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New composition of the family Nierstraszellidae (Mollusca: Polyplacophora) with description of two new genera and two new species

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ABSTRACT. The present contribution expands the family Nierstraszellidae Sirenko, 1992 from a pair of deepwater species assigned to *Nierstraszella* Sirenko, 1992, to eight deepwater extant species in three genera, two of them new to science. These species are typically found on deep-sea sunken wood, implying a homologous ecological specialization shared for all species within the family. This systematic revision reflects a new understanding of a distinctive and ancient lineage within the chiton order, Lepidopleurida Thiele, 1909, whose revision has been challenged by inaccessible deepwater habitat of its members. Here we integrate both SEM and molecular studies, and recast Nierstraszellidae as one of multiple, mostly still unresolved, monophyletic lineages within Lepidopleurida. The type genus, *Nierstraszella,* is newly restricted to its type species, *N. lineata* (Nierstrasz, 1905), and two new genera are introduced. ***Rissochiton*** gen. nov. includes five similar species found in the Indo-West Pacific Ocean, all once grouped uncomfortably as *Leptochiton rissoi* (Nierstrasz, 1905). We distinguish type species ***R.*** *rissoi* by morphology and DNA from four other similar species, including ***R. formosaensis*** sp. nov. and ***R. quincuncialis*** sp. nov. A second new genus, ***Astrochiton*** gen. nov., has a neotropical distribution that is disjunct from other Nierstraszellidae. The two species, our selected type species, *Lepidopleurus binghami* Boone, 1928, from the Caribbean Sea and Gulf of Mexico, and ***A.*** *incongruus* (Dall, 1908) from the tropical Eastern Pacific. The results of a phylogenetic analysis, based on combined mitochondrial *cox1* and 16S gene regions and corresponding to morphological affinities, support all three genera as independent lineages. Together, Nierstraszellidae is strongly supported as monophyletic relative to multiple included outgroups from across and outside of Lepidopleurida. Within Nierstraszellidae, a geographic split is evident between Indo-West Pacific and neotropical species. The molecular analysis also reveals a strong phylogeographic pattern within *N. lineata.* that is inconsistent with regular gene flow, hinting at cryptic species diversity. Together, our analyses support three genera that are united by features of the girdle, radula, and patterns of strong variability in the number of pores of aesthetes in the aesthete group. In contrast to other Lepidopleurida, members of Nierstraszellidae have a surprising amount of intraspecific variability in their tegmental sculpture, with some individuals having tegmentum granules in rows, while others have no trace of granules. Based on the number and location of the pores of the aesthetes, the Jurassic species *Leptochiton shapovalovi* Sirenko, 2013 is provisionally assigned to ***Rissochiton***, which has implications for the antiquity of the family.

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Обновленный состав семейства Nierstraszellidae (Mollusca: Polyplacophora) с описанием двух новых родов и двух новых видов

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РЕЗЮМЕ. Настоящая работа расширяет семейство Nierstraszellidae Sirenko, 1992, от пары глубоководных видов, отнесенных к роду *Nierstraszella* Sirenko, 1992, до восьми современных глубоководных видов в трех родах, два из которых являются новыми для науки. Их общее типичное обитание на затонувшей в глубоководных районах древесине для всех членов семейства Nierstraszellidae подразумевает гомологичную экологическую специализацию. Эта систематическая ревизия отражает новое понимание древней линии в отряде хитонов Lepidopleurida Thiele, 1909, ревизия которой была затруднена из-за недоступности глубоководных местообитаний ее членов. В статье мы используем как сканирующий электронный микроскоп, так и молекулярные исследования и пересматриваем семейство Nierstraszellidae как одну из нескольких, в основном все еще не разрешенных, монофилетических линий в пределах Lepidopleurida. Типовой род *Nierstraszella* теперь ограничен своим типовым видом *N. lineata* (Nierstrasz, 1905), и описываются два новых рода. Род ***Rissochiton*** n. gen. включает пять сходных видов, обитающих в тропической западной части Тихого океана, которые ранее объединялись в группу *Leptochiton rissoi* (Nierstrasz, 1905). Мы отличаем типовой вид ***R.*** *rissoi* по морфологии и ДНК от четырех других сходных видов, включая ***R. formosaensis*** sp. nov. и ***R. quincuncialis*** sp. nov. Второй новый род, ***Astrochiton*** gen. nov., имеет неотропическое распространение, которое изолировано от других представителей семейства Nierstraszellidae. Вид *Lepidopleurus binghami* Boone, 1928, выбранный нами как типовой вид рода ***Astrochiton*** gen. nov., обитает в Карибском море и Мексиканском заливе, а ***A.*** *incongruus* (Dall, 1908), второй вид этого рода, обитает в тропической восточной части Тихого океана. Результаты филогенетического анализа, основанного на объединенных последовательностях митохондриальных генов *cox1* и 16S и соответствующих морфологическим сходствам, подтверждают, что все три рода являются независимыми линиями. В совокупности, Nierstraszellidae убедительно подтверждается как монофилетическая группа относительно множества включенных внешних групп из разных районов Lepidopleurida. Молекулярный анализ дополнительно выявляет сильную филогеографическую закономерность внутри *N. lineata*, которая не согласуется с обычным потоком генов, указывая на скрытое видовое разнообразие. В совокупности наши анализы подтверждают существование трех родов, объединенных признаками мускулистого пояса, радулы и закономерностями сильной изменчивости числа пор у эстетов. В отличие от других лепидоплеурид, представители семейства Nierstraszellidae демонстрируют удивительно высокую внутривидовую изменчивость в скульптуре тегментума: у некоторых особей гранулы тегментума расположены рядами, тогда как у других гранул нет совсем. На основании количества и расположения пор эстетов юрский вид *Leptochiton shapovalovi* Sirenko, 2013 предварительно отнесен к роду ***Rissochiton***, что свидетельствует о древности семейства.

Introduction

Resolving the species status of chitons once broadly identified as *Leptochiton rissoi* (Nierstrasz, 1905) has proven to be increasingly difficult in recent years. Besides *L. rissoi*, three more species with similar morphology are currently accepted as valid: *L. vietnamensis* Sirenko, 1998, *L. longispinus* Saito, 2001 and *L. incongruus* (Dall, 1908). Sigwart [2009] transferred *Lepidopleurus andamanicus* E. A. Smith, 1906 to *Nierstraszella*, based on morphological similarities, but Sigwart *et al.* [2011] noted that molecular comparisons instead favored grouping this species more closely with *L. vietnamensis* than with the type species of *Nierstraszella* Sirenko, 1992, *N. lineata* (Nierstrasz, 1905). A more detailed analysis of *L. binghami* (Boone, 1928), from the Caribbean Sea and the Gulf of Mexico, allowed us to establish its relationship with the East Pacific and Indo-West Pacific species treated here. Collectively, across Lepidopleurida, all these species have surprisingly similar sculpturing of the tegmentum, girdle spicules, and radular teeth. Likewise, our molecular analysis strongly supports Nierstraszellidae Sirenko, 1992, here broadened to include eight species, as a basal monophyletic lineage within Lepidopleurida. Interestingly, we also found consistent morphological and molecular evidence for dividing the family into *Nierstraszella* and two new genera. The study of materials collected by expeditions organized by Philippe Bouchet in the western Pacific Ocean together with additional material for molecular comparisons from the Philippines, Japan, and the vicinity of the Caribbean Sea allowed us to complete a morphological and molecular revision of the family, also leading to the discovery of two new species that undoubtedly belong to this group.

Material and methods

Morphology has been examined in more than 120 specimens of the genera ***Rissochiton*** gen. nov. in more than 40 samples from East Indian Ocean to Solomon Islands and in the Gulf of Panama. The specimens have been mainly collected during the expeditions of Muséum National d'Histoire Naturelle (MNHN) in 2000–2014, which were organized by Philippe Bouchet: AURORA 2007, BOA 1, KAVIENG, MADEEP, PANGLAO 2005, PAPUA NIUGINI, SALOMON 1, SALOMON 2, and TAIWAN 2000, some of which were part of the TROPICAL DEEP SEA BENTHOS set of cruises (doi.org/10.18142/257). One sample was collected in the Indian Ocean on the Russian R/V *Vitjaz* (1975), and another in the Philippines on the R/V *Professor Mesyatsev* (1979). For ***Astrochiton*** *binghami,* we studied 77 specimens from 35 samples from the Caribbean Sea or the Gulf of Mexico, stored in INVEMAR or NMNH. For *Astrochiton incongruus* we studied five specimen from four samples from Mexico to Panama We also studied 19 specimens of *N. lineata* from eight samples collected off South Vietnam (R/V *Odyssey*, 1984), off the Philippines (PANGLAO 2005), or off New Guinea (PAPUA NIUGINI, 2012 and KAVIENG, 2014). Six of the specimens from the Philippines were collected during the California Academy of Sciences' Hearst Philippine Biodiversity Expedition of 2011 under a Gratuitous Permit (GP-0057-11) nearest to the municipalities of Cavite, Bataan, and Batangus. This work was part of the joint Department of Agriculture-NFRDI-California Academy of Sciences Memorandum of Agreement for the ongoing implementation of the National Science Foundation-funded biodiversity expedition in the Verde Island Passage. Specimens were collected in accordance with terms and conditions of the gratuitous permit and under the supervision of BFAR Fisheries Regulatory and Quarantine Division and NFRDI.

Altogether, 23 specimens of the family were studied under Scanning Electron Microscopy (SEM), following the methods of Sirenko [2015, 2018]. Each studied specimen was boiled for 10–15 minutes in 7% KOH solution to remove organic material and isolate valves (usually valves I, IV, V and VIII), girdle portions, and radula, and then prepared conventionally to scan on an FEI SEM Quanta 250 scan SEM. The rest of the radula and girdle were dried and put in Canada balsam in case examination under a light microscope was needed.

A ratio of the widths of either (left or right) apophysis to jugal sinus was estimated by direct measurement of these widths in a rostral view of either valve 4 or 5 with calipers. The ratio can also be adequately computed from a rostral view image such as those included in our figures. This calculation is not accurate in dorsal or ventral views because the width of the apophyses would then be confounded by valve height.

Bathymetric ranges are reported as inner values of the shallowest and deepest stations as explained by Bouchet *et al.* [2008]. The chresonymy for each species is incomplete, including only name use in selected relevant literature.

To integrate our morphological descriptions with a phylogenetic estimate from DNA sequence comparison, we also assembled and sequenced a representative selection of the species treated here, and selected outgroup specimens from other chiton genera. Altogether, 47 of the 58 Nierstraszellidae specimens and 14 of the 28 outgroup specimens are from MNHN expeditions. As summarized in Table 1 and Supplementary Table S1, we obtained DNA sequence data mostly provided by MNHN personnel from two mitochondrial gene regions reported here, 16S ribosomal DNA (16S) and cytochrome *c* oxidase subunit I (*cox1*). We first dissected small tissue clips from the foot or girdle of the MNHN specimens in January 2018 after preliminary identifications had been completed by one of us (BS). Later, these molecular voucher specimens were re-examined in more detail to evaluate how they corresponded to the morphological distinctions reported here. The DNA extraction, PCR, and sequencing, and assembly protocols used at the MNHN were described by Zuccon *et al.* [2012]. Besides the MNHN material, 27 selected other specimens were included by one of us (DE) in our analyses; most were sequenced with methods described by Eernisse *et al.* [2018]. One of these added specimens is a *Nierstraszella lineata* voucher specimen from Japan (SBMNH-704671; de0100) that has both a complete mitochondrial genome sequence [Irisarri *et al.*, 2020] and a phylogenomic data set available [Varney *et al.*, 2024] from its use as an outgroup in those studies. For PCR amplification, we used commonly employed primer pairs: 16Sar/16Sbr [Palumbi *et al.*, 1991] and LCO 1490/HCO 2198 [Folmer *et al.*, 1994]. All new sequences are available in GenBank under accession numbers for 16S (PZ353059- PZ353120) and *cox1* (PZ353242-PZ353282 and PZ359893).

We assembled sequence data sets as summarized in Table 1 for 41 specimens with both 16S and *cox1* and separate gene data sets that included an additional 26 specimens with only 16S or 19 with only *cox1*. All Phylogenetic analysis employed separate alignments of each gene region using default parameters for MAFFT v. 7 [Katoh *et al.*, 2019]. The main combined-gene analysis is based on a concatenation of the two alignments for a data set where all but one of 42 included specimens are represented by both 16S and *cox1* sequences. Separate gene tree estimates, with more inclusive taxon representation, were obtained with a likelihood approach. Although parsimony and distances approaches were also explored and found to produce similar results, all analyses presented are based on maximum likelihood analysis using RAxML [Stamatakis, 2014] using default parameters as implemented at RAxML HPC-BlackBox v. 8.2.12 [Kozlov *et al.*, 2019].

Because the extent of intra- and interspecific sequence variation for deep-water chitons is little explored, we computed average pairwise distance across and within all Nierstraszellidae species using simple “p” distance as calculated by PAUP* [Swofford, 2002] v. 4.0a (build 169). We also compared our separate morphological species identifications with an estimate of species delimitation provided by the ABGD software [Puillandre *et al.*, 2012] for the more complete 16S data set.

Abbreviations

BL, body length. CASIZ, California Academy of Sciences (Invertebrate Zoology), San Francisco California, USA. CSUF, California State University Fullerton, USA. de, prefix abbreviation combined with unique identifier number for both DNA extractions and corresponding specimen vouchers formerly in the collections of D.J. Eernisse at CSUF. ICML-EMU, Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, UNAM, in Mazatlán, Sinaloa, Mexico. INVEMAR, Instituto de Investigaciones Marinas y Costeras, Colombia. MNHN, Muséum National d’Histoire Naturelle, Paris, France. NCB, Naturalis

Table 1. Specimens used in molecular analyses.
Species names followed by an asterisk are our reidentifications differing from earlier authors. The order of names corresponds approximately to their order in Figures 30, 31A, and 31B. Full data on Genbank accession numbers and geographical coordinates are provided in Supplementary Table S1.

Taxon	Specimen ID	MNHN Expedition	Station	Locality	Depth (m)
Callochiton puniceus	CASIZ-245258; de0107			Atlantic Ocean, Scotia Sea	93
Callochiton steinenii	CASIZ-245257; de2934			S. Georgia S. Sandw. Is., Shag Rocks	199
Ischnochiton rissoi	SBMNH-719321; de9591			Italy, Liguria	2
Stenosemus simplicissimus	CASIZ-245492; de2490			S. Georgia & S. Sandwich Islands	~200
Tonicia schrammi	UF450488; de4464			USA, Florida, off St. Petersburg	~30
Acanthochitona avicula	SBMNH-719323; de2080			USA, California, San Onofre	0
Acanthochitona avicula	SBMNH-719322; de2078			USA, California, San Onofre	0
Plaxiphora aurata	SBMNH-360540; de3409			Chile, Isla Grande de Chiloe, Matao	0
Belknapchiton macleani	NHMUK-20170073			Peru-Chile Trench	4050
Belknapchiton belknapi	SBMNH-704669; de6922			USA Alaska, Chatham Strait	440
Belknapchiton belknapi	ICML-EMU-11381; de4508			Mexico, off Baja Calif. Sur	657
Leptochiton nexus	SBMNH-704673; de2183			USA, California, off San Pedro	28
Hanleyella oldroydi	SBMNH-704674; de1424			USA, California, off San Pedro	28
Leptochiton cf. *darioi*	MNHN-IM-2013-56241	GUYANE 2014	CP4363	French Guiana	197-200
Leptochiton cf. *darioi*	MNHN-IM-2013-56688	GUYANE 2014	CP4363	French Guiana	197-200
Leptochiton rugatus	SBMNH-704670; de2509			USA, California, San Onofre	0
Leptochiton foresti	MNHN-IM-2013-66690	KAVIENG 2014	CP4418	Papua New Guinea	335-340
Leptochiton saitoi	MNHN-IM-2013-66494	EXBODI	CP3807	New Caledonia	352-372
Leptochiton saitoi	MNHN-IM-2013-66504	EXBODI	CP3800	New Caledonia	279-282
Leptochiton aff. *perscitus*	MNHN-IM-2013-66599	PANGLAO 2005	CP2361	Philippines	516-543
Leptochiton samadiae	MNHN-IM-2013-66624	PAPUA NIUGINI	CP4036	Papua New Guinea	505
Leptochiton samadiae	MNHN-IM-2013-66625	PAPUA NIUGINI	CP4036	Papua New Guinea	505
Leptochiton vanbellei	MNHN-IM-2013-66574	PAPUA NIUGINI	CP4039	Papua New Guinea	1022
Leptochiton vanbellei	MNHN-IM-2013-66637	PAPUA NIUGINI	CP3982	Papua New Guinea	724
Leptochiton dykei	MNHN-IM-2013-66600	PAPUA NIUGINI	CP3994	Papua New Guinea	650
Leptochiton dykei	MNHN-IM-2013-66641	PAPUA NIUGINI	CP3970	Papua New Guinea	573
Leptochiton rogeri	MNHN-IM-2013-40452	PAPUA NIUGINI	CP3994	Papua New Guinea	650
Leptochiton rogeri	MNHN-IM-2013-66634	PAPUA NIUGINI	CP3982	Papua New Guinea	724
Astrochiton *binghami*	MNHN-IM-2013-60073	KARUBENTHOS 2	CP4513	Guadeloupe	406-644
Astrochiton *binghami*	MNHN-IM-2013-60162	KARUBENTHOS 2	CP4512	Guadeloupe	409-532
Astrochiton *incongruus*	SIO S0219: M17067			off Costa Rica, Rio Bongo Scar	661
Nierstraszella lineata	SBMNH-704671; de0100			Japan, Mie, Owase	350
Nierstraszella lineata	MNHN-IM-2013-66512	MADEEP	CP4337	Solomon Sea, Ainto Bay	287-447
Nierstraszella lineata	MNHN-IM-2013-66513	MADEEP	CP4337	Island Region, Papua New Guinea	287-447
Nierstraszella lineata	CASIZ-187870; de3217			Philippines, Luzon Island	325
Nierstraszella lineata	CASIZ-187921(a); de3358			Philippines, Luzon Island	456
Nierstraszella lineata	MNHN-IM-2013-66514	MADEEP	CP4337	Island Region, Papua New Guinea	287-447
Nierstraszella lineata	MNHN-IM-2013-66631	PAPUA NIUGINI	CP3994	Papua New Guinea	648-652
Nierstraszella lineata	MNHN-IM-2013-66632	PAPUA NIUGINI	CP3994	Papua New Guinea	648-652
Nierstraszella lineata	CASIZ-187885(c); de3352			Philippines, Luzon Island	281
Nierstraszella lineata	CASIZ-187929; de3359			Philippines, Luzon Island	478
Nierstraszella lineata	ZSM-20034397			Japan, Suruga Bay	not listed
Nierstraszella lineata	MNHN-IM-2009-10307	SANTO2006	AT92	Vanuatu	722-780
Nierstraszella lineata	MNHN-IM-2009-10301	SANTO2006	AT92	Vanuatu	722-780
Nierstraszella lineata	MNHN-IM-2009-10308	SANTO2006	AT127	Vanuatu	562-580
Nierstraszella lineata	none listed	PANGLAO 2005	CP2380	Philippines	150-163
Nierstraszella lineata	CASIZ-187885(a); de3350			Philippines, Luzon Island	281
Nierstraszella lineata	CASIZ-187885(b); de3351			Philippines, Luzon Island	281
*Nierstraszella lineata**	1816P1			China	–
*Nierstraszella lineata**	1956P1			China	–
Rissochiton *vietnamensis*	MNHN-IM-2013-46415	MADEEP	CP4339	Island Region, Papua New Guinea	510-743

