories: i) linked to the active above ground life of toads and hence, “environmentally linked”, or ii) linked to the gestation period, “reproductively linked”. Obviously, these phases are non-exclusive, as both overlap during the first months after emergence and the last months of gestation.

“Environmentally linked” developments start with emergence and end with the beginning of the dormant life underground which coincides with mating (shown in blue in Figure 12). Within this category fall spermatogenesis, the follicular phase of the ovary, development of the oviductal tube (not shown on Figure 12) and the presence and activity of female and male glycoprotein type 1 cells (gonadotrop cells). The glycoprotein type 1 cells were shown to produce luteinizing hormone (LH), which is generally linked to gonad development and testosterone and oestradiol synthesis. Human gonadotrop cells produce as well follicle stimulating hormone (FSH), which in turn stimulates the granulosa cells, which produce progesterone in Nimba toads (Xavier 1971). Oestradiol and progesterone together trigger oviduct development (Xavier 1971). Hence, all these processes lead to ovulation, mating and finally successful establishment of the gestation. In males, the glycoprotein type 1 and 2 cells are linked to spermatogenesis and nuptial pad development; both are most developed in July and August, just prior to the mating season. As all these processes start with emergence, an environmental trigger for this development could be assumed.

"Reproductively linked" developments start with mating and the establishment of the gestation and end with the birth of juveniles (shown in yellow on Figure 12). This category focusses mainly on females. The uterine secretion phase, the ovarian luteal phase, the presence and activity of protein type 2 cells and obviously foetal development are within this category. The female protein type 2 cells were classified as somatotropic cells. During the dry season, foetal development is slow, the uterus is secreting and stretching slowly and within the ovary corpora lutea are producing progesterone. The developments within this category are nevertheless as well influenced by the environment, as most reproductive organs start slowly decreasing their presence and activity after emergence, including progesterone levels, with the exception of foetal development, which increases in speed after emergence.

The uterine apoptosis and proliferation phases and the presence and activity of protein type 1 cells (shown in red in Figure 12) do not fit in either of these categories. The uterine apoptosis phase starts slowly at the end of gestation with the production of glycogen, which is linked to foetus development (stage III) but not with emergence. During apoptosis the whole uterine mucous layer is replaced, hence this is the phase with the most immediate impact on the uterus. The uterine proliferation phase fits into the environmentally linked definition in that it leads to ovulation and mating at the end of the rainy season, but nevertheless, contains the uterus foetuses until parturition, and preparations for a new gestation can only start after the epithelial cells are replaced during the apoptosis phase. Hence, the secretion and the proliferation phase cannot overlap, as they do in other organs. The presence and activity of the protein type 1 cells were linked to prolactin secretion.

In Nimba toads the reproductive cycle is tightly linked to the seasons. In most other viviparous amphibians an environmental dependency is assumed, but detailed data rarely exist (Wake 2015b). For oviparous caecilians it is known that they may retain the fertilised eggs within the oviduct until a suitable breeding site is found and timing seems to be correlated with the onset of the rainy season (Gomes et al. 2012, Wake 2015a, 2015b). In *S. atra* the duration of gestation is longer at higher altitudes (Wunderer 1910) and is further prolonged by unsuitable environmental conditions (Vilter 1986). In squamate reptiles it was hypothesised that the cold climate at high elevations and high latitudes (Tinkle and Whitfield Gibbons 1977, Watson et al. 2014) or the less variable female body temperature, compared to the surroundings (Shine 1995), favours a viviparous reproduction. Nimba toads occur in an environment with fluctuating temperatures and at high elevation (>1,200 asl). Likewise all *Nectophrynoides* occur between 800 and 2700 m asl (Clarke 1988, Menegon et al. 2004, 2007, Channing et al. 2005, Channing and Howell 2006, Loader et al. 2009), with lower temperatures compared to the lowlands. Nevertheless, the possibly viviparous Central American *C. laticeps* occurs between 10 and 1,500 m asl, and *E. jasperi* and *L. larvaepartus* occur at low elevations (Wake 1978, Iskandar et al. 2014), and most viviparous caecilians are lowland species (Wake 1980b, 1993, Gomes et al. 2012). In caudates, high as well as low elevation species with a viviparous reproduction are known (Wake 2015b). For *L. larvaepartus* it was hypothesised that viviparity might have evolved due to competition avoidance (Iskandar et al. 2014). In pueriparous, adelphophagous subspecies of *S. salamandra* it is hypothesised that scarcity of open water and harsh environments promoted viviparity (García-París et al. 2003, Buckley et al. 2007, Velo-Antón et al. 2012, Escoriza and Ben Hasssine 2014). Within the Nimba mountains high altitude grasslands standing open water is only present during some months during the rainy season at two locations, temperature fluctuations are large and competition quite likely scarce as only two other anuran species occur within the same area (Guibé and Lamotte 1958, L. Sandberger-Loua 2016a). It is likely that scarcity of open water and harsh environments promoted as well viviparity in Nimba toads, or supported the survival of this unique reproductive mode in these special and isolated conditions.

Conservation

Most amphibian species with derived reproductive modes are threatened (Wake 2015b). This is particularly true for Nimba toads, which are listed under the IUCN red list as critically endangered (IUCN SSC Amphibian Specialist Group January 11, 2017/2016). Across a total range of 4 km² the total toad population was estimated to comprise 16 million individuals in August in the 1950s (Lamotte 1959) and 14 million in 1966 (Xavier 1971). A calculation based on an assumed equal range size, our annual monitoring data (2007–2016; 1,160 examined plots of 5 × 5 m², of those 178 in August, and 88 in high density areas in August compare Sandberger-Loua et al. 2016a), would result in 2.8 million toads in August (population size oscillates throughout season). This translates into an 82% decrease in toad numbers since 1959, which quite likely underestimates the decrease as our distribution estimate is smaller than 4 km², and we only included numbers from areas with high toad abundances to calculate the average number of toads per 1 m². The excellent studies, summarised in this review, are based on > 3,000 females, several hundred foetuses and an unknown number of males (F. Xavier included about 3,000 females and several hundred foetuses and newborns in her doctoral thesis alone, Xavier 1971). During our ten years of field work we recorded less than 61% of the number of females sacrificed to understand the toad's reproduction (1,844 females in total recorded within 29,000 m² of high altitude grasslands searched for 1,740 person hours). Between the 1950s and 2007 two mining exploration campaigns were carried out in the area (Poilecot and Loua 2009), the Nimba mountains were first declared a World Heritage Site (1981/ 1982) and 10 years later (1992) listed as World Heritage Site in Danger (UNESCO 1992). Some anuran species with derived and unique reproductive modes are already considered extinct (*Rheobatrachus silus*, *R. vitellinus*, *E. jasperi*, Wake 2015b) and hence, protection of the reproductive diversity within anurans is important. Considering their complex life cycle, in which reproductive and seasonal cycles are tightly linked, understanding and protecting the Nimba toad's threatened environment is of utmost importance.

Future work

The strong link between the Nimba toad's reproductive and life-cycle with the Nimba mountains seasonality and other environmental factors indicates that these conditions might have favoured the evolution or at least the maintenance of viviparity. Hence, ecological studies on *N. occidentalis* and the other species within the Nimba toad's clade (*Didynamipus*, *Altiphrynoides*, *Schismaderma*, *Nectophrynoides*), several of which have derived reproductive modes as well, may give insights into the evolutionary drivers of viviparity in African bufonids. Comparatively little is known about the other species with and without derived reproductive modes within this clade. For example, the reproductive mode of *D. sjostedti* is only assumed to be direct development (Grandison 1981, Gonwouo et al. 2013) and little else is known (Gonwouo et al. 2013). Of the two Ethiopian *Altiphryonides* species, some information exist on the reproductive mode (Wake 1980b), but little on the ecology. For *A. osgoodi* it may be impossible to study the ecology as it is feared to be extinct (Gower et al. 2013). Within *Nectophrynoides*, most ecological information exists for *N. asperginis* (Channing et al. 2006), which is extinct in the wild. This emphasises two reasons why ecological studies are needed for all species in this clade: first, they may give insights into the evolution of viviparity and second, they may help to protect these threatened species from extinction.

Conclusion

Viviparity is rare in anurans and the only known matrotrophic anuran is the Nimba toad. In Nimba toads three observations support matrotrophy: first, newborn Nimba toads are 15 times larger and > 200 times heavier than the egg. Second, amino acids injected into the mother were recorded first within the digestive system and liver and later in other areas of the foetuses. Third, foetal size at birth is linked to environmental conditions during the last third of the gestation period, during which females are active and most of the foetal growth occurs. We have identified six characteristics linked to viviparity specific of Nimba toads, which provide strong evidence that viviparity evolved independently in this species. These characteristics comprise three traits which are common in other amphibians, but not usually found in other viviparous species (small and yolk poor eggs, mucoprotein secretion by oviduct/ uterus epithelium, labial papillae of the foetuses), two behavioural or ecologically important traits ("behavioural birthing" and the developmental break during the dry season) and one characteristic which to our knowledge is not known from any other amphibian, but from mammals (complete apoptosis and rebuilding of the uterine epithelium after parturition). Apart from the mucoprotein secretion of the oviduct/ uterus which is found in all amphibians before fertilisation - but in Nimba toads additionally after fertilisation - these traits are more likely present in oviparous species with free-swimming tadpoles than in direct developing and lecitotrophic viviparous species. The other three unique traits can be regarded as adaptations to an unpredictable environment and time constraints due to the environments seasonality. Most reproductive developments can be placed in either of two categories: i) linked to the gestation period, "reproductively linked", or ii) linked to the active above ground life of toads and hence, "environmentally linked". Hence, it is likely that the harsh unpredictable environment and scarcity of open water promoted viviparity in Nimba toads, or supported the survival of this unique reproductive mode in these special and isolated conditions. Considering their complex life cycle, in which reproductive and seasonal cycles are tightly linked, understanding and protecting the Nimba toad's threatened environment is of utmost importance.

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Taxonomical study on a sample of land and freshwater snails from caves in central Brazil, with description of a new species

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Abstract

A sample of land and freshwater snails, mainly pulmonates, was recently collected in caves in Goiás and Bahia states, Brazil. Twenty-one species were found in the material. The following species are reported for the first time for Goiás state: *Cecilioides consobrina* (Ferussaciidae), *Dysopeas muibum* and *Stenogyra octogyra* (Subulinidae), *Entodina jekylli* and *Prohappia besckei* (Scolodontidae; also reported for the first time for Bahia state), *Pupisoma dioscoricola* (Valloniidae). A new species from Goiás is described herein: *Gastrocopta sharae* **sp. n.** (Gastrocoptidae). The new records and species addressed here constitute important findings, helping to fill distributional gaps and improving the knowledge of the local molluscan fauna, an essential step for future conservation efforts.

Key Words

Bahia
caves
Gastropoda
Goiás
Gastrocopta sharae sp. n.
stygofauna
troglofauna

Introduction

The Brazilian continental molluscan fauna is still poorly known and is deemed to have so many undescribed species as to triple the presently known number (Simone 1999, 2006). Since cave-dwelling invertebrates, in general, have received scarce attention from researchers in Brazil (Trajano and Bichuette 2010), it should be no surprise that cave-dwelling land and freshwater snails are even less known (a few exceptions are: Bichuette and Trajano 1999, 2003, Simone 2013, Salvador et al. 2016). This lack of study is alarming, especially from a conservationist point of view, since caves usually have very fragile ecosystems with a high degree of endemic species (Trajano 2000, Gallão and Bichuette 2012, Silva and Ferreira 2015).

Some recent expeditions (April/2012–January/2013) by Dr. M. E. Bichuette (Universidade Federal de São Carlos; São Carlos, Brazil) and her team to cave systems in Goiás and Bahia states, central Brazil, recovered many land and freshwater snails. This whole material was deposited in the malacological collection of the Museu de Zoologia da Universidade de São Paulo (MZSP, São Paulo, Brazil) and is studied here. The sample studied herein includes the description of a new species and occurrence of another twenty species, some of which are new records for Bahia and/or Goiás states.

Material and methods

All the material studied here was collected by M. E. Bichuette and her team and deposited in the MZSP. All the specimens were collected in caves (see Table 1 for all the localities) and comprise both empty shells and living an-

Table 1. List of all localities, i.e., the caves (or "grutas" in Portuguese), where the present material was collected, alongside their city/municipality, state, coordinates (see also Fig. 1), date of collection, the biome of the surrounding area, the microhabitat where the snails were collected and if there is a water body inside each cave.

Locality	City	State	Coordinates	Collection date	Biome	Substrate	Water body
Gruta Cantinho	Igatu/Andaraí	BA	12°51'49.9"S 41°19'26.9"W	01/Apr/2013	Campos Rupestres	wet sand	yes
Gruta do Catão	São Desidério	BA	12°22'07.0"S 44°52'03.2"W	03/Nov/2012	Cerrado/ Caatinga	wet sand, clay	yes
Gruta do Renatão	São Desidério	BA	12°26'35.6"S 44°56'26.7"W	03/Nov/2012	Cerrado/ Caatinga	clay	no
Gruta das Dores	Mambaí	GO	14°24'38.0"S 46°11'35.5"W	30/Apr/2013	Cerrado	clay	yes
Gruta Fundo de Quintal	Mambaí	GO	14°29'16.0"S 46°07'08.4"W	29/Oct/2012	Cerrado	clay	yes
Gruta Judite	Mambaí	GO	14°24'26.5"S 46°11'43.7"W	01/May/2013	Cerrado	clay	yes
Gruta da Tarimba	Mambaí	GO	14°24'43.0"S 46°10'29.6"W	28/Oct/2012, 29/Apr/2013	Cerrado	clay	yes
Gruta Pasto de Vacas I	Mambaí	GO	14°26'19.4"S 46°10'40.9"W	02/May/2013	Cerrado	clay	yes
Gruta Revolucionários	Posse	GO	14°14'03.0"S 46°20'41.8"W	30/Apr/2013, 03/May/2013	Cerrado	clay	yes

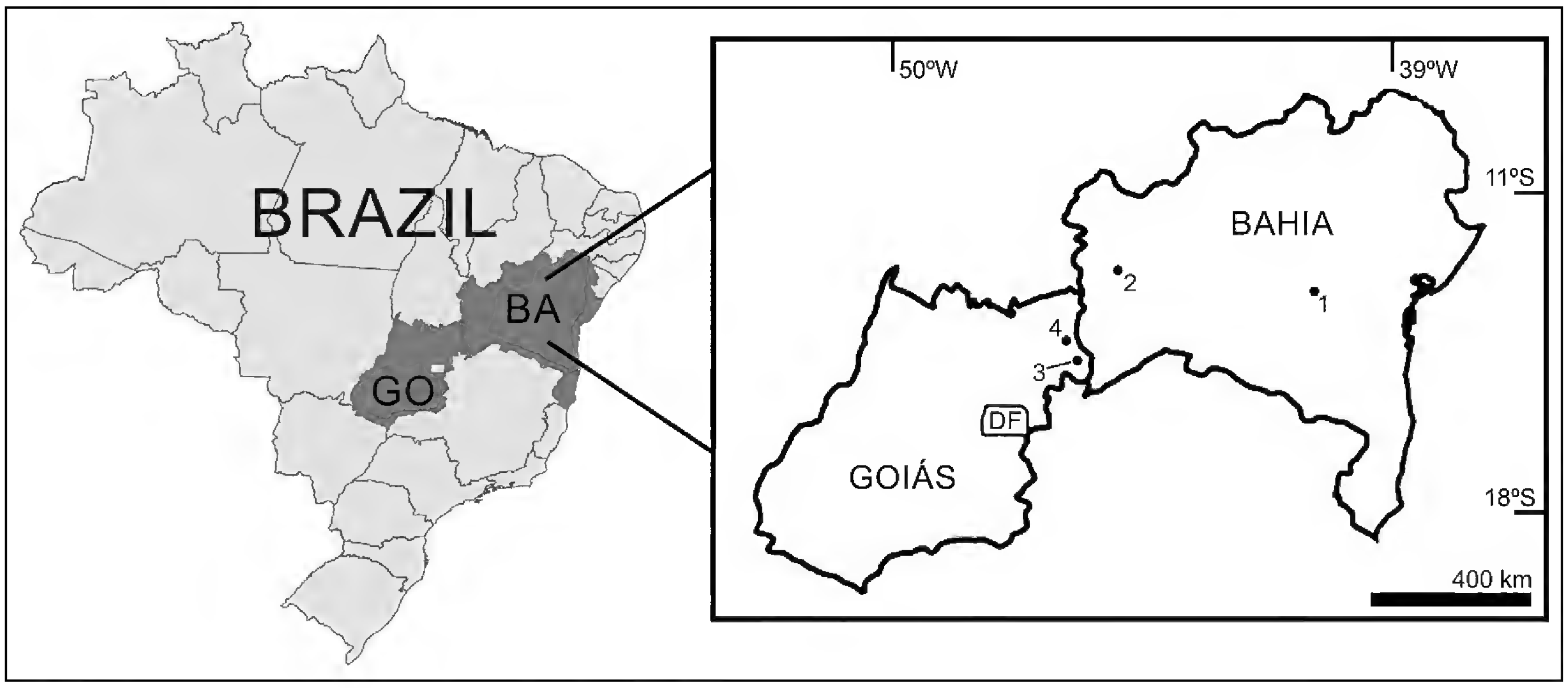

Figure 1. Map showing the Brazilian states of Bahia and Goiás, with the cities where the caves are located (see also Table 1): **1**, Igatu/Andaraí; **2**, São Desidério; **3**, Mambaí; **4**, Posse. Abbreviations: GO, Goiás state; BA, Bahia state; DF, Distrito Federal.

imals. Brief descriptions of each locality can be found in Table 1, alongside their precise coordinates (see also Fig. 1). Localities from Goiás all fit into the Cerrado Biome, while those in Bahia are either Campos Rupestres (montane subtropical savannah) or a transition between the Cerrado and the Caatinga.

Identification was conducted based on the work of Simone (2006), the original descriptions, and additional material housed in the collection of the MZSP. Unfortunately, some species could not be identified beyond genus level, either due to poor preservation of the specimens or to very young age. The complete list of species, as well as a relation of all the studied material, can be found in Table 2. Species that deserve further notice, such as those with new records, are figured and discussed in the Systematics session below. Measurements were made with a digital caliper or with the aid of the Zeiss Axiovision SE64 Rel 4.8 imaging software. The following abbreviations are used herein: shell dimensions: H = shell length, D = shell greatest width, h = aperture height, d = aperture width; institutions: NHMUK = Natural History Museum (London, UK); NMSW = National Museum Wales (Cardiff, UK).

Systematics

Pulmonata
Stylommatophora
Superfamily Pupilloidea
Family Gastrocoptidae
Genus *Gastrocopta* Wollaston, 1878

Gastrocopta sharae sp. n.

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Figs 2–6

Type material. Holotype: MZSP 122725 (Figs 2–4). Paratype: MZSP 122726, from type locality (Figs 5–6).

Table 2. List of all species found on the present material, with information on locality data, whether it is a new occurrence (species with new records are analyzed more thoroughly in the text) and record number of the MZSP collection. Abbreviations: **BA,** Bahia state; **GO,** Goiás state; **Can,** Gruta Cantinho; **Cat,** Gruta do Catão; **Dor,** Gruta das Dores; **FdQ,** Gruta Fundo de Quintal; **Jud,** Gruta Judite; **PdV**, Pasto de Vacas I; **Ren,** Gruta do Renatão; **Rev,** Gruta Revolucionários; **Tar,** Gruta da Tarimba; **hol,** holotype; **par,** paratype; **sh,** shell; **spc,** specimen.

Species	Family	New record?	Cave(s)	Collection Nr. (MZSP)
Neritimorpha				
Helicina angulata Sowerby, 1873	Helicinidae	–	Ren (BA)	MZSP 122761 (1 spc)
Caenogastropoda				
Pomacea sp.	Ampullariidae	–	Cat (BA)	MZSP 122776 (1 sh)
Idiopyrgus souleyetianus Pilsbry, 1911	Pomatiopsidae	–	Cat (BA)	MZSP 122772 (1 sh), 122773 (5 sh), 122774 (6 sh), 122775 (3 sh)
Pulmonata - Hygrophila				
Biomphalaria sp.	Planorbidae	–	Cat (BA), PdV (GO)	MZSP 122768 (17 sh), 122769 (1 sh), 122770 (5 sh), 122771 (3 sh), 122777 (1 sh)
Aplexa marmorata (Guilding, 1828)	Physidae	–	Jud (GO)	MZSP 122730 (1 spc)
Pulmonata - Stylommatophora				
Solaropsis sp.	Camaenidae	–	Tar (GO)	MZSP 122727 (2 spc)
Radiodiscus sp.	Charopidae	–	Tar, Rev (GO)	MZSP 122816 (1 sh), 122817 (9 sh), 131089 (2 sh), 131090 (1 sh)
Zilchogyra sp.	Charopidae	–	Dor (GO)	MZSP 122734 (1 sh)
Cecilioides consobrina (d'Orbigny, 1841)	Ferussaciidae	yes	Tar, Rev (GO)	MZSP 131578 (1 sh), 131579 (1 sh), 122756 (1 sh), 122759 (1 sh)
Gastrocopta sharae sp. nov.	Gastrocoptidae	yes	Rev (GO)	MZSP 122725 (hol), MZSP 122726 (par)
Cyclodontina sexdentata (Spix, 1827)	Orthalicidae	–	Cat (BA)	MZSP 122763 (1 spc)
Ringincella luetzelburgi Weber, 1925	Orthalicidae	–	Ren (BA)	MZSP 122762 (2 sh)
Entodina jekylli Baker, 1913	Scolodontidae	yes	Tar, Rev (GO)	MZSP 122735 (10 sh + 4 spc), 122757 (1 sh), 131091 (5 sh + 1 spc), 131092 (2 sh), 131093 (3 sh)
Happia sp.	Scolodontidae	–	Cat (BA)	MZSP 122767 (1 spc)
Happia glaberrima	Scolodontidae	–	Rev (GO), Cant (BA)	MZSP 122822 (1 spc), 122824 (1 sh), 122825 (2 sh), 122826 (4 spc), 1228227 (1 spc)
Prohappia besckei (Dunker, 1847)	Scolodontidae	yes	Can, Ren (BA); Tar, Rev (GO)	MZSP 122736 (4 sh + 1 spc), 122758 (1sh), 122760 (4 sh + 1 spc), 122764 (1 sh), 131094 (4 sh), 131095 (7 sh), 131096 (3 sh), 131097 (3 sh), 131098 (1 spc), 131099 (1 sh)
Allopeas micra (d'Orbigny, 1835)	Subulinidae	–	FdQ (GO)	MZSP 122729 (1 sh) MZSP 122732 (1 sh)
Dysopeas muibum (Marcus & Marcus, 1968)	Subulinidae	yes	Tar (GO)	MZSP 131100 (1 sh)
Leptinaria sp.	Subulinidae	–	Cat, Ren (BA)	MZSP 122765 (1 sh), 122766 (1 sh)
Leptinaria concentrica (Reeve, 1849)	Subulinidae	–	Rev (GO)	MZSP 122828 (1 spc)
Stenogyra octogyra (Pfeiffer, 1856)	Subulinidae	yes	Dor, Jud, Tar (GO)	MZSP 122728 (1 sh), 122731 (1 spc), 122733 (2 sh)
Pupisoma dioscoricola (C.B. Adams, 1845)	Valloniidae	yes	Tar, Rev (GO)	MZSP 122737 (1 sh), 122738 (1 sh), 122739 (1 sh), 131101 (1 sh)

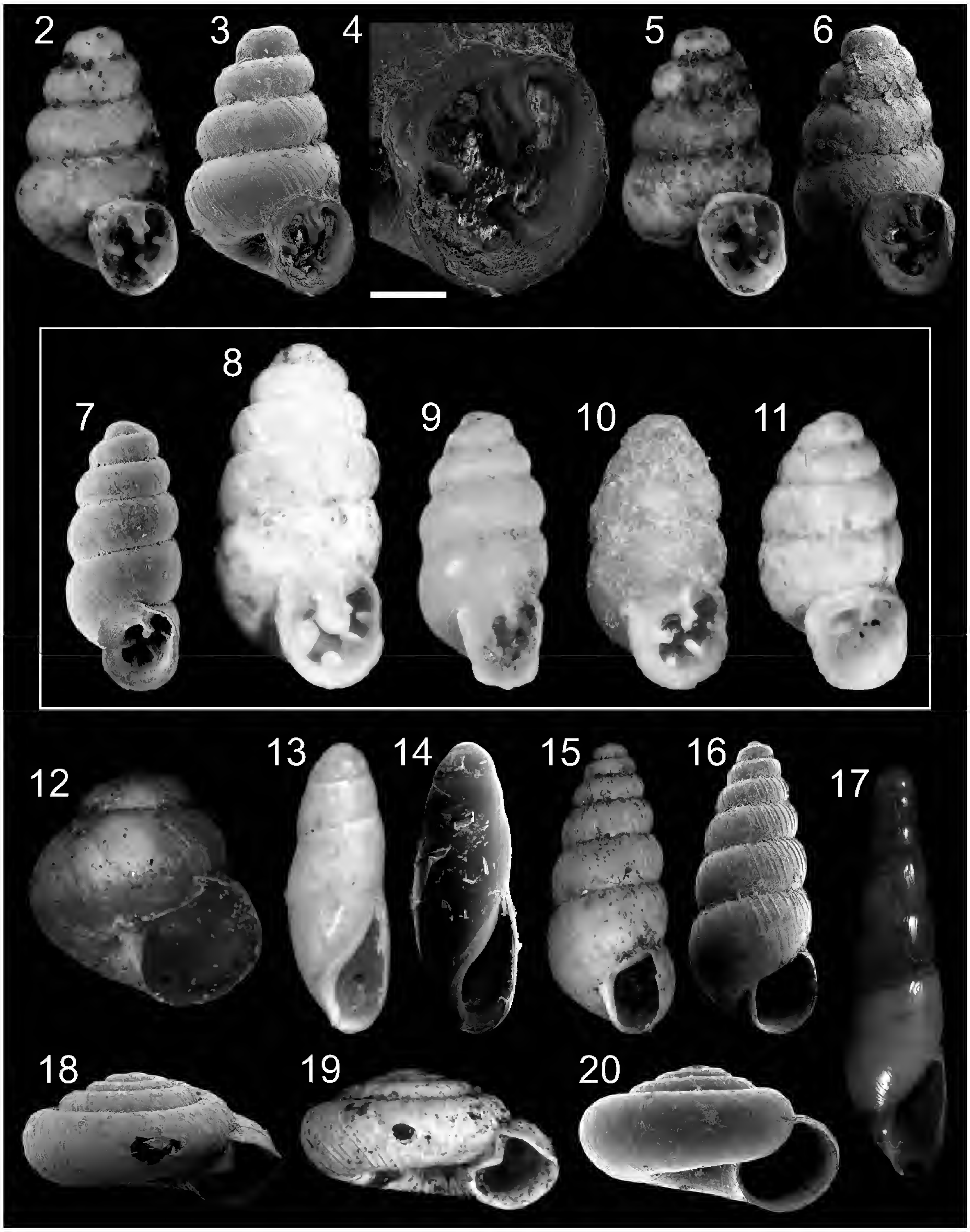
Type locality. BRAZIL, Goiás, Mambaí, Gruta Revolucionários (col. M.E. Bichuette, J.E. Gallão, D.M. Shimonsky, P.P. Rizzato, R. Borghezan; 29/iv/2013).

Distribution. Known only from the type locality (Fig. 1).

Etymology. The name refers to Shar, a fictional goddess of darkness, caverns, and secrets, from the Faerûnian pantheon of the Forgotten Realms campaign setting of the Dungeons and Dragons role-playing game.

Diagnosis. Shell pupilloid-conical. Four apertural barriers: two lamellae and two teeth). Anguloparietal lamella shaped like narrow gutter, bent towards palatal region.

Description. Shell minute (H < 2 mm), pupilloid-conical; greatest width of shell on body whorl (D/H = 0.6); body whorl ca. 1/2H; spire angle 48°. Whorl profile greatly convex; suture well-marked. Protoconch (ca. 1½ whorl) round, smooth; transition to teleoconch clearly marked by change to teleoconch sculpture. Teleoconch sculptured by strongly prosocline faint axial riblets. Aperture rounded to lightly quadrangular (d/h = 0.8; h/H = 0.4); peristome reflexed; parietal callus distinctive. Apertural barriers totaling four (Fig. 3): upper palatal tooth, lower palatal tooth, columellar lamella, anguloparietal lamella. Anguloparietal lamella shaped like narrow gutter, bent towards palatal region. After the anguloparietal lamella, the strongest barriers are the



Figures 2–20. *Gastrocopta sharae* sp. n., holotype (MZSP 122725, H = 1.9 mm, D = 1.1 mm). **2.** Apertural view; **3.** Apertural view, SEM image; **4.** Close-up of the aperture, showing dentition; scale bar = 200 µm. **5–6.** *Gastrocopta sharae* sp. n., paratype (MZSP 122726, H = 1.9 mm, D = 1.1 mm). **5.** Apertural view; **6.** Apertural view, SEM image. **7–11.** Other *Gastrocopta* spp. from Brazil, shown in apertural view. All images in scale to one another and to *G. sharae* (Figs 2, 3, 5, 6). **7.** *G. barbadensis*, from Trindade Island, SEM image (MZSP 104736, H = 1.9 mm); **8.** *G. iheringi*, probable syntype, from Bolacha, Rio Grande do Sul state (MZSP 7519, H = 2.5 mm); **9.** *G. oblonga*, from Brazil, precise provenance unknown (NMSW unnumbered, H = 2 mm); **10.** *Gastrocopta servilis*, from Fortaleza, Ceará state (MZSP 7520, H = 2 mm); **11.** *Gastrocopta solitaria*, possible holotype, from Fernando de Noronha Archipelago (NHMUK unnumbered, H = 2 mm). **12.** *Pupisoma dioscoricola*, apertural view (MZSP 131101, H = 1.6 mm, D = 1.6 mm). **13–14.** *Cecilioides consobrina* (MZSP 131579, H = 1.9 mm, D = 0.6 mm). **13.** Apertural view; **14.** Apertural view, SEM image. **15–16.** *Dysopeas muibum* (MZSP 131100, H = 5.4 mm, D = 2.3 mm). **15.** Apertural view; **16.** Apertural view, SEM image. **17.** *Stenogyra octogyra*, apertural view (MZSP 122731, H = 14.3 mm, D = 3.7 mm). **18–19.** *Entodina jekylli* (MZSP 131092, H = 1.6 mm, D = 3.1 mm). **18.** Apertural view, SEM image; **19.** Apertural view. **20.** *Prohappia besckei*, apertural view, SEM image (MZSP 131096, H = 1.0 mm, D = 1.8 mm).

lower palatal tooth and columellar lamella. Umbilicus narrow, deep.