Taxon	Specimen ID	MNHN Expedition	Station	Locality	Depth (m)
Rissochiton *vietnamensis*	MNHN-IM-2013-66569	MADEEP	CP4339	Island Region, Papua New Guinea	510-743
Rissochiton *vietnamensis*	MNHN-IM-2013-66614	PAPUA NIUGINI	CP3994	Papua New Guinea	648-652
Rissochiton *vietnamensis*	MNHN-IM-2013-66621	PAPUA NIUGINI	CP4006	Papua New Guinea	440-475
Rissochiton *vietnamensis*	MNHN-IM-2013-66613	PAPUA NIUGINI	CP3994	Papua New Guinea	648-652
Rissochiton *vietnamensis*	MNHN-IM-2013-66620	PAPUA NIUGINI	CP4006	Papua New Guinea	440-475
Rissochiton *vietnamensis*	MNHN-IM-2013-66570	MADEEP	CP4339	Island Region, Papua New Guinea	510-743
Rissochiton *vietnamensis*	MNHN-IM-2013-66622	PAPUA NIUGINI	CP4006	Papua New Guinea	440-475
Rissochiton *vietnamensis*	MNHN-IM-2013-66615	PAPUA NIUGINI	CP3994	Papua New Guinea	650
Rissochiton *vietnamensis**	none listed	BOA1	CP2462	Vanuatu	618-641
Rissochiton *vietnamensis**	none listed	PANGLAO 2005	CP2356	Philippines	1764
Rissochiton *andamanicus*	MNHN-IM-2013-16529	PAPUA NIUGINI	CP3961	Papua New Guinea	513
Rissochiton *andamanicus*	MNHN-IM-2013-66519	MADEEP	CP4337	Island Region, Papua New Guinea	287-447
Rissochiton *andamanicus*	MNHN-IM-2013-66520	MADEEP	CP4337	Island Region, Papua New Guinea	287-447
Rissochiton *andamanicus*	MNHN-IM-2013-66521	MADEEP	CP4337	Island Region, Papua New Guinea	287-447
Rissochiton *andamanicus*	MNHN-IM-2013-66571	PAPUA NIUGINI	CP4008	Papua New Guinea	500-555
Rissochiton *andamanicus*	MNHN-IM-2013-66572	PAPUA NIUGINI	CP4008	Papua New Guinea	500-555
Rissochiton *andamanicus*	MNHN-IM-2013-66573	PAPUA NIUGINI	CP4008	Papua New Guinea	500-555
Rissochiton *andamanicus*	MNHN-IM-2013-66645	AURORA 2007	CP2658	Philippines	422-431
Rissochiton *andamanicus*	none listed	PANGLAO 2005	CP2385	Philippines	982-989
Rissochiton quincuncialis sp. nov.	MNHN-IM-2013-66578	PAPUA NIUGINI	CP4039	Papua New Guinea	1022
Rissochiton quincuncialis sp. nov.	MNHN-IM-2013-16743	PAPUA NIUGINI	CP3963	Papua New Guinea	960-980
Rissochiton quincuncialis sp. nov.	MNHN-IM-2013-44877	MADEEP	CP4251	Papua New Guinea	842-933
Rissochiton quincuncialis sp. nov.	MNHN-IM-2013-66579	PAPUA NIUGINI	CP4039	Papua New Guinea	1022
Rissochiton quincuncialis sp. nov.	MNHN-IM-2013-66580	PAPUA NIUGINI	CP4039	Papua New Guinea	1022
Rissochiton *rissoi*	MNHN-IM-2013-16739	PAPUA NIUGINI	CP3963	Papua New Guinea	960-980
Rissochiton *rissoi*	MNHN-IM-2013-66646	AURORA 2007	CC2704	Philippines	1347-1392
Rissochiton *rissoi*	MNHN-IM-2013-66647	AURORA 2007	CP2684	Philippines	1413-1449
Rissochiton *rissoi*	MNHN-IM-2013-44878	MADEEP	CP4251	Papua New Guinea	842-933
Rissochiton *rissoi*	MNHN-IM-2013-17061	EXBODI	CP3917	New Caledonia	753-951
Rissochiton *rissoi*	MNHN-IM-2013-17022	PAPUA NIUGINI	CP3965	Papua New Guinea	980-985
Rissochiton *rissoi*	MNHN-IM-2013-66679	PAPUA NIUGINI	CP3967	Papua New Guinea	980
Rissochiton *rissoi**	none listed	SALOMON2	CP2246	Solomon Islands	618-626
Rissochiton *rissoi**	none listed	PANGLAO 2005	CP2385	Philippines	982-989
Rissochiton cf. *rissoi*	MNHN-IM-2013-66695	KAVIENG 2014	CP4435	Papua New Guinea	1218-1252
Rissochiton cf. *rissoi*	MNHN-IM-2013-66696	KAVIENG 2014	CP4435	Papua New Guinea	1218-1252

Biodiversity Center, Leiden, Netherlands. NMNH, National Museum of Natural History, Washington, D.C., USA. Stn, station. SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, USA. SIO, Benthic Invertebrate Collection, Scripps Institute of Oceanography. UF, University of Florida Museum of Natural History, USA. YPM, Yale Peabody Museum, Newhaven, Connecticut, USA. ZIN, Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia. ZMA, Zoölogisch Museum Amsterdam, Netherlands, but now material is held in Naturalis Biodiversity Center, Leiden.

Systematics

Class Polyplacophora Gray, 1821
Subclass Neoloricata Bergenhayn, 1955
Order Lepidopleurida Thiele, 1909
Family Nierstraszellidae Sirenko, 1992

Family distribution. East Indian Ocean, West Pacific (from South Japan, Taiwan and Vietnam up to New Guinea and Solomon Islands), Gulf of Panama, Gulf of Tehuantepec, Mexico, Caribbean Sea, Gulf of Mexico, 260–4800 m, Jurassic–Recent.

Diagnosis. Animals of small and medium size (up to 45.0 mm). Tegmentum with or without granules. Pores of aesthetes with caps. Number of pores in one aesthete group is 6 to 45. Apophyses are wide. Ratio of width of an apophysis to the width of the jugal sinus is 0.53–1.45. Girdle clothed with ribbed or smooth spicules and scattered smooth needles. Radula is uniform. Central tooth narrow with longitudinal narrow rib and slightly widened base, first lateral tooth with a narrow blade and a long outward, forwardly directed wing, major lateral teeth with a bidentate cusp, the inner denticle much smaller. On each side are 8–21 gills arranged from valve VI to the anus in chitons, corresponding to BL 3.2–23.0 mm, accordingly. Xylophagy is likely a shared feeding mode, and specimens are typically associated with sunken wood.

Family composition. The family consists of three extant genera, including two restricted to the Indo-West Pacific: *Nierstraszella*, ***Rissochiton*** gen. nov., and a disjunct neotropical genus, ***Astrochiton*** gen. nov. Despite much that is unknown about their ecology, the frequent association with sunken wood known from most species, and details of their intestinal tract (often observed to be filled with wood fibers and detritus) as summarized by Sirenko [2001, 2004], imply that xylophagy is shared by all species in the family, but is also known for other species of Lepidopleurida from the deep sea. Additionally, we propose that *Leptochiton shapovalovi* Sirenko, 2013, described from Jurassic deposits of the Middle Russian Sea, is provisionally attributed to this family. Evidence includes similarity with extant species, including the fossil valve sculpture of the tegmentum, the large number of aesthete pores (18–26), and the pattern of the aesthete locations within each clustered group. In addition, it was found in clay with numerous remains of fossil wood, consistent with the xylophagous lifestyle that is characteristic of this family [Sirenko, 2013].

Genus *Rissochiton* gen. nov.

Zoobank registration: urn:lsid:zoobank.org:act:0C65AC0A-E085-4D73-AC8B-528194FA6A28

Type species. *Lepidopleurus rissoi* Nierstrasz, 1905 (here designated).

Etymology. Named after Antoine Risso, French naturalist of the 18th to 19th centuries (b. 1777, d. 1845).

Genus distribution. East Indian Ocean, West Pacific (from South Japan, Taiwan and Vietnam up to New Guinea and Solomon Islands), 260–4800 m. Jurassic–Recent.

Diagnosis. Small to medium sized chiton. Tegmentum with or without granules. Number of pores in one aesthete group is 6 to 20. Girdle clothed with ribbed spicules and scattered smooth needles

Genus composition. The genus consists of five Recent species: ***Rissochiton** rissoi, **R.** vietnamensis, **R.** andamanicus, **R. formosaensis*** sp. nov. and ***R. quincuncialis*** sp. nov. The fossil *Leptochiton shapovalovi* Sirenko, 2013 is conditionally placed in this genus.

Remarks. In ***R.** rissoi* and ***R.** vietnamensis*, the longitudinal arrangement of tegmentum granules on the central areas prevails, while in the other three species (***R.** andamanicus, **R. formosaensis*** sp. nov. and ***R. quincuncialis*** sp. nov.) the granules, or in their absence the aesthete groups, are arranged in quincunx. Complicating a simple division into two groups, ***R. formosaensis*** sp. nov. and ***R. quincuncialis*** sp. nov., also have a longitudinal arrangement of granules on the antemucronal areas, and ***R.** vietnamensis* occasionally has a quincuncial arrangement of granules on jugal areas. To further clarify, granules on the surface of tegmentum are small, often rounded or oval calcareous bumps, not to be confused with groups of adhering aesthete caps on a smooth tegmentum surface (false granules).

Key for identification of species of genus ***Rissochiton*** gen. nov.

Jump to step in parentheses if false.

1(8) Any granules on tegmentum are real, not merely aesthete cap groupings 2
2(5) Granules of tegmentum in central areas arranged in longitudinal rows 3
3(4) Ratio of width of apophysis to width of jugal sinus less than 1.0 ***R.** vietnamensis*
4(3) Ratio of width of apophysis to width of jugal sinus exceeds 1.0 ***R**. rissoi*
5(2) Granules of tegmentum in central areas of intermediate valves arranged in quincunx 6
6(7) Ratio of width of apophysis to width of jugal sinus less than 0.9 ***R. formosaensis*** sp. nov.
7(6) Ratio of width of apophysis to width of jugal sinus exceeds 0.9 ***R. quincuncialis*** sp. nov.
8(1) No real granules, but possibly false granules consisting of aesthete caps on a smooth tegmentum surface ***R**. andamanicus*

Rissochiton *rissoi* (Nierstrasz, 1905), comb. nov.

(Figs 1–6)

Lepidopleurus rissoi Nierstrasz, 1905: 6, figs 5, 52–55; Ferreira, 1979: 163, figs 30–32.

Leptochiton rissoi. – Ferreira, 1981: 36, figs 1–2 (=*L. americanus* Kaas, Van Belle, 1985) (not *Lepidopleurus rissoi* Nierstrasz, 1905, fide Kaas, Van Belle [1985]).

Leptochiton (*Leptochiton*) *rissoi*. – Kaas, Van Belle, 1985: 110, fig. 48, map 24.

Type material. Lectotype (ZMA. MOLL 138601) designated by Ferreira [1979].

Type locality. Celebes Sea, N of Manado, 3°27.1’N 125°18.7’E, 2053 m, *Siboga* St. 126.

Material examined. 25 specimens. Lectotype; **Indian**

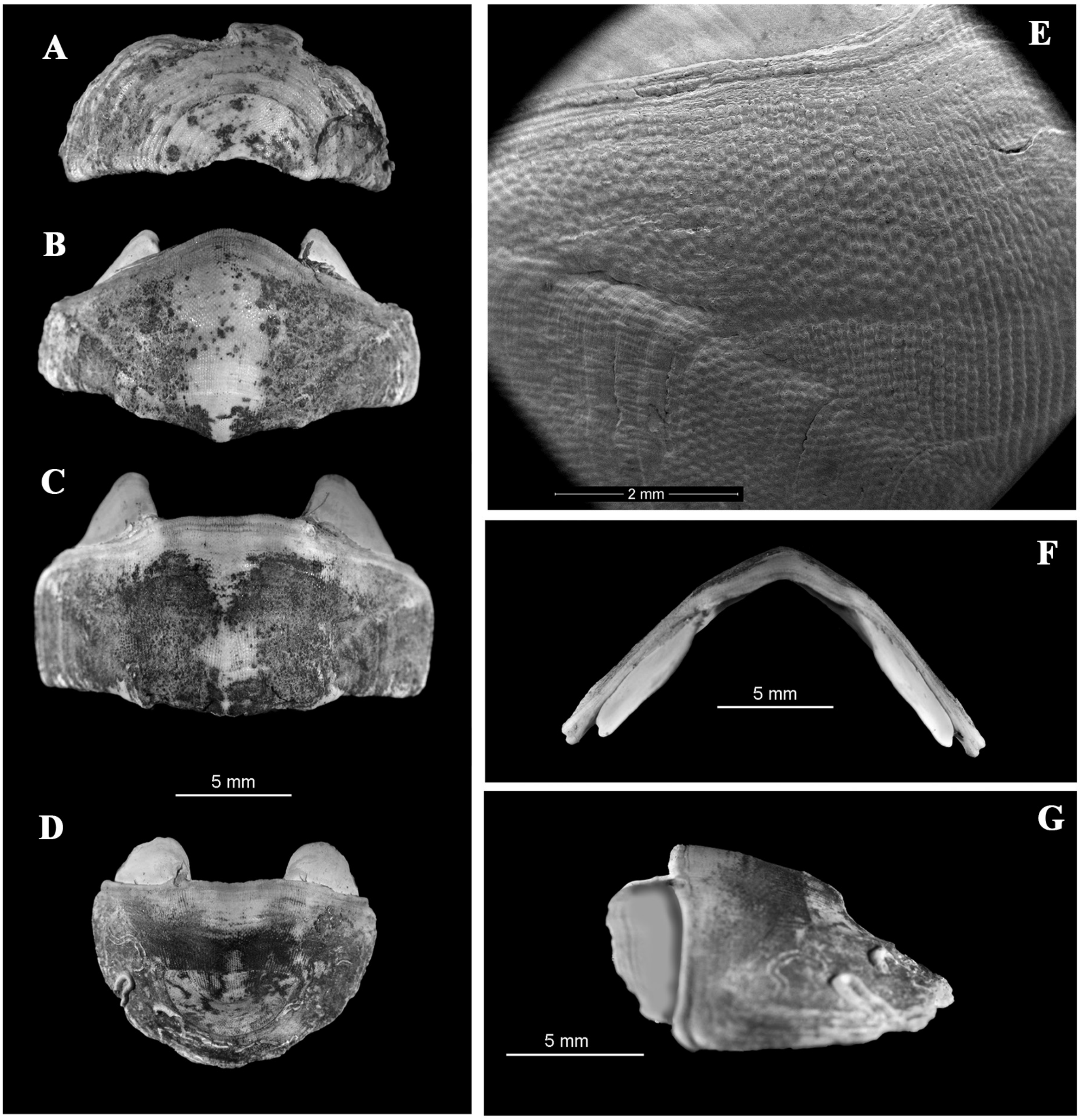

FIG. 1. ***Rissochiton*** *rissoi*, Indian Ocean, off Sumatra Island, BL 45.0 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. **E.** Valve VI, detail of tegmentum in central and lateral areas. **F.** Valve V, rostral view. **G.** Valve VIII, lateral view.

Ocean, off Sumatra Island, R/V Professor Mesyatsev, cruise 7, trawl N7, 3°46'–3°31'N, 95°00'–95°52'E, 800–875 m, 1 spm, BL 45.0 mm, 28.02.1979; **Pacific Ocean, Philippines**, PANGLAO 2005, stn CP2386, 08°49'N, 123°02'E, 2120–2149 m, 1 spm (MNHN-IM-2012-25436), BL 9.0 mm, 29.05.2005; **Solomon Islands,** SALOMON 1, stn CP1752, 09°07'S, 159°53'E, 896–912 m, 1 spm (MNHN-IM-2012-25435), BL 35.0 mm, 25.09.2001; stn CP1754, 09°00'S, 159°49'E, 26/09/2001, 1169–1203 m, 2 spms (MNHN-IM-2012-25434), BL 9.0–10.0 mm, 26.09.2001; SALOMON 2, stn CP2253, 07°27'S, 156°15'E, 1200–1218 m, 1 spm (MNHN-IM-2013-25433), BL 13.0 mm, 02.11.2004; SALOMON BOA, stn CP2779, 09°01'S, 159°44'E, 1090–1214 m, 1 spm (MNHN-IM-2012-25432), BL 18.0 mm, 12.09.2007; **New Guinea**, PAPUA NIUGINI, stn CP3963, 05°06'S, 145°63'E, 960–980 m, 1 spm (MNHN-IM-2013-16920), BL 04.0 mm, 30.11.2012; stn CP4039, 04°19'S, 145°37'E, 1000–1045 m, 6 spms (MNHN-IM-2012-25431), BL 11.0–30.0 mm, 17.12.2012; MADEEP, stn CP4256, 02°51'S, 150°56'E, 1200–1274 m, 2 spms (MNHN-IM-2013-45018 + MNHN-IM-2019-22780), BL 7.0–10.0 mm, 24.04.2014; KAVIENG 2014, stn CP4434, 02°19'S, 150°47'E, 1066–1200 m, 4 spms (MNHN-IM-2013-67021 + MNHN-IM-2019-22781 + MNHN-IM-2019-22782 + MNHN-IM-2019-22783), BL 10.0–14.0 mm, 30.08.2014; stn CP4436, 02°16'S, 150°45'E, 1128–1135 m, 4 spms (MNHN-IM-2013-67023 + MNHN-IM-2019-22784 + MNHN-IM-2019-22785 + MNHN-IM-2019-22786), BL 8.0–15.0 mm, 30.08.2014.

Distribution. Indian Ocean (off Sumatra Island), Pacific Ocean, Philippines, Indonesia, New Guinea, Solomon Islands, 875–2120 m, more common deeper than 1000 m.