Dimensions (in mm). Holotype: 4¼ whorls; H = 1.9; D = 1.1; h = 0.7; d = 0.6. **Paratype:** 4¼ whorls; H = 1.9; D = 1.1; h = 0.7; d = 0.6.

Discussion. The minute pupilloid shell and the pattern of apertural barriers, especially the presence of an anguloparietal lamella (formed by the fusion of the angular and parietal lamellae), place the present specimens in *Gastrocopta*. They are sufficiently different and easily diagnosable from all known *Gastrocopta* species in Brazil, which warrants the description of a new species: *Gastrocopta sharae* sp. n. Although each of the diagnostic features of *G. sharae* can be found separately in congeners (e.g., Pilsbry 1916–1918), their occurrence together is unique for this species.

Gastrocopta sharae can be easily distinguished by its strongly conical shell (Figs 2, 3, 5, 6). Nearly all Brazilian species have more pupiform/cylindrical shells: *G. barbadensis* (Pfeiffer, 1853) (Fig. 7), known from the Caribbean Islands, Venezuela, Fernando de Noronha Archipelago and Trindade Island (Cunha et al. 2015); *G. iheringi* (Suter, 1900) (Fig. 8), known only from Rio Grande do Sul state (Simone 2006); *G. oblonga* (Pfeiffer, 1852) (Fig. 9), known from Suriname to Argentina (Simone 2006); and *G. servilis* (Gould, 1843) (Fig. 10), known from Ceará and Rio de Janeiro states (Simone 2006). *Gastrocopta solitaria* (Smith, 1890) (Fig. 11), from Fernando de Noronha Archipelago, is somewhat conical, but not nearly as much as *G. sharae*.

Likewise, *G. sharae* is easily diagnosable by its narrow gutter-like anguloparietal lamella (Fig. 4), slightly bent towards the palatal region of the aperture. All the Brazilian species present a bifid weak anguloparietal lamella, with the single exception of *G. iheringi* (Fig. 8). The latter also has a gutter-like lamella, but it is much broader and straight (i.e., not bent towards the palatal region). Moreover, *G. iheringi* is much taller than *G. sharae*, reaching a shell length of 2.5 mm; this might not seem a large difference at first sight, but differences of this magnitude are usually considered to be interspecific in the family.

Family Valloniidae
Genus *Pupisoma* Stoliczka, 1873
Pupisoma dioscoricola (C.B. Adams, 1845)

Fig. 12

Synonymy see Hausdorf (2007). Complement:
Pupisoma dioscoricola: Salgado and Coelho 2003: 153.
Pupisoma discoricola [sic]: Simone 2006: 308 (fig. 9).
Pupisoma (*Ptychopatula*) *dioscoricola*: Hausdorf 2007: 1483 (Figs 1–2, 6).

Type locality. USA, Texas, Brownsville. Paralectotypes are from Mexico, San Luis Potosí, Valles Falls and Choy Cave.

Previously known distribution. From Florida, USA, to southern Brazil and northern Argentina, including the Caribbean islands (Hausdorf 2007).

New occurrence. Goiás. Mambaí: Gruta da Tarimba. Posse: Gruta Revolucionários.

Remarks. Despite the species being known throughout the Americas, the present record fills a gap in the species distribution (see the revision of Hausdorf 2007: fig. 6).

Superfamily Achatinoidea
Family Ferussaciidae
Genus *Cecilioides* Férussac, 1814
Cecilioides consobrina (d'Orbigny, 1837)

Figs 13–14

Achatina consobrina d'Orbigny 1837: 89 (pl. 11 bis, Figs 10–12); d'Orbigny 1841: 170.
Caecilioides (*Caecilianopsis*) *consobrina*: Hylton Scott 1948: 254; Morretes 1949: 131.
Cecilioides (*Karolus*) *consobrina*: Figueiras 1963: 87; Quintana 1983: 80.
Cecilioides consobrina: Parodiz 1957: 131; Salgado and Coelho 2003: 154; Simone 2006: 182 (fig. 666); Aguirre et al. 2007: 10 (fig. 4.5); Miquel et al. 2007: 114; Miquel and Aguirre 2011: 109 (fig. 8).

Type locality. Near Matanzas, Cuba.

Previously known distribution. From the Caribbean Islands to central-northern Argentina (Miquel and Aguirre 2011) and Uruguay (Figueiras 1963).

New occurrence. Goiás. Mambaí: Gruta da Tarimba. Posse: Gruta Revolucionários.

Remarks. The present record is the first occurrence for Goiás and fills a gap in the species distribution in Central Brazil.

Family Subulinidae
Genus *Dysopeas* Baker, 1927
Dysopeas muibum Marcus & Marcus, 1968

Figs 15–16

Pseudopeas (*Dysopeas*) *muibum* Marcus and Marcus 1968: 199 (Figs 11-19)
Dysopeas muibum: Simone 2006: 185 (fig. 673); Simone and Salvador 2016: 29, fig. 97, table 1.

Type locality. São Paulo, São Paulo state, Brazil.

Previously known distribution. Known only from its type locality (Marcus and Marcus 1968; Simone 2006) and Nanuque, Minas Gerais state (Simone and Salvador 2016).

New occurrence. Goiás. Mambaí: Gruta da Tarimba.

Remarks. The present record greatly expands this species distribution: ca. 720 km to the northwest.

Genus *Stenogyra* Shuttleworth, 1854

Stenogyra octogyra (Pfeiffer, 1856)

Fig. 17

Bulimus octogyrus Pfeiffer 1856: 45.
Opeas octogyrum: Pilsbry 1906: 206 (pl. 29, Figs 75–79); Baker 1913: 644; Salgado and Coelho 2003: 155.
Stenogyra octogyra: Simone 2006: 188 (fig. 695).

Type locality. Caracas, Venezuela.

Previously known distribution. Venezuela and Brazil (Pará, Ceará, Rio Grande do Norte and Mato Grosso states) (Simone 2006).

New occurrence. Goiás. Mambaí: Gruta das Dores, Gruta Judite, Gruta da Tarimba.

Remarks. The present record fills a gap in the species' previously known distribution in Brazil.

Superfamily Rhytidoidea
Family Scolodontidae
Genus *Entodina* Ancey, 1887

Entodina jekylli Baker, 1913

Figs 18–19

Entodina jekylli Baker 1913: 630 (pl. 22, Figs 11–13); Morretes 1949: 137; Baker 1963: 239; Salgado and Coelho 2003: 169; Simone 2006: 224 (fig. 851).

Type locality. Camp 39 of Stanford expedition, Madeira-Mamoré railway ca. 284 km above Porto Velho, Rondônia, Brazil.

Previously known distribution. Known only from type locality.

New occurrence. Goiás. Mambaí: Gruta da Tarimba. Posse: Gruta Revolucionários.

Remarks. There are two further possible records of this species from Peru and Bolívia (Ituarte et al. 2008; Ramírez et al. 2012), but the specimen figure by Ituarte et al. (2008: 83, text fig.), referred to as *Systrophia* (*Entodina*) aff. *jekylli*, is quite different from the type specimen figured by Simone (2006: 244, fig. 851B). The present specimens do compare well with the types; however, they lack the palatal tooth typical of the species (Baker 1913). This could be simple morphological variation (intraspecific differences in dentition are common in pulmonate snails), represent juvenile or sub-adult specimens or, less likely, even be an indicative that the present material represents a new species. The present record greatly extends the species distribution, ca. 2000 km southeast.

Genus *Prohappia* Thiele, 1927

Prohappia besckei (Dunker in Pfeiffer, 1847)

Fig. 20

Helix Besckei Dunker *in* Pfeiffer 1847: 81; Hidalgo 1870: 37.
Happia (*Prohappia*) *besckei*: Morretes 1949: 139.
Happia besckei: Salgado and Coelho 2006: 169.
Prohappia besckei: Simone 2006: 228 (fig. 873); Simone and Salvador 2016: 29 (Figs 98–100, table 1).

Type locality. Brazil (restricted to Rio de Janeiro by Hidalgo 1870).

Previously known distribution. Brazil: Minas Gerais, Rio de Janeiro and Santa Catarina states (Simone 2006; Simone and Salvador 2016). Paraguay (Morretes 1949; Simone 2006).

New occurrence. Bahia. Igatu/Andaraí: Gruta Cantinho. São Desidério: Gruta do Renatão. **Goiás.** Mambaí: Gruta da Tarimba. Posse: Gruta Revolucionários.

Remarks. The shell morphology of the present specimens compare very well to *P. besckei*; the size of the specimens from Goiás, however, is much smaller (D ~ 2 mm), slightly larger than half the normal size. This could represent a variation of the species in a cave environment, but the sample is too small to be of any significance. The present record extends the species distribution ca. 600 km to the north.

Discussion

Many records reported here are the first for either Goiás or Bahia states (Table 2). These findings are especially important as they not only extend the geographical distribution of some species but also fill "distribution gaps" of some others; for instance, one species, *Entodina jekylli*, was previously known only from its type locality. The present records are among the few concerning molluscan cave fauna. Most caves in Brazil have no legal protection and are threatened by mining activities, but still harbor new discoveries (e.g., Simone 2013). Better known geographical distributions, as well as the presence of endemic taxa, can improve arguments for conservation. It is our hope that the present work is a step towards proper legal protection of such fragile ecosystems.

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Diamond in the rough: a new species of fossorial diamond frog (*Rhombophryne*) from Ranomafana National Park, southeastern Madagascar

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Abstract

We describe a new species from the cophyline microhylid genus *Rhombophryne,* a group of fossorial and terrestrial frogs endemic to Madagascar. Found during herpetofaunal surveys of moist montane forest in the remote north of Ranomafana National Park, *Rhombophryne nilevina* **sp. n.** exemplifies two difficulties that hinder taxonomic progress in Malagasy cophyline frogs: micro-endemicity and highly secretive habits. Known from only two adult male specimens, this new species is nonetheless easily distinguishable from all other known *Rhombophryne* using morphological data, and osteological data collected here via X-ray Micro-Computed Tomography, or "micro-CT". This species is now the largest known *Rhombophryne*, and the only one known from Ranomafana National Park, which will make it the southern-most member of the genus pending a forthcoming taxonomic revision involving *Plethodontohyla* and *Rhombophryne*. Pairwise distances of the mitochondrial 16s rRNA marker show a minimum genetic distance of 4.9% from other nominal *Rhombophryne*. We also describe recordings of an advertisement call, emitted from a burrow by the holotype. *Rhombophryne nilevina* **sp. n.** is not known to be found syntopically with other *Rhombophryne*, nor to be present elsewhere in Ranomafana National Park, but it probably does co-occur with a few ecologically similar *Plethodontohyla* species. Although the type locality is within a protected area, we suggest an IUCN listing of Data Deficient for *R. nilevina* **sp. n.**, as its area of occupancy is largely undetermined within the park.

Introduction

Over the past several decades, integrative approaches to taxonomy have shown that Madagascar's anuran fauna is one of the most spectacular on earth, with current estimates approaching 600 species; 99.9% of which are endemic to the island (reviewed in Vieites et al. 2009, Perl et al. 2014). This estimate continues to rise as more candidate species are newly discovered, with ~465 species estimated in Vietes et al. (2009), and ~530 in Perl et al. (2014). Many recent candidate species have been found from very few localities, and are presumably restricted to small ranges (e.g., Rosa et al. 2014, Hutter et al. 2015). Among clades of Malagasy frogs, the subfamily Cophylinae Cope, 1889 (family Microhylidae Günther, 1858) faces one of the steepest taxonomic gaps, with more candidate species existing than described species (Vieites et al. 2009, Perl et al. 2014, Scherz et al. 2016a). This phenomenon is likely explicable by the many challenges they present to systematists, including secretive habits, small range sizes, and numerous morphologically cryptic species.

Rhombophryne Boettger, 1880 is a particularly enigmatic cophyline genus consisting of 16 valid nominal species (Scherz et al. 2016a,b), found primarily in rainforest habitats of northern and eastern Madagascar. In addition to fossorial or otherwise secretive habits, the apparently

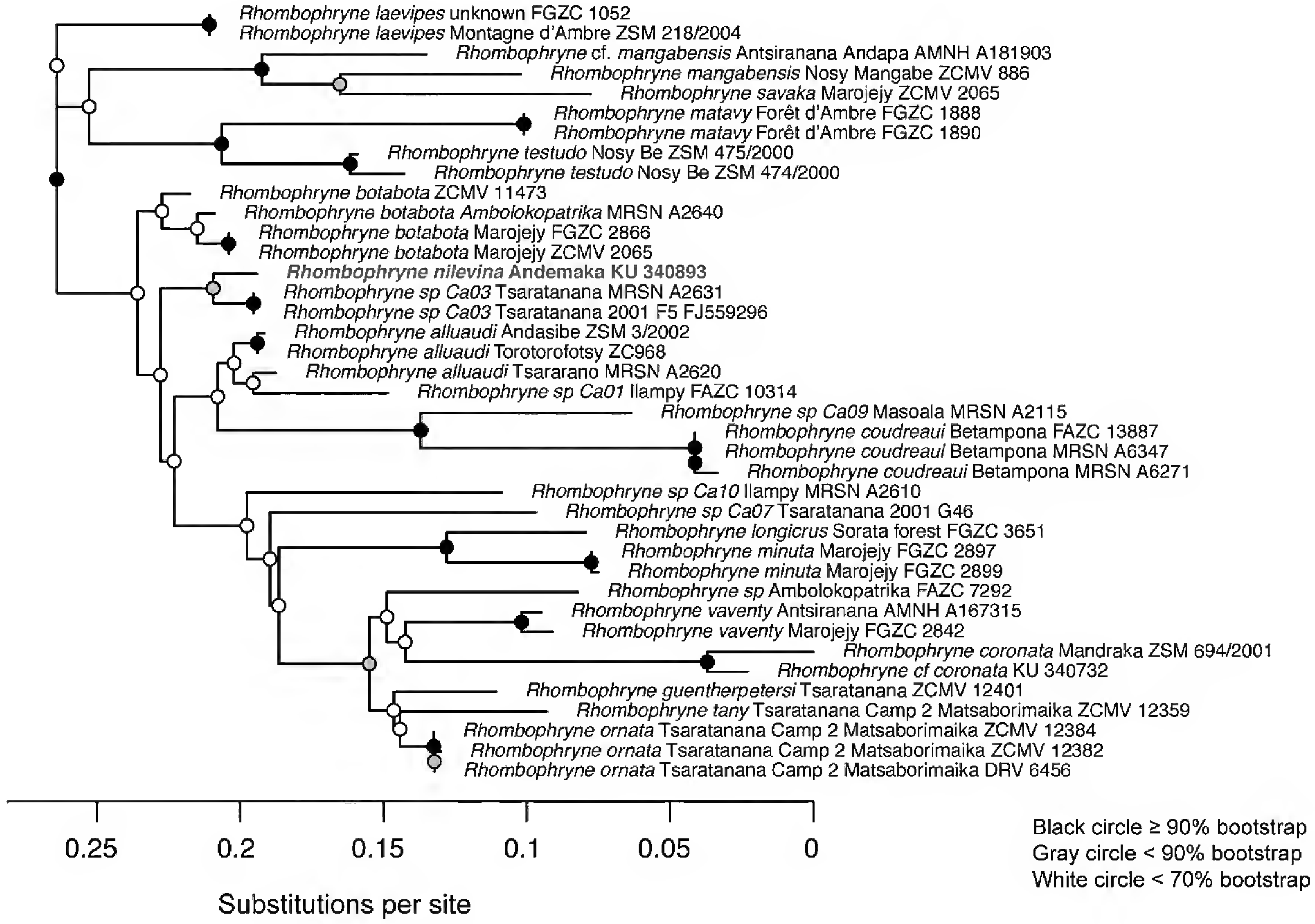

Figure 1. Phylogenetic relationships between *Rhombophryne* species estimated using maximum likelihood in RaxML using the mitochondrial 16S rRNA barcode fragment. *Rhombophryne nilevina* sp. n. is highlighted with blue bold text. Outgroups are removed from the tree figure for aesthetic purposes.

small ranges of many species have historically impeded data collection, and thus taxonomic progress, in the genus (Glaw et al. 2010). However, fueled by the application of integrative taxonomic approaches, the number of described *Rhombophryne* has swelled in recent years, with 8 species described since 2010 (D'Cruze et al. 2010, Glaw et al. 2010, Scherz et al. 2014, 2015a,b, 2016b), and only a few already-published candidate species left to be described (Scherz et al. 2016b), although several more have been identified and will be described soon (Fig. 1 and Scherz, Crottini, et al. unpubl. data).

We herein describe *Rhombophryne nilevina* sp. n., discovered during herpetofaunal surveys of moist montane forest in the remote north-western corner of Ranomafana National Park, southeastern Madagascar, in January of 2015. We diagnose *R. nilevina* sp. n. from its congeners using morphological and osteological characters collected with the help of X-ray Micro-Computed Tomography (micro-CT). We also describe the male advertisement call of the new species, which is distinct from all other known vocalizations in the genus.

Methods

Specimen collection

We collected specimens during the day through targeted searching, using the advertisement call to locate males. We euthanized specimens using 20% benzocaine, fixed them in ~10% formalin solution buffered with sodium phosphate to pH 7.0, and transferred them to 70% ethanol for long-term storage after approximately two weeks. We deposited the holotype in the Biodiversity Institute of the University of Kansas (KU) and a paratype in the Mention Zoologie et Biodiversité Animal, Faculté des Sciences, Université d'Antananarivo (formerly Département de Biologie Animale of the Universiteé d'Antananarivo; UADBA).

DNA barcoding and phylogenetic analysis

Immediately following euthanasia, we removed the tongue and placed it in 95% EtOH. We extracted genomic DNA using standard phenol-chloroform extraction protocol and amplified a fragment of the mitochondrial rRNA marker 16S using a previously published protocol (Hutter et al. 2015). We include a total of seven newly generated 16S sequences in this study; one of *R. nilevina* sp. n., one tentatively assigned to *R. coronata*, and five outgroup sequences (Table 1). We acquired sequences of the same 16S fragment for other *Rhombophryne* from Genbank. Prior to alignment, we removed identical sequences using the "Find Duplicates" option in Geneious version 6 (Kearse et al. 2012). All retained sequences and their accession numbers are listed in Table 1. We aligned sequences with the MAFFT (Katoh and Standley 2013) plugin version 1.3 for Geneious, using the the "E-INS-i" algorithm and otherwise default settings. We inferred phylogenetic re-

Table 1. GenBank Accession numbers for all sequences used in phylogenetic analysis. Asterisks indicate newly generated sequences.

Species	Locality	Voucher number	Accession
*Platypelis barbouri**	Ambatomandondona	KU 340681	KY288471
*Platypelis pollicaris**	Torotorofotsy	KU 340614	KY288472
*Platypelis tuberifera**	Vohidrazana	CRH 286	KY288470
*Plethodontohyla inguinalis**	Vohidrazana	KU 340642	KY288474
Rhombophryne alluaudi	Andasibe	ZSM 3/2002	DQ019606
Rhombophryne alluaudi	Torotorofotsy	ZCMV 968	EU341105
Rhombophryne alluaudi	Tsararano	MRSN A 2620	AY594105
Rhombophryne cf. *coronata**	Vohidrazana	KU 340732	KY288476
Rhombophryne coronata	Mandraka	ZSM 694/2001	EU341103
Rhombophryne coudreaui	Betampona	FAZC 13887	FJ559299
Rhombophryne coudreaui	Betampona	MRSN A 6271	HM364771
Rhombophryne coudreaui	Betampona	MRSN A 6347	HM364772
Rhombophryne guentherpetersi	Tsaratanana	ZCMV 12401	KU937796
Rhombophryne laevipes	Montagne d’Ambre	ZSM 218/2004	EU341104
Rhombophryne laevipes	Montagne d’Ambre	FGZC 1052	KM509189
Rhombophryne longicrus	Sorata forest	FGZC 3651	KR025897
Rhombophryne mangabensis	Nosy Mangabe	ZCMV 886	KU724181
Rhombophryne matavy	Foret’d Ambre	FGZC 1888	FJ559298
Rhombophryne matavy	Foret’d Ambre	FGZC 1890	GU195641
Rhombophryne cf. *mangabensis*	Antsiranana, Andapa	AMNH 181903	KM509192
Rhombophryne minuta	Marojejy	FGZC 2897	EU341100
Rhombophryne minuta	Marojejy	FGZC 2899	EU341106
Rhombophryne ornata	Tsaratanana Camp Matsaborimaika	DRV 6456	KP895582
Rhombophryne ornata	Tsaratanana Camp Matsaborimaika	ZCMV 12382	KP895583
Rhombophryne ornata	Tsaratanana Camp Matsaborimaika	ZCMV 12384	KP895584
Rhombophryne savaka	Marojejy	ZCMV 2065	KU724176
Rhombophryne serratopalpebrosa	Ambolokopatrika	FAZC 7292	EU341111
Rhombophryne sp. Ca01	Ilampy	FAZC 10314	FJ559295
Rhombophryne sp. Ca03	Tsaratanana	MRSN A 2631	AY594107
Rhombophryne sp. Ca03	Tsaratanana	ZSM 667/2001	FJ559296
Rhombophryne botabota	Ambolokopatrika	MRSN A 2640	AY594104
Rhombophryne botabota	Marojejy	FGZC 2866	EU341102
Rhombophryne botabota	Marojejy	ZCMV 2065	FJ559297
Rhombophryne sp. Ca07	Tsaratanana	2001 G46	EU341108
Rhombophryne sp. Ca09	Masoala	MRSN A 2115	AY594110
Rhombophryne sp. Ca10	Ilampy	MRSN A 2610	AY594111
Rhombophryne nilevina sp. n. *	Andemaka	KU 340893	KY288475
Rhombophryne botabota	Makira	ZCMV 11473	KU724173
Rhombophryne tany	Tsaratanana Camp Matsaborimaika	ZCMV 12359	KP895585
Rhombophryne testudo	Nosy Be	ZSM 474/2000	KC180070
Rhombophryne testudo	Nosy Be	ZSM 475/2000	EU341110
Rhombophryne vaventy	Antsiranana	AMNH A167315	DQ283409
Rhombophryne vaventy	Marojejy	FGZC 2842	EU341107
*Scaphiophryne marmorata**	Torotorofotsy	KU 340620	KY288473

lationships with RaxML 8.2.6 (Fig. 1; Stamatakis 2014), using the -f a option to search for a maximum likelihood tree and conduct 1000 rapid bootstrap replicates, under the GTR model of sequence evolution and with gamma distributed rate variation. Finally, we calculated raw pairwise genetic distances from the alignment using the dist.dna function of the ape package in R (Table 2, Paradis et al. 2004, R Development Core Team 2016).

Morphology

We took morphological measurements using a digital caliper to 0.01 mm, rounded to 0.1 mm. We note that only the holotype was measured, as the paratype was unavailable for study. Measurements follow the standard for this genus and are repeated here verbatim from Scherz et al. (2015b): “SVL (snout–vent length), HW (maximum head width), HL (head length, from the maxillary commissure to the anterior-most point of the mouth), ED (horizontal eye diameter), END (eye–nostril distance), NSD (nostril–snout tip distance), NND (internarial distance), TDH (horizontal tympanum diameter), TDV (vertical tympanum diameter), HAL (hand length, from the metacarpal–radioulnar articulation to the tip of the longest finger), LAL (lower arm length, from the carpal–radioulnar articulation to the

Table 2. Raw genetic distances at the 16s rRNA gene fragment between analysed taxa and *Rhombophryne nilevina* sp. n. (KU 340893).

Taxon	Distance
Rhombophryne sp. Ca03 (Tsaratanana)	3.80%
Rhombophryne alluaudi (Andasibe, Torotorofotsy, Tsararano)	4.89–5.98%
Rhombophryne botabota (Ambolokopatrika, Marojejy, Makira)	5.98%
Rhombophryne sp. Ca01 (Ilampy)	7.61%
Rhombophryne minuta (Marojejy)	9.78–10.32%
Rhombophryne sp. Ca10 (Ilampy)	10.87%
Rhombophryne tany (Tsaratanana Camp 2 Matsaborimaika)	11.41%
Rhombophryne laevipes (Montagne d'Ambre)	11.41%
Rhombophryne guentherpetersi (Tsaratanana)	12.50%
Rhombophryne vaventy (Antsiranana, Marojejy)	11.96–12.50%
Rhombophryne testudo (Nosy Be)	11.96%
Rhombophryne coronata (Mandraka)	11.96%
Rhombophryne sp. Ca07 (Tsaratanana)	12.50%
Rhombophryne mangabensis (Nosy Mangabe)	13.04%
Rhombophryne sp. "Ambolokopatrika" (Ambolokopatrika)	13.04%
Rhombophryne longicrus (Sorata)	11.96%
Rhombophryne cf. *mangabensis* (Andapa)	12.50%
Plethodontohyla inguinalis (Vohidrazana)	13.59%
Rhombophryne ornata (Tsaratanana Camp 2 Matsaborimaika)	13.59%
Rhombophryne coudreaui (Betampona)	14.13%
Rhombophryne sp. Ca09 (Masoala)	13.59%
Platypelis pollicaris (Torotorofotsy)	15.76%
Rhombophryne cf. *coronata* (Vohidrazana)	15.22%
Platypelis barbouri (Ambatomandondona)	16.30%
Rhombophryne matavy (Forêt d'Ambre)	19.02%
Platypelis tuberifera (Vohidrazana)	18.48%
Scaphiophryne marmorata (Torotorofotsy)	23.37%

center of the radioulna–humeral articulation), UAL (upper arm length, from the center of the radioulna–humeral articulation to the trunk, measured along the posterior aspect of the arm), FORL (forelimb length, given by the sum of HAL, LAL, and UAL), FOL (foot length, from the tarsal–metatarsal articulation to the tip of the longest toe), TARL (tarsal length, from the tarsal–metatarsal articulation to the tarsal–tibiofibular articulation), FOTL (foot length including tarsus, from the tibiotarsal articulation to the tip of the longest toe, given by the sum of FOL and TARL), TIBL (tibiofibula length), TIBW (tibiofibula width at thickest point, measured in dorsal aspect), THIL (thigh length, from the vent to the femoral–tibiofibular articulation), THIW (thigh width at thickest point, measured in supine position), HIL (hindlimb length, given by the sum FOL, TARL, TIBL, and THIL), IMCL (maximum length of inner metacarpal tubercle), IMTL (maximum length of the inner metatarsal tubercle)." A figure depicting the measurement scheme is presented in Scherz et al. (2015b).

Osteology

We performed micro-CT scanning on a phoenix|x nanotom m cone-beam scanner (GE Measurement & Control, Wunstorf, Germany), using a tungsten target and a 0.1 mm Cu filter. We employed settings of 140 kV and 80 µA, with a timing of 750 ms, for 2440 projections and a total scan time of 30 minutes. We assembled the scan files in datos|x 2 reconstruct CT software (GE Measurement & Control, Wunstorf, Germany), and imported them as an unsigned 8-bit volume into VG Studio Max 2.2 (Volume Graphics GMbH, Heidelberg, Germany). We used the phong renderer with a custom color palate and rendering curve to register and visualize the scan. Using the built-in function, we took high-resolution screenshots for the production of figures. The osteological information presented is based on volume rendering. Only slightly calcified cartilage can be visualized using micro-CT, so we omit descriptions of the cartilaginous structures of the pectoral girdle (sternal features and most of the suprascapula) and those associated with the skull (the hyoid plate and nasal cartilages in particular). A Digital Imaging and Communications in Medicine (DICOM) stack of the scan files and rotational video produced in VG Studio Max 2.2 are available at the following MorphoSource http://morphosource.org/Detail/ProjectDetail/Show/project_id/263

We exported the volume as an "Analyze Volume" under standard settings in VG Studio Max 2.2, and imported the resulting .hdr file into Amira 6.1 (FEI Visualization Sciences Group, Burlington MA, USA), where a surface model was produced essentially following Ruthensteiner and Heß (2008). This model is embedded in a Suppl. material 1. The model is provided solely for reader comprehension; surface models carry inherent bias due to the manual thresholding are therefore less reliable for osteological description than volume renderings (Scherz et al. in review).

We note that skeletal comparisons to other cophylines are based on largely unpublished micro-CT data produced by MDS, which will be involved in revisions of the genera of this subfamily over the next few years. However, micro-CT-based osteological accounts for *Rhombophryne, Stumpffia, Anilany*, and *Plethodontohyla* are found in Scherz et al. (2016a) and for *Cophyla* and *Platypelis* in Rakotoarison et al. (2015).

Bioacoustics

We recorded calls attributed to the holotype on two occasions using an Olympus LS-10 Linear PCM Field Recorder and a Sennheiser K6-ME66 super-cardioid shotgun microphone. The calls were recorded at a sampling rate of 44.1 kHz and 16 bits resolution in WAV format. Recordings were made at mid-day in overcast weather conditions. No precise temperature recordings are available, but we estimate that the ambient temperature was approximately 20° C at the time of recording. We note that the individual was not visible during the recordings, as it was calling from a burrow. We therefor e cannot be completely certain that the recordings are of the same individual, however, only a single individual at a time was heard calling from this location, and the collected individual was found with distended vocal sac shortly after

Table 3. The advertisement call recorded for *Rhombophryne nilevina* in comparison with that of *R. testudo*. Calls were recorded from males calling during the day that were subsequently collected as vouchers. Note envelope is the ratio of the time of peak amplitude to note duration. Data are the range and then the mean ± two standard deviations in parentheses, when appropriate. The call recording of *R. testudo* is from Vences et al. (2006).

Parameters		
Species	*R. nilevina*	*R. testudo*
Specimen number	KU 340897	NA
Locality	Ranomafana	Nosy Be
N – calls	7	4
Inter-call interval duration (s)	42.5–99.5 (68.77 ± 24.0)	5.98–10.1 (8.3 ± 2.1)
Call duration (ms)	505–544 (536 ± 1.7)	828–896 (853 ± 2.9)
Call envelope	0.601–0.787 (0.663 ± 0.073)	-
Number of amplitude peaks	3–5 (3.4 ± 0.5)	1
Fundamental frequency (Hz)	236.9–279.9 (261.5 ± 22.9)	258.4–279.9 (263.8 ± 10.8)
Dominant frequency throughout call (Hz)	528.3–538.8 (537.9 ± 9.2)	538.3–555.9 (542.8 ± 8.8)
Dominant frequency at peak amplitude (Hz)	528.3–538.8 (537.9 ± 9.2)	581.4–602.9 (586.8 ± 10.8)
First Harmonic (Hz)	775.2–818.3 (796.7 ± 17.6)	775.2–796.7 (791.3 ± 10.8)

the second recordings. Additionally, the measured call parameters from the two occasions are nearly completely overlapping (Fig. 4; Table 3).

We follow Rakotoarison et al. (2015) and define a call as individual temporally distinct segments separated by a return to the background noise between each of these segments. This definition is equivalent to single notes used in other call definitions (Duellman and Trueb 1994; mantellids: Hutter et al. 2015). We define calls as "amplitude modulated" when there are two or more clear amplitude peaks.

Following Rakotoarison et al. (2015) and Hutter and Guayasamin (2015), we report the following call variables: call duration (ms); inter-call interval (s); number of amplitude peaks; note envelope shape (time at peak amplitude / call duration); dominant frequency (Hz), measured throughout call and at peak amplitude; fundamental frequency (Hz); and first harmonic frequency (Hz). Call rate was not calculated because of insufficient sample size. We used Raven Pro 1.4 to measure temporal and spectral call characteristics. Digital recordings are deposited at the University of Kansas Biodiversity Institute digital archive and are available upon request.

Registration of nomenclature

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:ACD2A947-B1B8-4B12-8FDF-1260C94B0AF8. The online version of this work will be archived and made available from the following digital repositories: CLOCKSS and Zenodo.

Results

We discovered a large-bodied cophyline microhylid frog near Andemaka within Ranomafana National Park in eastern Madagascar. Several obvious differences in morphology exist between the collected specimens and all known described and undescribed cophyline microhylids. Analysis of a fragment of its mitochondrial 16S rRNA gene recovered it with a close relationship to an undescribed population of *Rhombophryne* from northern Madagascar (sp. Ca03 from Vieites et al. 2009; Fig. 1). However, this population is quite distinct from the newly collected frogs morphologically (Scherz et al., unpubl. data). We also note that the 16S tree is largely unresolved, likely due to a limited number of characters it includes. Ongoing multi-locus analyses suggest that *R. nilevina* is quite phylogenetically distinct from all known *Rhombophryne,* including sp. Ca03 (A. Crottini, pers. comm.). Our 16S analysis also shows a minimum genetic distance of 4.9% between our new taxon and all valid, nominal *Rhombophryne* species (Table 2). We therefore describe it as a new species:

Rhombophryne nilevina sp. n.

http://zoobank.org/DAD2876A-D5C4-4D7B-B712-B22013161FC4

Suggested common English name: The buried diamond frog

Suggested common Malagasy name: Sahona diamondra nilevina

Suggested common French name: La grenouille de diamant enterré

Holotype. KU 340897 (CRH 798), an adult male collected at mid-day on February 8th 2015 by Shea Maddock Lambert, Emile Rajeriarison, and Ralaivao Jean Fulgence in montane rainforest near the former village of Andemaka in Ranomafana National Park (ca. 21.1287°S, 47.5054°E, elevation ca. 1240m a.s.l.; Fig. 2).

Paratype. UADBA-A Uncatalogued (CRH 799), an adult male collected the morning of February 7th 2015 by Shea Maddock Lambert and Ralaivao Jean Fulgence, otherwise with the same collection information as the holotype.

Diagnosis. A frog assigned to the cophyline genus *Rhombophryne* on the basis of its divided vomer, the

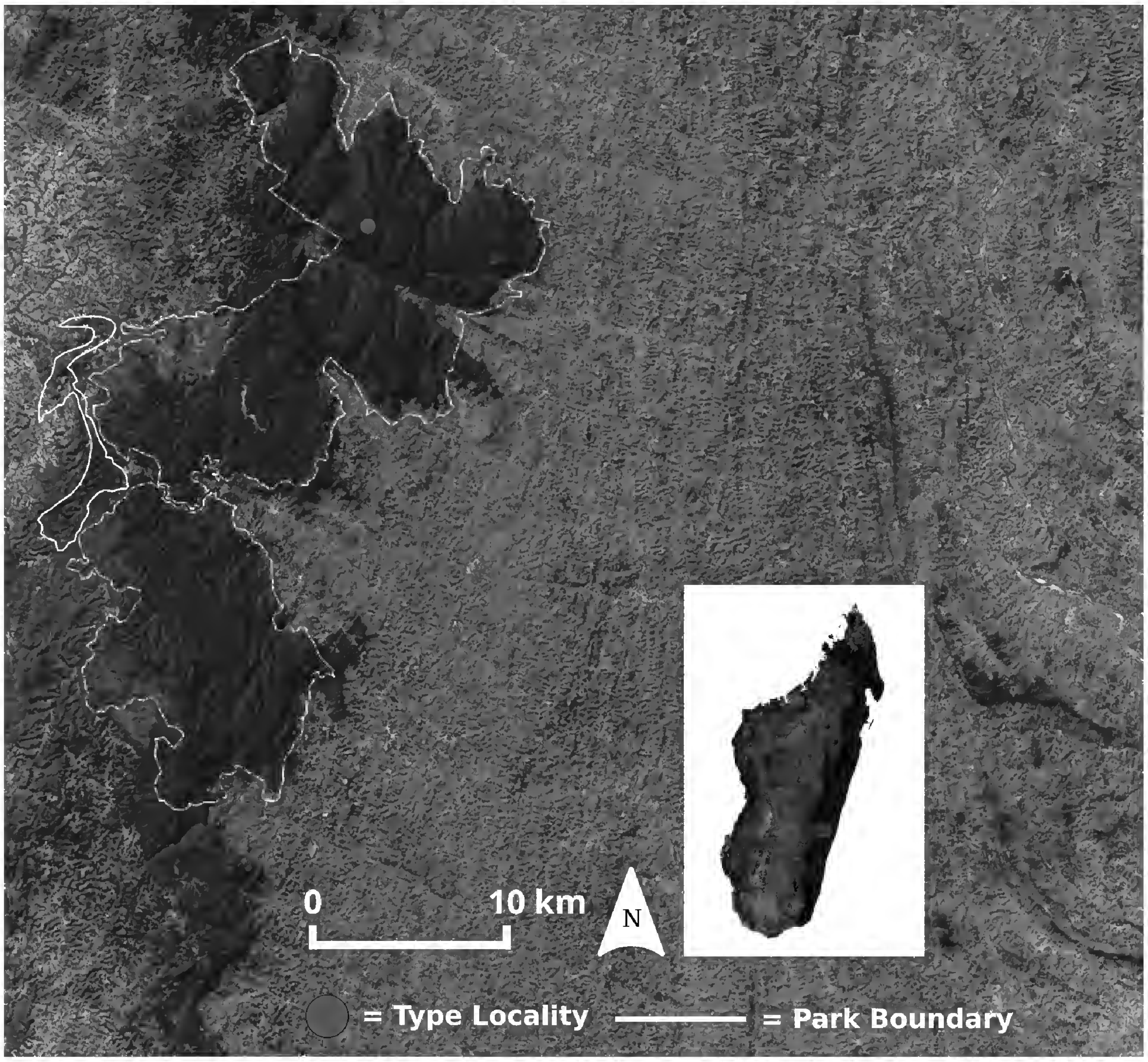

Figure 2. Map of Ranomafana National Park and the type locality of *Rhombophryne nilevina* sp. n.. Map is a composite of Landsat 8 satellite imagery and a hillshade layer created from SRTM 1 Arc-Second Global digital elevation data. Data available from the U.S. Geological Survey.

possession of clavicles and knob-shaped terminal phalanges (see Scherz et al. 2016a). This species is characterized by the following suite of characters: large size (SVL at least up to 57.2 mm), wide, short head (HW 180.7% of HL), tympanum 58.6% of eye, forelimb 51.1% of SVL, tibia 42.2% of SVL, hindlimb 152.5% of SVL, large inner metacarpal and metatarsal tubercles, supratympanic fold distinct and raised, running from the posterior corner of the eye straight over the tympanum, then sharply down behind it, extending to join the front of the arm, distinct vomerine teeth forming curved rows posteromedial to the oblong choanae, separated medially by a small cleft, second finger shorter than fourth finger, fifth toe distinctly shorter than third, without finger or toe reduction, finger and toe tips not enlarged. Additionally, *R. nilevina* is separated from all nominal species of *Rhombophryne* by an uncorrected pairwise distance of at least 4.9% in the fragment of the 16S rRNA gene, and by at least 3.8% from all known candidate species in this genus.

Rhombophryne nilevina is the largest species in the genus *Rhombophryne*, and can be distinguished based on this character alone from all other described species (SVL 57.2 mm vs. maximums of 56.3 mm and 52.9 mm for the next two largest species, *R. laevipes* and *R. vaventy*, respectively). This species differs from all of its congeners as follows: from all members of the *R. serratopalpebrosa* group (*R. serratopalpebrosa*, *R. coronata*, *R. vaventy*, *R. ornata*, *R. tany*, and *R. guentherpetersi*, plus two species under description by Scherz et al. in review) by the absence of superciliary spines (vs. presence); from *R. testudo*, *R. coudreaui*, and *R. matavy* by less wide head (HW 180.7% vs. 187.6–242.4% of HL in *R. testudo* and *R. matavy*), longer forelimb (FORL 51.1% vs. 35.4–49.8% of SVL), longer hindlimb (HIL 152.5% vs. 117.4–140.8% of SVL), and the possession of a clavicle (vs. lack thereof); from *R. longicrus* and *R. minima* by its wider head (HW 180.7% vs. 122.5–142.8% of HL), shorter forelimb (FORL 51.1% vs. 70.4–74.7% of SVL), and shorter hindlimb (HIL 152.5% vs. 178.5–183.8% of SVL); from *R. savaka* and *R. mangabensis* by its longer forelimb (FORL 51.1% vs. 40.9–47.9% of SVL), well ossified clavicles (vs. poorly ossified), and absence of black inguinal spots and a mid-vomerine diastema (vs. presence in *R: savaka*); and from *R. alluaudi*, *R. laevipes*, and *R. botabota* by its wider head (HW 180.7% vs. 144.2–173.8% of SVL), absence of light dorsolateral stripes (vs. presence in *R. alluaudi*), absence of a stark color border between the dorsal and lateral parts of the head (vs. presence in *R. botabota*), absence of inguinal ocellations (vs. presence in *R. laevipes* and *R. alluaudi*).

Rhombophryne nilevina is morphologically similar to terrestrial members of the genus *Plethodontohyla*, but aside from being distinguishable from this genus by the combination of the possession of clavicles with knob-shaped terminal phalanges, this species can be distinguished from *P. inguinalis* by its smaller size (SVL 57.2 vs. 62.2–99.1 mm), the absence of enlarged fingertips, absence of dark inguinal spots (vs. occasional presence), and absence of a strong dorsolateral color border (vs. occasional presence); from *P. notosticta*, *P. guentheri*, *P. fonetana*, and *P. mihanika* by the absence of enlarged fingertips, absence a strong dorsolateral color border (vs. presence in all but *P. fonetana*), and shorter forelimb (FORL 51.1% vs. 57.5–71.9% of SVL); and from *P. bipunctata*, *P. tuberata*, *P. brevipes*, and *P. ocellata* by the absence of inguinal spots (vs. presence in all but *P. tuberata*) and larger size (SVL 57.2 vs. 24.6–44.7 mm) and from *P. tuberata* by the presence of smooth skin (vs. granular skin).

Although the bioacoustic repertoires of cophylines is far from completely known, bioacoustically, this species' call is strongly distinct from the other known calls by being strongly amplitude modulated (Fig. 4). To the human ear, this call most closely resembles the genetically distant *R. testudo* (Table 2), but the call of *R. testudo* differs by having a much longer duration and lacking significant amplitude modulation (Fig 4). No other known calls can be confused with those of this species.

Description of the holotype. *Morphology of the holotype.* An adult male specimen in an excellent state of preservation. The vocal sac is still somewhat loose and malleable. The tongue was removed as a tissue sample.

Body rotund; dorsal and ventral skin smooth, with subtle bumps on the dorsal skin (more rugose in life). Head considerably wider than long (HW 180.7% of HL), snout rounded in dorsal and lateral view; nostrils protuberant, directed laterally, closer to the snout than the eye; canthus rostralis distinct and concave; loreal region concave and oblique; tympanum indistinct, oval, horizontally 58.6% of eye diameter; pupil dilated in preservative but more or less round in life (Fig. 3a, 3d); supratympanic fold distinct and raised, running from the posterior corner of the eye straight over the tympanum, then sharply down behind it, extending to join the front of the arm; tongue removed as a tissue sample, was attached anteriorly and posteriorly free; vomerine teeth distinct, forming curved rows posteromedial to the choanae; choanae relatively large, oblong.

Arms strongly built, relatively short; fingers without webbing, short, with distinct, rounded subarticular tubercles, relative lengths 1<2<4<3, the second finger marginally shorter than the fourth (and marginally longer than the first), without enlarged terminal discs; inner metacarpal tubercle strong, oblong, 28.1% of hand length; outer metacarpal tubercle indistinct, round. Legs relatively long and thick (HIL 152.5% of SVL; TIBL 42.2% of SVL), position of the tibiotarsal articulation when adpressed along the body not possible to assess without breaking the hindlimbs; toes long, unwebbed, with indistinct round subarticular tubercles, relative toe lengths 1<2<5<3<4, third toe distinctly longer than fifth; inner metatarsal tubercle present and distinct, 12.7% of foot length; outer metatarsal tubercle absent.

Coloration of the holotype. In preservative, the holotype is chocolate brown dorsally with a loosely reticulated pattern of ebony to burnt umber markings, including an indistinct interocular bar. There are no inguinal spots. The loreal region has a grey marking in it. The forelimb is as the dorsum, with dark patches on the elbow and a crossband on the forearm. A distinct light annulus is present before the terminus of each finger. The hindlimb is dorsally as the back, with three dark crossbands on the thigh and shank. The posterodorsal thigh has weak cream spots, as does the anterior thigh. The dorsal foot is brown speckled with cream. The toes are even more flecked with cream, and also possess a light annulus before the terminal phalanges. The ventral abdomen is brown with numerous small cream flecks. The chin is darker and mostly solid dark brown. The ventral arms are as the trunk. The subarticular and metacarpal tubercles are lighter in color than the rest of the hand. The ventral hindlimbs are as the abdomen. The color in life was as in preservative (Fig. 3).

Osteology of the holotype (Fig. 5, Suppl. material 1). The skeleton of the holotype is typical of *Rhombophryne*. It is well ossified and robust. The right femur shows signs of an old break toward its distal end that has healed.

Anterior braincase laterally closed by the sphenethmoid. Interior braincase containing calcified material. Nasal in medial contact with contralalteral and posterior contact with frontoparietal. Frontoparietal broadening anteriorly from narrow waist anterior to lateral flanges, possessing a strong, posteriorly elongated dorsal process. Prechoanal vomer simple, triradiate. Neopalatine and postchoanal vomer distinguishable. Vomerine teeth not medially fused, without diastemata, oriented oblique to antero-posterior body axis, curved. Maxillary teeth minute. Otic capsule dorsally poorly ossified.

Sternum not ossified. Clavicle robust, curved. Humerus proximally broad, distally rather narrow; possessing a well-developed crista ventralis along roughly 50% of its length; crista lateralis weak. Terminal phalanges of fingers and toes with small distal knobs. Phalangeal formula of fingers 2-2-3-3; of toes 2-2-3-4-3. Femur without cristae. Prepollex strong, blade-like, half length of first metacarpal. Prehallux strong, approximately half length of first metatarsal.

Neural spines decrease in size posteriorly, the sixth and seventh lacking spines altogether. Neural arches of atlas fused. Dorsal crest of urostyle running roughly 80% along its shaft. Iliosacral articulation type IIA sensu Emerson 1979. Iliac shafts with well developed dorsal tubercles and deep oblique grooves; dorsal crests running most of their length. Pubis partially ossified.

Variation. The paratype UADBA-A Uncatalogued (CRH 799) strongly resembles the holotype, but has a slightly

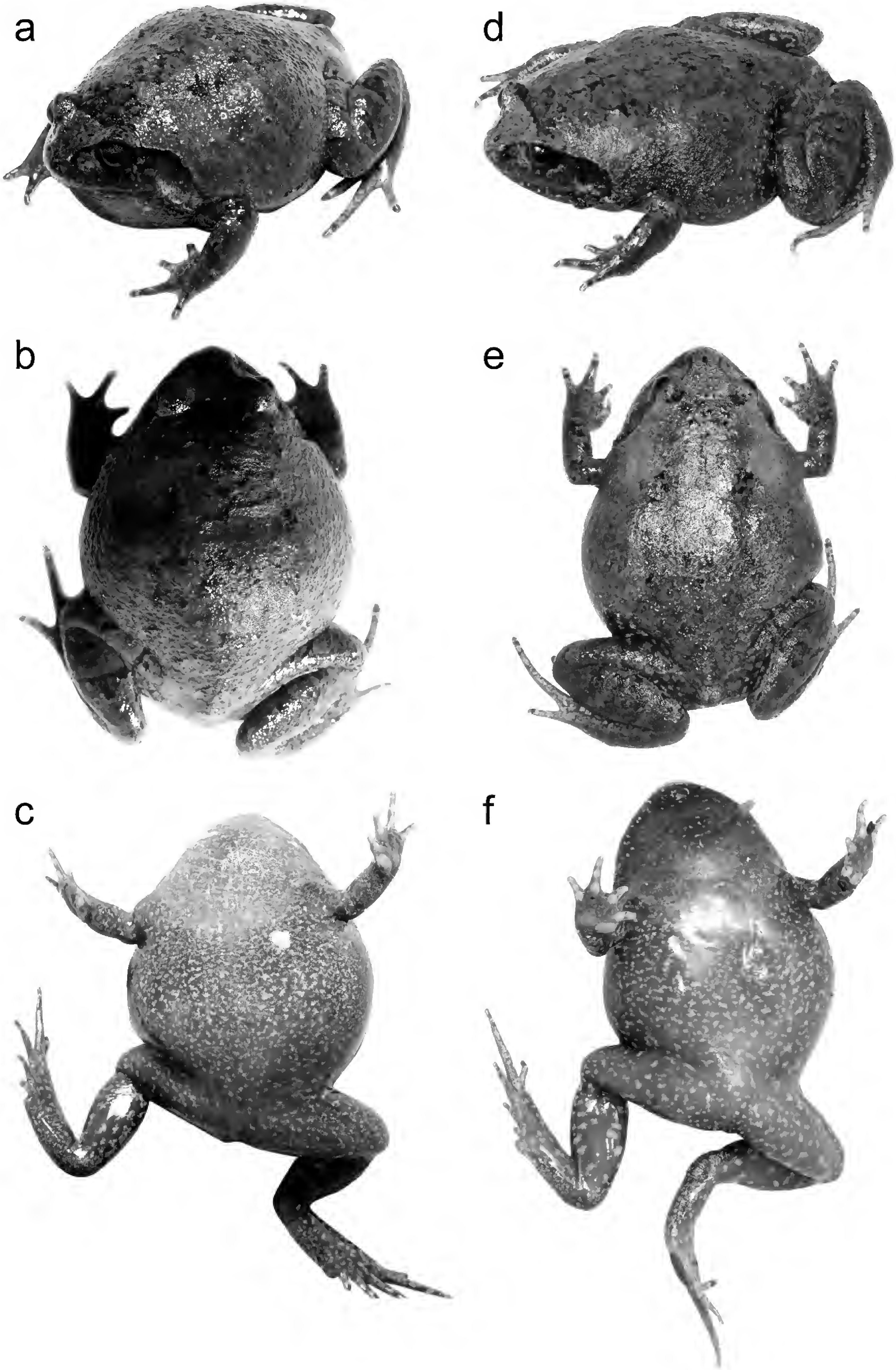

Figure 3. Photos in life of *Rhombophryne nilevina* sp. n. (**a**) Dorsolateralview of the holotype (KU 340893). (**b**) Dorsal view of the holotype. (**c**) Ventral view of the holotype. (**d**) Dorsolateral view of the paratype (CRH 799, UADBA-A Uncatalouged). (**e**) Dorsal view of the paratype. (**f**) Ventral view of the paratype.

more distinct color border between the lateral and dorsal head (see Fig. 3 for comparison).

Bioacoustics. We analysed a total of seven calls from *R. nilevina*, and compared these to the call of *R. testudo* (Fig. 4; Table 3). We presume that the calls we recorded come from one individual, the holotype (see **Materials and methods**). We further assume that the recorded call is an advertisement call, as no other call types (except distress calls) are known from cophylines. This call sounds like a slow groan to the human ear.

Each call is rapidly pulsed, with 3–5 (3.5 ± 0.534) amplitude modulated peaks occurring throughout the call, and peak amplitude occuring in the last 50% of the call. The call duration is 505–544 (536 ± 1.7) ms with an inter-call interval duration of 42.5–99.5 (68.8 ± 24.0) s. The fundamental frequency is 236.9–279.9 (261.5 ± 22.9) Hz. The mean dominant frequency throughout the call was 528.3–555.9 (537.9 ± 9.2) Hz and the first harmonic frequency is 775.2–818.3 (796.8 ± 17.6) Hz (Fig. 4).

Etymology. The specific epithet "nilevina" is a Malagasy word meaning "buried." This name was chosen to recognize the fossorial habits of this species. It is to be treated as an invariable noun in apposition.

Available names. Due to morphological and size similarities, as well as geographic distribution, two existing names must be considered for this species: *Phrynocara laeve* Boettger, 1883, and *Plethodontohyla laevis tsianovohensis* Angel, 1936. Both of these names are currently considered to be junior synonyms of *Rhombophryne alluaudi*. We examined the morphology and osteology of the holotypes of both of these taxa (*P. laeve:* SMF 4286; *P. laevis tsianovohensis:* MNHN 1936.47), and our new species differs critically from both in the possession of a well-developed clavicle (vs. absence/strong reduction; Scherz unpubl. data). Their taxonomy, as well as that of *Rhombophryne alluaudi*, will be discussed in a future article, and we here simply rule out the possibility that they are conspecific with *R. nilevina* sp. n. based on the presence vs. absence of a clavicle. The type specimen of *P. laevis tsianovohensis* was collected from Tsianovoha, which is around 60 km south of Ranomafana, suggesting the possibility of sympatry or parapatry with *R. nilevina*.

Natural history. Both known specimens of *R. nilevina* were obtained from a relatively flat, poorly drained section of moist montane forest adjacent to a stream, with the holotype found along the bank of this stream. Nearby habitats include a swamp with many large *Pandanus* and steep forested slopes with relatively smaller trees. However, the calls of *R. nilevina* seemed to emanate mostly from the flatter, forested area. Males were heard calling during the day, particularly during overcast conditions and after rainfall. Advertisement calls were not heard at night, however, the night-time chorus of other frogs, including *Boophis*, *Spinomantis*, *Gephyromantis*, and *Anodonthyla*, may have interfered with detection. When heard from a distance, the call is reminiscent of that of an owl. When heard from close proximity, the call sounds like a groan, and is far less melodic. Both specimens were both located by auditory tracking, and found calling from underground: one from a cavity under the roots of a large tree, and the other from a burrow in soft, moist soil alongside the stream. In order to collect the holotype from its burrow, excavation was required. Based on these observations and suggestive morphology, we presume that *R. nilevina* spend much of their lives underground, possibly coming to the surface for short periods during rainfall, similar to other fossorial *Rhombophryne* species (Glaw and Vences 2007, D'Cruze et al. 2010). We also note that *R. nilevina* was discovered in the middle of the wet season, and after a week-long period of particularly heavy, sustained rain.

Distribution. *Rhombophryne nilevina* has thus far been detected at a single site, near the former village of Andemaka, in the north-west of Ranomafana National Park (Fig. 2). This locality is relatively high-elevation for Ranomafana National Park (ca. 1240 m). To our knowledge, *R. nilevina* has not been detected by any previous survey, including several conducted by CRH and SML at similarly high-elevation sites in the northern (Miaranony), central (Vohiparara), and southern (Maharira) regions of Ranomafana. Nevertheless, we do not rule out here the possibility that *R. nilevina* occurs elsewhere in the park. This is in large part due to the secretive habits and potentially ephemeral activity periods of this species (see **Natural history**). In addition, much of the high-elevation forest of Ranomafana is difficult to access and thus remains sparsely or completely unsurveyed for herpetofauna. Although it is possible that *R. nilevina* has been overlooked in other eastern rainforest patches, current information suggests that this species is endemic to Ranomafana National Park, and potentially to a much smaller area within the park.

Conservation status. Although the type locality of *R. nilevina* is within Ranomafana National Park, its occupancy within the park is potentially highly restricted, elevationally and geographically, as it has not been detected in any other herpetological surveys of the park. However, its secretive lifestyle means that it icould be easily overlooked. Given this large uncertainty in area of occupancy, we suggest an initial IUCN categorization of Data Deficient. If *R. nilevina* is for instance, restricted to the type locality, then habitat destruction, chytrid fungus (recently detected in Madagascar, Bletz et al. 2015), and/or climate change could easily place the only population of *R. nilevina* sp. n. at risk of extinction.

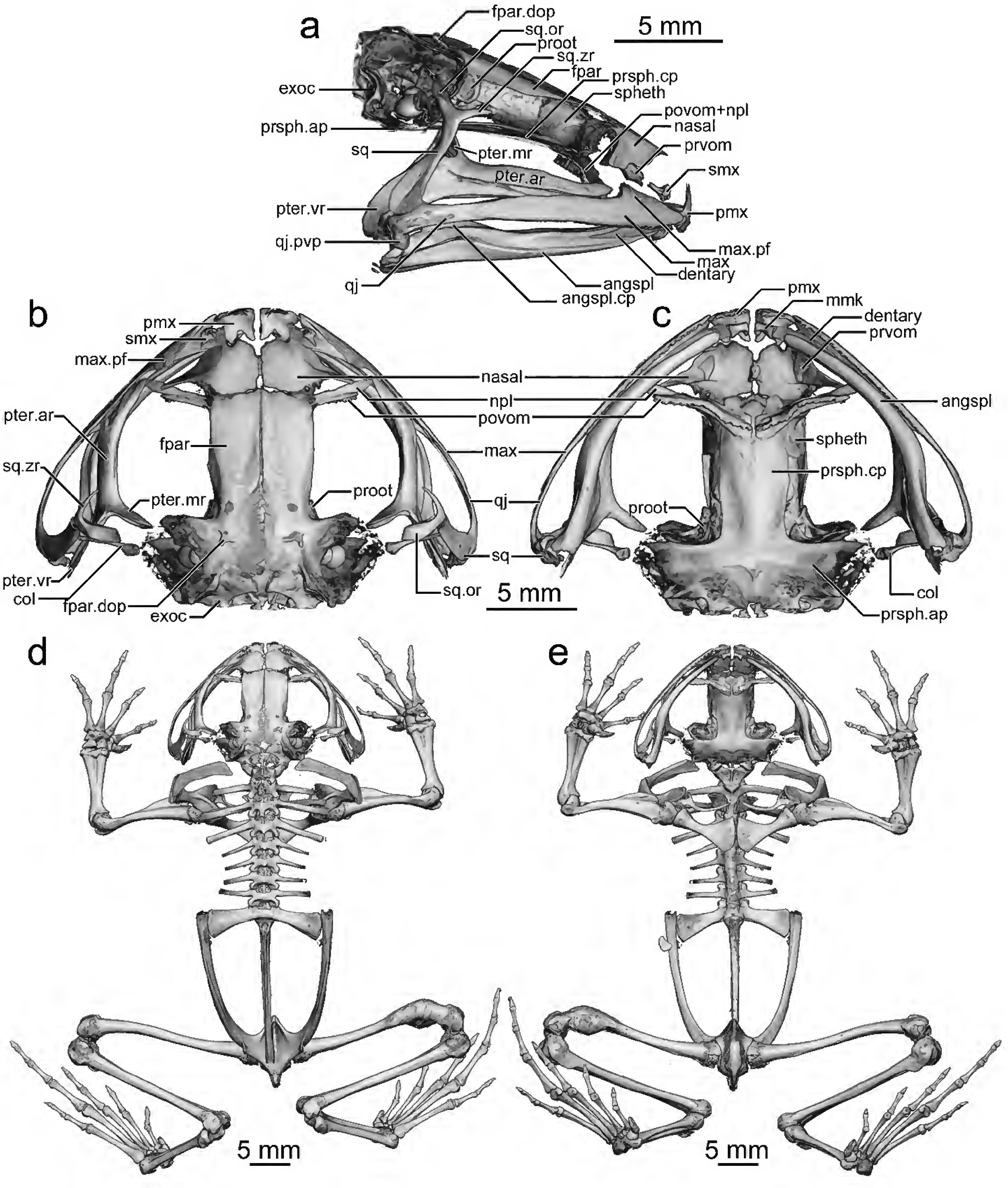

Figure 4. The osteology of *Rhombophryne nilevina* sp. n. Skull in (**a**) lateral, (**b**) dorsal, and (**c**) ventral view; and full skeleton in (**d**) dorsal and (**e**) ventral view. Abbreviations: angspl, angulosplenial; angspl.cp, angulosplenial coronoid process; col, columella; exoc, exoccipital; fpar, frontoparietal; fpar.dop, frontoparietal dorsal process; max, maxilla; max.pf, maxillary pars fascialis; mmk, mentomeckelian bone; npl, neopalatine; pmx, premaxilla; povom, postschoanal vomer; proot, prootic; prvom, prechoanal vomer; prsph.ap, parasphenoid alary process; prsph.cp, parasphenoid cultriform process; pter.ar, pterygoid anterior ramus; pter.vr, pterygoid ventral ramus; pter.mr, pterygoid medial ramus; qj, quadratojugal; qj.pvp, quadratojugal posteroventral process; smx, septomaxilla; spheth, sphenethmoid; sq, squamosal; sq.or, squamosal otic ramus; sq.zr, squamosal zygotic ramus.