Remarks. We compared lectotype of this species (ZMA. MOLL 138601) with other studied specimens and found the specimen from off Sumatra

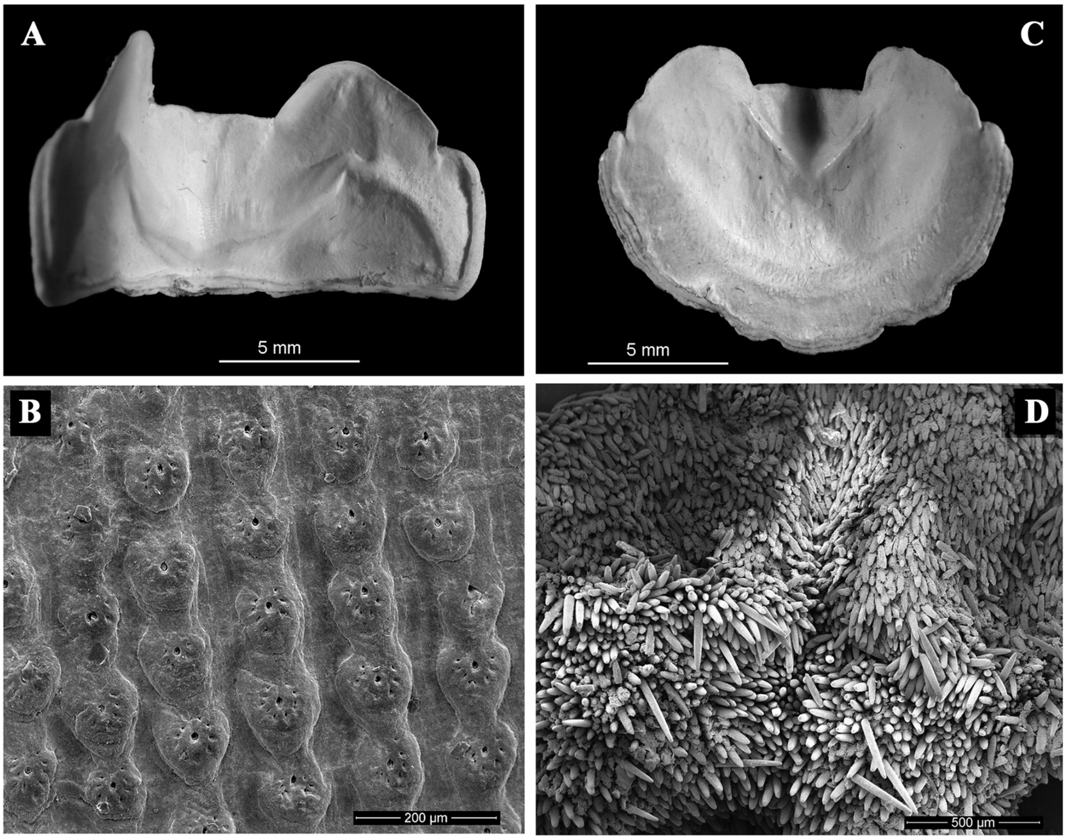

FIG. 2. ***Rissochiton*** *rissoi*, Indian Ocean, off Sumatra Island, BL 45.0 mm. **A.** Valve IV, ventral view. **B.** Valve VI, detail of tegmentum in central area. **C.** Valve VIII, ventral view. **D.** Dorsal spicules and needles, virginal needles, ventral spicules.

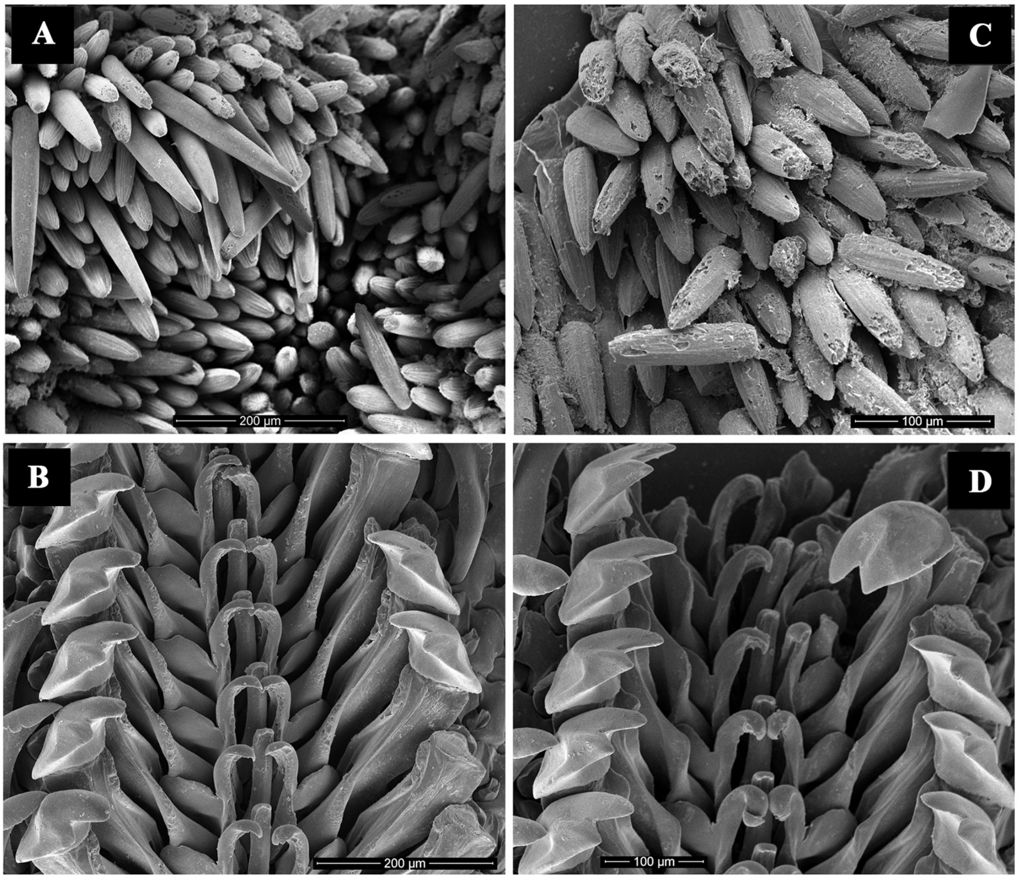

FIG. 3. ***Rissochiton*** *rissoi*, Indian Ocean, off Sumatra Island, BL 45.0 mm. **A.** Dorsal spicules and needles. **B**, **D.** Central, first lateral and major lateral teeth of radula, more anterior part (B). **C.** Dorsal spicules.

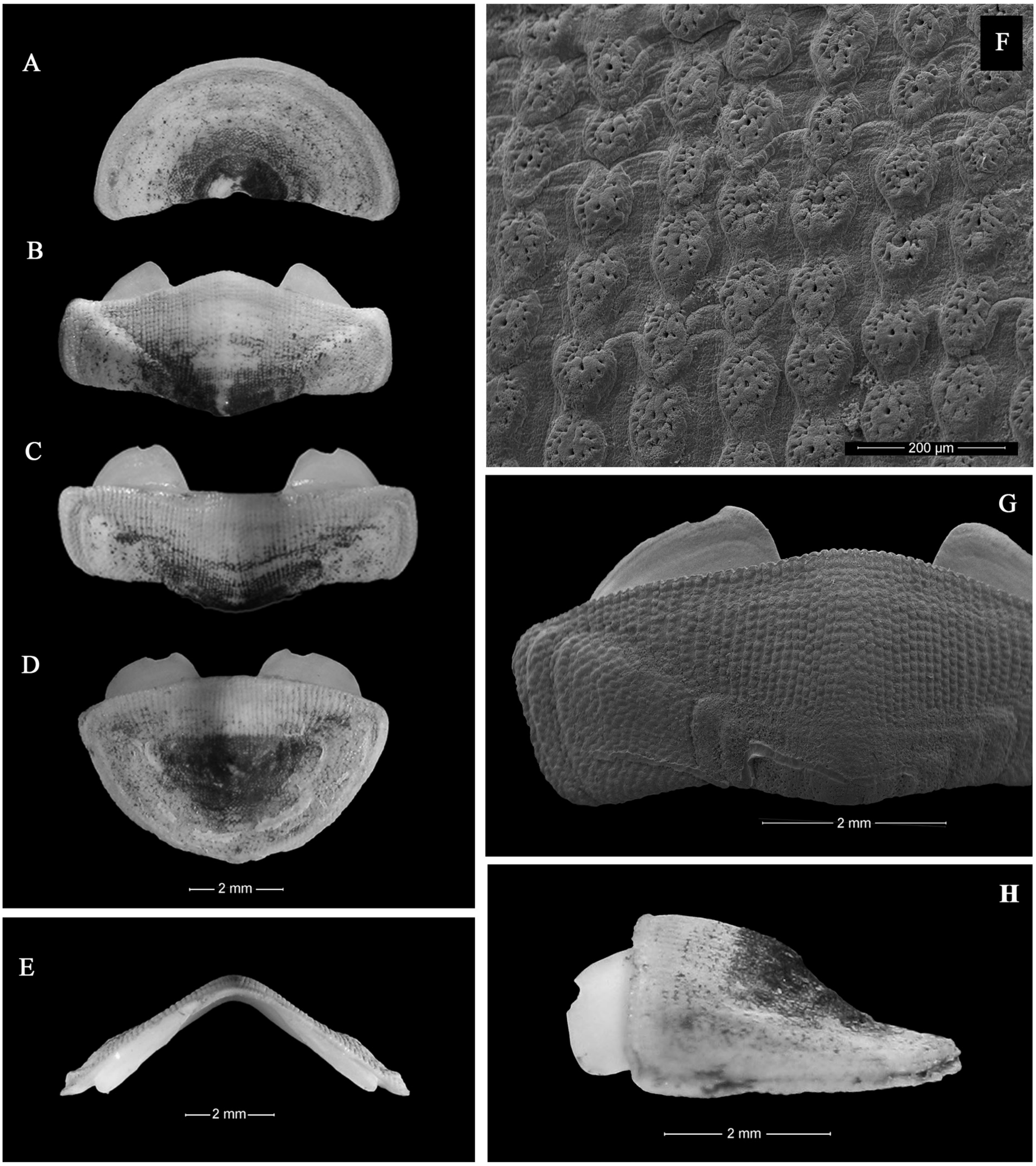

FIG. 4. **Rissochiton** *rissoi*, Solomon Islands, (MNHN-IM-2012-25432), BL 18 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. **E.** Valve V, rostral view. **F.** Valve V, detail of tegmentum in central areas. **G.** Valve VII, dorsal view. **H.** Valve VIII, lateral view.

Island in the Indian Ocean to be most similar to it. Kaas and Van Belle [1985] reported and illustrated a major lateral tooth of radula of the lectotype to be unidentate but they were mistaken. These teeth are bidentate in the lectotype, as in all the radulas of the specimens shown here (Figs. 3B, 3D, 6A). The number of pores of aesthetes in one aesthete group in this species varies from 6 to 20, regardless of body size, which together with longitudinal arrangement of rows of granules, is like ***R.*** *vietnamensis*. However, as detailed in Remarks for the latter species, the apophyses are much wider in ***R.*** *rissoi*, and this is the main difference between them. The ratio of the width of the apophysis to the width of the jugal sinus is always greater than 1 in ***R.*** *rissoi* (vs less than 1 in ***R.*** *vietnamensis*). The color of the shell in ***R.*** *rissoi* is usually white, whereas it is yellowish in ***R.*** *vietnamensis*.

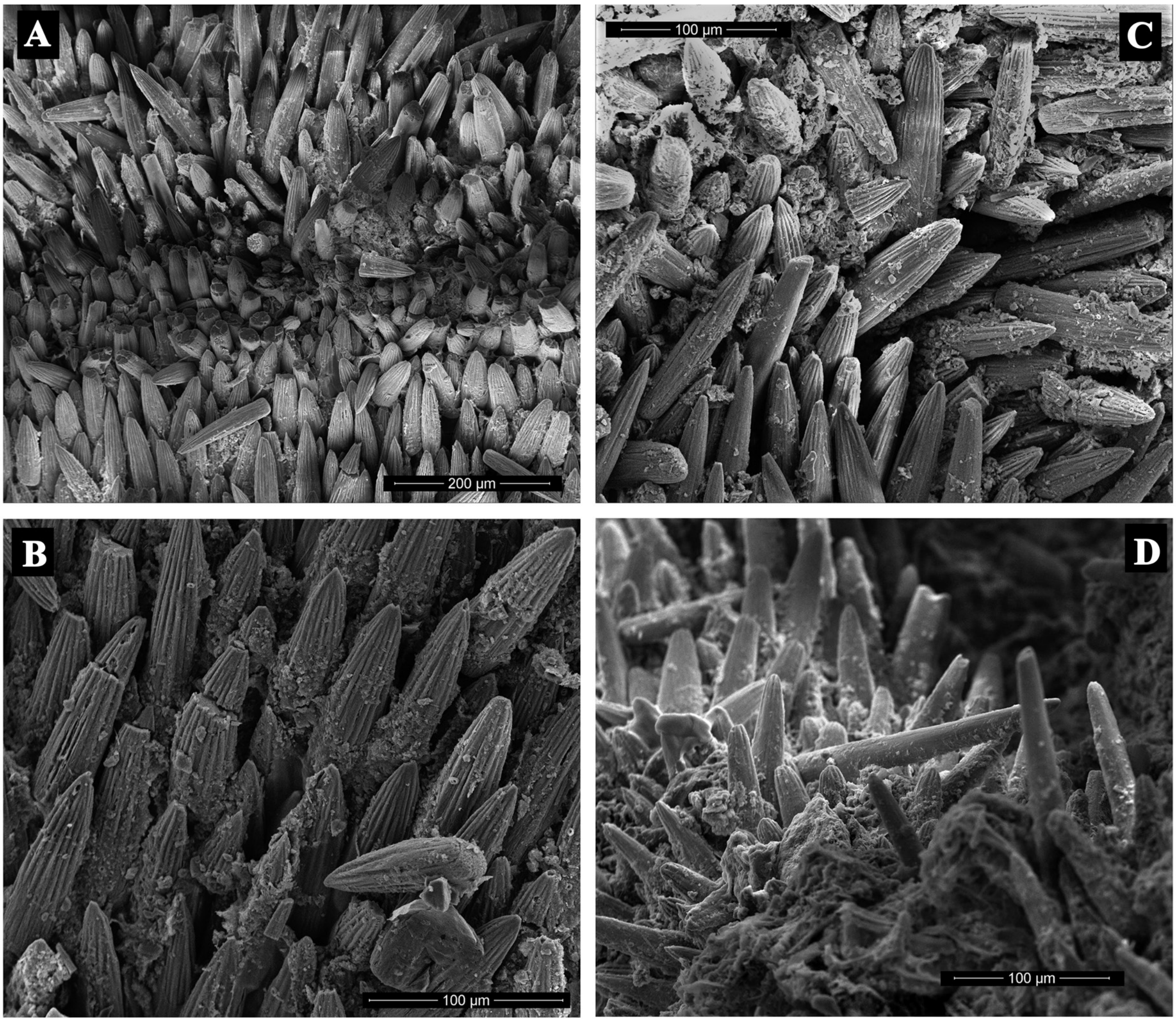

FIG. 5. ***Rissochiton** rissoi*, Solomon Islands, (MNHN-IM-2012-25432), BL 18 mm. **A, C.** Dorsal spicules, marginal needles and ventral spicules. **B.** Ventral spicules. **D.** Marginal needles and dorsal spicules.

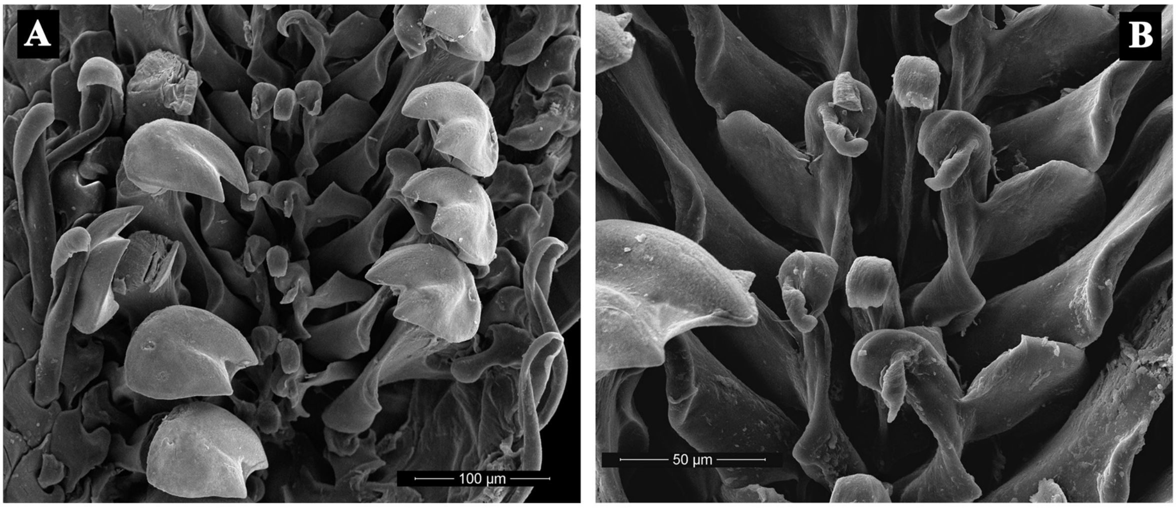

FIG. 6. ***Rissochiton** rissoi*, Solomon Islands, (MNHN-IM-2012-25432), BL 18 mm. **A.** Part of radula. **B.** Central and first lateral teeth of radula.

***Rissochiton** vietnamensis* (Sirenko, 1998), comb. nov.

(Figs 7–9)

Leptochiton vietnamensis Sirenko, 1998: 1, figs 1–3; 2001: 45, figs 31–47, 168–171; 2004: 112, 115, table 1; Schwabe, 2006: 19–22, pl. 1 figs A–D, pl. 2 figs A–F; Sigwart *et al.*, 2011: 567, 569, table 3, fig. 2; Yearsley, Sigwart 2011: table 1.

Leptochiton longispinus Saito, 2001: 111, figs 6, 7, pl. 1: 4–6; Sirenko, 2020: 473, figs 6–8. (new synonymy herein).

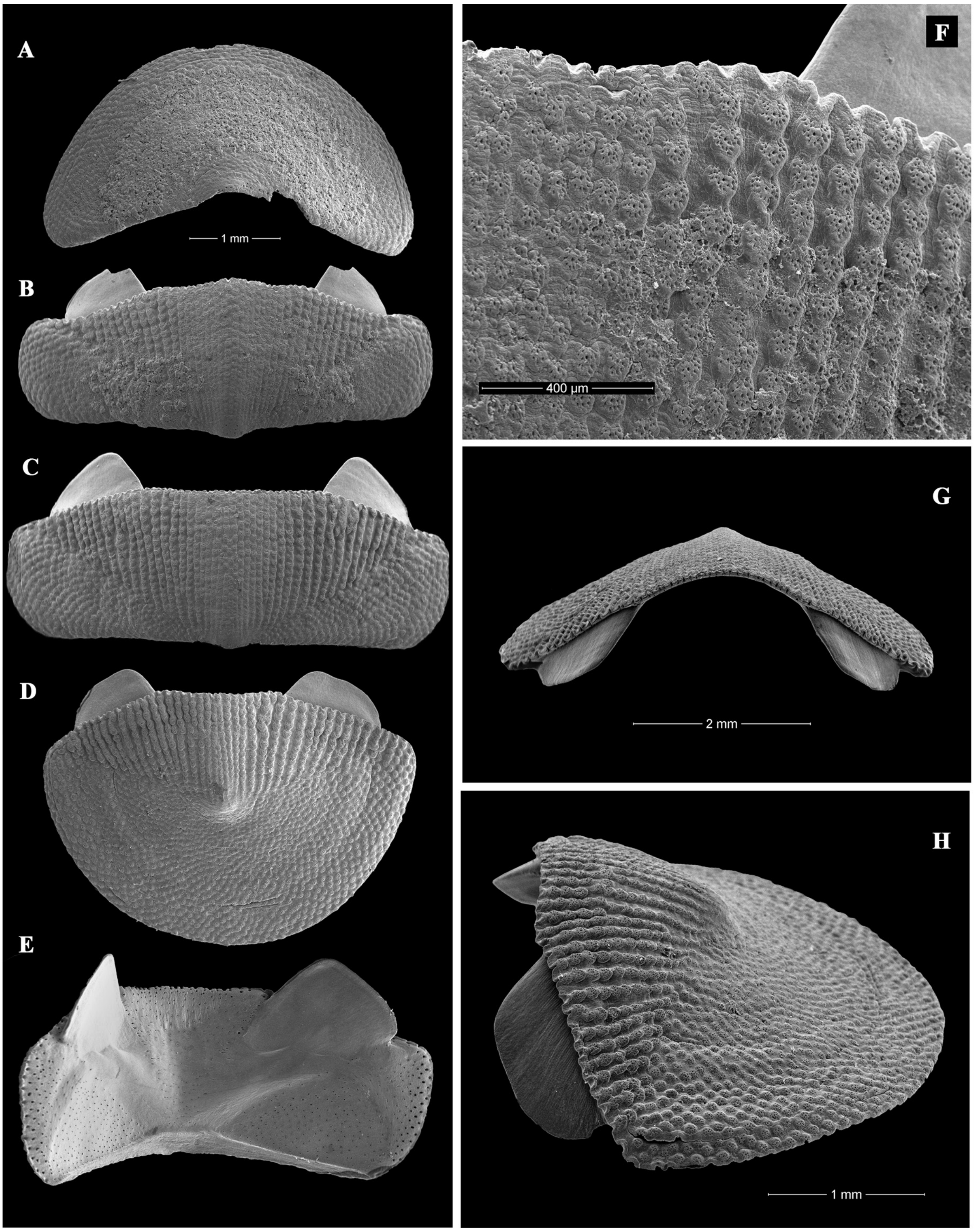

FIG. 7. ***Rissochiton** vietnamensis*, Papua New Guinea, stn CP4000 (MNHN-IM-2013-49572), BL 10 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. **E.** Valve IV, ventral view. **F.** Valve V, detail of tegmentum in central area. **G.** Valve V, rostral view. **H.** Valve VIII, lateral view.

Leptochiton rissoi. – Sirenko, 2020: 475, figs 9–11 (not of Nierstrasz 1905).

Type material. Holotype (ZIN 2145), paratype (ZIN 2146).

Type locality. South China Sea, 11°09'S, 110°02´E, 700 m.

Material examined. 56 specimens. **Philippines, Sulu Sea**, R/V Vitjaz,, cruise 57, stn.7237, 7°39.9'–7°31.1'N, 121°32.2'–121°22.5'E, 4800 m, 21 spms (ZIN 2376) BL 9.0–16.0 mm, 28.02.1975; AURORA 2007, stn CC2701, 14°48'N, 123°16'E, 709–718 m, 1 spm (MNHN-IM-2013-67052), BL 13.0 mm, 27.05.2007; **Solomon Islands**, SALOMON 1, stn CP1751, 09°10'S, 159°53'E, 749–799 m, 2 spms (MNHN-IM-2012-25430), BL 7.0–9.0 mm, 25.09.2001; **New Guinea**. PAPUA NEUGINI, stn CP3964, 05°07'S,

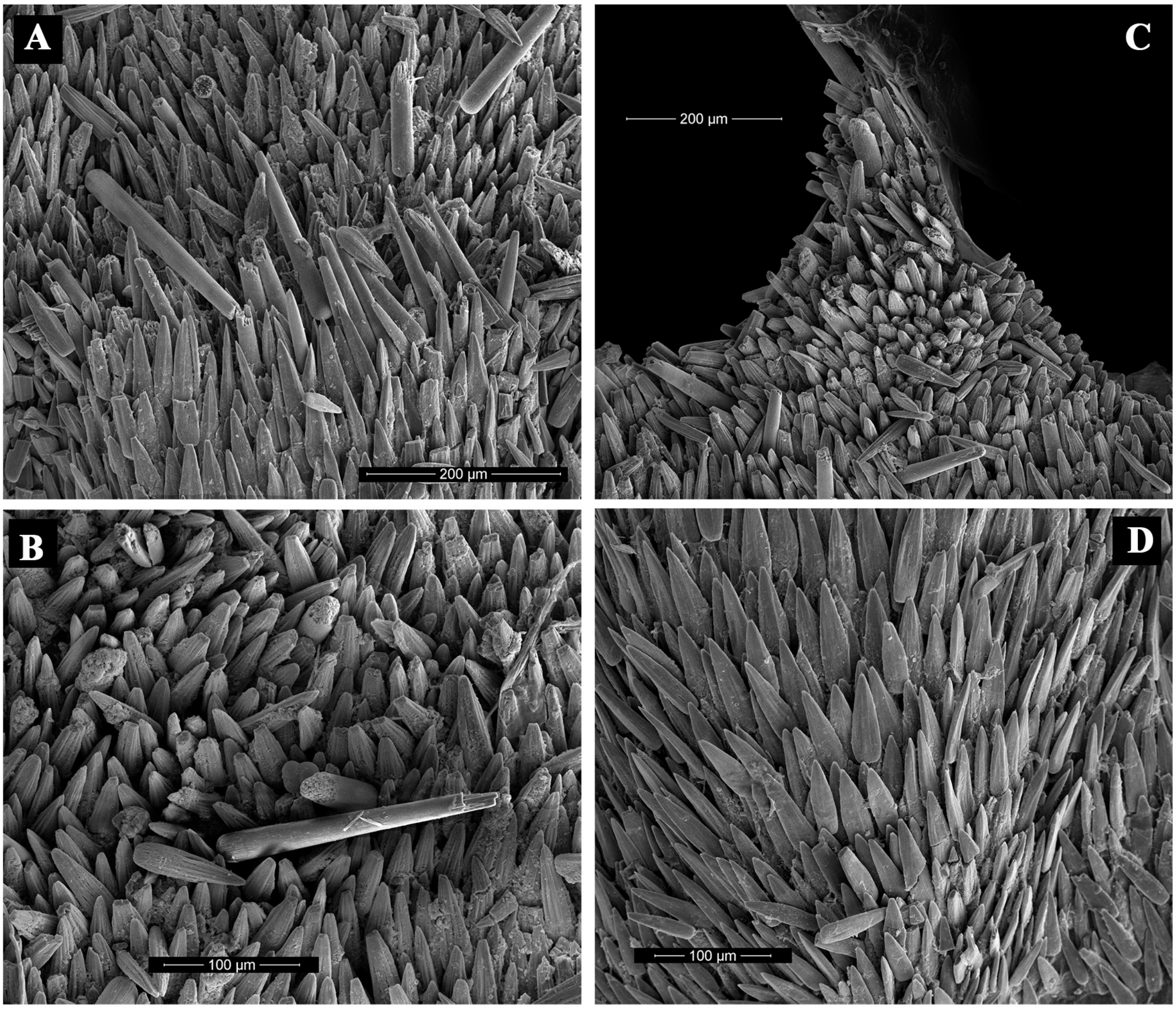

FIG. 8. ***Rissochiton** vietnamensis*, Papua New Guinea, stn CP4000 (MNHN-IM-2013-49572), BL 10 mm. **A.** Dorsal spicules and needles, marginal needles and ventral spicules. **B.** Dorsal spicules and needles. **C.** Sutural spicules and needles. **D.** Ventral spicules.

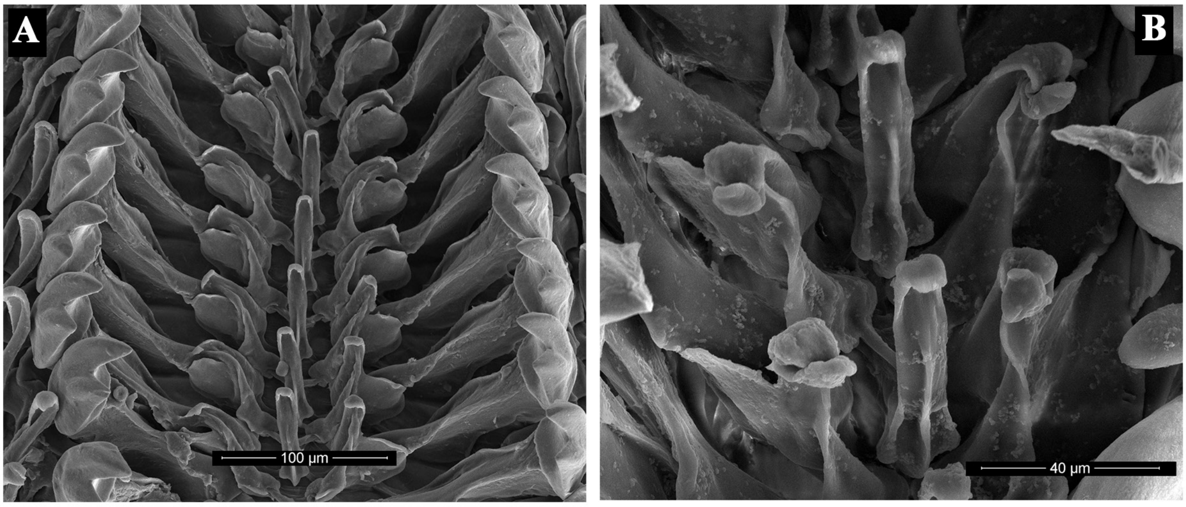

FIG. 9. ***Rissochiton** vietnamensis*, Papua New Guinea, stn CP4000 (MNHN-IM-2013-49572), BL 10 mm. **A.** Part of radula. **B.** Central, first lateral teeth of radula.

145°50'E, 527–539 m, 1 spm (MNHN-IM-2013-16749), BL 8.0 mm, 30.11.2012; stn CP4000, 06°47'S, 147°14'E, 650 m, 1 spms (MNHN-IM-2013-49572), BL 10.0 mm, 10.12.2012; stn CP4038, 04°27'S, 145°34'E, 800–840 m, 4 spms (MNHN-IM-2012-25429), BL 5.0–14.0 mm, 17.12.2012; stn CP4077, 04°02'S, 144°56'E, 860–885 m, 2 spms (MNHN-IM-2013-49572 + MNHN-IM-2019-22792), BL 4.0–6.0 mm, 24.12.2012; MADEEP, stn CP4246, 04°07'S, 148°09'E, 22/04/2014, 695–899 m, 2 spms (MNHN-IM-2013-45230+ MNHN-IM-2019-22793), BL 10.0–11.0 mm, 22.04.2014; stn CP4260, 02°54'S, 151°05'E, 350–847 m, 2 spms (MNHN-IM-2013-45118, MNHN-IM-2013-67005), BL 11.0 mm, 25.04.2014; stn CP4266, 04°35'S, 152°25'E, 575–616 m, 3 spms (MNHN-IM-2013-45118, MNHN-IM-2013-67005 + MNHN-IM-2019-22794), BL 7.0–9.0 mm, 26.04.2014; stn CP4330, 06°08'S, 149°12'E, 315–625 m, 4 spms (MNHN-IM-2013-45983, MNHN-IM-2013-67004 + MNHN-IM-2019-22795 + MNHN-IM-2019-22796), BL 8.0–9.0 mm, 6.5.2014; KAVIENG 2014, stn CP4423, 02°20'S, 150°38'E, 550–649 m, 4 spms (MNHN-IM-2013-58140, MNHN-IM-2013-67027 + MNHN-IM-2019-22797 + MNHN-IM-2019-22798), BL 7.0–8.0 mm, 28.08.2014; stn CP4429, 02°19'S, 150°39'E, 685–824 m, 1 spm (MNHN-IM-2013-67019), BL 08.0 mm, 29.08.2014; stn CP4434, 02°19'S, 150°47'E, 1066–1200 m, 1 spm (MNHN-IM-2013-67021), BL 11.0 mm, 30.08.2014.

Distribution. Indian Ocean (Andaman Sea), Philippines, Vietnam, New Guinea, Solomon Islands, 539–4800 m, more common at depths less than 800 m.

Remarks. ***R.*** *vietnamensis* is very similar to ***R.*** *rissoi* and differs from the latter in having wider jugal sinus, ratio of width of apophyses to width of jugal sinus is 0.69–0.83 in ***R.*** *vietnamensis* and 1.05–1.27 in ***R.*** *rissoi*. Moreover, the tail valve is wider than the head valve in ***R.*** *vietnamensis* (vs tail valve narrower than head valve in *R. rissoi*), lateral areas are less raised in ***R.*** *vietnamensis* than in ***R.*** *rissoi*, and color of valves is yellowish in ***R.*** *vietnamensis*, and white in ***R.*** *rissoi*.

Rissochiton *andamanicus*
(E. A. Smith, 1906), comb. nov.
(Figs 10–12)

Lepidopleurus andamanicus E. A. Smith, 1906: 251; Annandale, Stewart, 1909: pl. 23: figs 4, 4a; Winckworth, 1940:19.

Leptochiton (*Leptochiton*) *andamanicus*. – Kaas, Van Belle 1985: 118, fig. 52, map 38.

Nierstraszella lineata. – Sirenko,1992: 84, Schwabe *et al.*, 2008: 6 (part, not *Lepidopleurus lineatus* Nierstrasz 1905).

Nierstraszella andamanica. – Sigwart, 2009: 453, figs 1, 2, 4–7 (synonymy); Sigwart, Sirenko, 2012: 26 (synonymy); Sirenko, 2018: 329, fig. 37H.

Type material. Lectotype (BMNH 1906.10.12.86), designated by Kaas & Van Belle [1985]; and three paralectotypes (BMNH 1906.10.12.87-89).

Type locality. Bay of Bengal, off N Sentinel Id, Andaman Is, 432 m.

Material examined. 9 specimens. **Philippines,** PANGLAO 2005, CP2385, 08°51'S, 123°10'E, 982 m, 5 spms (MNHN-IM-2012-25428), BL 4.0–9.0 mm, 29.05.2005; CP2388, 09°27'S, 123°35'E, 762–786 m, 1 spm (MNHN-IM-2013-67046), BL 8.0 mm, 30.05.2005; **New Guinea,** BIOPAPUA, stn CP3710, 05°22'S, 145°48'E, 372–384 m, 2 spms (MNHN-IM-2013-67002 + MNHN-2019-22799), BL 4.0–6.0 mm, 05.10.2010; MADEEP, stn CP4331, 06°07'S, 149°12'E, 260 m, 1 spm (MNHN-IM-2013-46026), BL 9.0 mm, 06.05.2014.

Distribution. East Indian Ocean (Andaman Islands), West Pacific (Philippines, Indonesia, Vanuatu, Solomon Islands), 195–1775 m.

Remarks. All features of the shell, girdle and radula correspond to those of other species of the genus ***Rissochiton*** gen. nov. except for a lack of granules on the tegmentum, this species has a smooth tegmentum with no real granules on the tegmentum. There are only false granules created by caps sticking out of the pores of aesthetes that are easily removed with a knife.

Rissochiton formosaensis sp. nov.
(Figs 13–15)

Zoobank registration: urn:lsid:zoobank.org:act: D8815571-CBBF-4CDE-99B6-B5813F9B2F88

Leptochiton vietnamensis, – Sirenko, 2016: 45, figs 123–155, not of Sirenko, 1998.

Leptochiton sp. – Sirenko, 2018: 325, fig. 36A.

Type material. Holotype (MNHN-IM-2000-38521), paratype (MNHN-2000-38522).

Type locality. Taiwan, stn CP38, 21°32.1'N, 120°48.1'E, 1314–1317 m.

Etymology. Named after Formosa Island (former name of Taiwan Island).

Material examined. 12 spms **Taiwan**, Bashi channel N/O Fishery Researcher 1, TAIWAN 2000, stn CP38, 21°32'N, 120°48'E, 1314–1317 m, holotype MNHN-IM-2000-38521, BL 15.0 mm and paratype (MNHN-IM-2000-38522), BL 15.0 mm, 01.08.2000. Vanuatu. BOA1, stn CP2462, 16°38'S, 164°57´E, 618-641 m, 3 spms (MNHN-IM-2012-25428), BL 6.0–12.0 mm. **Solomon Islands.** SALOMON 1, stn CP1751, 09°10'S, 159°53´E, 749–799 m, 2 spms (MNHN-IM-2012-24527); stn CP1752, 09°07'S, 159°53´E, 896–912 m, 1 spm (MNHN-IM-2012-25426); stn CP1755, 08°58'S, 159°47´E, 1288–1313 m, 1 spm (MNHN-IM-2012-25425); SALOMON 2, stn CP2253, 07°26'S, 156°15´E, 1200–1218 m, 1 spm (MNHN-IM-2012-25424); SALOMON BOA3, stn CP2787, 08°31'S, 160°39´E, 570–885 m, 3 spms (MNHN-IM-2012-25423), BL 10.0–13.0 mm; **New Guinea**, PAPUA NIUGINI, stn CP3971, 04°37'S, 145°51'E, 832 m, 6 spms (MNHN-IM-2013-40465 + MNHN-IM-2019-22787 +MNHN-IM-2019-22788 + MNHN-IM-2019-22789 + MNHN-IM-2019-22790 + MNHN-IM-2019-22791), BL 7.0 mm, 04.12.2012.

Distribution. Taiwan, Vanuatu, Solomon Islands, 641–1314 m.

Diagnosis. Animal of a small size (maximal BL 15.0 mm). Shell low elevated, carinated. Intermediate valves rectangular. Head valve slightly narrower than the tail valve, mucro anterior, anterior slope convex, posterior slope almost straight. Tegmentum with low, rounded oval granules arranged in quincunx in all areas. Each granule with 6–8 pores of aesthetes. Jugal sinus rather wide, ratio of width of apophyses to width of jugal sinus 0.63–0.83. Girdle densely

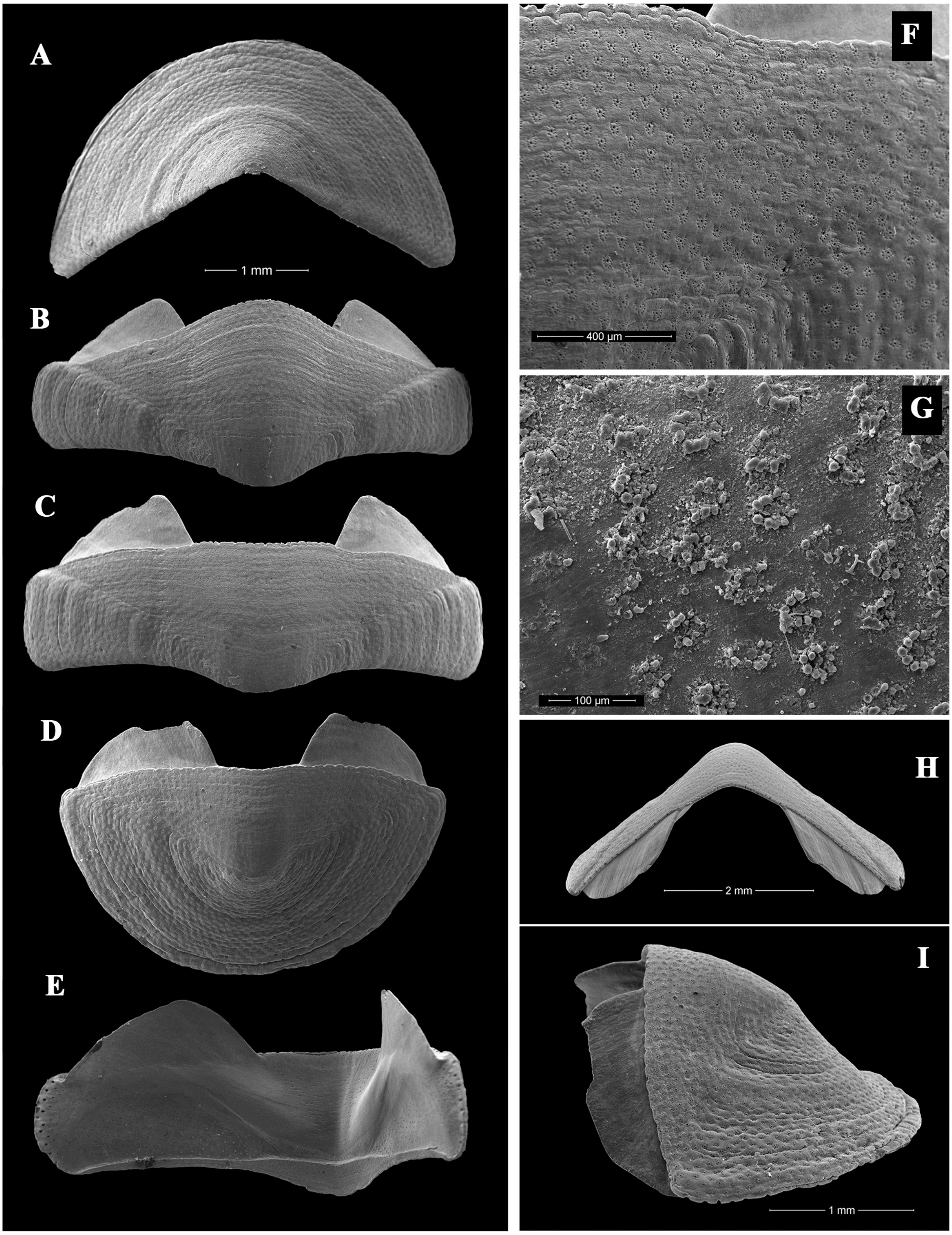

FIG. 10. ***Rissochiton** andamanicus*, Philippines, stn CP2385, (MNHN-IM-2012-25428) BL 9.0 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. **E.** Valve IV, ventral view. **F.** Valve V, detail of treated tegmentum in central and lateral areas. **G.** Valve VII, detail of untreated tegmentum in central area. **H.** Valve V, rostral view. I. Valve VIII, lateral view.

covered with short, sharply pointed, longitudinally ribbed dorsal spicules and scattered long, smooth needles. Central teeth of radula narrow, elongate, widest at base, with longitudinal narrow rib and small, rounded blade, major lateral tooth with a bidentate cusp, the inner denticle much smaller. Gills 13 per side arranged from valve VI to the anus.