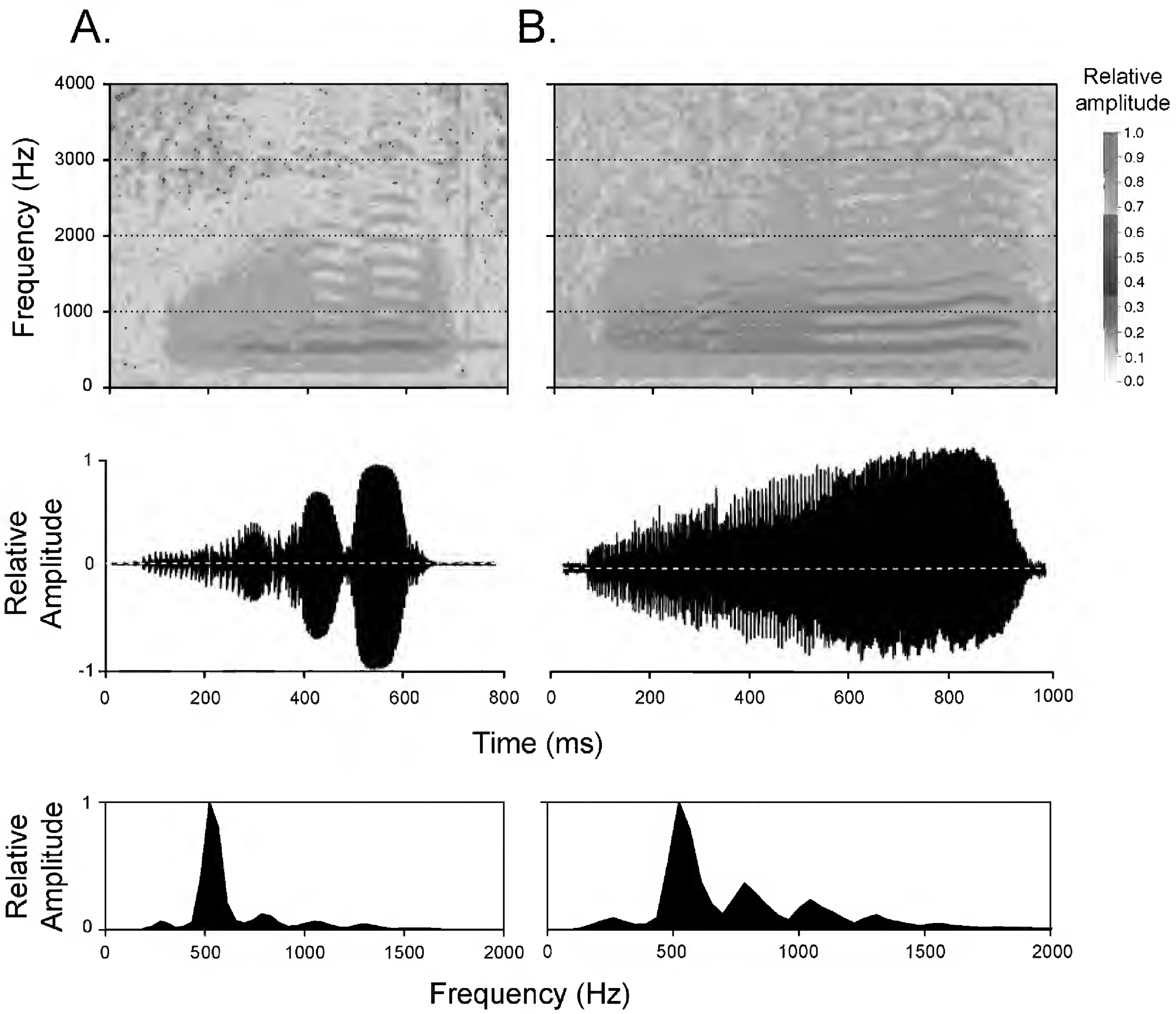

Figure 5. Comparative spectrograms (top), oscillograms (center) and power spectra (bottom) between the calls of (**A**) *Rhombophryne nilevina* sp. n. and (**B**) *R. testudo* (from Vences et al. 2006). Spectrogram was created using a Hanning window size of 1024.

Discussion

The discovery of *Rhombophryne nilevina*—never previously identified as a candidate species despite being found in one of the most well-surveyed National Parks of Madagascar—highlights the importance of continued field work for the advancement of systematics in Malagasy anurans. In particular, field surveys should help reveal diversity in clades containing species with small ranges and secretive life histories, including *Rhombophryne* and other cophyline frogs. Cophylines have already shown great promise as a model system for studying ecomorphological and reproductive mode evolution (e.g. Andreone et al. 2005, Wollenberg et al. 2008), and the continued discovery and description of novel species will only further this potential.

Rhombophryne nilevina is remarkable in several respects, including its morphology. Most obvious is its large size, the largest recorded for the genus, narrowly exceeding *R. laevipes* (Glaw & Vences, 2007; Scherz et al. unpubl. data). In addition, the relatively long legs, wide head, and rotund body shape contribute to the distinctive appearance of this species. In total, the morphology of *R. nilevina* is sufficiently divergent from all other *Rhombophryne* species that it cannot be immediately assigned to a complex or species cluster.

In addition to morphological distinctiveness, *Rhombophryne nilevina* is currently the southernmost distributed species of *Rhombophryne,* excluding records of *Rhombophryne alluaudi* from the far south of Madagascar, which are due to confusion surrounding the identity of that species (Scherz, Bellati, Crottini et al. unpubl data). It also has a strongly amplitude-modulated call unlike that of any congeners (although few call recordings are available for this genus).

Our limited genetic data suggests that *R. nilevina* may have affinities with *Rhombophryne* sp. Ca3 from Tsaratanana in northern Madagascar, but we consider this relationship tentative and ongoing multi-locus analyses suggest that *R. nilevina* represents a relatively early-diverging, phylogenetically distinct species of *Rhombophryne* (A. Crottini, pers. comm.). Given the limited information available at this time, the phylogenetic affinities of *R. nilevina* will need to be clarified in a future revision of the genus.

Acknowledgements

We thank the Malagasy authorities for issuing permits; field research was conducted under permit number 303/14/MEF/SG/DGF/DCB.SAP/SCB; specimens were exported under 017N-EV01/MG14. We also thank MICET and Centre ValBio for facilitating fieldwork. Finally, SML would like to thank Ralaivao Jean Fulgence and Emile Rajeriarison for their exceptional work in the field during the Andemaka expedition. If not for their dedication and ability, *R. nilevina* would surely remain undiscovered.

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Supplementary material 1

File S1

Authors: Shea M. Lambert, Carl R. Hutter, Mark D. Scherz

Data type: Adobe PDF file

Explanation note: This file contains a PDF-embedded interactive 3D model of the skeleton of the holotype of *Rhombophryne nilevina* sp. n., KU 340897, generated via X-ray micro-Computed Tomography. The model can be opened in Adobe® Acrobat Pro or Reader, versions IX and above. To activate it, click the image.

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PENSOFT.

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Loveridge's Angolan geckos, *Afroedura karroica bogerti* and *Pachydactylus scutatus angolensis* (Sauria, Gekkonidae): new distribution records, comments on type localities and taxonomic status

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Abstract

In 1944 Loveridge described two new geckos from Angola, *Afroedura karroica bogerti* and *Pachydactylus scutatus angolensis.* The descriptions of both species have vague and confusing type localities and refinements are suggested based on early expedition reports, historical accounts from the region, and a review of cartographic material. Numerous new distribution records are reported for both species from expeditions undertaken from 1956–2016 by the authors or their colleagues. The taxonomic status of both species has changed, but new material from diverse habitats, altitudes and geological substrates indicates that further taxonomic adjustments are likely in order to reflect additional cryptic diversity.

Resumo

Em 1944, Loveridge descreveu duas osgas novas de Angola: *Afroedura karroica bogerti* e *Pachydactylus scutatus angolensis.* As descrições de ambas as espécies têm localidades-tipo vagas e confusas. Neste trabalho são sugeridos mais detalhes relativos a estas espécies, com base em relatórios de expedições, relatos históricos da região e revisão de material cartográfico. São relatados numerosos registos novos de distribuição para estas espécies, com base em expedições levadas a cabo entre 1956 e 2016 pelos autores ou colegas seus. A situação taxonómica das duas espécies alterou-se, mas material novo proveniente de habitats, altitudes, e substratos geológicos diversos, indicam que é provável que ocorram mais ajustes taxonómicos de forma a refletir uma diversidade críptica ainda maior.

Introduction

Studies on the herpetofauna of Angola have entered a new phase following increased collaboration on regional and national biodiversity surveys, multi-authored modern taxonomic reviews, and the emergence of young Angolan scientists (Branch 2016). Almost all recent surveys (e.g. Huntley 2009; Brooks 2012, 2013; Ceríaco et al. 2014, 2016; Ernst et al. 2014; Huntley and Francisco 2015; Conradie et al. 2016), have uncovered new national and regional distribution records (Branch and McCartney 1992; Branch and Conradie 2013; Conradie and Bourquin 2013; Ernst et al. 2014), as well as new species of amphibians (Conradie et al. 2012a, 2013) and reptiles (Conradie et al. 2012b; Stanley et al. 2016). However, problems arise when attempting to integrate these new findings with early literature and original species descriptions. Comparison is complicated by numerous factors, particularly the generally vague locality details for type material in early descriptions. It is not always obvious which localities or regions in these descriptions refer to modern towns in different parts of the country that have similar or identical names, and may be affected by the variant spellings of explorers and researchers. Exacerbating this is the loss of almost all of the material studied by José Vicente Barbosa du Bocage, the father of Angolan herpetology, in a fire that destroyed the Museu Bocage collections in 1978. As a consequence, many type specimens are no longer available and replacement 'topotypic' material requires confidence in the documentation of type localities. To illustrate these problems we consider two recent examples, *Afroedura karroica bogerti* Loveridge, 1944, and *Pachydactylus scutatus angolensis* Loveridge, 1944, where knowledge of the vague type localities given in the original description have become more defined following recent investigation and the integration of new and early observations. Both taxa are subsequently been elevated to specific status (see below).

Taxonomy

Angolan Flat Gecko (*Afroedura bogerti*)

History. The Angolan Flat Gecko (*Afroedura bogerti*) is a beautiful and zoogeographically interesting species. For many years knowledge of the species was based on a single specimen collected during the Vernay Angola Expedition (VAE) in 1925. Charles Bogert, after whom the gecko is named, was the Curator of Herpetology at the American Museum of Natural History (AMNH), and prepared a detailed report on the snakes collected by the VAE (Bogert 1940). He never published on the extensive lizard collections, but did draw Loveridge's attention to a specimen that he thought might be a new species, and for which a superb drawing had been prepared (fig. 1 in Loveridge 1944). Loveridge confirmed this assessment and described the species in Bogert's honour. He considered it closely related to a South African species, *Oedura karroica* Hewitt, 1925, but did not consider the few African representatives of *Oedura* to be congeneric with Australian *Oedura* Gray, 1842, which had been based on the Australian species *Oedura marmorata* Gray, 1842. He therefore placed all African representatives of *Oedura* in a new genus, *Afroedura,* with his new subspecies, *Afroedura karroica bogerti* as the genotype.

Taxonomic status of *Afroedura bogerti.* Onderstall (1984) investigated relationships between *Afroedura* species, and on morphological grounds recognized three species groups. He examined material collected by WDH in 1971 and 1974, and based on its possession of two pairs of scansors per digit and a verticillate tail placed it in his '*transvaalica*' group, along with *A. transvaalica* (Hewitt, 1925) and *A. loveridgei* Broadley, 1963. His '*africana*' group, which included *A. karroica,* was characterized by having three pairs of scansors per digit and a verticillate tail, and he therefore elevated *A. bogerti* to a full species (Onderstall 1984). Based on material collected in 2009 from Tambor in the Iona National Park (see below), significant genetic divergence of *A. bogerti* from all other *Afroedura* (Jacobsen et al. 2014; Makhubo et al. 2015) confirmed its specific status. However, there remains confusion over its phylogenetic relationships. Jacobsen et al. (2014) and Makhubo et al. (2015) found that *A. bogerti* was part of the *A. transvaalica* group, although they differed in the latter group's relationships to other species groups. This association remains of zoogeographic interest as the range of *A. bogerti* is separated by nearly 2000 km from other members of the *A. transvaalica* group (sensu Jacobsen et al. 2014). However, among Angolan geckos it is easily recognized by its dorso-ventrally flattened body, smooth homogenous dorsal scalation, possessing 1-2 pairs of scansors under the fourth toe, and the verticillate tail.

Type locality of *Afroedura karroica bogerti.* In his description of *Afroedura k. bogerti*, Loveridge (1944) noted that the type specimen (AMNH 47841) was an adult male from Namba (Mombolo), Cuanza Sul Province, Angola, collected by Harry and Allan Chapman, between September and November 1925. Although the locality was not defined in more detail by Loveridge, Bogert (1940) had previously given general geographical co-ordinates for Mombolo (12°10'S, 14°50'E), but did not mention Namba. Crawford-Cabral and Mesquitela (1989) mapped the vertebrate collections recorded from Angola but overlooked Loveridge's (1944) two gecko descriptions. They did record Bogert's (1940) Mombolo (as 'Mombola') using the details given in his paper, and also listed Namba (Missão da Namba, 11°55' S, 14°51'E), approximately 27 km north of Bogert's Mombolo locality. It should be noted that the geographical co-ordinates listed for both these localities are relatively vague and provide only degrees and minutes.

PROVINCIA DE ANGOLA

Titulo de Concessão

POR

Aforamento

Passado a favor de William James Bushnell Chapman

Processo de concessão n.º 100/914

Direção da Agrimensura de Loanda,
em 28 de Janeiro de 1930.

Ficou o prédio a que se refere êste título com o n.º 1, na folha n.º Sul 233 do compartimento n.º 191, secção –, do cadastro e descrito no Tombo Geral da propriedade.

Figure 1. A: (left) Photograph of the original "Titulo de Concessao" (28 January 1930) confirming William Chapman's ownership of the farm that was purchased by the Kath-Brock family. **B**: (right) the farm map from the "Titulo de Concessao" showing 'Alengo Sandula' at middle of lower boundary.

There is no detailed history or route for the VAE, but a brief summary of the expedition is given in the Mammals of Angola (Hill and Carter 1941, p: 3). It records (salient comments abstracted):

> *Messrs. Herbert Lang and Rudyerd Boulton, collectors, went to Angola in April, 1925, and remained there for about three months. Landing at Lobito, near Catumbela, a few animals were secured here. The expedition went to Hanha Estate (not the Hanha usually given on maps), an oil palm plantation near the coast, some thirty-two kilometers north of Lobito. The party then went south by way of Huambo where they were joined by Messrs. A. S. Vernay, Alan and Charles Chapman………… At the end of August the expedition united at Capelongo and returned by way of Caconda to Huambo…… At Huambo the party again divided…… Boulton and Charles Chapman went to Namba in the Mombolo region.*

The geographical locations of sites detailed in Hill and Carter (1941) are again relatively vague: i.e. Chipepe, near Cassongue (12°S, 15°E); Monte Victoria Verdun (12° 05'S, 15°E); and Namba (Mombolo) (11°35 S, 14°25' E).

Although Loveridge (1944) recorded that the type specimen of *A. k. bogerti* was collected during the VAE, he specifically states that it was "*collected by Harry and Allan Chapman, between September and November, 1925.*" This was after the American members of the VAE had departed. This discrepancy is probably explained by a comment in Hill and Carter (1941, p: 5) where they note that their mammal material included "*…..fifty mammals … purchased from Mr. C. P. Chapman, collected at Chipepe, Namba, and Monte Victoria Verdun.*", and it is thus possible that Loveridge's type specimen was obtained in the same way.

Many of these locations are discussed in the recently published 'Reminiscences' of William Chapman, the father of Charles, Harry and Alan Chapman (Stassen 2010). The latter two sons (note corrected spelling of Alan, not Allan) are the collectors of the type specimen of *A. k. bogerti* (Loveridge 1944). William Chapman was the son of the famous South African explorer James Chapman (Chapman 1868), and one of the original 'Trek Boers', who moved away from British rule in the Cape region, and eventually settled (1881–1928) in southern Angola.

Chapman notes "*Ernst Meyer had selected a farm in the Mombolo country at the base of a mountain range called Namba*" (Stassen 2010, p: 295). He later comments "*The next day I crossed the Etala stream* [a tributary of the Cuchem] *with my wagon and went up to the small plain below the koppie on which I subsequently built my*

Figure 2. The ruins of farm Monte Verde, surrounded by eucalyptus trees (middle distance), overlay those of William Chapman's farm Monte Victoria-Verdun. Viewed from an intrusive rock outcrop on the lower northern slopes of Sandula Hill.

house" (Stassen 2010, p: 297). He called it Monte Victoria-Verdun (Stassen 2010, p: 25 notes it was originally called Sandula, but see below).

It was noted (Stassen 2010, p: 13) that William Chapman:

> ….. *liked the company of scientific explorers and quite a number of them were invited to stay for some time on his farm. As a result the type specimens of quite a few species of fauna and flora were recorded at Sandula, Namba or Chipepe, the farms of the Chapman clan near Mombolo.*

A thorough examination of official detailed cartographic material supported by the historical accounts, allowed us to identify the possible location of Chapman's farm on topographic maps as "Fazenda Monte Verde", located on the northeastern slopes of the Lupangue mountains, close to the headwaters of the Etala stream, which drains between rock outcrops from the mountain. We were able to confirm this following a site visit (5-6 November 2016), and from inspection of the original "Titulo de Concessão", dated 28 January 1930 (Fig. 1A), that confirms the farm's ownership by William Chapman. The farm was purchased by the Kath-Brock family, who renamed it as Monte Verde. The original farm map attached to the title deed reveals that the "koppie" (hill) noted by Chapman was originally called Sandula (Fig. 1B). The brick farm buildings of the Brock family (12°10'09"S, 15°01'42"E, 1798m a.s.l.) were built on, and incorporate some of, the original Chapman house, but both are now derelict, whilst Sandula Hill (12°11'04"S, 15°01'41"E, 2242m a.s.l) is locally now called Monte Verde. This prominence is capped in granite outcrops, with intrusive rock outcrops on its lower slopes and is close to the farm site. These outcrops form suitable habitat for flat geckos (Fig. 2).

Stassen (2010, p25) notes "*Mombolo is a small village on the Benguela highlands in the Cuanza Sul district and is also called Omambolo, Nakamombolo or Makamombolo*". Although two small quimbos (villages) to the southwest of Chapman´s farm have been identified in the cartographic material referenced as Mombolo, we consider that the name is more correctly associated with the general region to the south of *Missão da Namba*, as is shown in the Carta de Angola at the scale of 1/100 000, where the area immediately to the south of Missão da Namba is named Mombolo. This is an extensive grassy area named as the Anhara do Mombolo, and at the southern edge of which lies the present town of Maka-Mombolo (12°11'54"S, 14°52'06"E, 1760m asl) mentioned by Stassen (2010, p25). Local people refer to extensive flat natural grasslands as 'mombolos', areas suitable for planting staple crops. Missão da Namba is a Seventh-day Adventist church established by James Delmes Baker, who settled in the area in November 1928 (Anon, 2017).

The Lynes-Vincent bird expedition (1930–31) was a specialist trip for *Cisticola* species in Central and West Africa (Lynes and Sclater 1933, 1934). On 1 March 1931 the expedition visited "Chipepe (Mombolo loc. 5900ft)", identified in the official topographic maps as *Fazenda Quipepe* (11°59'30"S, 14°56'10"E), having driven 140 miles from Huambo, via Bailundo. The expedition then spent 2–8 March 1931 at "Namba (nr. Chipepe) 5700 ft. to 6700ft.", where they were assisted by "Herr Köster" (probably Paul Friedrich Heinrich Köster who married William Chapman's daughter Sarah, and who remained in the Mombolo region after the 'Trek Boers' moved to Namibia in 1928; Stassen 2010).

Although our studies and site visits give greater detail to the probable origin of the type specimen of *A. k. bogerti*, the exact location of its capture remains unknown,

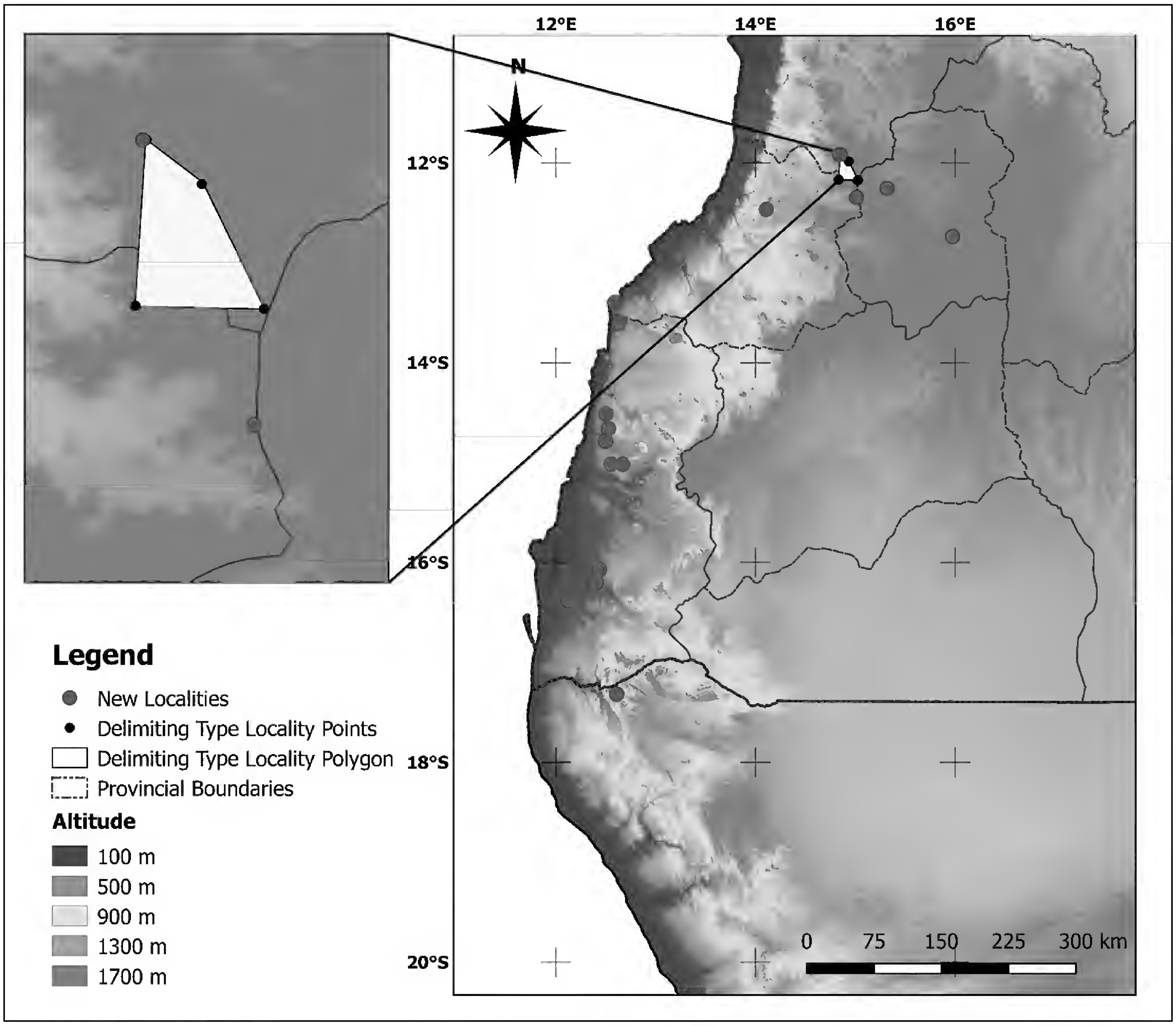

Figure 3. Geographical distribution of *Afroedura bogerti*. Insert (left) shows the polygon that encompasses the area from which the type specimen was collected. The problematic Namibian specimen is included.

and cannot be determined with greater accuracy based on existing knowledge. We conclude that the vague type locality, i.e. "Namba (Mombolo)" refers to a general area that probably corresponds to a polygon that can be delimited by the points (detailed above) of William Chapman's farm (Monte Victoria-Verdun, later Monte Verde), Chipepe/Quipepe, the farm of one of his sons, Missão da Namba, and Maka-Mombolo (Fig 3.). This is also adjacent to Mombolo (Missão da Namba, AO018, 11°55'S, 14°51'E), an Important Bird Area for the conservation of a number of Angolan birds (Birdlife 2016).

New distribution records for *Afroedura bogerti*. Following its discovery in 1925 the next specimen of this species was collected by Dr C. Koch on a Transvaal Museum Expedition to southwest Angola in September 1956. Collected near Caraculo (15°01'36.7"S, 12°39'07.57"E), this specimen (TM 24545) was not mentioned by FitzSimons (1959) in his description of new reptiles (e.g. *Pachydactylus caraculicus* and *Prosymna visseri*) collected during Koch's expedition. It did, however, direct subsequent searches when one of us (WDH) visited Angola (1971 and 1974) to specifically search for geckos of the genera *Pachydactylus, Rhoptropus* and *Afroedura*. These surveys obtained significant new *A. bogerti* material from various localities, including: TM 40263–68, 40279–95 (23 specimens), Caraculo, Namibe Province, 27 March 1971; TM 40508–20 (13 specimens), Tambor, Namibe Province, Angola (16°04'00.1"S, 12°26'59.9"E), 1 April 1971; TM 40536–37 (two specimens) Furnas (? – plotted as nearest rock outcrops to centre of quarter-degree square (QDS) 1612Ab in original field notes), Namibe Province (1612Ab, 16°23'30.0"S, 12°08'30.0"E), 1 April 1971; TM 41132–44 (13 specimens), turn off to Morro do Chapéu Armado, Namibe Province (14°31'42.8"S, 12°30'06.8"E), 18 April 1971; TM 41211–16 (six specimens), Lucira road, 5 km south of Catara River, Namibe Province (13°36'15.5"S, 12°38'44.0"E), 19 April 1971; TM 45366–68 (3 specimens), 10 km west of Soque, Huambo Province (12°21'45.2"S, 15°01'42.5"E), 10

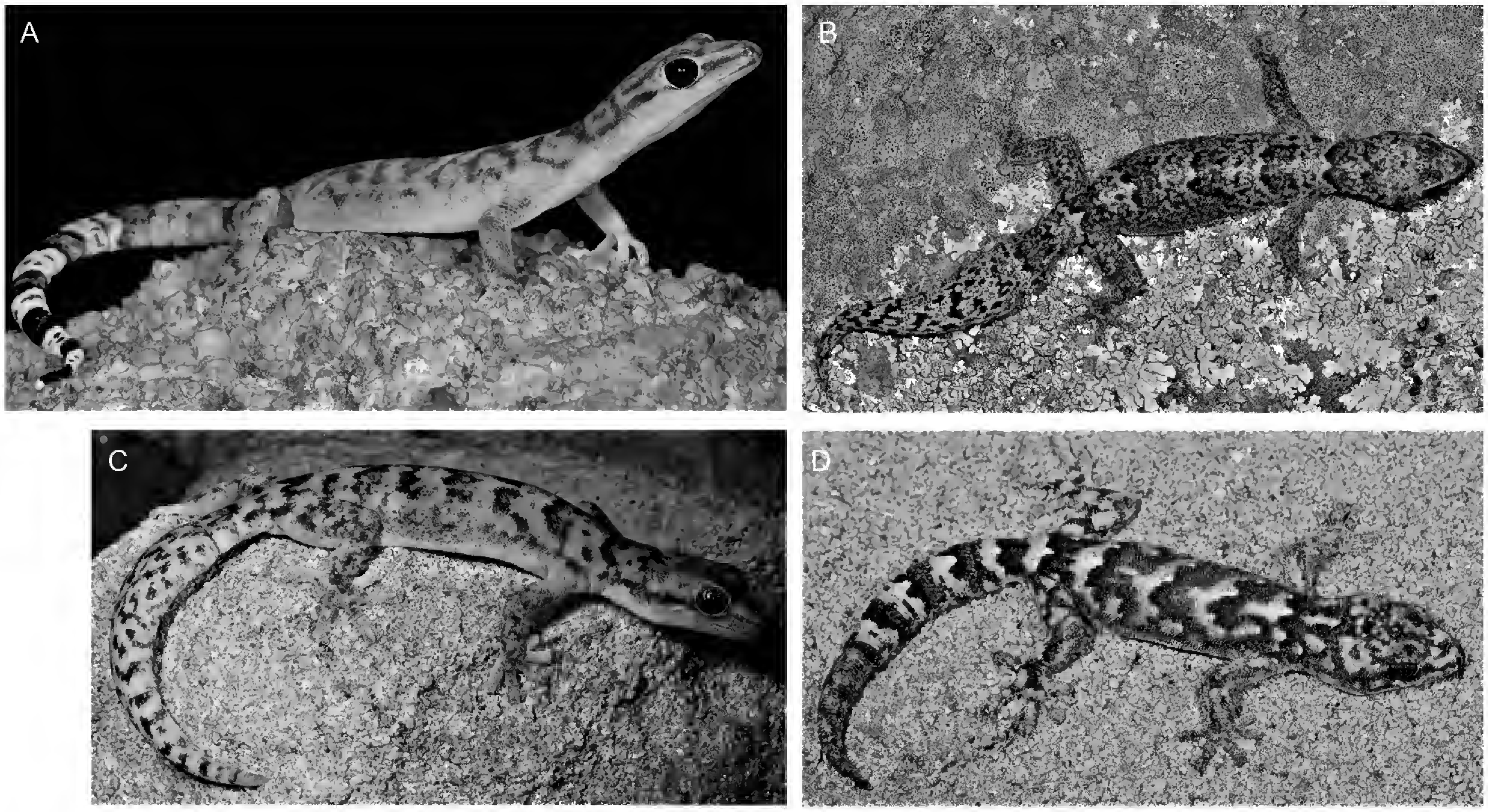

Figure 4. Regional variation in colouration and habitus of *Afroedura bogerti* from Angola **A** Omauha Lodge, Namibe Province **B** 52 km N Caraculo, Namibe Province **C** Praia do Meva, Benguela Province (P Vaz Pinto). **D** Candumbo Rocks, Huambo Province (L Verburgt). All photos by WR Branch, except where noted.