Description. Holotype 15.0 mm. Shell elongate

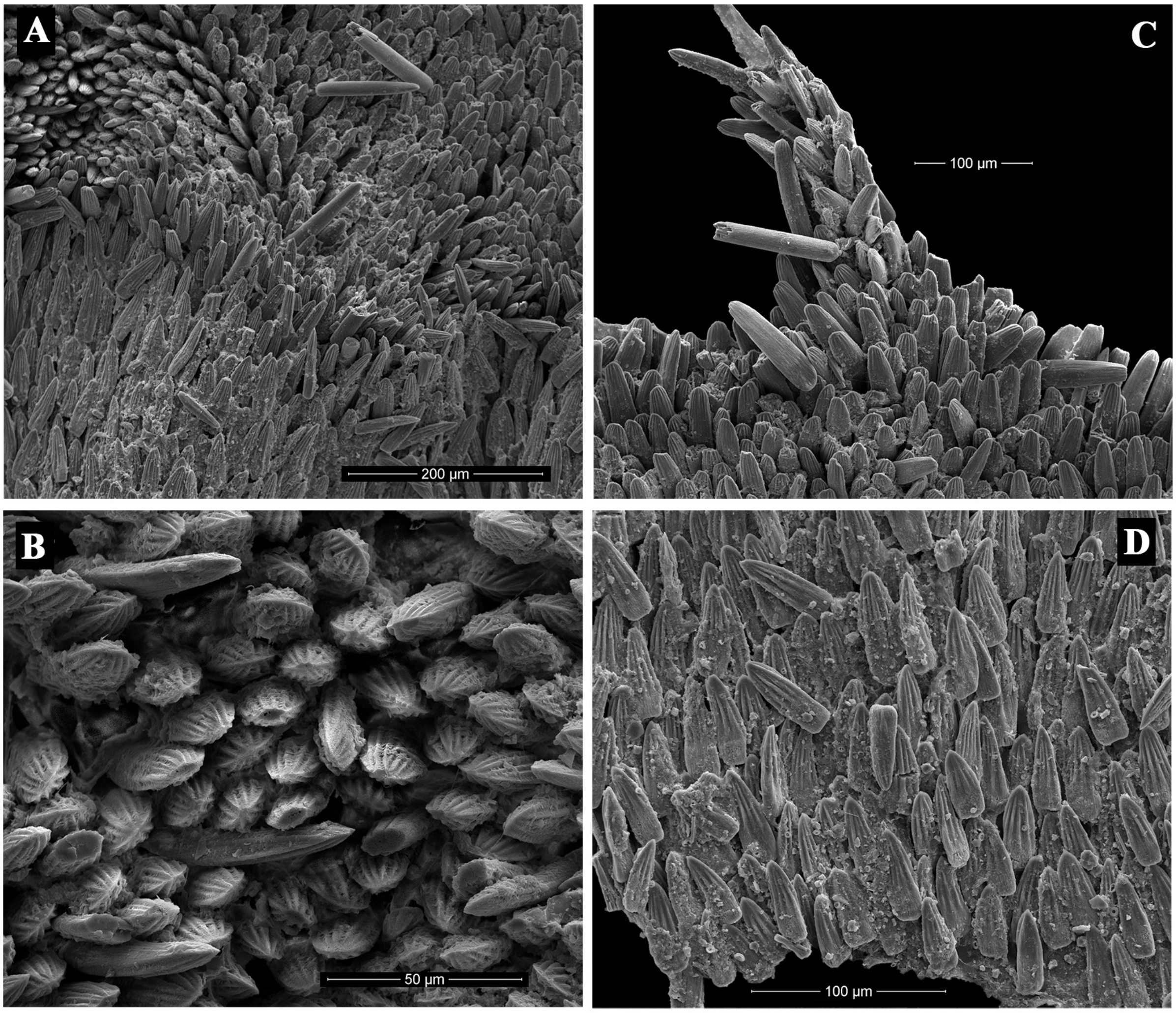

FIG. 11. ***Rissochiton*** *andamanicus*, Philippines, stn CP2385, (MNHN-IM-2012-25428) BL 9.0 mm. **A.** Dorsal spicules and needles, marginal needles and ventral spicules. **B.** Dorsal spicules. **C.** sutural needles and spicules. **D.** Ventral spicules.

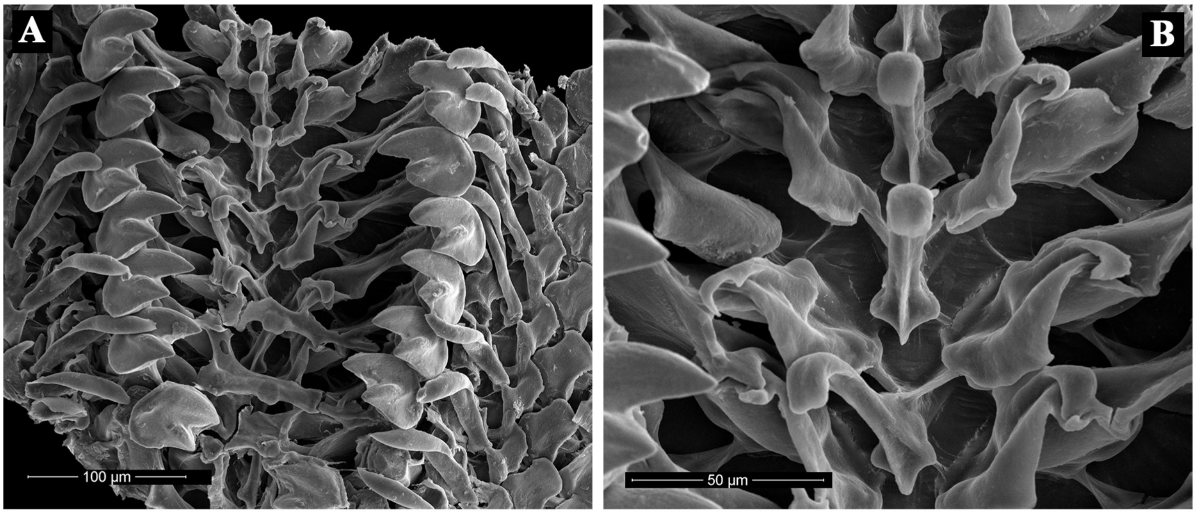

FIG. 12. ***Rissochiton*** *andamanicus*, Philippines, stn CP2385, (MNHN-IM-2012-25428) BL 9.0 mm. **A.** Part of radula. **B.** Central, first lateral teeth of radula.

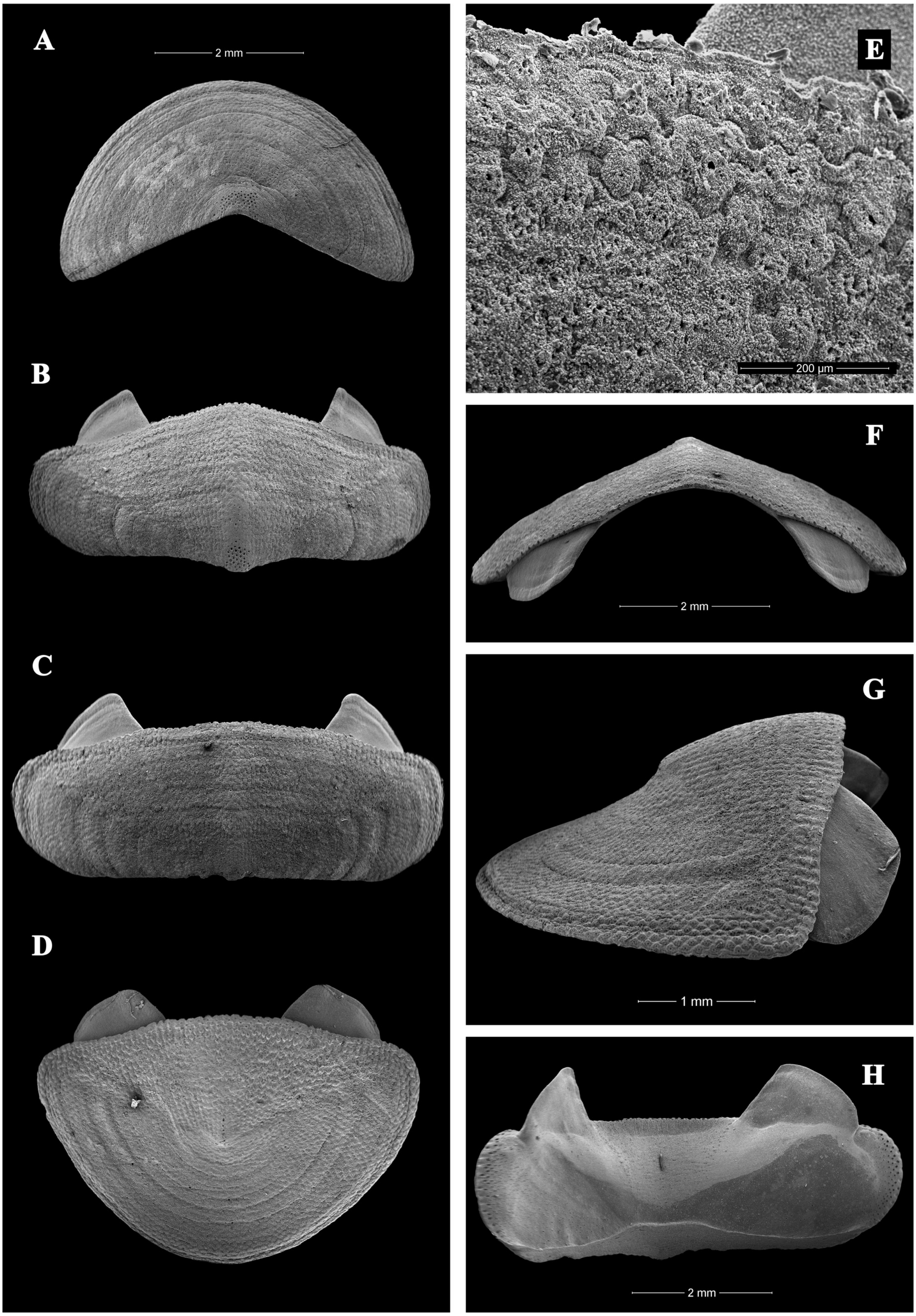

FIG. 13. ***Rissochiton formosaensis*** sp. nov., Taiwan, stn CP38, holotype, (MNHN-IM-2000-38521), BL 15.0 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. E. Valve V, detail of tegmentum in central area. **F.** Valve V, rostral view. **G.** Valve VIII, lateral view. **H.** Valve IV, ventral view.

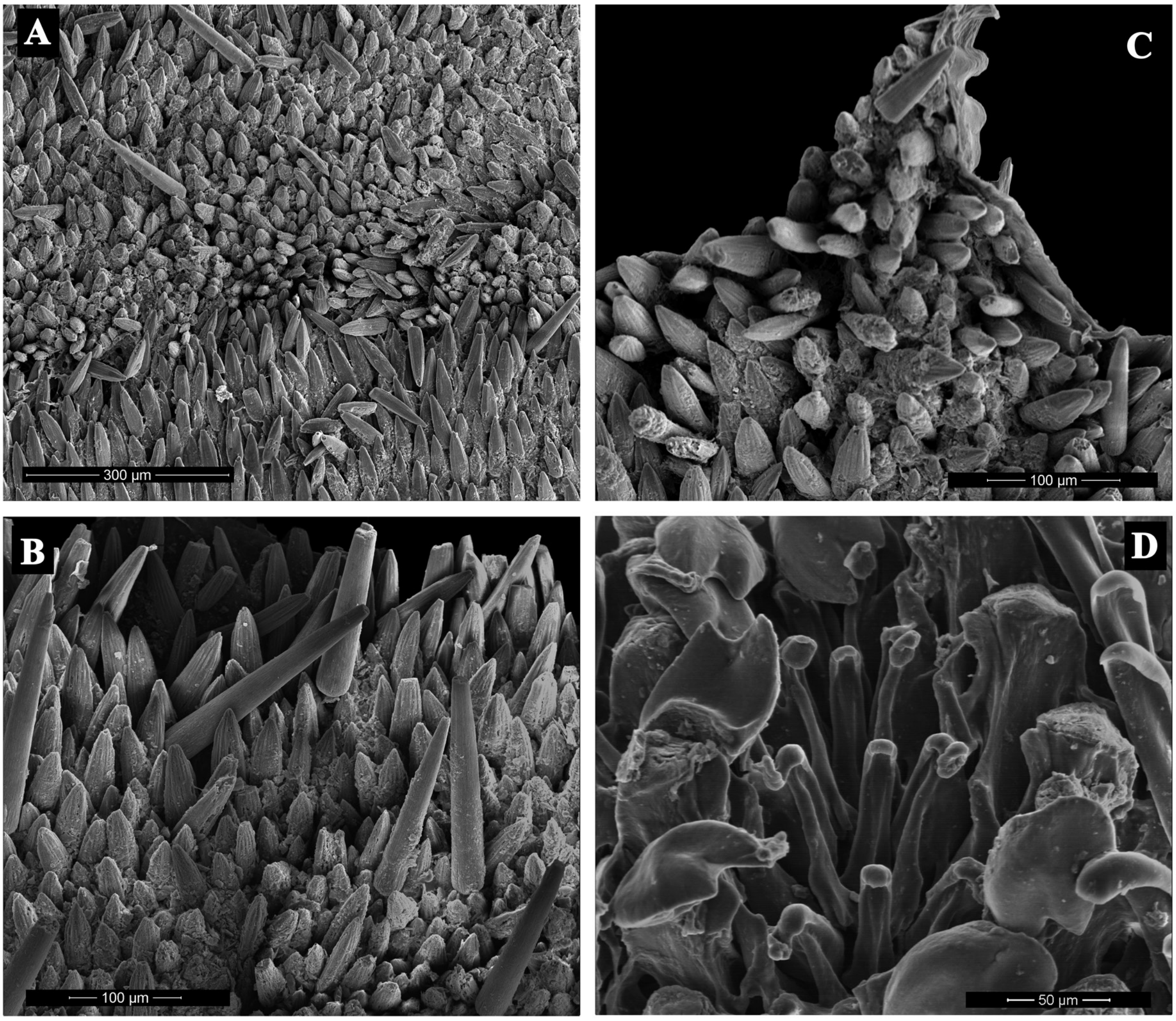

FIG. 14. ***Rissochiton formosaensis*** sp. nov., Taiwan, stn CP38, holotype, (MNHN-IM-2000-38521), BL 15.0 mm. **A.** Dorsal spicules and needles, marginal needles, ventral spicules. **B.** Dorsal spicules and needles. **C.** Sutural spicules and needles. **D.** Part of radula.

oval, low elevated (elevation ratio in valve V 0.28). Valves carinated, not beaked, side slopes slightly convex, the color of tegmentum white,

Head valve semicircular, hind margin V-shaped. Intermediate valves almost rectangular, anterior margin convex especially in valve II, posterior margins nearly straight in all intermediate valves except valve II where there is a small projecting apex, lateral margins rounded. Head valve slightly narrower than the tail valve, mucro anterior, antemucronal slope convex, posterior slope almost straight.

Tegmentum sculptured with rounded oval granules, arranged in quincunx in all areas except antemucronal area of tail valve where there are several longitudinal rows in pleural area. Each granule has 1 megalaesthete and 6–8 micraesthetes. Pores of aesthetes closed with short caps.

Articulamentum well developed, apophyses short, jugal sinus rather wide, ratio of width of apophyses to width of jugal sinus 0.63.

Girdle rather narrow, width of girdle near valve V 1.2 mm. Girdle densely covered with short, sharply pointed dorsal spicules (70–80 x 24 µm) and scat-

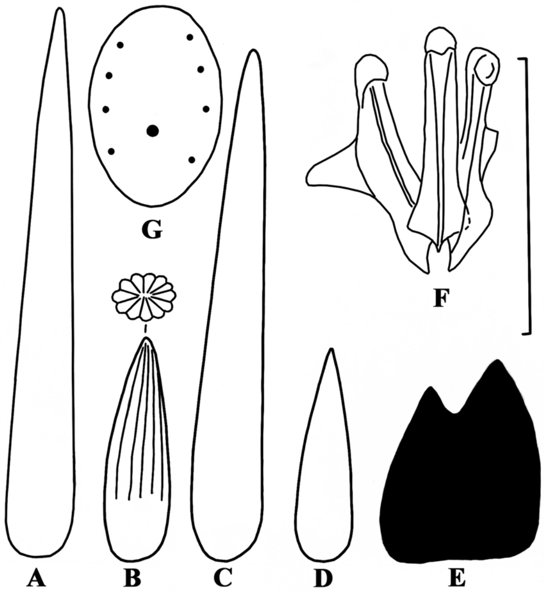

FIG. 15. ***Rissochiton formosaensis*** sp. nov., Taiwan, stn CP38, holotype, (MNHN-IM-2000-38521), BL 15.0 mm. **A.** Sutural and dorsal needle. **B.** Dorsal spicule. **C.** Marginal needle. **D.** Ventral spicule. E. Head of major lateral tooth of radula. **F.** Central and first lateral teeth of radula. **G.** Aesthete group in central area. Scale bar: 100 µm.

tered long, smooth needles (200–220 x 26 µm), there are about 11–12 short ribs around each dorsal spicules, Sutural and marginal needles similar to dorsal ones. Ventrally girdle covered with elongate sharply pointed smooth scales (75 x 23 µm).

Radula of holotype 6.0 mm long with 51 transverse rows of mature teeth. Central tooth narrow, elongate, widest at base, with longitudinal narrow rib and small, rounded blade, major lateral tooth with a bidentate cusp, the inner denticle much smaller.

Gills 13 per side arranged from valve VI to the anus.

Remarks. A specimen of this species from New Guinea (stn. CP 3971) have 10–13 micraesthetes per one megalaesthete in central area. ***R. formosaensis*** sp. nov. differs from ***R. quincuncialis*** sp. nov. by having wider jugal sinus, ratio of width of apophyses to width of jugal sinus 0.63–0.83 (vs 1.0–1.1 in ***R. quincuncialis*** sp. nov.), tail valve wider than the head valve (vs head valve wider than the tail valve in ***R. quincuncialis*** sp. nov.).

Rissochiton quincuncialis sp. nov.

(Figs 16–21)

Zoobank registration: urn:lsid:zoobank.org:act:F8CD2860-7B53-4874-BF76-85CE38B8A5DC

Type material. Holotype MNHN-IM-2000-38523, paratype MNHN-IM-2013-44879.

Type locality. Solomon Islands, 10°19’S, 161°54’E, 686–864 m.

Etymology. From the Latin *quïncũnciãlis*, also as *quincunciālis* or *quincuncialis*, referring to the granules of tegmentum in the central area, which are arranged in staggered order (Figs. 16B, D).

Material examined. 21 specimens. **Solomon Islands**, SALOMON BOA, stn CP2821, 10°19’S, 161°54’E, 686–864 m, holotype (MNHN-IM-2000-38523)), BL 17.0 mm, 19.09.2007; **New Guinea**, PAPUA NIUGINI, stn CP3963, 05°06’S, 145°53’E, 960–980 m, 1 spm (MNHN-IM-2013-16920), BL 7.0 mm, 30.11.2012; stn CP3967, 05°07’S, 145°53’E, 980 m, 1 spm (MNHN-IM-2013-16974), BL 6.0 mm, 30.11.2012; stn CP4033, 04°52’S, 145°53’E, 780–780 m, 1 spm, BL 27.0 mm, 16.12.2012; stn CP4038, 04°27’S, 145°34’E, 800–840 m, 5 spm (MNHN-IM-2012-25422), BL 8.0–18.0 mm, 17.12.2012; stn CP4039, 04°19’S, 145°37’E, 1000–1045 m, 2 spms (MNHN-IM-2012-25421), BL 17.0–23.0 mm, 17.12.2012; MADEEP, stn CP4251, 3°30’S, 148°02’E, 842–933 m, paratype (MNHN-IM-2013-44879), BL 24.0 mm, 23.04.2014; stn CP4264, 04°34’S. 152°24’E, 430–523 m, 1 spm (MNHN-IM-2013-45253), BL 7.0 mm, 26.04.2014; stn DW4277, 05°44’S. 154°03’E, 386–390 m, 1 spm (MNHN-IM-2013-49568), BL 12.0 mm, 28.04.2014; stn CP4331, 06°07’S, 149°12’E, 260 m, 1 spm (MNHN-IM-2013-46026), BL 7.0 mm, 06.05.2014; KAVIENG 2014, stn CP4429, 02°19’S, 150°39’E, 685–824 m, 1 spm (MNHN-IM-2013-67019), BL 10.0 mm, 29.08.2014; stn CP4482, 02°41’S, 150°04’E, 761–825 m, 1 spm (MNHN-IM-2013-58805), BL 8.0 mm, 05.09.2014.

Distribution. Solomon Islands and New Guinea, 260–1000 m, more common at less than 800 m.

Diagnosis. Animal of a small and medium size (maximal BL 27.mm). Shell low elevated, carinated. Intermediate valves almost rectangular, their width is almost 3 times the length. Tail valve slightly narrower than the head valve, mucro anterior, anterior slope convex, posterior slope almost straight. Tegmentum with low, rounded oval granules arranged in quincunx in all areas. Each granule with 11–13 pores of aesthetes. Ratio of width of apophyses to width of jugal sinus 1.1. Girdle densely covered with long, bluntly pointed dorsal spicules and scattered long, smooth needles. Central teeth of radula elongate, widest at base, with small, rounded blade, head of major lateral tooth with a short bifid head. Sixteen long and thin gills per side arranged from valve V to the anus.

Description. Holotype 17.0 mm. Shell elongate oval, low elevated (elevation ratio in valve V 0.28). Valves carinated, not beaked, side slopes slightly convex, the color of tegmentum white,

Head valve semicircular, hind margin V-shaped. Intermediate valves almost rectangular, anterior margin convex, posterior margins nearly straight, lateral margins rounded. Tail valve slightly narrower than the head valve, mucro anterior, antemucronal slope convex, posterior slope almost straight.

Tegmentum sculptured with rounded oval granules, arranged in quincunx in all areas except antemucronaol area. Each granule has one megalaesthete and 11–13 micraesthetes. Pores of aesthetes closed with short caps.

Articulamentum well developed, apophyses short, wide, width of apophyses about 1.1 times more than the width of the jugal sinus.

Girdle narrow, width of girdle is 3.7 times less than the width of valve V. Dorsally girdle densely covered with long, bluntly pointed dorsal spicules (124 x 21 µm) and scattered long, smooth needles (250 x 28 µm), there are about 10 short ribs around each dorsal spicules, Sutural and marginal needles similar to dorsal ones. Ventrally girdle covered with elongate sharply pointed smooth scales (118 x 20 µm).

Radula of holotype 5.0 mm long with 55 transverse rows of mature teeth. Central tooth elongate, widest at base, with small, rounded blade, first lateral teeth with a small outward bent cusp and a peculiar long and narrow outer wing, major lateral tooth with a short bifid head, the main denticle strong, sharply triangular, the exterior one smaller.

Sixteen long and thin gills per side arranged from valve V to the anus.

Remarks. Paratype (BL 24 mm) from Papua New Guinea has higher elevated valves (dorsal elevation 0.40). New species differs from ***R. vietnamensis*** by having wider apophyses, ratio of width of apophyses to width of jugal sinus 1.1 (vs 0.69–0.83 in ***R. vietnamensis***) and quincuncially arrangement of granules

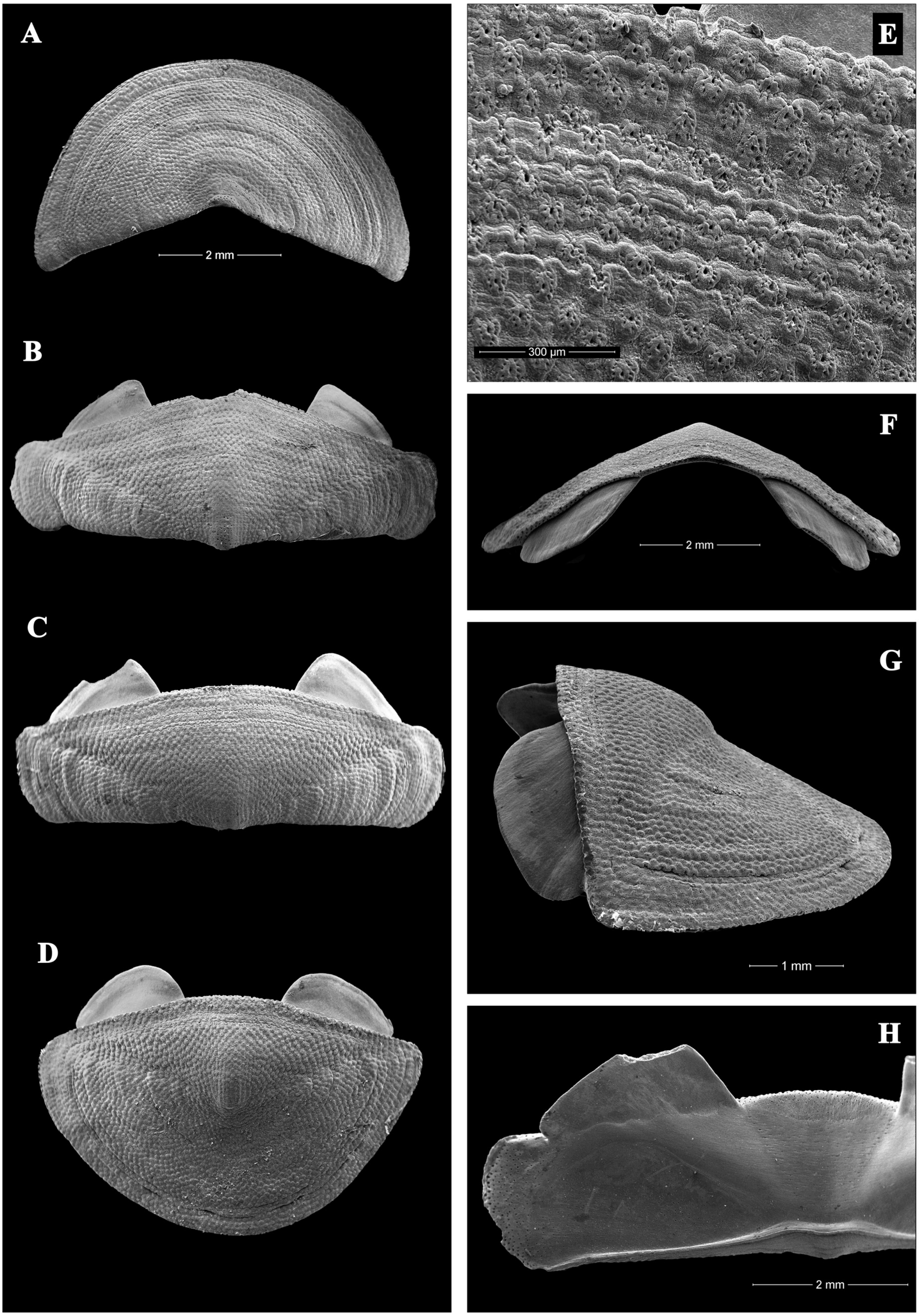

FIG. 16. ***Rissochiton quincuncialis*** sp. nov., Solomon Islands, stn CP2821, holotype, (MNHN-IM-2000-38523), BL 17.0 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. E. Valve V, detail of treated tegmentum in central area. **F.** Valve V, rostral view. **G.** Valve VIII, lateral view. **H.** Valve IV, ventral view.

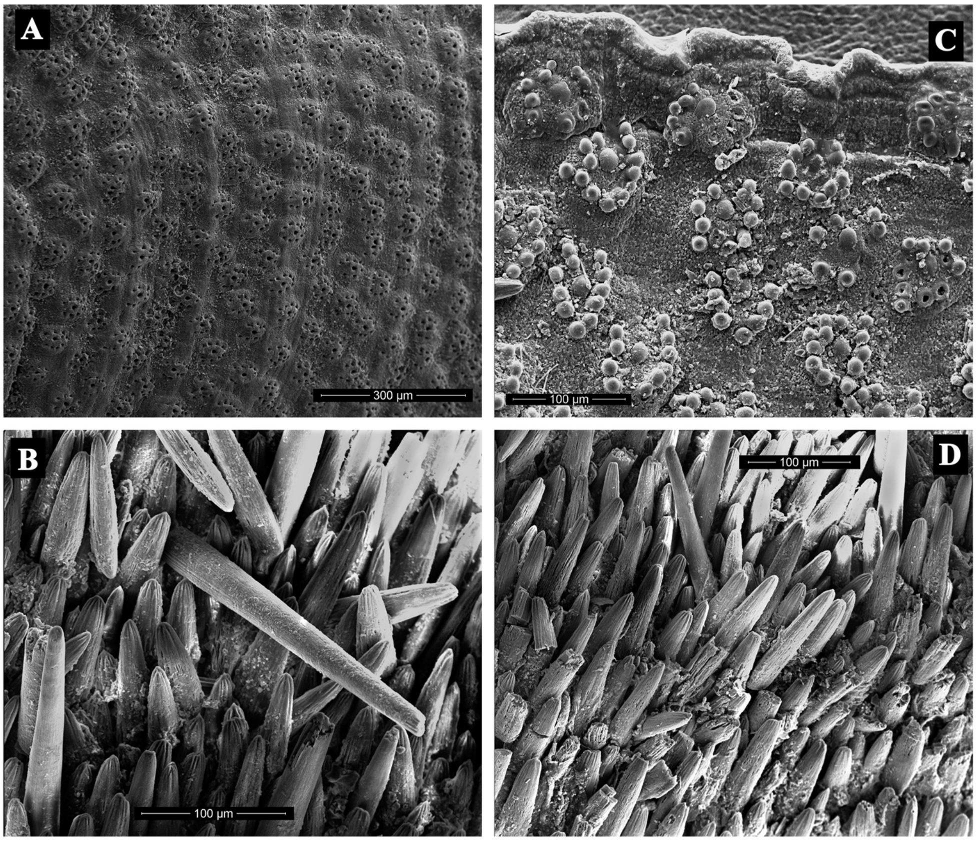

FIG. 17. ***Rissochiton quincuncialis*** sp. nov., Solomon Islands, stn CP2821, holotype, (MNHN-IM-2000-38523), BL 17.0 mm. **A.** Valve V, detail of tegmentum in lateral area. **B, D.** Dorsal spicules and needles. **C.** Valve VII, detail of untreated tegmentum in central area.

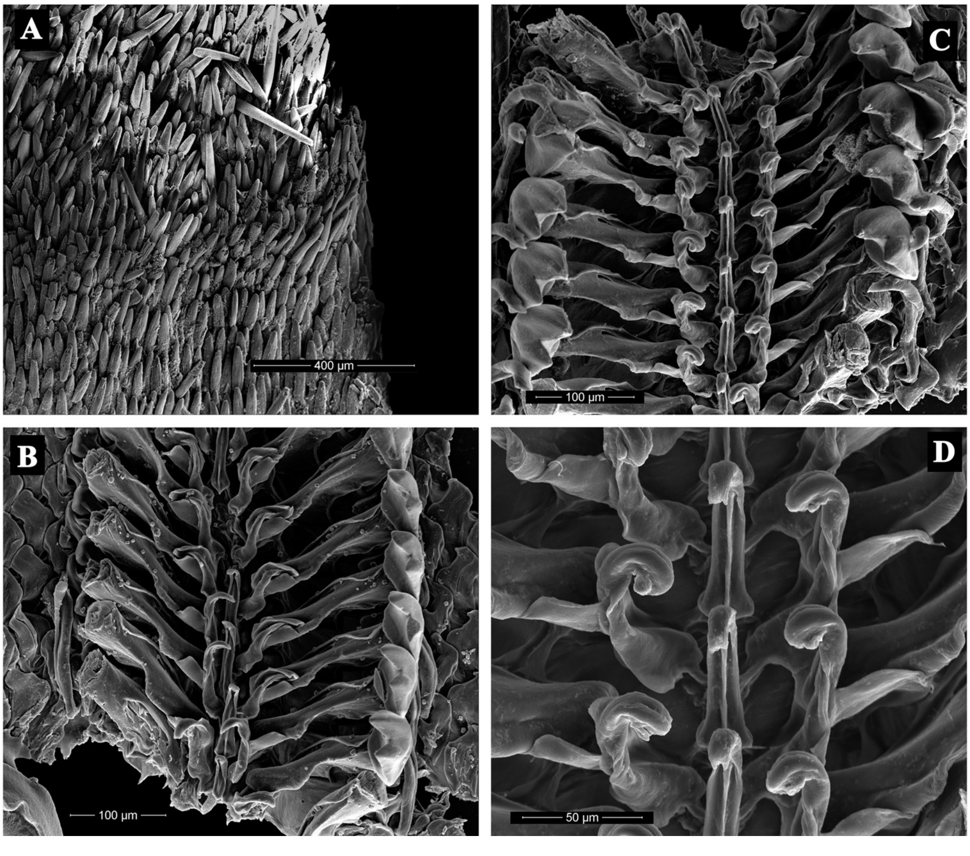

FIG. 18. ***Rissochiton quincuncialis*** sp. nov., Solomon Islands, stn CP2821, holotype, (MNHN-IM-2000-38523), BL 17.0 mm. **A.** Dorsal spicules, marginal needles and ventral spicules. **B, C.** Part of radula. **D.** Central and first lateral teeth of radula.

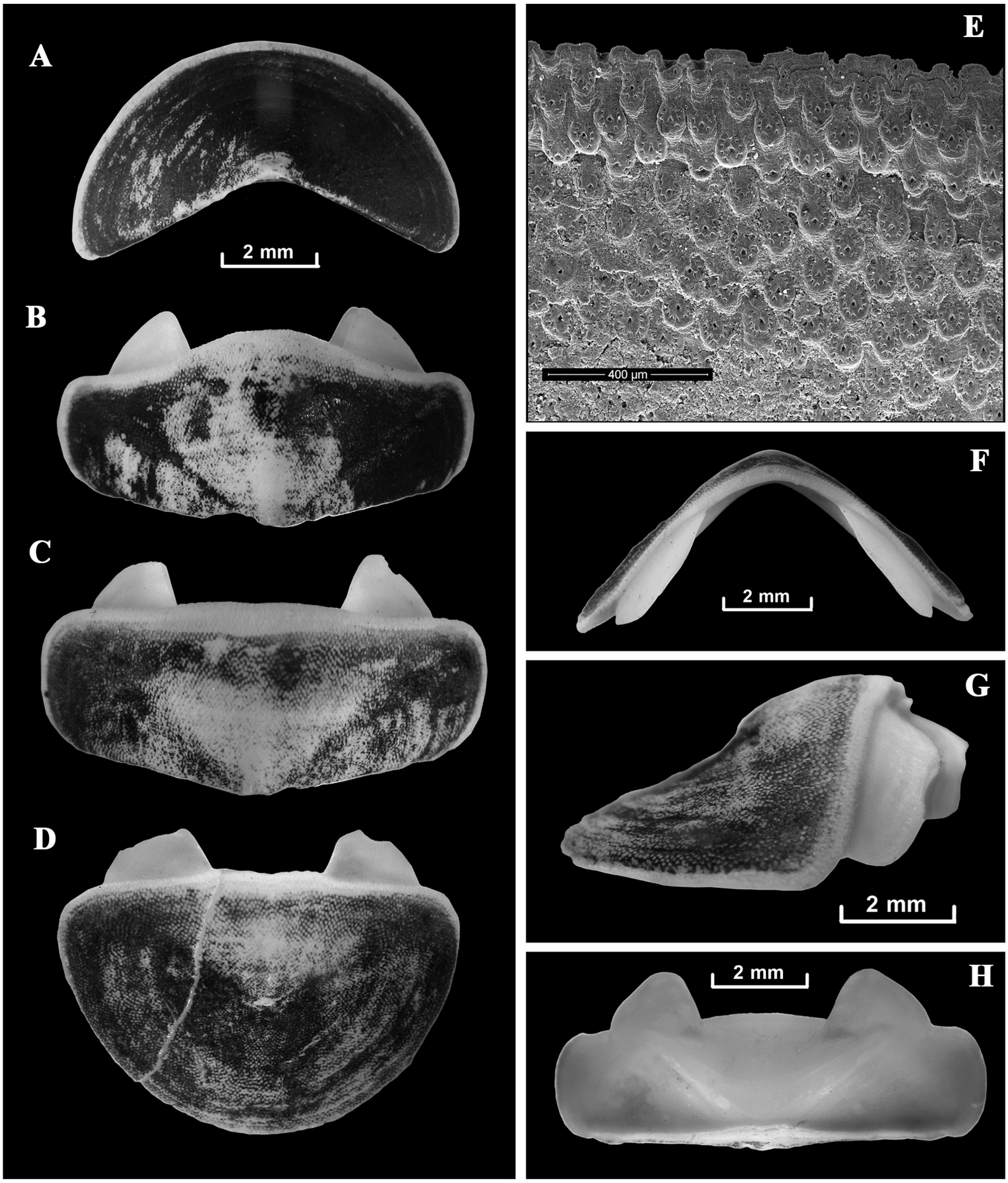

FIG. 19. ***Rissochiton quincuncialis*** sp. nov., Papua New Guinea, stn CP4251, paratype, (MNHN-IM-2013-44879), BL 24.0 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. E. Valve V, detail of treated tegmentum in central area. **F.** Valve V, rostral view. **G.** Valve VIII, lateral view. **H.** Valve IV, ventral view.

in central and antemucronal areas (vs longitudinal rows of granules in ***R.*** *vietnamensis*).