May 1974; TM 45374, 1 km south Luimbale, Huambo Province (12°15'13.3"S, 15°19'00.8"E), 10 May 1974; TM 45381–98 (18 specimens), Candumbo Rocks, 16 km west of Vila Nova, Huambo Province (12°44'09.6"S, 15°58'27.8"E), 11 May 1974; TM 46587–90 (four specimens), 3 km west of Bocoio, Benguela Province (12°28'58.0"S, 14°06'24.8"E), 28 May 1974; TM 46631–34 (four specimens), Numba (= Namba), on track from Atome to Cassongue (vicinity of Missão da Namba), Cuanza Sul Province (11°55'01.9"S, 14°51'39.1"E), 29 May 1974.

Following a hiatus in field surveys to Angola during the protracted civil war (1975–2002), no additional material was added until international collaborative biodiversity surveys began in 2009. During the first of these (Huntley 2009) additional material was collected: PEM R17936–37 (two specimens), Omauha Lodge, 15 km south of Tambor, Namibe Province (16°12'02.2"S, 12°24'06.6"E, 341m), 18 January 2009; PEM R18041–42 (two specimens), CAS 248780–81 (two specimens donated by PEM), 0.5 km south of Tambor, Namibe Province (16°04'26.9"S, 12°25'59.8"E, 352m), 21 January 2009. Subsequent field work in the ProNamib region north of Namibe (2012, 2015) and in the Huambo region (2016) resulted in additional material from new localities: PEM R21595, Granite outcrops in sandy veld, 50 km E Namibe on main tar road to Leba, Namibe Province (15°00'56.1"S, 12°33'18.1"E, 516m a.s.l.), 8 December 2012; PEM R21596, small granite outcrops in succulent veld, 52 km N on tar road on road to Lucira from junction with Lubango-Namibe road, Namibe Province (14°39'29.0"S, 12°31'37.8"E, 586m a.s.l.); AG 137-41 (to be accessioned into PEM collection), 5 specimens, 1 km east of Farm Mucongo, Namibe Province (14°47'01"S, 12°29'49"E, 314m a.s.l.), 7 November 2015; PEM R22488-89, 2 specimens, Praia do Meva (near Santa Maria), Benguela Province (13°23'48"S, 12°35'23"E, 10m a.s.l.), 28 December 2015; PEM R22490-91, 2 specimens, 1 km west Kandumbo on road to Boas Aguas, Huambo Province (12°44'10.1"S, 15°58'27.9"E, 1777m a.s.l.), 11 March 2016.

Currently Angolan *Afroedura bogerti* is known from approximately 15 localities that appear to fall into disjunct populations occurring above and below the Great Escarpment, and in diverse habitats and on different geological substrates. Colouration and scalation varies between the known populations of *A. bogerti* (Fig. 4) and preliminary morphological and genetic analysis corroborates the existence of cryptic diversity within the species (Branch et al. 2017). Molecular sequences for *A. bogerti* incorporated into recent phylogenies of the genus were based on tissues collected from lowland populations within the Angolan Namib region (Jacobsen et al. 2014, Tambor CAS 248780–81; Makhubo et al. 2015, Omauha Lodge, PEM R17936–37). A flat gecko, referred to as *Afroedura* cf. *bogerti,* was discovered in a rock crevice on the summit of the Otjihipa Mountains, northern Opuwo District, Namibia (approx. 17°18'18"S, 12°36'35"E, 1170m) in 1992 (Branch 1998; Griffin 2003). However, no voucher material is available in the State Museum, Windhoek (A.M. Bauer, pers. comm. May 2016), and the taxonomic status of the Namibian population cannot be assessed until further material becomes available.

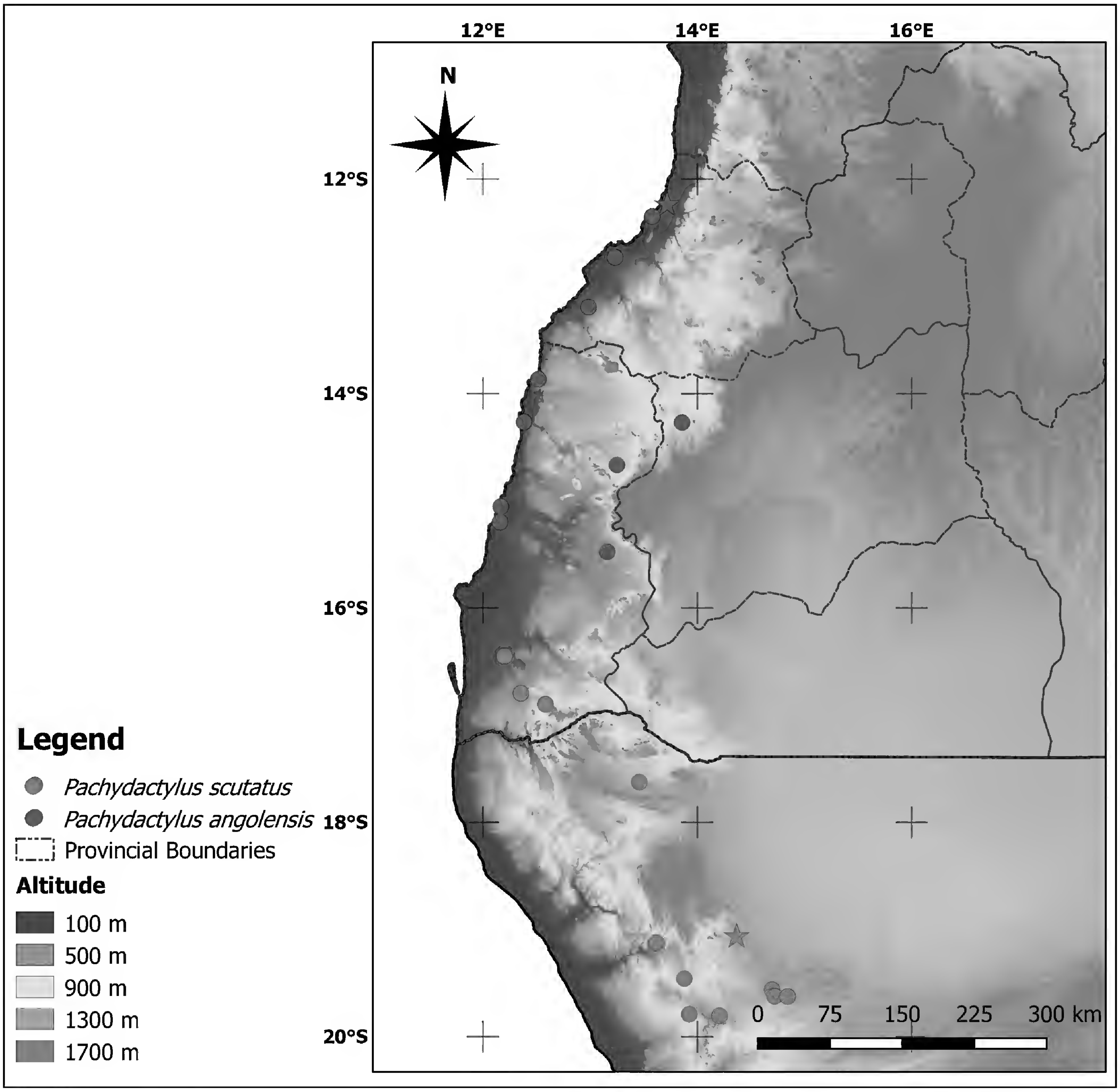

Figure 5. Distribution of *Pachydactylus angolensis* and *Pachydactylus scutatus* in Angola. Stars = type localities. For additional Namibian localities for *P. scutatus*, see Bauer et al. (2002).

Angolan Thick-toed Gecko (*Pachydactylus angolensis*)

History. In the same paper in which he described *Afroedura k. bogerti*, Loveridge also described the small terrestrial gecko *Pachydactylus scutatus angolensis* Loveridge, 1944. Loveridge's (1944) description was based on three specimens. The holotype (AMNH 47874) was "an adult male from Hanha, Benguela Province, Angola, collected by Arthur Vernay, Herbert Lang and Rudyerd Boulton, May 17, 1925". One of the two paratypes was also collected at the type locality but on 13 May 1925, and the other collected earlier "from Lobito Bay, Angola … by Herbert Lang, April 24, 1925". These dates, unlike those for *A. bogerti*, indicate that the geckos were actually collected during the VAE.

Taxonomic status of *Pachydactylus angolensis*. Bauer et al. (2002), in a review of Namibian *P. scutatus* Hewitt, 1927 (including the description of *P. parascutatus* Bauer, Lamb and Branch, 2002), elevated *P. angolensis* to a full species, noting the consistent nasal arrangement. A recent molecular phylogeny of the genus *Pachydactylus* (Heinicke et al. 2017) confirms the specific status of *P. angolensis*, but reveals its sister relationship to *P. caricul icus* not *P. scutatus*. With the elevation of *P. angolensis* to specific status, *P. scutatus* was considered to be restricted to Namibia north of the Brandberg. However, WDH (unpubl.) had already collected the first Angolan *P. scutatus* from Iona National Park (TM 40751), and others from Espinheira (TM 40615–18), when he visited the region in April 1971. Recent material from the latter locality has also been reported by Ceríaco et

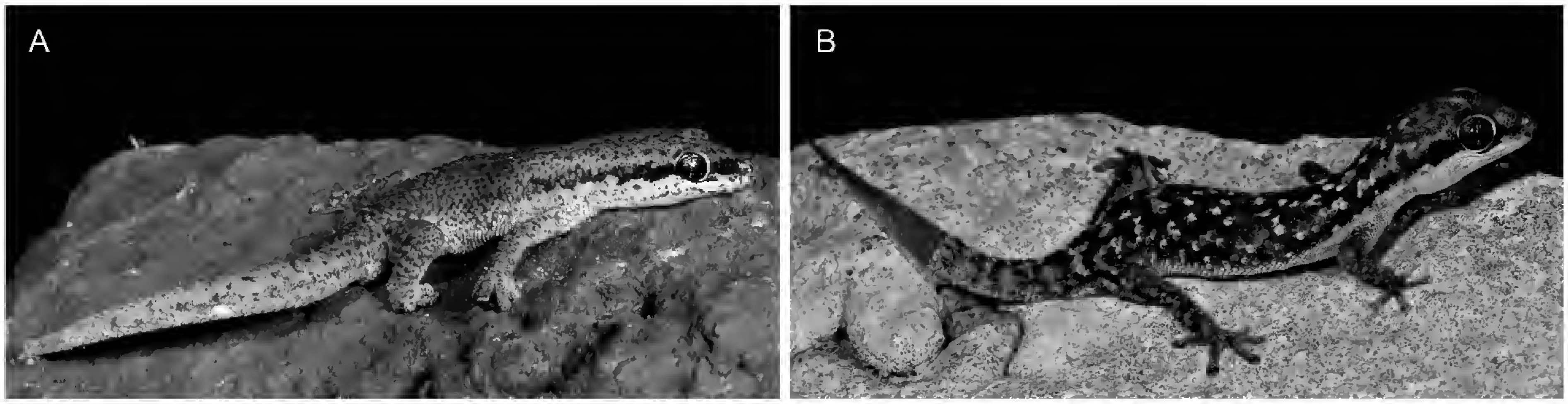

Figure 6. Regional variation in colouration of *Pachydactylus angolensis* from Angola. **A** *P. angolensis* – inland form (Serra da Tchivira: photo P. Vaz Pinto) **B** *P. angolensis* – coastal form (Chimalavera Regional Natural Park: photo WR Branch).

al. (2016). The TM geckos from Iona and Espinheira have the characteristic narrow and dark-edged white nape band illustrated in Boone and Barts (2006) which is not evident in *P. angolensis* or mentioned in its description (Loveridge 1944). Thick-toed geckos (*Pachydactylus*) are poorly represented in Angola, with only seven currently recognized species recorded; *P. cariculicus, P. scutatus, P. angolensis, P. punctatus, P. oreophilus, P rangei* and *P. vanzyli*. This contrasts dramatically with *Pachydactylus* diversity in Namibia (38 species) and South Africa (30 species). *Pachydactylus angolensis* can be distinguished from most Angolan *Pachydactylus* (e.g. *P. cariculicus, P. punctatus, P. rangei* and *P. vanzyli*) by its keeled dorsal scalation, from *P. oreophilus* by its smaller size, and from *P. scutatus* by lacking a dark-edged white nape band and by the exclusion of the first upper labial and rostral from the nostril (*P. scutatus* has a well developed nape band, and both the first upper labial and rostral enter the nostril).

Type locality of *Pachydactylus scutatus angolensis*. Angolan localities referenced under the toponym "Hanha" may cause confusion. Two main places are of concern, and both are situated in Benguela Province: Hanha do Norte (also Hanha Estate) and Hanha do Cubal. Bauer et al. (2002) noted that the holotype was ".. collected at Hanha (probably Hanha do Norte in quarter degree square 1213Bc; another locality, Hanha do Cubal, 1314Aa is also in the same province)". The above assumption is here accepted, insomuch as it avoided confusion between the two localities, and furthermore is corroborated by the fact that Hill and Carter (1941) had earlier noted that the VAE did not visit Hanha do Cubal, but rather the Hanha Estate oil palm plantation. Unfortunately, although the geographic description of Hill and Carter (1941) is basically correct, the co-ordinates they give (13°30' S, 14°30' E) are incorrect and refer to another Hanha toponym that lies southeast of the estate. It is indicated on a 1934 map of the region, and is now known as Cambondongolo (13°21'0"S, 14°24'0"E). To avoid further confusion we recommend that the type locality for *Pachydactylus scutatus angolensis* Loveridge, 1944 be restricted to - Hanha do Norte (12°14'42"S, 13°42'27"E), approximately 20 km northeast of Lobito, Benguela Province, Angola. This site is illustrated in fig. 1 of Hill and Carter (1941).

New distribution records for *Pachydactylus angolensis*. *Pachydactylus angolensis* remains poorly-known from Angola. Additional material (Laurent 1964) was collected soon after the original description, and other specimens were collected from various localities in Namibe Province by Koch during his expedition in September 1956 (see above), including: Lungo (TM 24406), Lucira (TM 24445, 24449) and Bentiaba (TM 25454–55, 25459, 25476, 25478–79). These discoveries, and others from 24 km south of Benguela (TM 39110–11), stimulated WDH to collect more material in 1971 from Saco do Giraul (TM 40328–29), Lucira (TM 41172), 30 km north Dombe Grande (TM 41266), and in 1974 from Hanha (TM 46558). More recently Ceríaco et al. (2016) recorded a specimen from the Namibe-Lubango road, near Mangueiras (15°2'37"S, 13°9'36"E).

Recent collections of geckos currently attributed to *P. angolensis* are grouped into coastal and inland populations (Fig. 5), with coastal populations (<300m a.s.l.) usually associated with consolidated marine deposits, while inland populations (>600m a.s.l.) are found in granite or intrusive outcrops. Preliminary morphological investigation indicates variation in dorsal colouration and habitus (Fig. 6) between these populations that are indicative of further cryptic diversity in Angolan geckos, and will be investigated with integrative morphological and genetic studies (Branch in prep.).

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A new genus of Parastenocarididae (Copepoda, Harpacticoida) from the Tocantins River basin (Goiás, Brazil), and a phylogenetic analysis of the Parastenocaridinae

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Abstract

Eirinicaris antonioi **gen.** et **sp. n.** (Parastenocaridinae) is described from the Brazilian rocky savannas, an ecosystem under heavy anthropogenic pressure. The subfamily is distributed worldwide, with representatives in Africa, Asia, Australia, Europe, and North America. This is the first time a non-*Remaneicaris* Parastenocaridinae is described from a Neotropical region indicating that Parastenocaridinae species were already present in a vast geographical area, before the split of the Gondwana. The new taxon is included within the subfamily Parastenocaridinae based on the following characters: 1) segments 5, 6, and 7 of the male antennules forming a functional unit for clasping the female; 2) segment 7 with small process at the inner margin, forming an incipient "pocket-knife" structure with segment 6; 3) last segment pointing medially when closed; 4) the endopod of female leg 3 one-segmented and spiniform, without distal seta; 5) the apophysis and terminal seta of the exopod of male leg 3 are fused; 6) the genital field is rectangular and much broader than the height in the female; 7) the group of three lateral setae I, II, and III of the furca and the dorsal seta are situated at the same level in the female; and 8) the basis of leg 1 has an inner seta. The new taxon can be distinguished from all other Parastenocaridinae genera by the unique sexually dimorphic telson and furca. In the male, the dorsal seta is inserted at the midlength of the furca and setae I, II, and III are displaced anteroventrally. A phylogenetic analysis of the subfamily Parastenocaridinae is given based on the description of the type species of each genus and available descriptions of all Parastenocaridinae species. *Eirinicaris* gen. n. is the sister taxon of a clade formed by *Kinnecaris* and *Monodicaris,* sharing with them the long male and female leg 5 with a long spiniform process, and with *Kinnecaris*, a distal pore on the spiniform process.

Introduction

Copepods of the family Parastenocarididae Chappuis, 1940, are typical representatives of fresh groundwater meiofauna (Corgosinho and Martínez Arbizu 2005). They can be found in different microbiotopes such as the hyporheic zone of alluvial aquifers along rivers, lakes and human-made structures such as dug or artesian wells, as well as associated with mosses and other semi-terrestrial environments such as phytotelmata (Menzel 1916, Chappuis 1931, Jocque et al. 2013).

The taxonomy and phylogenetic relationships among the species of Parastenocarididae are far from resolved with many genera being potentially paraphyletic or polyphyletic. Most of the confusion can be attributed to Jakobi (1972) who divided the family into 26 genera using a very unorthodox model and was strongly criticized by Schminke 1976. Consequently, the use of Jakobi's (1972) generic names (i.e. *Michelicaris* Jakobi, 1972; *Stammericaris* Jakobi, 1972; *Minutacaris* Jakobi, 1972; *Nanacaris* Jakobi, 1972; *Clujensicaris* Jakobi, 1972; *Phreaticaris* Jakobi, 1972; *Pannonicaris* Jakobi, 1972; *Proserpinicaris* Jakobi, 1972; *Italicocaris* Jakobi, 1972; *Fontinalicaris* Jakobi, 1972; *Entzicaris* Jakobi, 1972; *Lacustricaris* Jakobi, 1972; *Nipponicaris* Jakobi, 1972; *Oshimaensicaris* Jakobi, 1972; *Biwaecaris* Jakobi, 1972; *Enckellicaris* Jakobi, 1972; *Brinckicaris* Jakobi, 1972; *Kinnecaris* Jakobi, 1972; *Cafferocaris* Jakobi, 1972; *Macacocaris* Jakobi, 1972; *Remaneicaris* Jakobi, 1972; *Brasilibathynellocaris* Jakobi, 1972; *Pararemaneicaris* Jakobi, 1972; and *Siolicaris* Jakobi, 1972) was avoided and all species were included in the genus *Parastenocaris* Kessler, 1913, until Corgosinho and Martínez Arbizu (2005) redefined the genus *Remaneicaris,* highlighting the validity of all genera defined by Jakobi (1972). It is important to note the seminal work of Reid (1995), who redescribed *Parastenocaris brevipes* Kessler, 1913, and redefined Lang's (1948) *P. brevipes*-group, calling for a resolution of the taxonomy within the Parastenocarididae. Recently, Schminke (2010) shed more light on this subject and divided the family into two monophyletic subfamilies, Parastenocaridinae Chappuis, 1940, and Fontinilicaridinae Schminke, 2010, both well-defined by strong synapomorphies (Ranga Reddy et al. 2014).

Many genera were revised or proposed recently (viz. Cottarelli et al. 2010, Corgosinho et al. 2008, 2010a, 2012a, b, Karanovic and Cooper 2011, Karanovic et al. 2012, Schminke 2008, 2009, 2013, Ranga Reddy et al. 2014, 2016). Most of these contributions addressed some taxonomic uncertainties in Parastenocarididae by defining real monophyletic groups with clear geographical distributions. With exception of the monospecific genus *Iticocaris* Corgosinho, Martínez Arbizu & Previattelli, 2012, and the genus *Brasilibathynellocaris* from the neotropics, the remaining genera proposed or revalidated recently (i.e. *Stammericaris*, *Kinnecaris*, *Siolicaris*, *Proserpinicaris*, *Remaneicaris, Monodicaris* Schminke, 2009; *Asiacaris* Cottarelli et al., 2010; *Dussartstenocaris* Karanovic & Cooper, 2011; *Horstkurtcaris* Karanovic & Lee, 2012; *Cottarellicaris* Schminke, 2013; *Himalayacaris* Ranga Reddy, Totakura & Corgosinho, 2014; *Indocaris* Ranga Reddy, Totakura & Shaik, 2016), have European, Asian, African and Australian representatives.

The Neotropical fauna of Parastenocarididae is represented by the genera *Remaneicaris*, *Murunducaris* Reid, 1994, *Brasilibathynellocaris*, *Siolicaris*, *Iticocaris*, *Forficatocaris* Jakobi, 1972, and *Potamocaris* Dussart, 1979. With the exception of *Remaneicaris*, all the remaining genera belong to the subfamily Fontinalicaridinae.

In order to improve our knowledge on the biodiversity of Brazil, the National Council of Scientific Research (CNPq) launched in 2010 a call for proposals, to assess the biodiversity of neglected taxonomic groups in understudied Brazilian ecosystems. Our project focused on the microcrustaceans from the Brazilian rocky savannas. These environments fall into the category of azonal biomes (Walter 1985), which during the Pleistocene, extended to the lowlands of what today is occupied by the savanna ecosystems of Cerrado and Caatinga. Nowadays they appear as insular ecosystems at the top of hills, 800 m MSL (above the sea level). This biome is under high anthropogenic threat (Da Silva and Bates 2009) and is the source of headwaters of important Brazilian rivers such as São Francisco, Paraguay, Paraná and Tocantins, connecting biogeographical zones and biomes to the north, south and east of South America.

This contribution describes one of the several new species and genera discovered during an intensive sampling effort conducted in 12 rocky fields in the Brazilian inland. A non-*Remaneicaris* Parastenocaridinae is described from a Neotropical region for the first time and its phylogenetic position within the Parastenocaridinae is discussed.

Material and methods

Specimens of an undescribed taxon were found associated with moss in the littoral zone of the Água Fria River, tributary of the São Bartolomeu River, Tocantins hydrographic basin, 1230 m MSL. The sampling station, characterized by a rocky riverbed, is located at Chapada dos Veadeiros, Alto Paraíso de Goiás, Goiás State, Brazil: 14°5'30.89"S, 47°29'34.47"W (Fig. 1).

Samples of damp moss living next to the waterline were collected on August 12, 2012. The material was concentrated using a 50 µm mesh size net and preserved in 4% formalin. Animals were stained with rose Bengal and sorted with a stereomicroscope. Whole specimens and dissected material were mounted on slides in lactic acid for morphological inspection.

The terms 'furca' and 'telson' are used according to Schminke (1976). Terminology and homologization of maxillary and maxillipedal structures follow Ferrari and Ivanenko (2008). Therefore, by the application of serial homology, the nomenclature of Huys and Boxshall (1991) for Mx2 (Fig. 1.5.5, p. 26) is modified as follows: praecoxa of Mx2 is hereafter recognized as syncoxa (praecoxa and coxa), coxa is considered as the basis, and the basis is recognized as the first endopodal segment with claw. Drawings were made using an Olympus BX51 microscope equipped with a drawing tube, at a magnification of 400x and 1000x. Abbreviations: A1 (antennule); A2 (antenna); Md (mandible); Mxl (maxillula); Mx (maxilla); Mxp (maxilliped); enp (endopod); exp (exopod); benp (baseoendopod); P1 to P5 (legs 1 to 5); ap (apomorphy); pl (plesiomorphy); Urs (urosomite). The type material has been deposited in the invertebrate collection of the Museu de Zoologia da Universidade de São Paulo - MZUSP, São Paulo, Brazil. Specimens of both sexes were prepared for scanning electron microscopy (SEM) following protocols by Felgenhauer (1987), and Huys and Boxshall (1991).

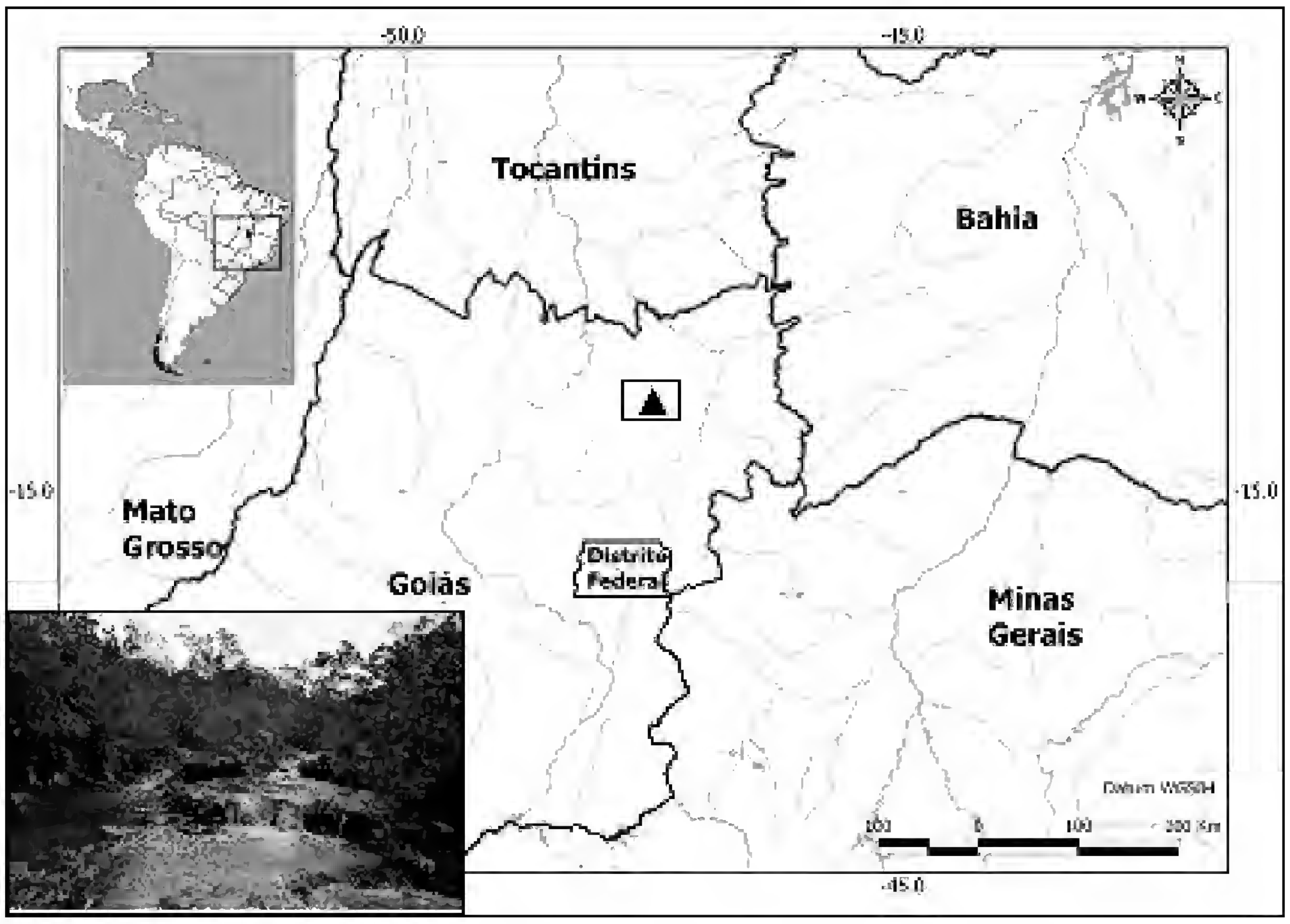

Figure 1. Study area. Type locality indicated with triangle. Insert shows the type locality (Água Fria River, National Park of the Chapada dos Veadeiros, Brazil) of *Eirinicaris antonioi* sp. n.

In order to determine the position of the new genus within Parastenocarididae, the method of phylogenetic systematics of Hennig (1966) was followed. The cladogram (Fig. 9) was generated using the program NONA (Goloboff 1999) for cladistic parsimony in interface with WINCLADA (Nixon 2002). This program uses a heuristic algorithm with unconstrained search and multiple TBR + TBR (searches for trees using tree bisection-reconnection method of branch-swapping, then repeats this process the number of times as indicated in the number of replications box) as search strategy for the best topology, and a Wagner algorithm that supports character reversal (allows 0 → n and n → 0 character changes) as a "similarity" algorithm. Character states are coded as binary (0-1) or multistate (0-n). We allowed the software to run characters as additive (0 ↔ 1 ↔ 2 = 2 steps; 0 ↔ 2 = 2 steps). The state for each character can be seen in the character list. The data matrix is given in Table 1. The polarisation of characters was done a priori (zero (0) represents the plesiomorphic condition, one (1) the apomorphic condition, and one (1) is plesiomorphic in comparison with two (2)) as in the ground pattern characters for Parastenocarididae (Corgosinho et al. 2007a), Parastenocaridinae and Fontinalicaridinae (Schminke 2010). Additional decisions of character polarity were obtained by comparing the Parastenocarididae ground pattern with the state of character present in *Psammonitocrella* Rouch, 1992, and other Ameiridae. The resulting cladogram is rooted. The term "ground pattern" is used here in the sense of 'Grundmuster' (Ax 1984: 156) and refers to all plesiomorphies and autapomorphies present in each taxon ('Stammart' sensu Ax 1984). Uninformative characters were not mapped. Unsupported nodes in the tree are hard collapsed. Characters are ACCTRAN (fast) optimized.

The phylogenetic analysis is based on data from published literature. All the original descriptions and the descriptions of the species included in Lang's (1948) groups and Jakobi's (1972) genera of Parastenocaridinae were studied. The observation of the state of characters on outgroups and on the remaining species included within the Parastenocaridinae by Schminke (2010), which are not mentioned by Lang (1948) and Jakobi (1972), was possible by studying the drawings and descriptions present in a catalogue compiled by the first author.

When necessary in the text is used of the Newick (parenthetical) phylogenetic notation to discuss the species relationships within and between closely related clades.

Results

Subclass COPEPODA Milne-Edwards, 1840
Order HARPACTICOIDA Sars, 1903
Family PARASTENOCARIDIDAE Chappuis, 1940

Genus *Eirinicaris* gen. n.

http://zoobank.org/8F621641-4E8D-4D91-825D-81734B42BCEC

Diagnosis. A1 eight-segmented in male, seven-segmented in female. Male A1 haplocer, eight-segmented, haplocer, with small process in segment seven; segments 5, 6, and 7 forming a functional unit for clasping the female, in grasping position, segment 7 bent inwards against segment 6, segment 8 points in opposite direction. Allobasis of Mx with two endites; proximal endite with one seta; distal endite with two elements, one of them transformed into serrated spine; proximal endopodal segment drawn out into claw, distal endopodal segment with two setae. Basis of P1 without remarkable sexual dimorphism; with inner and outer seta, the former longer in male; enp

Table 1. Character matrix for phylogenetic reconstruction of the valid genera included by Schminke (2010) within the subfamily Parastenocaridinae. Character states polarized a priori; polarization from 0= most plesiomorphic to 4 = most apomorphic. ?= unknown state of the character.

Ameiridae	1110000000	0000000000	0000000000	0000000000	0100000000	0000000000	0000000000	00000000
Fontinalicaris	0001211111	1111111111	1111111110	0000000000	0100000000	0000000000	0000000000	00000000
Remaneicaris	0001111111	1111111111	1110100001	1011100111	1010000000	0000000000	0000000000	00000000
Himalayacaris	0001211111	1111111111	1111100001	0112111000	0100000000	0000000000	0000000000	00000000
Indocaris	0001211111	1111111111	1110100001	1011100111	1003000000	0000000000	0000000000	00000000
Parastenocaris	0001211111	1111111111	1111100011	1110000000	0103111111	1111000000	0000000000	00000010
Kinnecaris	0001211111	1111111111	1111100001	1110000111	1101111110	0000110001	1100000000	00000110
Monodicaris	0001211111	1111111111	1111100001	1110000111	1102111110	0000110001	1010000000	00000?10
Macacocaris	0001211111	1111111111	1111100001	1110000000	0102100000	0000000001	0010012000	00000002
Simplicaris	0001211111	1111111111	1111100011	1110000000	0101100000	0000000000	0000013010	02010000
Asiacaris	0001211111	1111111111	11111000?1	1110000000	0106100000	0000000000	0000004000	10000000
Stammericaris	0001211111	1111111111	1111100011	1110000000	0102100000	0000000000	0001011000	00000001
Cottarellicaris	0001211111	1111111111	1111100011	1110000000	0102100000	0000000000	0001101000	00000002
Clujensicaris	0001211111	1111111111	1111100001	1110000000	0106100000	0000000000	0000014000	00100000
Entzicaris	0001211111	1111111111	11111000?1	1110000000	0101100000	0000000000	0000002211	00000000
Italicocaris	0001211111	1111111111	11111000?1	1110000000	0101100000	0100000000	0000002100	00000000
Michelicaris	0001211111	1111111111	1111100001	1110000000	0101100000	0000000000	0000000000	00000003
Minutacaris	0001211111	1111111111	1111100011	1110000000	0101100000	0000000000	0000013000	00100000
Nanacaris	0001211111	1111111111	1111100001	1110000000	0105100000	0000000010	0000014010	00000000
Eirinicaris	0001211111	1111111111	1111100001	1110000000	0104121000	0000111110	0000000000	00000121
Horstkutcaris	0001211111	1111111111	1111100001	1110000000	0104100000	0000000000	0000002211	00000000
Lacustricaris	0001211111	1111111111	1111100011	1110000000	0101100000	0000000000	0000012010	01011003

not sexually dimorphic. P2 enp without marked sexual dimorphism. Male P3 with quadratic smooth coxa; basis short, quadratic, with row of spinules close to outer seta, without inner ornamentation; enp modified, aesthetasc-like; exp unisegmented, rectangular, longer than wide, with irregular inner margin and with medial hump, outer margin straight, with unevenly distributed spinules, distal margin flat, inner apophysis shorter than supporting segment, blade-shaped, without distal seta or spine, thumb slightly longer than apophysis, with broad base, proximal expansion on both sides and leaf-shaped distal blade. Female P3 with spiniform enp ⅔ as long as exp-1. Male P4 enp cylindrical, approximately half as long as exp-1, with three distal spinules and one medial outer spinule. Enp of female P4 spiniform, almost as long as exp-1, distally bipinnate. Male and female P5 well developed, a simple triangular plate reaching middle of genital somite in male, inner margin drawn into long and pointed, outwardly curved, spinous process with distal pore, without inner ornamentation, reaching beyond the genital field in female; armature consisting of very long outer basal seta and two additional setae, of which proximal most shorter. Male P6 large, tetra-lobbed fused plate covering genital area. Female P6 represented by naked opercular plate much broader than the height covering genital opening. Male telson with proximal lateral pore, transverse row of small spinules along entire dorsal surface, anterior to sensilla, and rows of spinules covering most of preopercular lateral margin. Female telson smooth, with proximal ventral pore and ventral tube pore near insertion of furca. Male furca irregular, with distal outer pore, longer than width, inner and dorsal margins convex, outer and ventral margins concave; dorsal, inner and outer margins covered by spinules; lateral setae I, II and III, and dorsal setae VII separated by wide gap, setae I, II, and III displaced to antero-ventral position, seta I modified into short spine, with broad base and acuminate tip, seta III 1/3 as long as furca, with one long peduncle and one distal aesthetasc-like structure, 1/2 size of seta II, seta II with broad base, a long peduncle and one distal aesthetasc-like structure; setae IV to VII smooth, dorsal seta (VII) medially inserted in a depression; seta IV inserted subdistally on outer margin, approximately as long as telson without furca, seta V distal, twice as long as seta IV, seta VI distal, 1/2 as long as seta IV; proximal bulges on inner and outer margins. Female furca rectangular with distal ventral pore, longer than wide, smooth, slightly tapering distally, with inner flat lobe; setae smooth, lateral setae I, II, and III, and dorsal seta VII inserted medially and more or less opposite to each other; lateral setae reduced to one small (seta III) and two tiny setae (setae I and II); two uncinate processes anterior to insertion of dorsal seta VII, setae IV, V and VI inserted distally, length and ornamentation of setae IV, V, and VI as for the male; seta VI inserted beneath flat lobe, small spinules close to its insertion.

Eirinicaris antonioi gen. et. sp. n.

http://zoobank.org/8F621641-4E8D-4D91-825D-81734B42BCEC
Figs 2–8

Type material. Male dissected holotype mounted onto three slides (sample VEA17/B/R/ROF/musgo; 20 Jan 2012; MZUSP 35273). One dissected female paratype

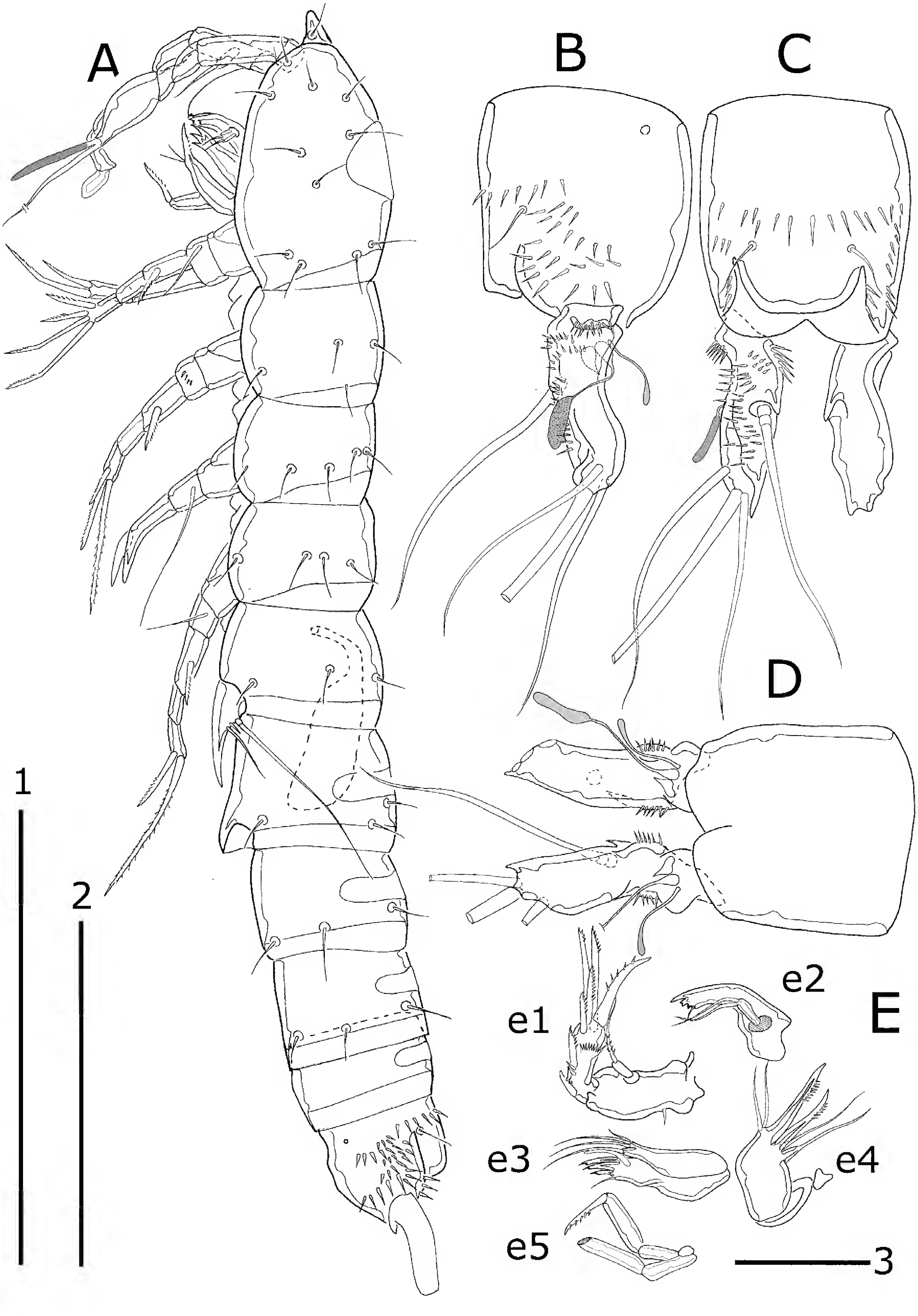

Figure 2. *Eirinicaris antonioi* sp. n. Male: **A** habitus, lateral view; **B** anal somite with caudal furca, lateral view; **C** anal somite with caudal furca, dorsal view; **D** anal somite with caudal furca, ventral view; **E** mouthparts; **e1** antennule; **e2** mandible; **e3** maxillulae; **e4** maxillae; **e5** maxilliped. Scale bars: **1** = 50 µm (**A**); **2 (B, C, D)** = 50 µm; **3 (E)** = 20 µm.

mounted onto one slide (sample VEA17/B/R/ROF/musgo; 20 Jan 2012; MZUSP 35274), one undissected female paratype (sample VEA15/C/CP/50; 20 Dec 2012; MZUSP 35274), and two undissected male paratypes mounted onto a single slide (sample VEA17/B/R/ROF/musgo; 20 January 2012; MZUSP 35274).

Type locality. National Park of the Chapada dos Veadeiros (North of Goiás, Brazil); Água Fria River; 1230 m MSL; speed of water current from low to medium; temperature 20 ±5°C; pH 5 ±1. Coordinates: 14°5’30.89”S, 47°29’34.47”W.

Etymology. The generic name is in honour of the first author’s wife, Eirini Grapsa, combining her first name with the ancient Greek substantive for shrimp, καρίς (caris). The specific epithet “antonioi” is posthumous homage to Antonio Alves Corgosinho Filho, father of the first author.

Description of male. Length 320µm (variability of the type series 314-328µm), measured from rostrum to end of telson excluding furca. Rostrum not fused to cephalothorax, with wide base and two sensilla on tip (Fig. 2A). Cephalothorax and Urs-2-5 with dorsal integumental window (Fig. 2A). Patterns of sensilla as depicted. Telson with transverse row of small spinules dorsally, anterior to sensilla, and with rows of spinules covering most of preopercular lateral margin (Figs 2A, B, C), without ornamentation ventrally (Fig. 2D), posteriorly clefted, conferring a bilobate shape posteriorly (Fig. 6D), with a pore on the ventro-lateral margin. Furca irregular, with inner and outer bulges proximally (Figs 2B–D and 6D–F) with distal outer pore (Fig. 6F, arrowed), about three times as long as width, inner and dorsal margins convex, outer and ventral margins concave; with dorsal, inner and outer spinules; with seven setae as follows: setae I, II and III and dorsal seta VII not aligned, separated by wide gap; setae I, II and III displaced anteroventrally; seta I modified into short spine, with broad base and acuminate tip; seta II with broad base, a long peduncle and one distal aesthetasc-like structure, twice as long as seta III, the latter 1/3 as long as furca, with a long peduncle and one distal aesthetasc-like structure; setae IV to VII smooth; seta IV inserted subdistally on outer margin, about as long as telson excluding the furca; seta V inserted distally, twice as long as seta IV; seta VI inserted distally next to seta V, shorter than seta IV; dorsal seta VII inserted in a depression located in the middle of the furca.

A1 (Figs 3A, B; 6A, B) eight-segmented, haplocer, with small process in segment seven (arrowed on Figs 3A, B; 6B); segments 5, 6, and 7 forming a functional unit for clasping the female, in grasping position, segment 7 bent inwards against segment 6, segment 8 points in opposite direction (Fig. 6B); segments armature as follows: 1 (0)/2(5)/3(4)/4(1)/5(3+ (1+ae))/6(0)/7(0)/8(7+ modified seta + (2+ ae)); segment 8 with seven slender setae, two seta fused basally to aesthetasc, and one modified seta, the latter as in Fig. 6C.

A2 (Fig. 2e1) allobasis without abexopodal armature, with small outer spinule proximally; one-segmented exp with one bipinnate seta; free endopodal segment bearing seven setae/spines, outermost strongly developed.

Labrum (not shown) triangular in lateral view.

Md as in Fig. 2e2. Coxal gnathobasis with distal teeth and one seta; palp one-segmented, with two distal setae.

Mx1 as in Fig. 2e3. Praecoxal arthrite with five elements (one surface seta, three claw-like pinnate spines, and one slender seta); coxal endite with one, basis with three setae.

Mx as in Fig. 2e4. Allobasis with two endites; proximal endite with one, distal endite with two elements, one of them transformed into serrated spine; proximal endopodal segment drawn out into claw, distal endopodal segment with two setae.

Mxp (Fig. 2e5) subchelate; syncoxa about 1/3 the length of basis; enp drawn into spinulose claw.

P1 (Figs 3B, 7A). Unarmed coxa ornamented with posterior row of spinules; inner seta of basis reaching tip of enp-1, with small row of spinules near insertion of enp, with comparatively smaller outer seta, with pore and row of spinules beneath outer seta; enp two-segmented, enp-1 nearly as long as exp-1 and exp-2 combined, with inner row of spinules (Fig. 7A), and two outer rows of spinules; enp-2 with one outer spine and one long geniculate seta, with posterior hyaline frill; exp three-segmented, exp-1 with outer spine, proximal and distal rows of spinules on outer margin, proximal and distal to outer spine, exp-2 unarmed, with row of inner spinules close to distal corner, exp-3 with outer row of spinules proximally, with two outer spines and two geniculate apical setae.

P2 (Figs 3C, 7A–B) coxa ornamented with posterior spinules; basis without outer seta, with row of spinules on outer margin and one outer pore; enp one-segmented, reaching middle of exp-1, armed with one distal seta, ornamented with one distal and two outer spinules; exp three-segmented, exp-1 with long outer spine, ornamented with medial row of outer spinules, with one long spinule and smaller spinule close to outer spine (Figs 3C, 7B), with hyaline inner frill; exp-2 unarmed, with distal row of spinules; exp-3 with one outer unipinnate spine, one distal unipinnate spine twice as long as outer element, and one bipinnate apical seta nearly twice as long as previous element, additionally with longitudinal row of spinules on distal third, proximal to outer spine and inner hyaline frill.

P3 as in Figs 3D, d1, d2 and 7B-C. Coxa quadratic, with posterior row of spinules; basis short, quadratic, with outer pore, with row of strong spinules close to exp; enp modified as claviform aesthetasc-like seta (Figs 3D, 7B–C); exp unisegmented, rectangular, about four times as long as wide, inner margin irregular, with one medial inner hump, outer margin straight, with unevenly distributed spinules, distal margin flat, inner apophysis shorter than exp, blade-shaped, without distal spine or seta, completely fused to exp, thumb slightly longer than apophysis, blade-shape, with broad base, curved inwards proximally.

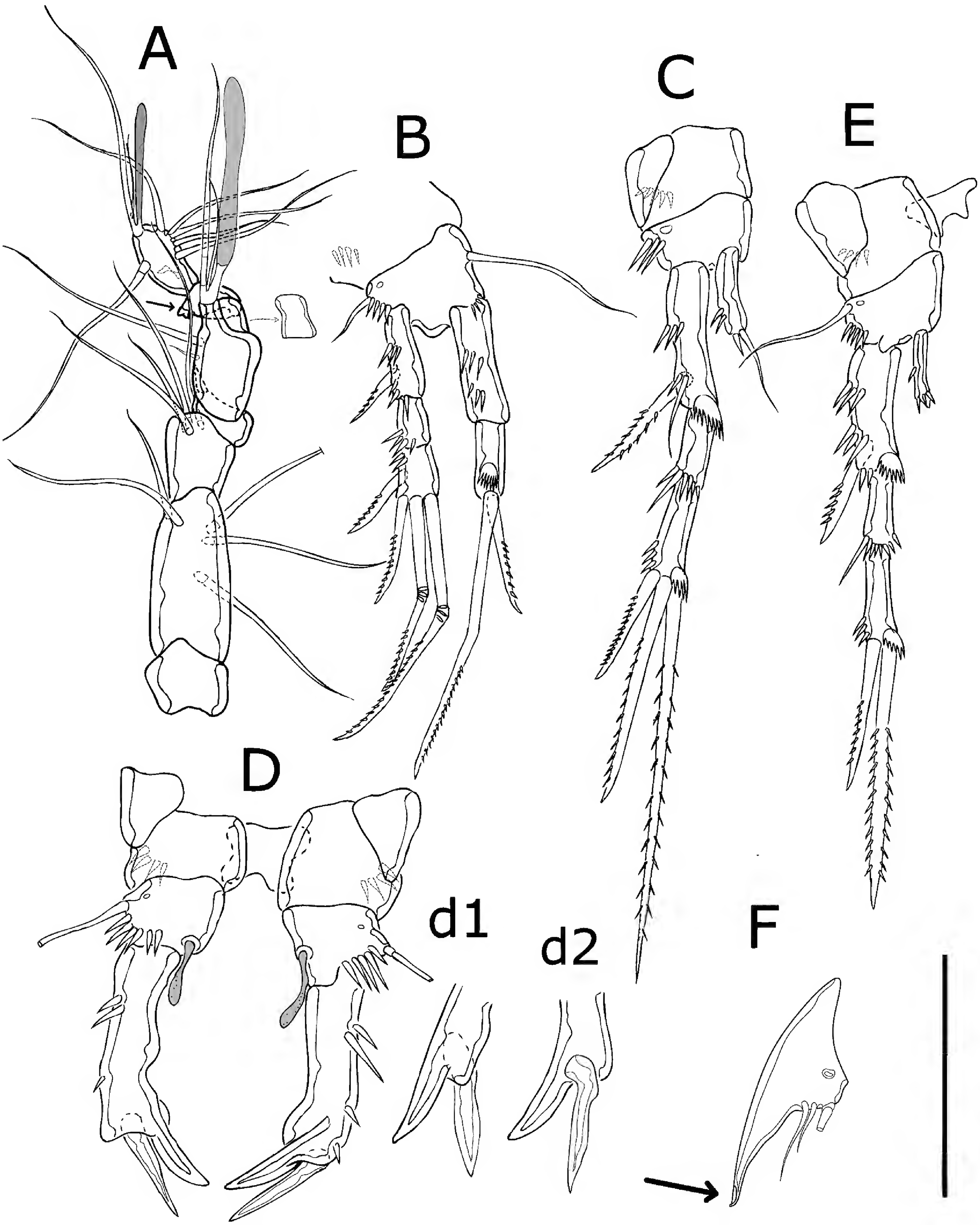

Figure 3. *Eirinicaris antonioi* sp. n. Male: **A** antennule, with process arrowed on segment seven, segment six laterally detached; **B** P1, anterior; **C** P2, anterior; **D** P3, anterior; **d1** distal part of exopod of P3 showing the apophysis, anterior; **d2** distal part of exopod of P3 showing the apophysis, posterior; **E** P4, anterior; **F** P5, with distal pore arrowed. Scale bar = 25µm.

P4 as in Figs 3E, 7B. Coxa with posterior row of spinules; basis with outer pore, outer seta, and row of outer spinules close to exp; enp cylindrical, with accuminate tip, approximately half the length of exp-1, with three distal spinules and one medial outer spinule; exp 3-segmented, exp-1 with long outer spine, ornamented with row of spinules proximally and subdistally, with comparatively smaller distal spinules, and inner hyaline frill; exp-2 un-

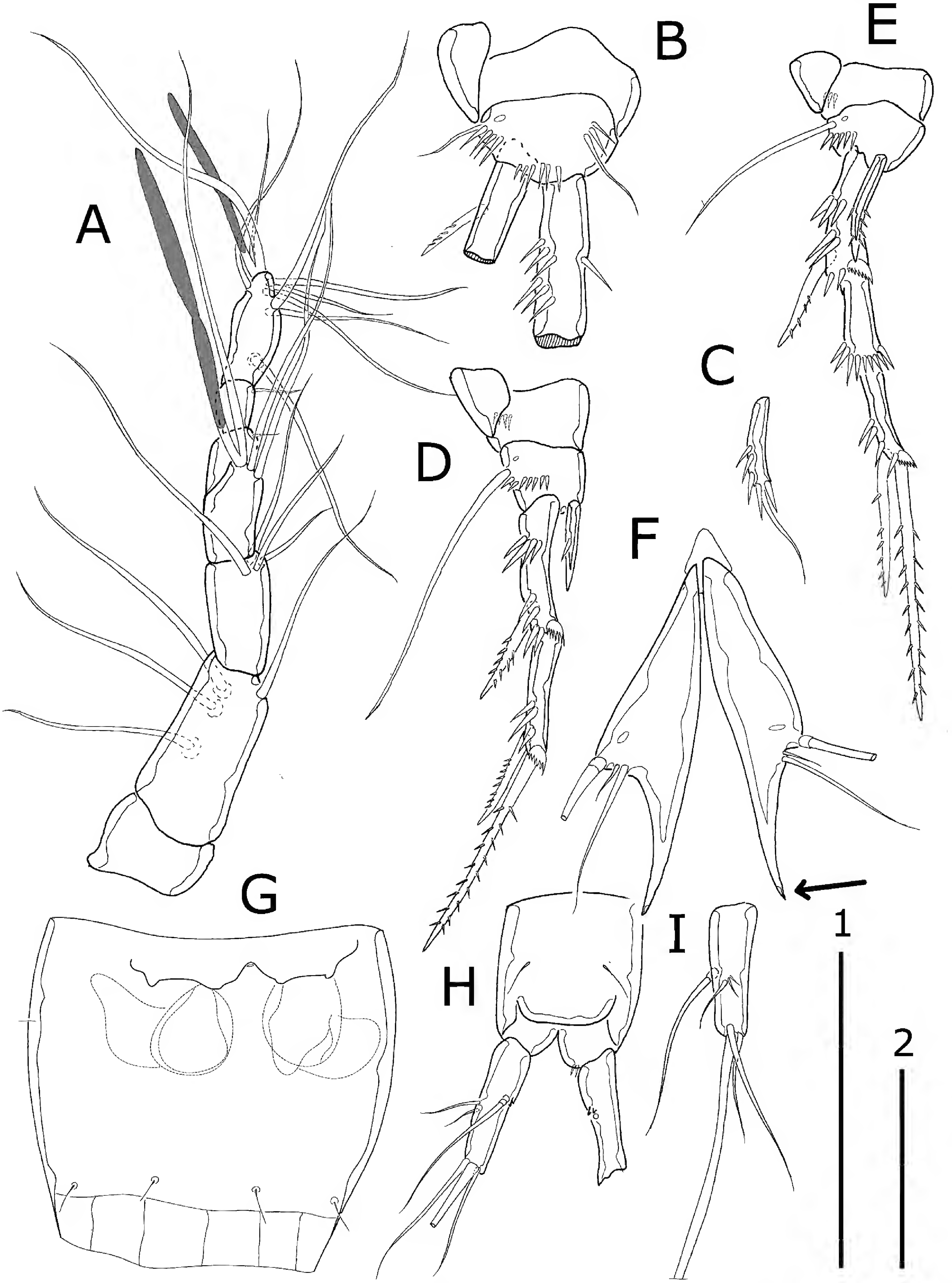

Figure 4. *Eirinicaris antonioi* sp. n. Female: **A** antennule; **B** P1, depicted with coxa, basis enp-1 and exp-1; **C** P2 enp; **D** P3, anterior; **E** P4 anterior; **F** P5, with distal pore arrowed; **G** genital field; **H** anal somite with caudal furca; **I** furca, lateral view. Scale bar 1 (**A, F**) and 2 (**C, D, E, G, H, I**) = 25μm.