Genus *Nierstraszella* Sirenko, 1992

Type species. *Lepidopleurus lineatus* Nierstrasz, 1905 by original designation [Sirenko, 1992].

Genus distribution. Widely distributed in the West Pacific, (from South Japan, Taiwan, Philippines and Vietnam up to New Guinea and Solomon Islands), 121–1767 m [Sigwart, Sirenko, 2012], Recent.

Diagnosis. Small to medium sized chiton (maximal 29.0 mm). Width of apophyses about 1.11–1.64 times more than the width of the jugal sinus (Table 2). Tegmentum with or without granules. Number of pores in one aesthete group up to 40-45. Girdle clothed with smooth (or rarely striated) spicules and scattered smooth needles.

Genus composition. The genus consists of one species: *Nierstraszella lineata.* Earlier treatments of the genus have also included *Lepidopleurus*

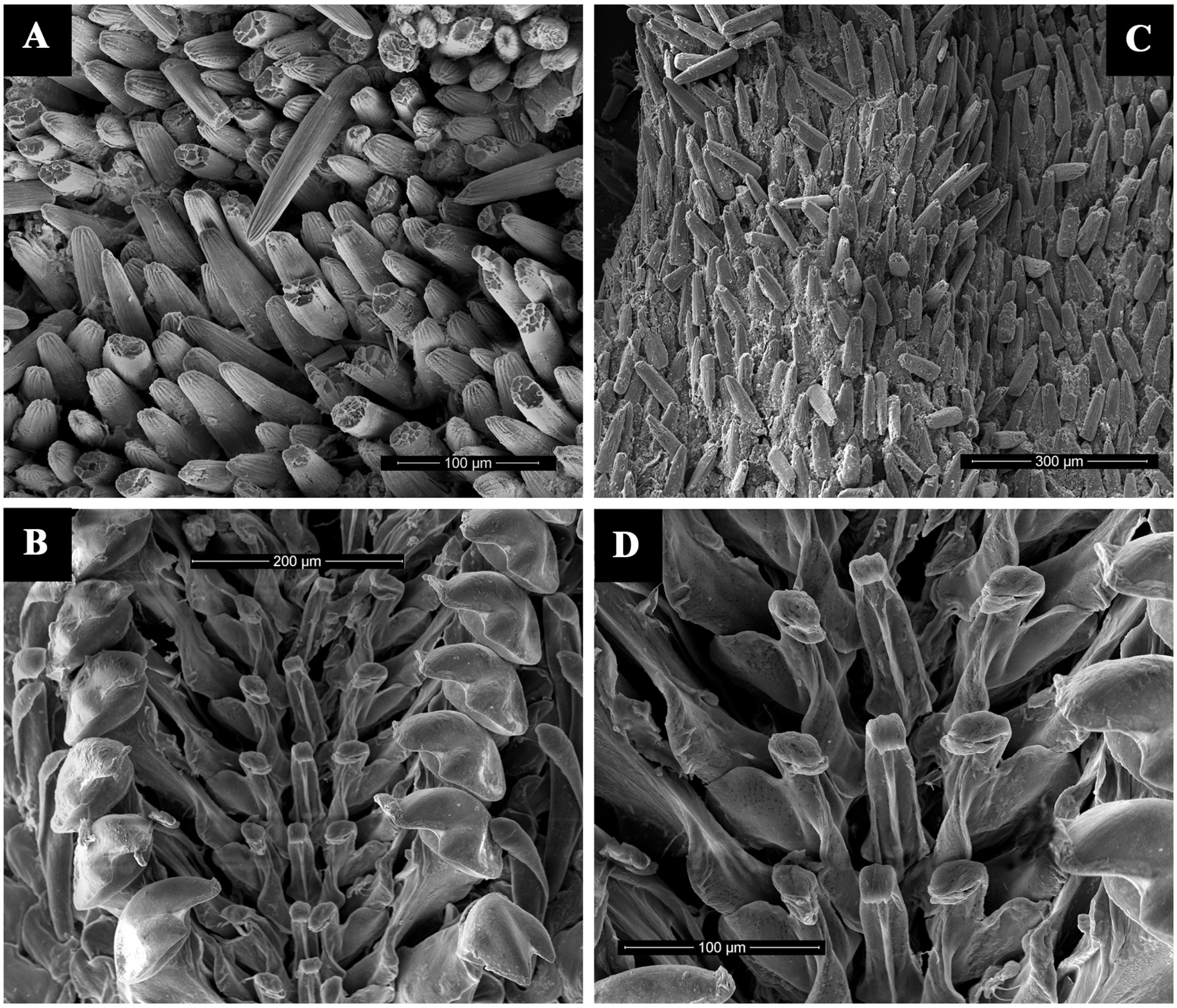

FIG. 20. ***Rissochiton quincuncialis*** sp. nov., Papua New Guinea, stn CP4251, paratype, (MNHN-IM-2013-44879), BL 24.0 mm. A, **C.** Dorsal scales. **B.** Part of radula. **D.** Central and first lateral teeth of radula.

andamanicus E. A. Smith, 1906, which is herein reassigned to ***Rissochiton*** gen. nov.

Remarks. The main difference between the genus *Nierstraszella* and the other two genera of the family Nierstraszellidae is the unique structure of the aesthete group. Each such group consists of two parts. The first part is often observed in other chitons of families Leptochitonidae and Nierstraszellidae, which consists of a megalaesthete with 20–25 micraesthetes situated around it. The second part contains about 20 micraesthetes, situated at close distance from each other. The length of the base to the micraesthetes caps of the second part of is two or three times longer than the entire first part. As a result of the adhesion of long micraesthete caps, the false impression of the presence of a granule is created.

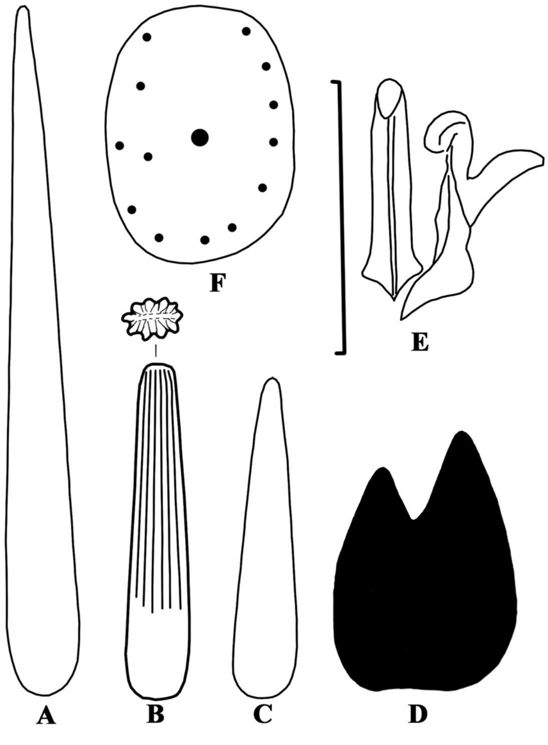

FIG. 21. ***Rissochiton quincuncialis*** sp. nov., Solomon Islands, stn CP2821, holotype, (MNHN-IM-2000-38523), BL 17.0 mm. **A.** Sutural, marginal and dorsal needle. **B.** Dorsal spicule. **C.** Ventral spicule. **D.** Head of major lateral tooth of radula. E. Central and first lateral teeth of radula. **F.** Aesthete group in central area. Scale bar: 100 µm.

Table 2. Comparison of some important features of shell and girdle for eight species in three genera: ***Rissochiton*** gen. nov., *Nierstraszella*, and ***Astrochiton*** gen. nov.

Species	Order of granules and groups of aesthetes in the central fields of tegmentum	Ratio of width of each apophysis to width of jugal sinus	Ratio of width of head valve to width of tail valve	Position of mucro	Number of aesthetes in one granule or aesthete group	Sculpture of dorsal spicules
Rissochiton *rissoi*	Longitudinal rows	1.05–1.50	0.96–1.00	Subcentral	7–21	Ribbed
R. *vietnamensis*	Longitudinal rows	0.69–0.83	0.98	Anterior	11–21	Ribbed
R. *andamanicus*	Quincuncialy	1.30–1.45	1.06	Anterior	11–14	Ribbed
R. ***formosaensis*** sp. nov.	Quincuncialy	0.63–0.83	0.94	Anterior	7–13	Ribbed
R. ***quincuncialis*** sp. nov.	Quincuncialy	1.00–1.10	0.97	Anterior	12–14	Ribbed
Nierstraszella lineata	Quincuncialy	1.11–1.64	1.03	Anterior	40–45	Smooth
Astrochiton *binghami*	Longitudinal ridges	1.14	1.01	Anterior	15–31	Smooth
A. *incongruus*	Longitudinal ridges	1.10	1.03	Subcentral	14–18	Ribbed

Nierstrszella lineata (Nierstrasz, 1905)
(Figs 22–24)

Lepidopleurus lineatus Nierstrasz, 1905: 8, figs 4, 48–51; 1906: 146, 157; Ferreira, 1979: 163, figs 23–24; 1980: 59.
Leptochiton lineatus. – Kaas, 1982: 87.
Leptochiton (*Leptochiton*) *lineatus*. – Kaas, Van Belle, 1985: 113, fig. 49, maps 22, 44.
Nierstraszella lineata. – Sirenko, 1992: 84, figs 3–7, 8A–D, 9; Saito, 2005: 104 (synonymy); Schwabe *et al*., 2008: 6, figs C–D (synonymy); Sigwart, 2009: 451, figs 1–3, 7, 8 (synonymy); Sigwart, Sirenko, 2012: 25 (synonymy); Sirenko, 2018: 329, fig. 37H.
Abbreviated synonymy (see above literature for details):
Lepidopleurus niasicus Thiele 1906: 13, pl. 29, figs 1–5; type locality: Indonesia, Northwest off Nias Island, 01°47.1’N 96°58.7’E, 660 m.
Leptochiton diomedeae Berry 1917: 1, pl. 1, figs 1–3, pl. 2 (holotype, USNM 215625, type locality: Japan, Honshu, 33°25.10’N 135°37.20’E, 446–463 m.
Lepidopleurus belknapioides Leloup, 1981: 317, fig 1, pl. 1: figs 1-3; *fide* Kaas, 1982: 87; type locality: Philippines, 13°46.9’N 120°29.5’E, 592–610 m.
Lepidopleurus philippinus Leloup 1981: 322, fig. 4, pl. 2, figs 1–3; type locality: Philippines, 13°50.5’N 120°28’E, 448–484 m.
Lepidopleurus porosus Leloup 1981: 322, figs 5–6, pl. 2, figs 4–6; type locality: Philippines, 13°40.7’N 120°30’E, 685–757 m.

Type material. Lectotype (ZMA Moll. 3.05.011), designated by Ferreira [1979].

Type locality. Off Roti Island, Indonesia, 10°39’S, 123°40’E, 520 m, R/V Siboga, stn. 297.

Material examined. 19 specimens, **Off South Vietnam**, R/V Odyssey, trawl 53, 11°03’6”N, 109°52’3”E, 490–500 m, 1 spm, BL 9.0 mm, 22.09.1984; trawl 56, 10°23’24”N, 109°45’8”E 490 m, 1 spm, BL 9.0 mm, 23.09.1984;, trawl 59, 10°33’N, 109°43’E, 310 m, 10 spms, BL 7.0–11.0 mm, 24.09.1984; trawl 60, 10°38’4”N, 109°50’5”E, 400 m, 1 spm, BL 7.0 mm, 24.09.1984; trawl 63, 10°46’N, 109°43’E, 300 m, 1 spm, BL 11.0 mm, 25.09.1984 R/V Gidrobiolog, stn.210, 11°25’1”N, 109°47’3”E, 300 m, 1 spm, BL 12.0 mm; **Philippines,** PANGLAO 2005 stn CP2385, 08°51’S, 123°10’E, 982–989 m, 1 spm (MNHN-IM-2012-25420), BL 6.0 mm, 29.05.2005; **New Guinea,** PAPUA NIUGINI, stn CP3693, 02°10’S, 147°17’E, 300 m, 2 spms (MNHN-IM-2012-25419), BL 7.0–8.0 mm, 30.11.2012; KAVIENG 20014, stn CP4420, 02°24’S, 150°36’E, 425–442 m, 2 spms (MNHN-IM-2013-25418 + MNHN-IM-2013-22800), BL 4.0–6.0 mm, 28.08.2014.

Distribution. West Pacific from South Japan, Taiwan, Philippines and Vietnam up to New Guinea and Solomon Islands, 121–1767 m.

Remarks. The studied specimen (BL 8.1 mm) from Vietnam has radula 3.2 mm long with 42 rows of transverse mature tooth and 13 gills at both sides arranged from valve V to anus. Our molecular analyses (Figs. 30–31) have revealed sequence differences between specimens of *N. lineata* from Papua New Guinea, Philippines, Japan, and Vanuatu, but with preliminary evidence for somewhat overlapping range between the first three of these localities (see Discussion). Despite the quite high levels of intraspecific variation within *N. lineata* (Table 3), it is not yet possible to relate this sequence variation to the somewhat overlapping geographic distribution of particular mitochondrial haplotypes, and sequenced specimens still lack evidence of correlated morphological contrasts. Moreover, the relevant type specimens of nominal species that are considered to be synonyms of *N. lineata* are in need of detailed examination (see abbreviated synonymy above). Sequence comparisons are based on limited geographic sampling, especially near relevant type localities, and some rarer *N. lineata* haplotypes are still represented by too few specimens. Overall, the present sequence differences suggest a broader partly parapatric species complex within the Indo-West Pacific. These contrasts will be challenging to explore given little if any diagnostic morphological differences in the specimens we have compared among our sampled specimens.

Genus ***Astrochiton*** gen. nov.

Zoobank registration: urn:lsid:zoobank.org:act:CAE23B39-238A-4D94-A4DF-41CDA0DCCBF5

Type species. *Lepidopleurus binghami* Boone, 1928 (here designated).

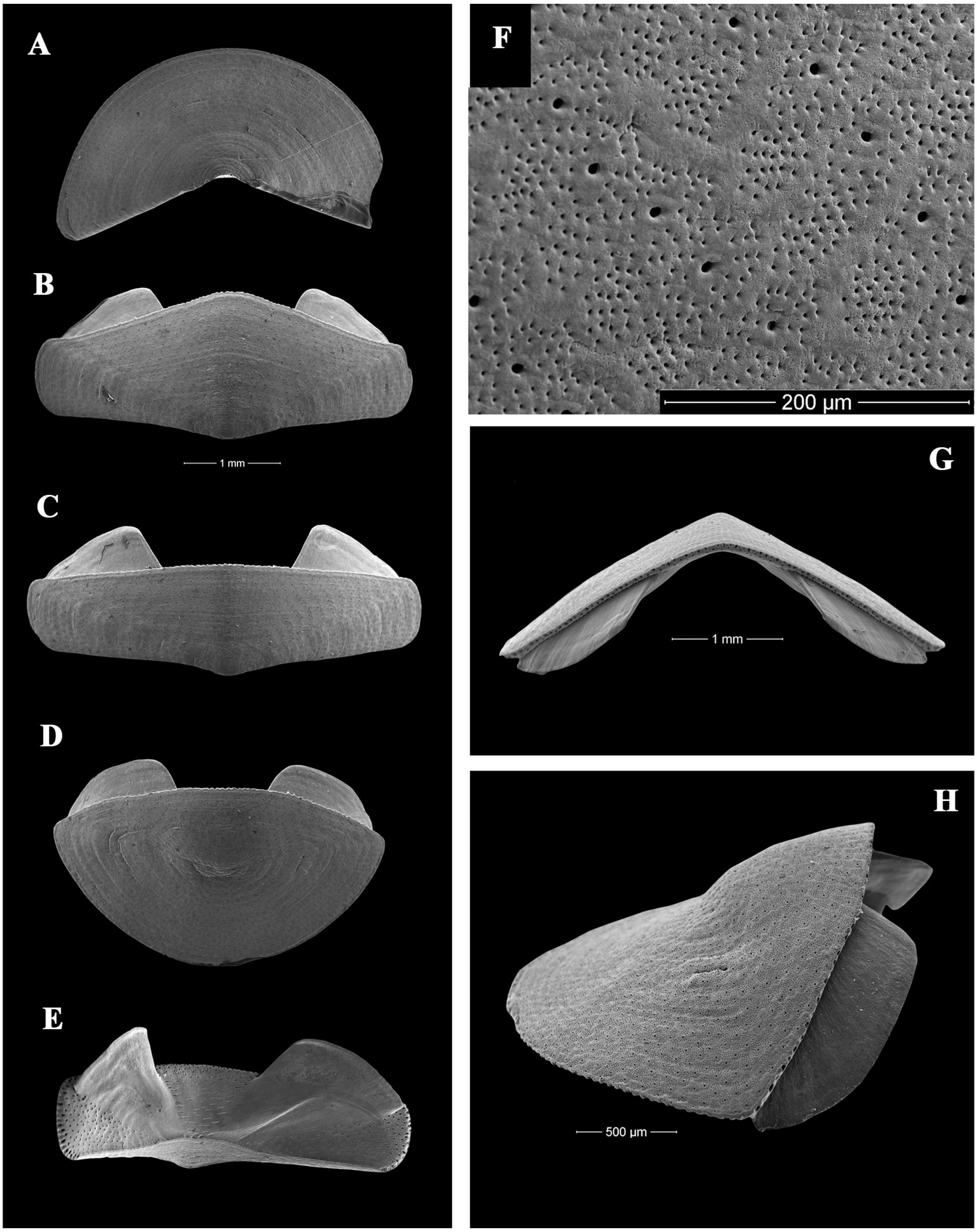

FIG. 22. *Nierstraszella lineata*, off South Vietnam, trawl 59, BL 8.1 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. **E.** Valve IV, ventral view. **F.** Valve V, detail of treated tegmentum in central area. **G.** Valve V, rostral view. **H.** Valve VIII, lateral view.

Etymology. Combines astro- from the Greek for star with chiton, referring to the association of the holotype of the type species (see below) living on the arm of a basket star, which is the first chiton reported to be found on any echinoderm, however atypical this might be for the genus.

Genus distribution. Caribbean Sea and Gulf of Mexico, Recent.