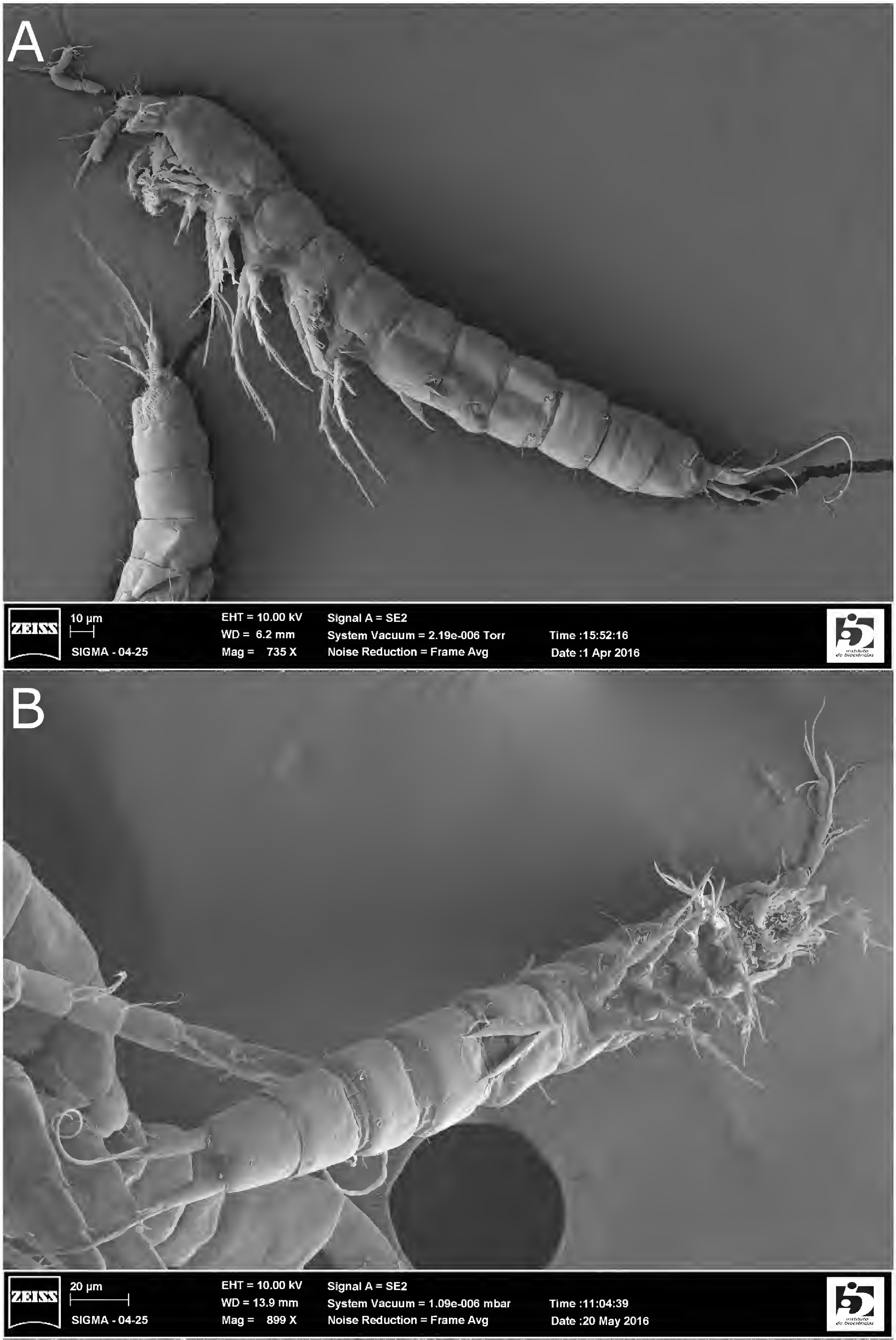

Figure 5. SEM image of *Eirinicaris antonioi* sp. n. **A** male habitus, lateral view; **B** female habitus, ventral view. Scale bar **A** = 10µm; **B** = 20µm.

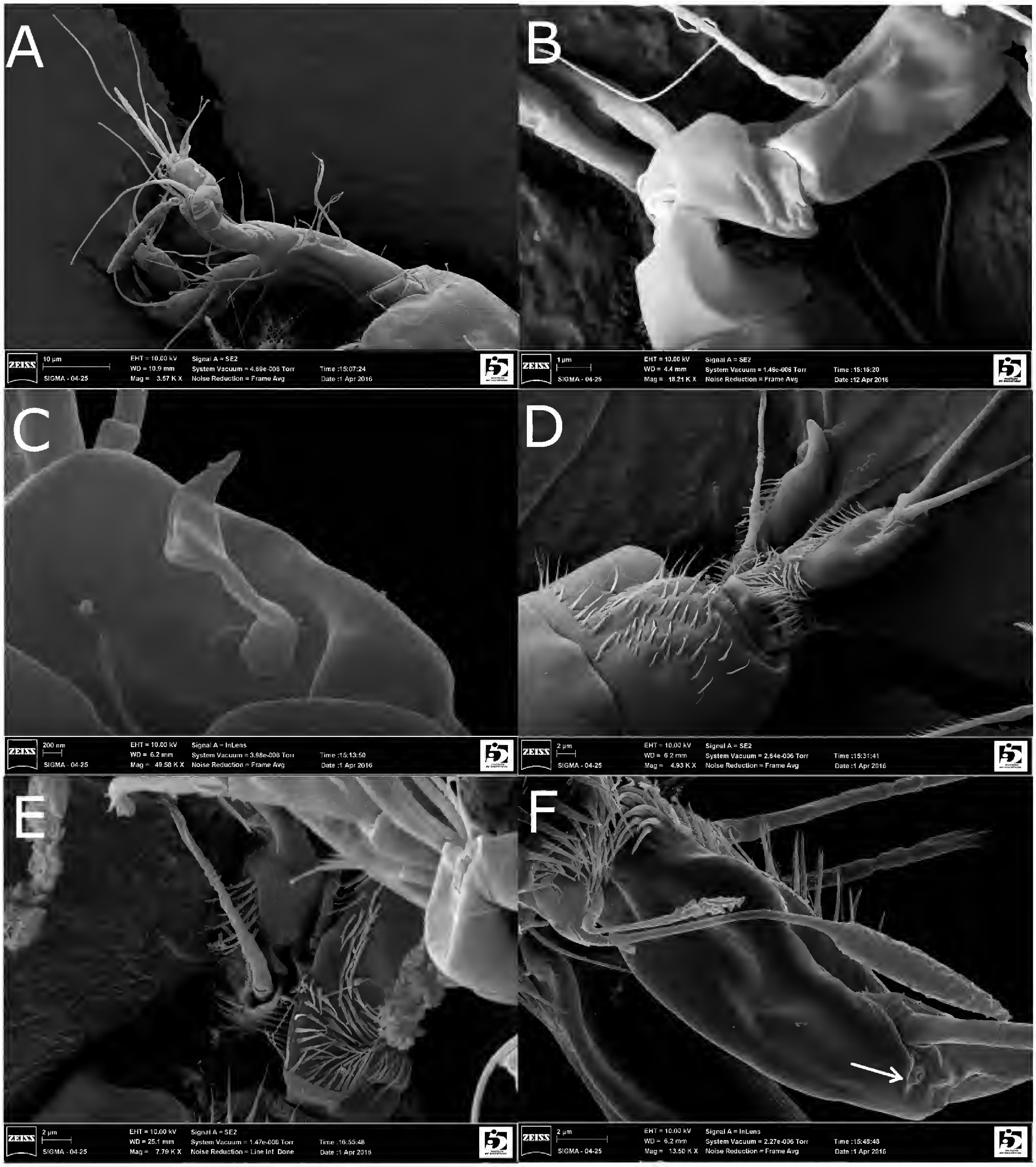

Figure 6. SEM image of *Eirinicaris antonioi* sp. n. Male: **A** antennule in lateral view; **B** antennule segments 6 (yellow) and 7 (coral); **C** antennule, segment 8 showing modified seta; **D** telson and furca, lateral; **E** furca, dorsal view; **F** furca, ventral view, showing modified setae I, II and III and distal pore arrowed. Scale bars **A** = 10µm; **B** = 1µm; **C** = 200µm; **D** = 2µm; **E** = 2µm; **F** = 2µm.

armed, with distal row of spinules (a long one on outer edge; arrowed), exp-3 with row of outer spinules subdistally, with one unipinnate outer spine, and one bipinnate distal seta nearly twice as long as outer element.

P5 (Figs 3F, 7D–E) well developed reaching slightly beyond middle of second urosomite; simple triangular plate with outer pore, distal inner margin a long and pointed, outwardly curved, spinous process with distal pore (arrowed on Figs 3F and 7D), without inner ornamentation; armature consisting of very long outer basal seta and two shorter elements, of which proximal one shortest.

P6 (Fig. 7E), large tetra-lobbed fused plate covering genital area.

Description of female. Length 310µm (variability of the type series 310-326µm), measured from tip of rostrum to end of telson, excluding furca. Sexual dimorphism ex-

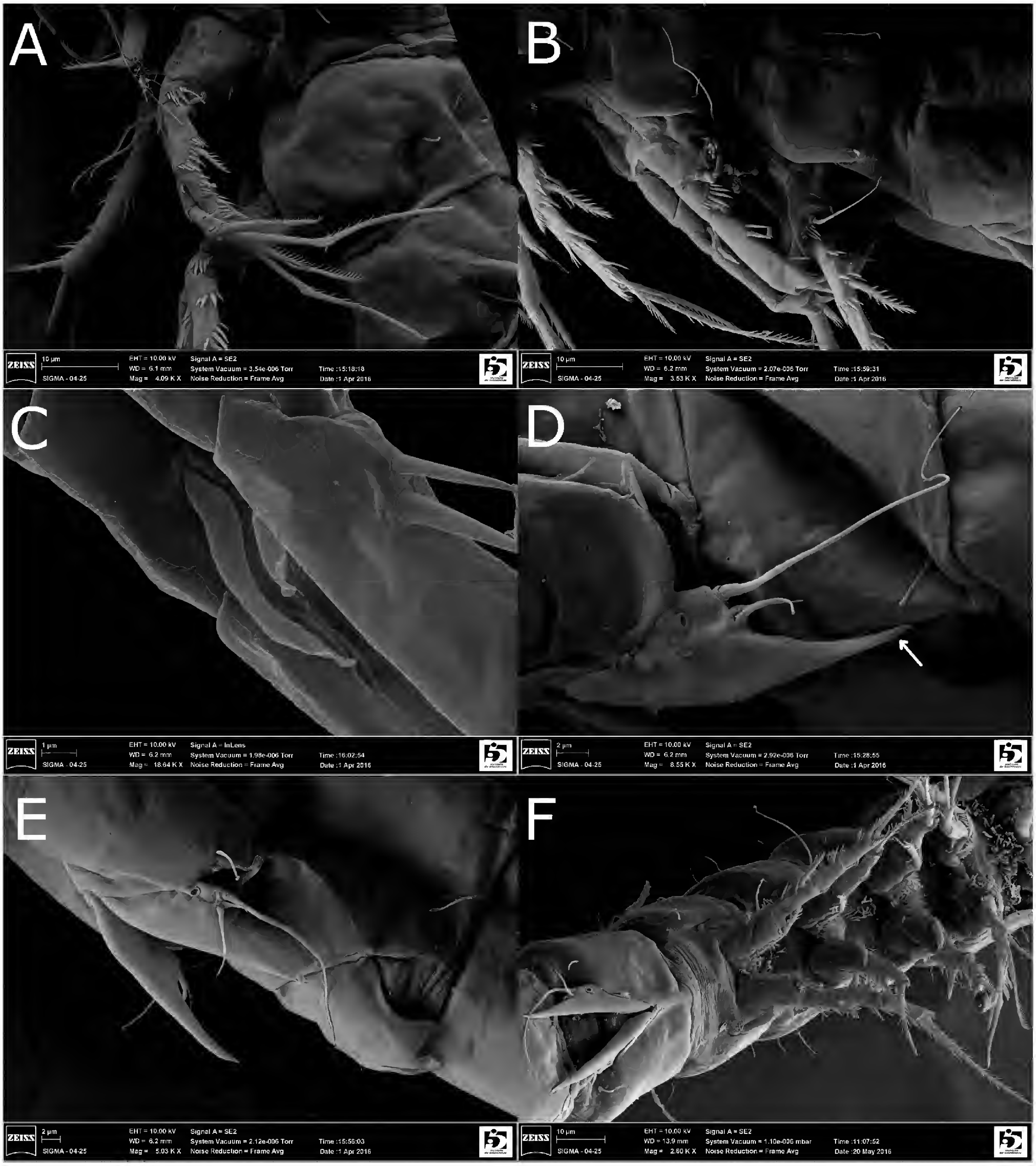

Figure 7. SEM image of *Eirinicaris antonioi* sp. n. Male: **A** P1 showing inner seta of basis; **B** P3 with endopod and thumb in colour, P4; **C** claviform aesthetasc representing the endopod of P3; **D** P5, lateral view, with distal pore arrowed; **E** P5 and P6. Female: **F** pro- and urosomites, ventral view showing endopods of P3 and P4, and P5 and P6. Scale bars **A** = 10µm; **B** = 10µm; **C** = 1µm; **D** = 2µm; **E** = 2µm; **F** = 102µm.

pressed in A1, P1, P3, P4, genital-double somite, number of integumental windows, telson and furca. Cephalothorax and Urs-2-4 with dorsal integumental windows; window on Urs-4 extending into ventral area (Figs 5B, 8A-B). Telson smooth, and small ventral tube pore near insertion of furca (Fig. 8A, arrowed); anal operculum smooth and convex (Figs 4H, 8B). Furca (Figs 4H-I, 5B, 8A-B) rectangular, with distal ventral pore (Fig. 8A, arrowed), three times as long as wide, smooth, slightly tapering distally, with seven smooth setae as follows: setae I, II and III, and dorsal seta VII inserted medially, aligned, the former three setae more or less opposite to the latter; lateral setae reduced to one small (seta I) and two tiny setae (seta II and III); with two uncinate processes anterior to insertion of dorsal seta (Fig. 4H, arrowed), setae IV, V and VI inserted distally, length and ornamentation of setae IV, V, VI, and VII as in male.

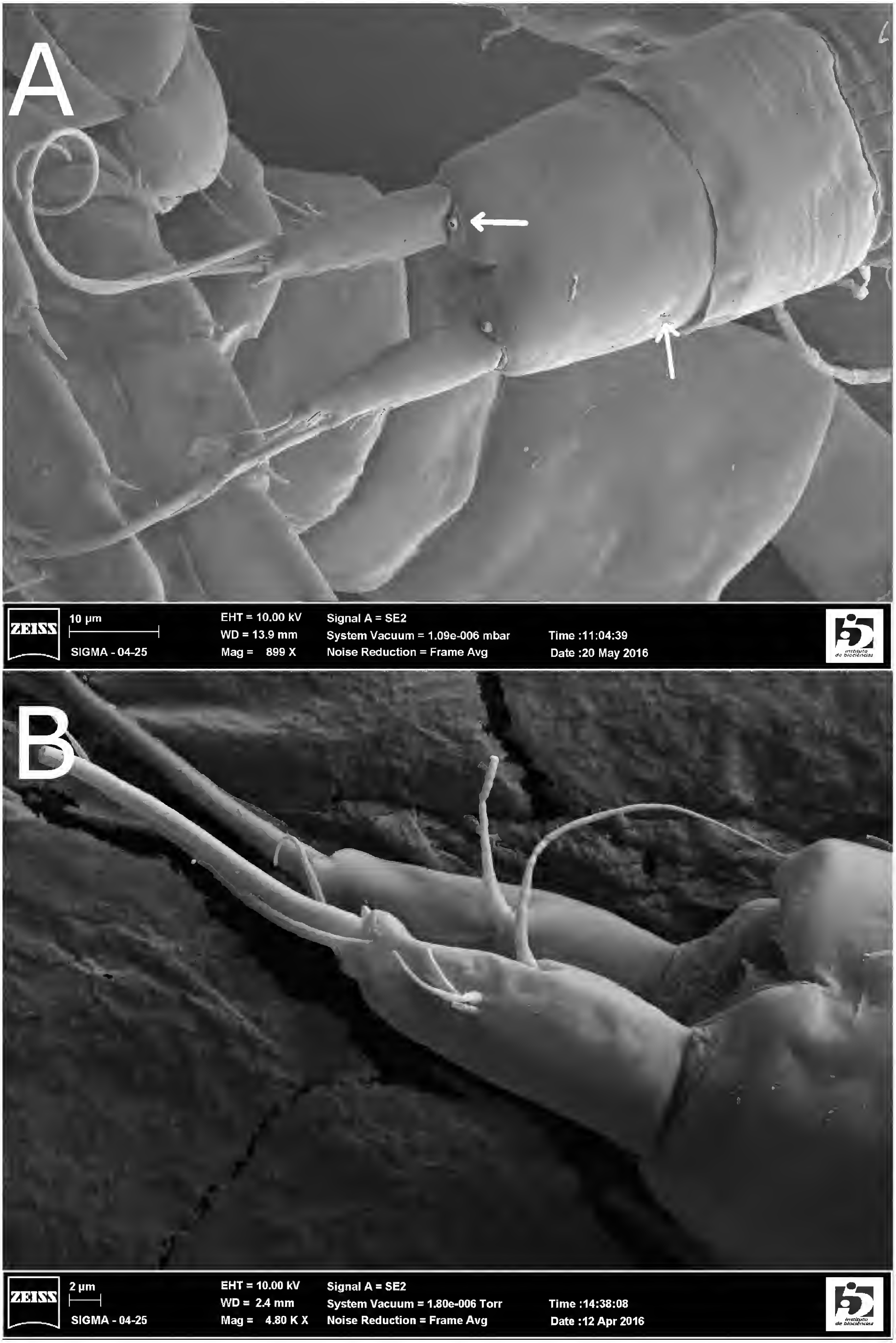

Figure 8. *Eirinicaris antonioi* sp. n. Female: **A** last urosomite, telson and furca, ventral view, proximal and distal pores arrowed; **B** telson and furca, lateral view. Scale bars **A** = 2µm; **B** = 10µm.

A1 seven-segmented (Figs 4A, 5B); armature as follows: 1(0)/2(4)/3(4)/4(2+ (1+ae))/5(1)/6(1)/7(7+ (2+ae)).

P1 (Fig. 4B) as in male, with comparatively shorter inner basal seta.

P2 enp (Fig. 4C), slightly dimorphic in ornamentation, with three outer and 2 distal spinules; exp three-segmented, exp-1 without long outer spinule close to the insertion of the outer spine.

P3 as in Figs 4D, 7F. Coxa with posterior row of spinules; basis with outer pore and row of spinules close to outer seta, the latter long; exp two-segmented, exp-1 with proximal row of spinules, outer spine, row of spinules around outer spine, and inner hyaline frill; exp-2 with subdistal row of outer spinules, with inner hyaline frill, outer unipinnate spine and distal bipinnate element; enp one-segmented, spiniform, with one outer spinule as shown, ⅔ the length of exp-1.

P4 (Figs 4E, 7F) coxa and basis as in male; exp-1and 3 as in male, enp-2 without long spinule on outer edge; enp (Fig. 4E) spiniform, about as long as exp-1, distally bipinnate.

P5 (Figs 4F, 5B, 7F) well developed, a simple triangular plate; distal margin a long and pointed, outwardly curved, spinous process with distal pore (Fig. 7F, arrowed), without inner ornamentation, reaching beyond genital field; armature as in male.

P6 (Figs 4G, 7F) represented by naked opercular plate much broader than height covering genital opening.

Discussion

After the revisionary work of Jakobi (1972), attempts to resolve the taxonomy and phylogenetic systematics within the Parastenocarididae resulted in the proposition of two subfamilies (Schminke, 2010), some new genera, and the redefinition of some other taxa (Table 2). However, some questions remain unanswered and the taxonomic and phylogenetic relationships within the family are far from complete.

Of the genera mentioned on Table 2, only *Simplicaris*, *Monodicaris*, *Asiacaris, Parastenocaris, Remaneicaris*, *Kinnecaris*, *Stammericaris*, *Cottarellicaris, Himalayacaris* and *Indocaris* belong to the Parastenocaridinae. Schminke (2010) also included the following genera within this subfamily: *Clujensicaris*, *Entzicaris*, *Italicocaris*, *Macacocaris*, *Michelicaris*, *Minutacaris*, and *Nanacaris*. Karanovic et al. (2012) synonymised *Lacustricaris* with *Parastenocaris*. However, following Schminke (2013), such course of action was premature since the type species of *Lacustricaris* is not *Proserpinicaris lacustris* (Chappuis, 1958) but *Lacustricaris budapestiensis* (Toeroek, 1935). Therefore, the genus *Lacustricaris* must be reinstated in the future.

The genus *Eirinicaris* strongly differs from all the above Parastenocaridinae genera by its unique sexually dimorphic telson and furca. *Eirinicaris* does not exhibit all the diagnostic characters of Parastenocaridinae, as proposed by Schminke (2010) and its phylogenetic position within this subfamily is discussed below.

List of characters and phylogenetic discussion. The characters are listed below and the state of each character is indicated within parentheses.

1. Inner spine on the basis of leg 1: sexually monomorphic (0); sexually dimorphic (1);
2. Seta on the distal endite of Mx: modified, brush-like (1); not modified (0);
3. Seta on the Md palp: modified, brush-like (1); unmodified (0);
4. No. of armature elements on praecoxal arthrite of Mxl: >5 (0); 5 (1);
5. No. of segments of male A1: 10 (0); 9 (1); 8 (2);
6. No. of segments of female A1: 8 (0); 7 (1);
7. No. of segments of the A2 enp: 2 (0); 1 (1);
8. No. of armature elements on triangular A2 exp: three spines/setae, at least 1 modified (0); 1 seta (1);
9. No. of segments on mandibular palp: 2 (0); 1 (1);
10. Accessory setae on the first enp/claw of Mx: present (0); absent (1);
11. Syncoxal seta of Mxp: present (0); absent (1);
12. P4: sexually dimorphic (1); monomorphic (0);
13. No. of endopodal segments of P1: 3 (0); 2 (1);
14. Inner seta on enp-1 of P1: present (0); absent (1);

Table 2. List of genera redefined after Jakobi (1972) followed by the respective synonyms and genera proposed after Jakobi (1972).

Genera redefined after Jakobi (1972) and synonyms	*Parastenocaris* (sensu Reid 1995 and Karanovic and Lee 2012a partim.; Junior synonym: *Biwaecaris*; *Brinckicaris*, *Enckellicaris*, *Oshimaensicaris*), *Remaneicaris* (Corgosinho and Martínez Arbizu 2005), *Kinnecaris* (Schminke 2008; Junior synonym: *Cafferocaris*), *Brasilibathynellocaris* (Corgosinho et al. 2010a; Junior synonyms *Paraforficatocaris*, *Pararemaneicaris*), *Siolicaris* (Corgosinho et al. 2012b), *Proserpinicaris* (Karanovic et al. 2012; Juinior synonyms *Nipponicaris*, *Pannonicaris*) and *Stammericaris* (Schminke 2013; Junior synonym *Phreaticaris*)
New genera proposed after Jakobi (1972)	*Potamocaris*, *Murunducaris*, *Simplicaris* Galassi and De Laurentiis, 2004, *Monodicaris*, *Asiacaris*, *Dussartstenocaris*, *Horstkurtcaris*, *Iticocaris*, *Cottarellicaris*; *Himalayacaris* and *Indocaris*.

15. No. of endopodal segments of P2: 2 (0); 1 (0);
16. Exp-2 of P2: with outer seta (0); without (1);
17. Exp-2 of P2: with inner seta (0); without (1);
18. No. of endopodal segments of P3: 2 (0); 1 (1);
19. Exp-2 of P4: with outer seta (0); without (1);
20. Exp-2 of P4: with inner seta (0); without (1);
21. No. of endopodal segments of P4: 2 (0); 1 (1);
22. Exp of male P3: not prehensile (0); prehensile (1);
23. Integumental windows: absent (0); present on Cphl and urosomites (1);
24. Armature of the first Mx endite: 2 (0); 1 (1);
25. P5 exp and benp: separate (0); fused (1);
26. Inner seta on the basis of P1: present (0); absent (1);
27. Ornamentation of basis of the male P4 between exp and enp: present (1); absent (0);
28. Shape of the genital operculum: broader than height (0); higher than width (1);
29. Exp of the male P3: with a proximal hump (1), without hump (0);
30. Length and shape of enp of female P3: short and rounded (0); long and spiniform (1);
31. Relative position of lateral setae I, II and III, and dorsal furcal setae VII: aligned (1); dorsal seta posterior to lateral setae (0);
32. Penultimate segment of the male A1: with apophysis (1); without apophysis (0);
33. Armature of the apophysis of male P3: with one distal spine (0); spine lost or reduced to a hyaline structure (1);
34. No. of armature elements on second endite of Mx: two setae and one spine (0); 3 (1); 2 (2);
35. P5 intercoxal sclerite: present (0); absent (1);
36. Enp of the male P4 fused to the basis: present (1); absent (0);
37. Flat strong spine on coxa of male P4: absent (0); present (1);
38. Medial ornamentation on the outer margin of P4 exp-3: absent (0); present (1);
39. Medial ornamentation on the outer margin of P4 exp-2: absent (0); present (1);
40. Medial ornamentation on the outer margin of P2 exp-3: absent (0); present (1);
41. Medial ornamentation on the outer margin of P2 exp-2: absent (0); present (1);
42. Enp of male P3: present (0); absent or reduced to a seta (1);
43. Position of outer setae of P4 exp-3: distal (0); subdistal (1);
44. Ornamentation of the basis of the male P4: simple row of spinules (0); with normal spinules of equal sizes (1); sclerotized, of different sizes (2); with strongly transformed spinules building a spinular complex or differently build into petaloid structures (3); lost but conserving the enp (4); loss of enp (5) loss of ornamentation and enp (6);
45. Length of the apophysis of the male P3: short (0); long (1);
46. Relative position of male setae I, II and III, and dorsal furcal setae VII: setae I, II, and III and seta VII inserted at distal third of the furca, or setae I, II and III anterior to the dorsal seta VII (0); at the same plane on furca's midlength (1); setae I, II and III located proximally in the ventral margin of the furca, dorsal seta VII on the distal third (2);
47. Relative position of female lateral and dorsal furcal setae: lateral and dorsal seta inserted at the distal 1/3 of the furca or setae I, II, and III are anterior to the dorsal seta VII (0); at the same plane on furca's midlength (1);
48. Shape of female furca: cylindrical (0); tapering distally (1);
49. Hyaline margin of male P3: present (1); absent (0);
50. Sexual dimorphism on P5: strong, based on difference of length (1); absent or based on differences of ornamentation (0);
51. Width of the proximal part of the endopod of male P4: narrow base (0); broad base (1);
52. Length and ornamentation of the endopod of the female P4: longer than exp-1with ornamentation at distal 1/3; shorter than exp-1 or as long as exp-1 (0);
53. Shape of exp-1 of the male P4: strongly concave at the inner margin (1); not concave (0);
54. Shape of exp of the male P3: inflate, with proximal and medial hyaline cushions (1); without this character (0);
55. Length of male P5: spiniform process reaching far beyond its own urosomite (1); short (0);
56. Length of female P5: spiniform process reaching far beyond its own urosomite (1); short (0);
57. Furca: dimorphic (1); monomorphic;
58. Enp of male P3: transformed into an aesthetasc-like seta (1); without this character (0);
59. Cuticle ornamentation of body somites: smooth (0); pitted (1);
60. Position of integumental window in the last and penultimate Urs: dorsal (0); lateral (1);
61. Size and shape of the inner process on the penultimate segment of the male A1: strong and sickle-shaped (1); different shape (0);
62. Ventral ornamentation of male Urs 3: two groups of spinules (1); absent (0);
63. Size of enp of the male P2: normally developed (0); strongly reduced (1);
64. Shape of the enp of the male P4: "Y"-shaped, proximally bifurcate, with a distal flagellum or lamella (1); of a different shape;
65. Shape of the apophysis of the male P3: foliaceous and acuminate (1); different (0);
66. Length of the thumb of the exopod of the male P3: longer or as long as apophysis (0), shorter than apophysis (1);
67. Shape of the enp of the male P4: foliaceous or triangular lamella (0); y-shaped enp (1); long spiniform (2); short, claw-like, outwardly curved (3); lost (4);

68. Shape of the apophysis on the male P3 exp: smooth (0); proximally dilated, with a soft median attenuation and a thinner distal lamella at the outer margin (1); proximally dilated, with a subtle median depression and a thinner distal lamella (2);
69. Length of furca relative to the telson: longer than telson (1); as long or shorter than telson (0);
70. Shape of the enp of the male P4: spiniform, curved inwards, sigmoid (1); different shape (0);
71. Enp of the male P2: present (0); absent (1);
72. P5 in both sexes: present (0); reduced (1); absent (2);
73. Shape of thumb of the exp of the male P3: a pointed spine (0); digitiform, with rounded tip (1);
74. Outer seta of basis of P4: present (0); absent (1);
75. P5 dimorphism: with a single seta in both sexes, elongate in male (1); with 2 or more setae (0);
76. Distal pore on the spiniform inner process of P5: present (1); absent (0);
77. Shape of male furca: cylindrical (0); tapering distally (1); allometric in growth (2);
78. Ornamentation of the proximal outer margin of the male P3: more than two spinules (0); two spinules (1); less than two spinules (2); not ornamented (3);

The phylogenetic study of the family Parastenocarididae is a difficult task, which means working up Jakobi's (1972 a, b) legacy (Schminke 2013). The family is notorious for its ill-defined genera (Galassi and De Laurentiis 2004), and researchers must deal with a plethora of poorly detailed descriptions, a high level of convergence, and ample distribution of plesiomorphic characters between and within groups and genera, making generic divisions difficult (Reid 1995, Galassi and De Laurentiis 2004, Karanovic 2005, Schminke 2010, Corgosinho et al. 2012a, b, Karanovic and Lee 2012a, b).

A phylogenetic hypothesis of the evolution of the subfamily Parastenocaridinae is herein proposed in order to discuss the phylogenetic position of the genus *Eirinicaris*. Recently, Schminke (2013) showed that meaningful conclusions could be drawn from available data. Meta-analysis of data collected from existing descriptions resulted in a single most parsimonious tree, with tree length, consistency index and retention index indicating a high level of convergence of characters within this subfamily (L=146, CI=68, RI=72) (Fig. 9).

The monophyletic status of the Parastenocarididae, Parastenocaridinae and Fontinalicaridinae were discussed in previous studies (Martínez Arbizu and Moura 1994; Schminke 2010; Ranga Reddy et al. 2014). Characters 1-29 are compiled from the contributions mentioned above. For polarization of these characters we recommend the studies of Martínez Arbizu and Moura (1994) and Ranga Reddy et al. (2014). The diagnostic characters for Parastenocaridinae and Fontinalicaridinae are proposed and discussed by Schminke (2010).

Parastenocaridinae. Schmincke (2010) proposes the following diagnostic characters for the Parastenocaridinae, avoiding to make inferences about the polarization of the characters: 1) the segments 5 and 7 form a functional unit for clasping the female. The segment 7 is sickle-shaped in some species, with an apophysis developed at the distal inner corner, and can fold back onto the fifth segment during copula whereas the segment 8 points medially; 2) female P3 enp is long and spiniform; 3) the apophysis of male P3 is unarmed in most of the species; 4) the coxa of male P4 lacks an inner row of spinules, but a row of spinules may be present near the insertion of endopod or medially of the basis; 5) except for species of *Kinnecaris*, *Monodicaris* and *Macacocaris*, all Parastenocaridinae share a small P5 in both sexes, not reaching far beyond its own somite; 6) female genital field is rectangular and much broader than high, and 7) the lateral setae I, II, and III occur at the same level as, and almost opposite to, the dorsal seta VII.

Eirinicaris can be included within the Parastenocaridinae because of the following synapomorphies (Characters 30–33):

a) Female P3 enp long, and spiniform, without distal seta (ap);
b) the group of three lateral setae of the furca (setae I, II and III), and the dorsal seta VII aligned (viz. female) (ap);
c) A1 is haplocer, with small process in segment 7 (this process is sickle-shaped in genera such as *Kinnecaris* and *Monodicaris*); segments 5, 6, and 7 forming a functional unit for clasping the female, in grasping position, segment 7 bends inwards against segment 6, segment 8 points in opposite direction (ap);
d) the apophysis and terminal seta of the exp of male P3 fused (ap);

In addition, *Eirinicaris* share the following symplesiomorphies with other Parastenocaridinae (Characters 26 and 28):

d) genital field rectangular, much broader than the height (pl);
e) basis of P1 with an inner seta (pl);

Length and shape of enp of female P3 (Character 30). Ranga Reddy et al. (2014) considered the female P3 with a terminal seta fused to the enp as a plesiomorphy for the Parastenocaridinae. However, we consider this character as an autapomorphy for the Parastenocaridinae, and the reduced, unarmed and linguiform enp as a plesiomorphy for the Fontinalicaridinae. Our decision is based on the observation of the copepodid development of the fontinalicaridin *Proserpinicaris phyllura* (Kiefer, 1938) described by Glatzel (1991). On both male and female copepodid IV the P3 enp is a linguiform structure, very similar to the adult. Hence, we consider the spiniform female P3 enp of Parastenocaridinae an autapomorphy.

Relative position of lateral and dorsal furcal setae (Character 31). This character is the best documented for the

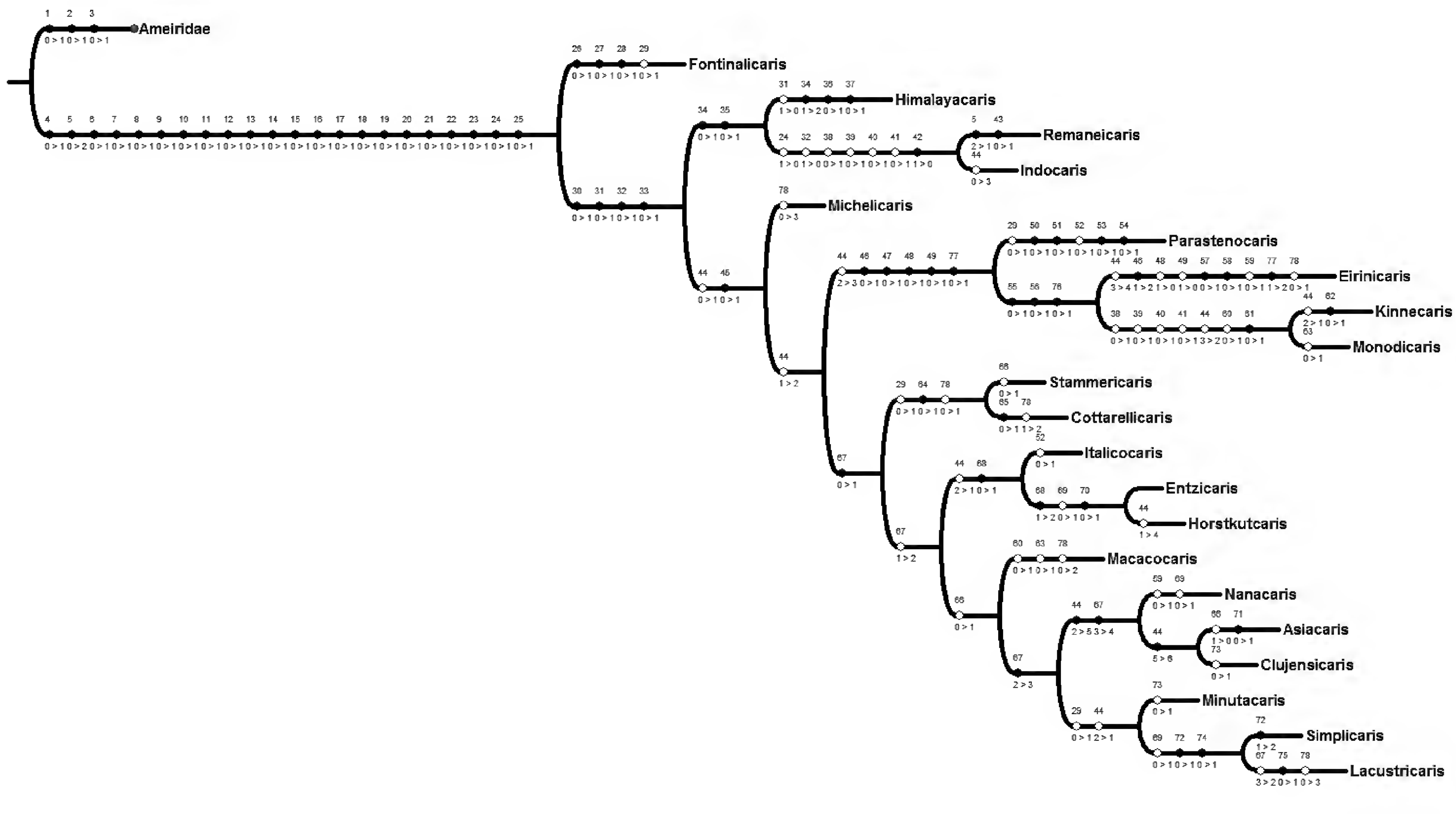

Figure 9. Phylogeny of the Parastenocaridinae reconstructed by applying Hennigian principles and criterion of putative parsimony based on the data matrix of Table 1. The cladogram was generated using the program NONA (Goloboff 1999) for cladistic parsimony, and in interface with WINCLADA (Nixon 2002). For details see Material and Methods. Characters as explained in the text; binary or multistate, polarized a priori; length of cladogram = 146. Circles represent autapomorphies, open circles represent autapomorphies by reversion of character state. Direction of character transformation indicated below each character.

family (Schminke 2010). There are three exceptions only in which the dorsal seta VII and the lateral setae I, II and III are not aligned. There is a slight gap between the lateral setae (setae I, II and III) and dorsal seta VII in *Remaneicaris euniceae* Corgosinho & Martínez Arbizu, 2005, and *Parastenocaris trichelata* Reid, 1995 (Schminke 2010). The lateral setae I, II and III are inserted at the middle of the furca, and the dorsal seta VII is inserted distally in *Himalayacaris alaknanda* Ranga Reddy, Totakura & Corgosinho, 2014. The anterior position of setae I, II and III, and the posterior situation of the dorsal seta VII is the condition described by Schminke (2010) for Fontinalicaridinae. This is a plesiomorphic condition also present in other Harpacticoida families such as Ameiridae Boeck, 1865, Cletodidae Scott T., 1904, Canthocamptidae Braddy, 1880, etc. With exception of *Eirinicaris* gen. n. and *Macacocaris*, the Parastenocaridinae condition, with lateral setae I, II and III, and dorsal seta VII aligned, and more or less opposite to each other, is observed in both male and female of those species for which both genders are described. In *Eirinicaris*, however, due to an allometric growth in the male, the lateral setae I, II and III are located proximally on the ventral margin, and the dorsal seta VII is inserted medially inside a depression, The normal condition for the subfamily is evident in the female of *Eirinicaris*. It has been suggested that the male and female of *Macacocaris* do not belong to the same species (Schminke 2009), given the presence of a parastenocaridin-like furca in the male, but a fontinalicaridin furca in the female. Although this is unusual, the sexually dimorphic furca observed for *Eirinicaris* proves that such dimorphism is possible.

Penultimate segment of the male A1 (Character 32), and geniculation. Similarly to other Parastenocaridinae with penultimate segment of the male A1 sickle-shaped, and with a functional clasping unit formed by segments 5, 6 and 7 (pocket-knife type, Schminke (2010)) as in *Kinnecaris* and *Monodicaris*, the functional unit for clasping is formed by the segments 5, 6 and 7 in *Eirinicaris* In both cases the terminal segment 8 of the male A1 points medially (ap). Galassi and De Laurentiis (2004) briefly addressed the different morphologies of the penultimate segment of the male A1 within the family Parastenocarididae. The study of the morphology of this segment in the Parastenocaridinae reveals some diverging morphologies. For example, in *P. brevipes* and many species of the genus *Parastenocaris* (sensu Reid 1995), the penultimate segment is strongly curved inwards, assuming a *quasi* horizontal conformation, conferring to the limb an appearance described as pocket-knife-like by Schminke (2010) and the last segment inserts subdistally or medially on the outer margin. Segment 7 has a medio-distal protrusion prolonged into a long process with rounded tip in *Simplicaris* (Galassi and De Laurentiis 2004: 420, Fig. 1C). However, segment 7 is aligned with the previous segment, and segment 8 inserts distally on segment 7, with the apophysis of the latter oriented obliquely to segment 8 when the A1 is in resting position. This is considered here a modification of the sickle-shaped segment 7 as described by Schminke (2010) for the parastenocaridin pocket-knife male antennule. The morphology of the penultimate male A1 segment of *Simplicaris veneris* (Cottarelli and Maiolini, 1980) is similar to *Parastenocaris brevipes*. Nothing can be said about the shape and strength of this the male antennular apophysis for the type species of the genera *Michelicaris*, *Italicocaris*, *Entzicaris*, *Horstkurtcaris, Nanacaris*, *Clujensicaris*, *Minutacaris* and *Lacustricaris*. The male A1 apophysis is present in *Parastenocaris*, *Kinnecaris*, *Monodicaris*, *Eirinicaris*, *Stammericaris*, and *Cottarellicaris*. The presence in *Macacocaris* is questionable and open to interpretation since Chappuis (1952) only made reference to the presence of a strongly prehensile male A1. Following Galassi and De Laurentiis (2004), the transformation of the penultimate segment of the male antennule may have appeared independently within the family Parastenocarididae and should be considered a derived state. Instead, we consider the modifications of the 5th and 7th segment of the male A1 as synapomorphies for the Parastenocaridinae (Ranga Reddy et al. 2014). However, the transformation series of the penultimate segment is difficult to establish. Hence, it is difficult to say how many times the male A1 apophysis have appeared and disappeared within the Parastenocaridinae and if they evolved from absent to incipient towards a strong sickle-shape apophysis or if any other kind of transformation is involved. To be sure, it is necessary to recollect and/or restudy the type species of *Michelicaris*, *Italicocaris*, *Entzicaris*, *Horstkurtcaris, Nanacaris*, *Clujensicaris*, *Minutacaris* and *Lacustricaris*, as well as closely related species and other Parastenocaridinae species not included in this study, since they do not belong and cannot be clearly included within any of the genera currently available taxonomically.

Armature of the apophysis of male P3 (Character 33). The apophysis is generally long and with a distal spine in Fontinalicaridinae, and the spine is usually missing in the Parastenocaridinae (see Schminke 2010). Some exceptions are known. Among the Fontinalicaridinae from the Neotropical region, some species of *Siolicaris* exhibit a short apophysis, and the distal spine of the apophysis is fused or lost in all species of the genus, except for *S. sandhya* (Ranga Reddy 2011). A long apophysis can be observed in *Iticocaris* and in *Brasilibathynellocaris* (Corgosinho et al. 2010a, 2012a), but no trace of a distal spine can be observed in the adult, with the exception of a heteromorphic male of *B. salvadorensis* (Noodt, 1962) and the copepodid V of the same species (Corgosinho et al. 2010a), with a 2-segmented P3 exp with a distal spine not fused to exp-2. *Dussartstenocaris idioxenos* Karanovic & Cooper, 2011, from Australia and *D. bisetosa* Ranga Reddy, Totakura & Shaik, 2016, are two examples of fontinalicaridins without the distal spine in the apophysis of the male P3 exp. Within the Parastenocaridinae, only *Himalayacaris alaknanda* has a distal hyaline spine in the short apophysis. A rounded hyaline cushion can be observed in some species closely related to *Parastenocaris brevipes* (see Reid 1995, Karanovic and Lee 2012a). We have no doubt that the armed apophysis of the male P3 exp is a plesiomorphic character, and the loss of this structure occurred several times within the Fontinalicaridinae This is considered here as a synapomorphy for the Parastenocaridinae, reverting to the primitive condition only in *H. alaknanda*.

The following two characters are considered symplesiomorphies for the Parastenocaridinae.

Inner seta on the basis of P1 (Character 26) The presence/absence of an inner seta on the basis of the P1 has been exhaustively discussed by Galassi and De Laurentiis (2004) and Schminke (2010). This character is considered here as a plesiomorphy for the whole family, disappearing and reappearing only within the Parastenocaridinae. The presence of a very long inner seta on the basis of P1 is an autapomorphy for *Eirinicaris* gen. n.

Shape of the genital operculum (Character 28). A genital operculum which is broader than the height, appears consistently in the females of all the species of Parastenocaridinae studied so far. Interestingly, at least two types of genital operculum are evident within the Parastenocaridinae. In *Eirinicaris*, *Simplicaris* and *Kinnecaris* (see Karanovic and Cooper 2011) the copulatory pore is covered by what Galassi and De Laurentiis (2004) described as "strongly sclerotized operculum represented by a single laminar plate running transversally across the genital double-somite". The copulatory pore is not covered completely by such plate in *Parastenocaris*. Instead, two lateral discrete plates representing the vestigial P6, form a sclerotized plate, partially covering the genital aperture and the median copulatory pores in *Parastenocaris* (see Karanovic and Lee 2012a).

Ranga Reddy et al. (2014) proposed a division of the Parastenocaridinae into two basic monophyletic groups: one composed by *Himalayacaris*, *Remaneicaris* and the *Parastenocaris tirupatiensis*-group (*Indocaris*), and a group composed of the remaining Parastenocaridinae, called here the crown-group. Our phylogenetic study confirms that Ranga Reddy's et al. (2014: 813) characters 34 (position of outer setae on third exopodal segment of leg 4) and 35 (spinules near the insertion of the endopod of male leg 4) support the clade formed by *Himalayacaris*, *Remaneicaris* and *Indocaris* as proposed by Ranga Reddy et al. (2014). Characters 38 to 41 appear convergently in two monophyletic groups (*Remaneicaris-Indocaris* and *Kinnecaris-Monodicaris*). Character 37 is an autapomorphy for *Himalayacaris*. Character 50 is autapomorphic for *Remaneicaris*. Character 62 is autapomorphic for *Kinnecaris*. For a discussion on the relationships within this group see Ranga Reddy et al. (2014).

The crown-group is supported in the present study by character 44 (ornamentation of the basis of the male P4) and character 45 (length of the apophysis of the male P3). These are discussed below.

Ornamentation of the basis of the male P4 (Character 44). A row of spinules on the basis of the male P4 close to the insertion site of the enp appears in derived groups within *Remaneicaris* (Corgosinho et al. 2010b; group D). It is absent in *R. ignotus* (Dussart, 1983), *R. meyerabichi* (Noodt, 1962), in the *R. argentina*-group (Corgosinho et al. 2010b; group A), and in the *R. analuizae*-group (Corgosinho et al. 2010b; group C). This character appears as a row of slender spinules inserted in a weakly chitinized zone in derived *Remaneicaris* groups; however these spinules are often omitted in original descriptions (Corgosinho et al. 2007). This ornamentation consists of strong petaloid elements in *Indocaris*, and increase in size from the inner to the outer margin, and is not as complex as in *Parastenocaris*. This ornamentation is not present in the ground pattern of *Remaneicaris*, and our phylogenetic hypothesis does not support the presence of such ornamentation in the groundpattern of the clade (*Himalayacaris* (*Remaneicaris*, *Indocaris*)). Therefore, the strong ornamentation on the basis of the enp is considered here a synapomorphy for the crown-group, occurring convergently in *Indocaris*.

Within the crown-group, this character evolves into a strong row of unequal spinules in *Stammericaris*, *Cottarellicaris* and *Monodicaris*. These spinules are strongly sclerotized and unequal in *Parastenocaris*, slender in *Kinnecaris* and are missing in *Eirinicaris*. Strong unequal spinules are present in *Kinnecaris giselae* Schminke, 2008. The condition observed in species of *Cottarellicaris*, *Stammericaris*, and in other species such as *P. palmerae* Reid, 1992, is not homologous to the condition observed for *Parastenocaris brevipes* and closely related species. In *Parastenocaris*, the spinular complex involves sclerotization, heteromorphy of the spinules, and the presence of anterior and posterior spinules on the basis. With exception of the enlargement and sclerotization of some spinules, nothing similar has been observed for *Cottarellicaris*, *Stammericaris*, and *P. palmerae*.

Length of the apophysis of the male P3 (Character 45). *Remaneicaris*, *Indocaris* and *Himalayacaris* have short apophyses which are, in general, as long as wide. Exceptions for this can be observed in *Indocaris inopinata* Ranga Reddy, Totakura & Shaik, 2016, and in *Indocaris tirupatiensis* (Ranga Reddy 2011). The shortest apophyses are found in *Indocaris imbricata* Ranga Reddy, Totakura & Shaik, 2016, and in *Himalayacaris alaknanda* Ranga Reddy, Totakura & Corgosinho, 2014, and in basal members of *Remaneicaris,* with some exceptions occurring in species belonging to more derived groups within *Remaneicaris* such as *R. membranaceae* (Noodt, 1965) and *R. oncophora* (Noodt, 1965) (Noodt 1965, Corgosinho 2007). The elongated apophysis seems to be also a derived character in *Indocaris*. Interestingly, *I. inopinata* displays an intermediate condition between *I. imbricata* and *I. tirupatiensis.* Hence, it seems more parsimonious to assume a shorter apophysis for the ground pattern of the Parastenocaridinae. A longer apophysis is a synapomorphy for the crown-group, and a convergent short apophysis appears both within the basal Parastenocaridinae as well as within the crown-group (viz. *Cottarellicaris*).

Following the above reasoning, the crown-group as defined here, can be divided into *Michelicaris* and two large monophyletic groups composed by the following genera:

a) Group-1: *Stammericaris*, *Cottarellicaris*, *Italicocaris*, *Entzicaris*, *Horstkurtcaris*, *Macacocaris, Nanacaris*, *Asiacaris*, *Clujensicaris, Simplicaris*, *Lacustricaris,* and *Minutacaris*;

b) Group-2: *Parastenocaris*, *Kinnecaris*, *Monodicaris,* and *Eirinicaris.*

Group-1. The monophyly of group-1 is supported on the ground of a complex series of transformations of the male P4 enp (Character 67).

Four main monophyletic subgroups were identified within group-1: (*Stammericaris*, *Cottarellicaris*); (*Italicocaris,* (*Entzicaris, Horstkurtcaris*)); *Macacocaris;* and ((*Clujensicaris,* (*Asiacaris, Nanacaris*)), (*Minutacaris,* (*Simplicaris, Lacustricaris*))).

Schminke (2013) redefined the genus *Stammericaris* and proposed *Cottarellicaris* to encompass similar species belonging to obviously distinct subgroups. Although Schminke correctly described and discussed in detail the diagnostic characters he proposed to each genus, he was reluctant to explicitly discuss the synapomorphies for both genera. However, he clearly defined the complex P4 enp as a character common to *Stammericaris* and *Cottarellicaris.* The presence of a seta or lamella inserted distally on the male P4 enp with a proximal bifurcation (what we call here "Y"-shaped enp) (Character 64) and the presence of at most two spinules on the proximal outer margin of the male P3 (Character 78) are considered here as synapomorphies for *Stammecaris* and *Cottarellicaris.* The "Y"-shaped enp is not exclusive for *Cottarellicaris* and *Stammericaris*, but can be also found in *Parastenocaris palmerae*. However, Karanovic and Lee (2012) attributed this species to *Parastenocaris* on the basis of the presence of hyaline processes on the inner margin of the basis of the male P4. We have discussed above the condition of this ornamentation within this group and we agree with Schminke (2012), not supporting the inclusion of *P. palmerae* in the genus *Parastenocaris.* Some of the characters proposed by Karanovic and Lee (2012a) are symplesiomorphies, allowing the inclusion of unrelated species within the genus *Parastenocaris.* As correctly mentioned by Schminke (2013), Reid (1995) conceded that the structure of the endopod P4 male complex and the long and spinulate endopod P4 female could be taken as an indication that *P. palmerae* is part of the *brevipes*-group, but she argued that the short female genital field, the P3 male and the setation of the caudal rami speak against it. In our view, the length of the female P4 enp and the shape and setation of the furca of *P. palmerae* clearly points against the inclusion of this species in *Par-*

astenocaris. Additionally, *P. palmerae* should be included in a group of species closely related to *Cottarellicaris* and *Stammericaris* as proposed by Schminke (2013), based on similar morphology of the male basal ornamentation shape of the "Y-shape-like" endopod of male P4, and similar morphology of the male P3 of *Stammericaris* and *P. palmerae*, sharing a long apophysis and shorter thumb, convergently appearing as autapomorphy for *Stammericaris* and as synapomorphy for a monophyletic group composed by (*Macacocaris*, ((*Nanacaris*, (*Asiacaris*, *Clujensicaris*)), (*Minutacaris*, (*Simplicaris*, *Lacustricaris*)))) (Character 66). Character 78 is discussed by Schminke (2013), who describes a maximum of one proximal and four distal spinules for *Cottarellicaris*, and two proximal and eight distal spinules for *Stammericaris*.

Italicocaris, *Entzicaris* and *Horstkurtcaris* share a P3 apophysis with a "recorted" outer margin (Character 68, shape of the apophysis on the male P3 exp), proximally dilated, with a median depression and a thinner distal lamella. It is important to stress that Karanovic and Lee's (2012b) diagnosis to the genus *Horstkurtcaris* is not supported by a single synapomorphy. Some characters such as "Male antennula seven-segmented, prehensile, with geniculation between third and fourth and fifth and sixth segments" are the result of inaccurate descriptions, since the male A1 is never seven-segmented in Parastenocarididae (Corgosinho et al. 2007). Additionally, the geniculation always occurs between 4th and 5th segment, and between 6th and 7th segments. Therefore, the use of the generic name *Horstkurtcaris* should be restricted to *H. nolli* (Kiefer, 1930) and *H. nolli alpina* (Kiefer, 1960) only, pending a revision and phylogenetic study of the Parastenocaridinae at the species level. The similarities between *Entzicaris* and *Horstkurtcaris* are considerable. Both *H. nolli* and *Entzicaris entzii* (Toeroek, 1935) share the morphology of the male P3, with an enpsigmoid in shape, curved to the inner margin (Character 70 in this study); the male P4 of *E. entzi* is different to that of *H. nolli* in the presence of a single spinule on the basis close to the insertion of the endopod. The female limbs are slightly different in ornamentation and length of the endopod, and both species possess a long furca with all the elements inserted distally. A remarkable difference can be observed in the male P5, being shorter, with the setae inserted distally, and with a feeble inner spiniform process in *H. nolli*. Chappuis (1940) showed a larger P5 of *H. nolli* with a conspicuous inner spiniform process, similar to what was described for *E. entzii*. These astounding similarities suggest that *H. nolli* and *E. entzii* are geographical variants of the same widely distributed species.

The third is composed solely by the genera *Macacocaris*; the fourth subgroup is composed by *Clujensicaris, Asiacaris*, *Nanacaris, Simplicaris*, *Minutacaris*; and *Lacustricaris*. In most of these species the male P3 exp is slender, slightly curved towards the inner margin, the apophysis is elongate, blade-shaped, with a rounded tip, without distal seta; the thumb ranges from smaller than the apophysis (Character 66; 0→1) as in *Simplicaris*, *Minutacaris*, *Nanacaris*, and *Clujensicaris*), to larger than the apophysis (Character 66; 1→0) as in *Asiacaris*. The monophyly of the group composed of *Nanacaris*, *Asiacaris*, *Clujensicaris*, *Minutacaris*, *Simplicaris* and *Lacustricaris* is supported by the presence of a short spiniform enp of the male P4 (Character 67), which is lost in *Nannacaris*, *Asiacaris* and *Clujensicaris*. This group also diplays a trend towards the reduction or loss of the armature of the basis of the male P4 as in *Asiacaris* and *Clujensicaris* (Character 44). This character appears convergently in *Himalayacaris alaknanda*. However, the male P4 enp is not completely lost in *H. alaknanda*, appearing as an inner uncinate bud on the basis.

The phylogenetic position of *Macacocaris* is difficult to decipher. *Macacocaris* shares many characters with other genera, such as the short enp of the male P4 (Character 63) as in *Monodicaris,* the pitted cuticle (Character 61) as in *Kinnecaris* and *Monodicaris*, strong and unequal ornamentation of the inner basis of the male P4 as in *Monodicaris*, *Parastenocaris*, *Stammericaris* and *Cottarellicaris*, and the dimorphic P5 (shorter in the male, with the elements arranged distally as in *Parastenocaris*). Additionally, the males of the genus *Macacocaris* males possess a strongly transformed A1, which Chappuis (1952) describes as "fortement préhensiles", probably similar to what can be observed for *Kinnecaris* and *Monodicaris.* Pending a full morphological and molecular study of this genus, and the redescription of *Macacocaris macaco* (Chappuis, 1952), its phylogenetic position is as inferred in the cladogram (Fig. 9).

Group-2. This group is composed of the genera *Parastenocaris*, *Kinnecaris, Monodicaris,* and *Eirinicaris.*

Schminke (2009) recognized the similarities and close relationship of *Kinnecaris* with *Monodicaris.* The recognition of the closer relationship between *Kinnecaris* and *Parastenocaris* can be traced back to Lang (1948), who pointed to the closer relationship between the *P. brevipes*-group and the *P. muscicola*-group, the latter composed at that time of *Kinnecaris caffer* (Chappuis, 1936) and *K. muscicola* (Chappuis, 1936).

> "The *Brevipes*-group must be closely related to the *Muscicola*-group. The enp of P4 is built in the same way in both groups, however, the *Brevipes*-group, which is the most derived group of both, have kept the basal tooth or finger-like processes." (free translation from Lang 1948, p. 1219).

Parastenocaris, *Kinnecaris* and *Monodicaris* share the tapering furca in the male and female in which the lateral setae I, II and III, and the dorsal seta VII are situated in the middle of the rami, setae I, II and III opposite to seta VII (Characters 46 an 47, for the male and female, respectively). The tapering furca and the position of setae I, II, and III aligned opposite to seta VII is observed in the female of *Eirinicaris* (Character 48), changing position of setae I, II, and III, their relative position to seta VII (with a large gap between them), the shape and ornamentation of the furca in the male as the result of the extreme dimorphism.

Eirinicaris is closely related to *Kinnecaris* and *Monodicaris*. These three genera share the long spiniform process on the male and female P5, reaching beyond the middle of the second (genital) urosomite (Characters 55 and 56 for the male and female, respectively), and proximal insertion of the lateral setae on the female. An interesting character, which was previously described for *Kinnecaris* by Karanovic and Cooper (2011), is the presence of a pore at the distal rim of the inner acute spiniform process of the P5 (Character 76). This pore is also present in *Eirinicaris*, but was not described for *Monodicaris*. The recent observations of an undescribed species of a new genus from Brazil (Corgosinho and Previattelli, pers. obs.) revealed the presence of this pore on the male P5. This is an indicative that this pore is widely distributed within the family, making possible that it could have been overlooked in *Monodicaris*.

On the morphology of *Eirinicaris* gen. n. *Eirinicaris* gen. n. is an intriguing genus with some unique characters. The basis of the male P1 possesses a very long inner seta, a character never reported for this family before. The telson and furca are very ornate in the males of this species, and the furca exhibits an extreme level of dimorphism with setae I, II and III situated proximally on the ventral side of the furca. Spinular ornamentation on the telson and furca is not uncommon within the family. The presence of spinular ornamentation on the telson is present in species closely related to the parastenocaridin *R. analuizae* Corgosinho & Martínez Arbizu, 2005 and *R. tridactyla* Corgosinho, Martínez Arbizu and Santos-Silva, 2007. Other species within this subfamily such as *P. spinicauda* Wells, 1964, *P. spinosa* Wells, 1964, *P. trisaetosa* Chappuis, 1954, also possess spinular ornamentation on the telson. Within the Fontinalicaridinae, *Parastenocaris nigerianus* Chappuis, 1959 and some species of *Forficatocaris* exhibit spinular ornamentation of the telson. Concerning the furca, normally the modification occurs in females (Schminke 1976). Such high levels of ornamentation on the telson and furca have never been described for the family. Similar levels of ornamentation can be observed only in freshwater Canthocamptidae Brady, 1880.

Equally impressive is the level of modification of the posterior seta of the last segment of the A1, the endopod of the P3 and the furcal setae I, II, and III in the males. The last segment of the male A1 possesses an additional modified aesthetasc-like seta ventrally. Additionally, the enp of the male P3, and the furcal setae II and III are transformed into aesthetasc-like structures. Within the Copepoda the aesthetascs are generally restricted to the A1. Aesthetascs are also present in the mouthparts of some Paranannopidae Por, 1986 (Gee and Huys 1991). To our knowledge, this is the first species of Copepoda with aesthetascs-like setae on the furca and leg 3 of male.

Distribution and ecology. Prior to this study, *Remaneicaris* was the only representative of Parastenocaridinae in the Neotropical zone. The discovery of *Eirinicaris* in Brazil extends the geographical distribution of other monophyletic groups of Parastenocaridinae to South America, hence, indicating that all the main phylogenetic lineages of Parastenocarididae were already present in a vast geographical area, before the split of Pangea.

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