Diagnosis. Small to medium sized chiton. Surface of tegmentum undulating in pleural area, groups of aesthetes are located on the tops of longitudinal ridges on the pleural areas, or in no particular order on the jugal and lateral areas without formation of granules. Number of pores in one aesthete group is 15–31 (Table 2) Girdle clothed with smooth or stri-

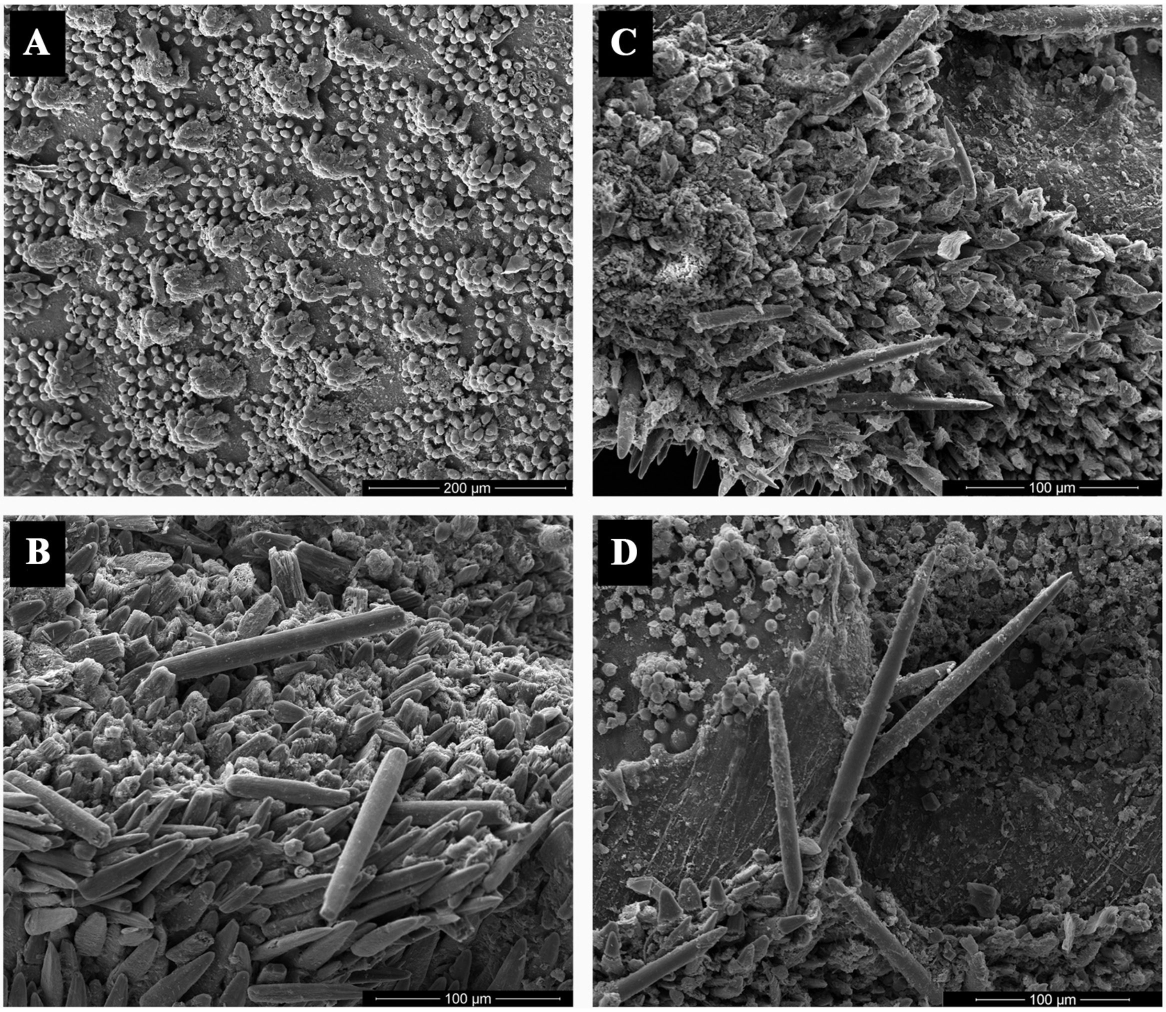

FIG. 23. *Nierstraszella lineata*, off South Vietnam, trawl 59, BL 8.1 mm. **A.** Valve VII, detail of untreated tegmentum in central area. **B.** Dorsal spicules and needles, marginal needles and ventral spicules. **C.** Dorsal spicules and needles. **D.** Sutural needles and spicules.

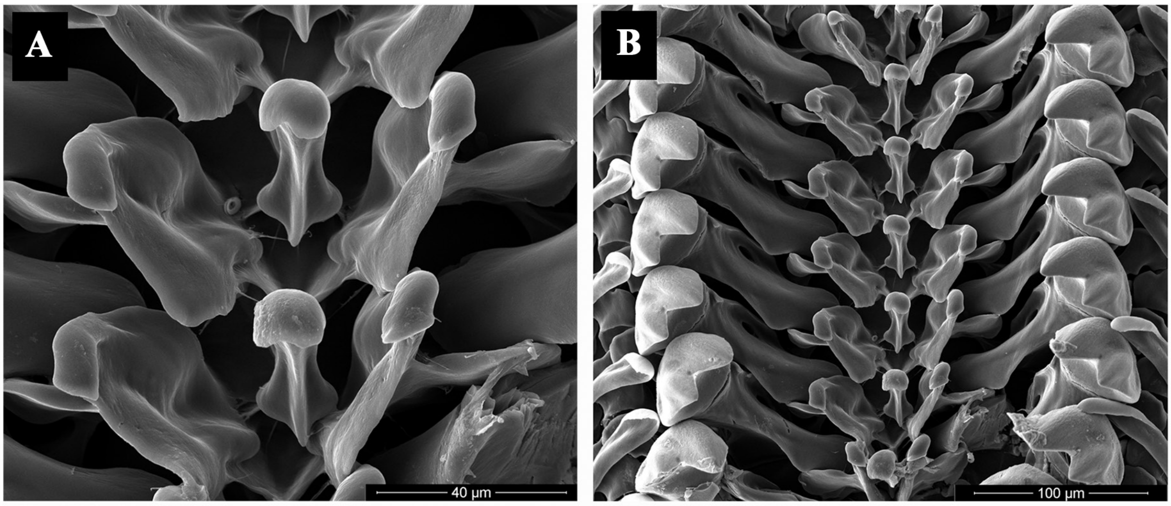

FIG. 24. *Nierstraszella lineata*, off South Vietnam, trawl 59, BL 8.1 mm. **A.** Central and first lateral teeth of radula. **B.** Part of radula.

ated pointed spicules and smooth needles, scattered or at the sutures.

Genus composition. Two species, ***A.*** *binghami* from the Caribbean and Gulf of Mexico and ***A.*** *incongruus* (Dall, 1908) from the tropical East Pacific.

Remarks. *A. binghami*, and *N. lineata* are characterized by the development of an excessively high number of aesthetes in one aesthete group, which significantly exceeds the number of aesthetes in other genera and families of order Lepidopleurida. Due to the strong variability in the sculpture of the tegmentum of ***A.*** *binghami*, which sometimes leads to the complete absence of granules on the tegmentum; those specimens become like *N. lineata*. This is especially true for young specimens of ***A.*** *binghami*. In addition to this subtle difference, our phylogenetic estimate based on mitochondrial sequence comparisons (Figs. 30, and discussed below) has revealed tthat this neotropical genus is weakly supported as sister taxon of the other two Indo-West Pacific genera together within Nierstraszellidae, or more conservatively as one of three basal lineages that form an unresolved trichotomy within the family. The Isthmus of Panama separates ***A.*** *binghami* from ***A.*** *incongruus*, with the most recent deep-water connection estimated to have occurred at least 4.1 Ma [Farmer *et al.*, 2025]. Substantial morphological difference between the two species implies this connection could have been even more ancient.

Astrochiton *binghami* (Boone, 1928), comb. nov.

(Figs 25–27)

Lepidopleurus binghami Boone, 1928:14, fig. 2.

Lepidopleurus (*Deshayesiella*) *binghami*. – Kaas, 1972: 18, figs 7–12.

Lepidopleurus pergranatus. – Götting, 1973: 247, pl. 8: fig. 1a–b [not of Dall, 1889]

Leptochiton (*Leptochiton*) *binghami*. – Kaas, Van Belle, 1985: 71, fig. 30, map 17.

Type material. Holotype (YPM 15636).

Type locality. Off British Honduras, N of Glover Reef, 912 m.

Habitat. The holotype was “found clinging to the arms of a huge Gorgonocephalid” [Boone, 1928: 1]. Gorgonocephalidae Ljungman, 1867 are ophiuroids commonly known as basket stars; they have highly branching arms that have been reported to measure up to 70 cm in length.

Material examined. 78 specimens. Caribbean Sea, Colombia, 09°45’N, 76°15’W, 270 m, muddy sand on sunken wood, 1 spm (INVEMAR, MOL 2263) BL 7.0 mm; 16 samples (18 specimens) the Caribbean Sea, from Colombia, INVEMAR; 19 samples (59 specimens) from Caribbean Sea and Gulf of Mexico, USNM.

Distribution. Caribbean Sea and Gulf of Mexico, 80–930 m.

Remarks. The studied under SEM specimen (BL 7.0 mm) from the Caribbean Sea, off Colombia has radula 3.2 mm long with 48 rows of transverse mature tooth and 11 gills at both sides arranged from valve VI to anus.

The study of ***A.*** *binghami* collected from vast expanses in the Caribbean Sea and in the Gulf of Mexico, and stored in INVEMAR and USNM, allowed us to establish in this species the age variability of the number of gills and the significant variability of the sculpture of the central area of the tegmentum. According to our data, chitons with a body length of 7.0, 8.0, 16.0, 18.0, 23.0 mm have 11, 13, 14, 14, 16 long gills, respectively. In different parts of the range of this species, there are specimens with well-developed longitudinal rows of granules in the central area, with poorly developed granules, or even completely devoid of any longitudinal rows and granules. The latter are very similar in the sculpture of the tegmentum to the *Nierstraszella lineata* and ***Rissochiton*** *andamanicus*. In the same station, one can find chitons with intermediate features from well-developed rows of granules in central area up to full absence of any rows.

Nierstrazella. lineata differs from ***Astrochiton*** *binghami* (Table 2) in having of a group of high adhesive caps in the aesthete group, 40–45 microaesthetes in the aesthete group (vs. 15–31 microaesthetes in ***A.*** *binghami*), and quincuncially arrangement of the aesthete groups in the tegmentum (vs. longitudinal ridges in the tegmentum of the pleural areas in ***A.*** *binghami*).

Astrochiton *incongruus* (Dall, 1908), comb. nov.

(Figs 28–30)

Lepidopleurus incongruus Dall, 1908: 355; Thorpe in Keen, 1971: 882

Leptochiton incongruus. – Ferreira, 1979: 157, fig. 29.

Leptochiton (*Leptochiton*) *incongruus*. – Kaas,Van Belle, 1985: 88, fig. 38, map 8.

Type material. Holotype (USNM 122969).

Type locality. Gulf of Panama, 07°09’45”N, 80°50’00”W, 589 m.

Material examined. 5 specimens. Holotype. Off Panama, *Galathea* Expedition, 07°15’N, 79°21’W, 915 m, on sunken tree-trunk. Other specimens: 1 spm from 661 m depth associated with natural wood fall in the vicinity of methane seeps off Costa Rica, cruise SO2019, locality Rio Bongo Scar (Scripps_M17067, figured in Seid *et al.*, 2025 as *Leptochiton incongruus*; new images and DNA sequence herein), BL 6.2 mm curled, 1 spm, (ZIN 2445, Gulf of Tehuantepec, Mexico (scientific exchange), BL 13 mm, 2 spms off Manzanillo, Colima (ICML-EMU-10003, TALUD XII, 2008, R/V El Puma, St. 28, 18°50’31”N, 104°34’23”W, 1100–1106 m, benthic sledge), BL 19 and 14 mm somewhat curled, examined, photographed and identified by DE at ICML-EMU as *L.* cf. *incongruus*, 2013, courtesy of M. Hendrickx.

Distribution. Besides the Gulf of Panama type locality, specimens examined were collected at

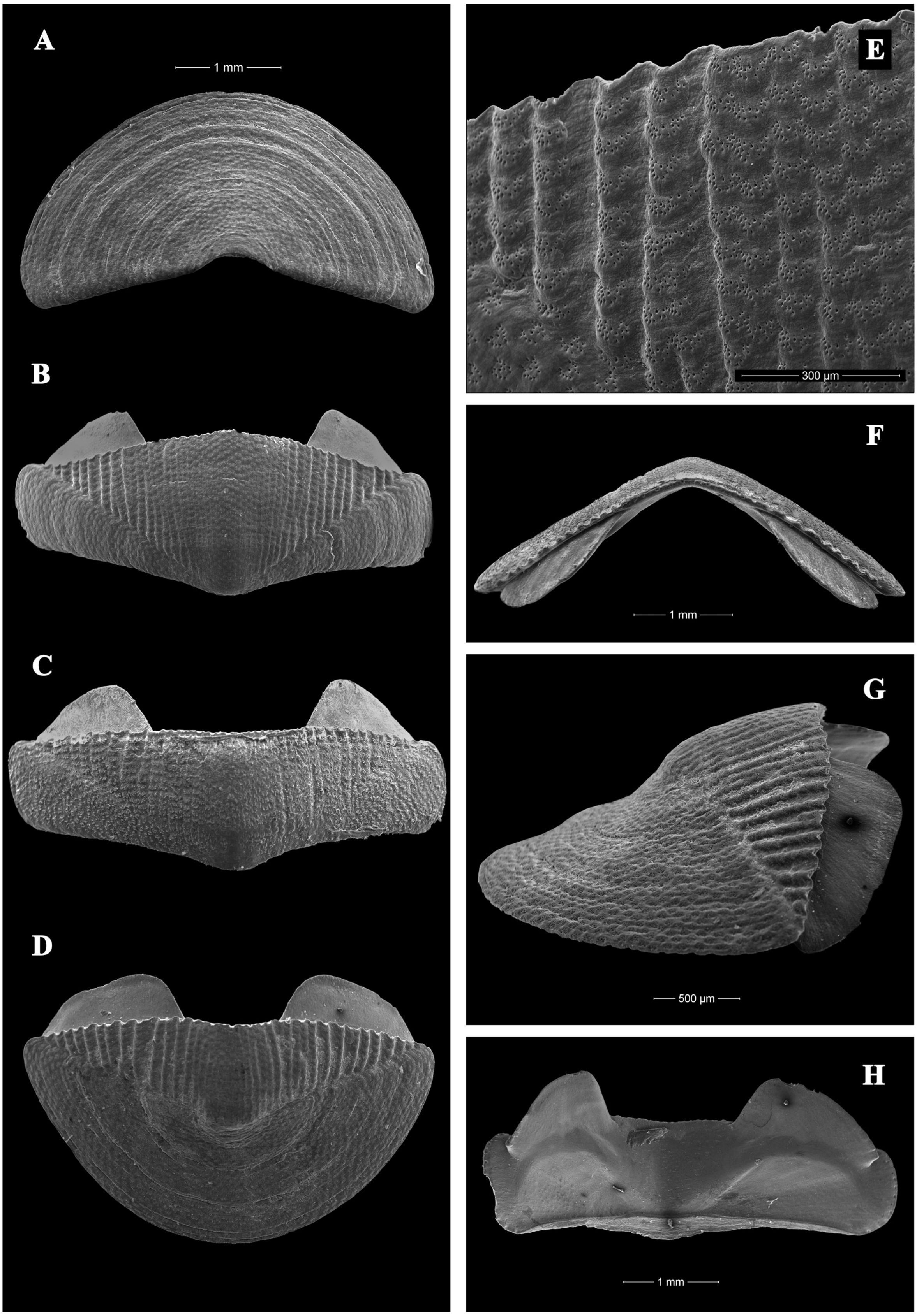

FIG. 25. ***Astrochiton*** *binghami*, Caribbean Sea, off Colombia, (INVEMAR, MOL 2263) BL 7.0 mm. **A.** Valve I, dorsal view. **B.** Valve II, dorsal view. **C.** Valve V, dorsal view. **D.** Valve VIII, dorsal view. E. Valve V, detail of treated tegmentum in central area. **F.** Valve V, rostral view. **G.** Valve VIII, lateral view. **H.** Valve IV, ventral view.

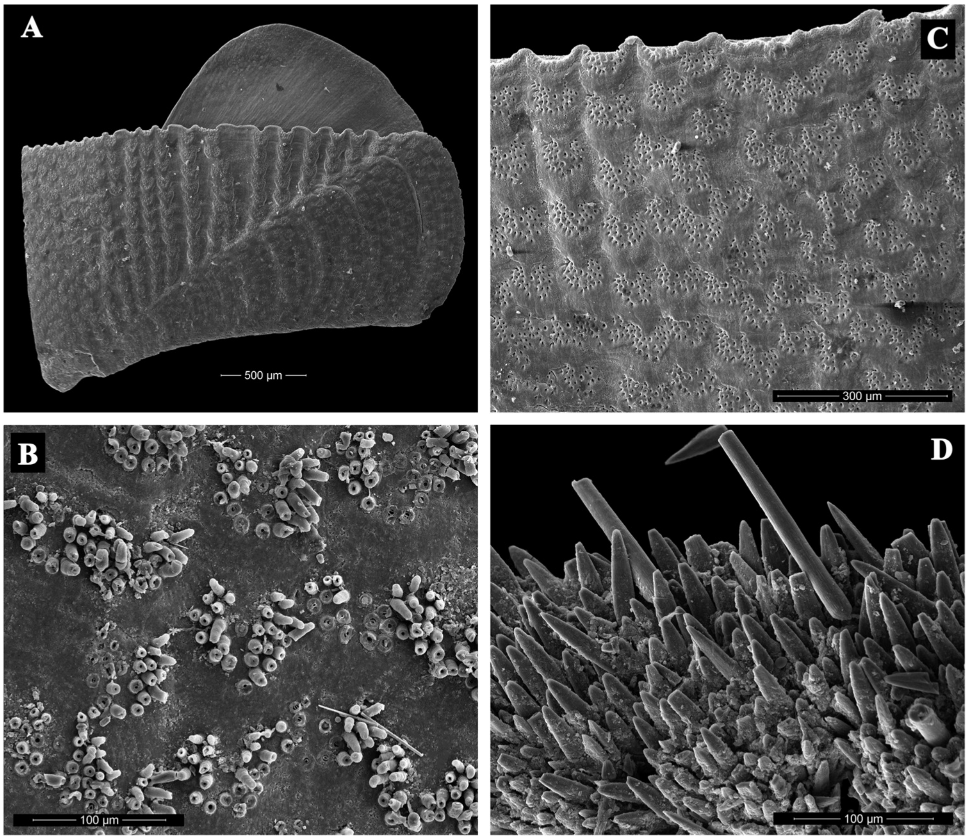

FIG. 26. ***Astrochiton*** *binghami*, Caribbean Sea, off Colombia, (INVEMAR, MOL 2261) BL 9.0 mm (A), INVEMAR, MOL 1641), BL 16.0 mm (B, C), (INVEMAR, MOL 2263) BL 7.0 mm (D). **A.** Half of treated valve V. **B.** Untreated valve VI, detail of central area. **C.** Treated valve VII, detail of central area. **D.** Dorsal spicules and needles.

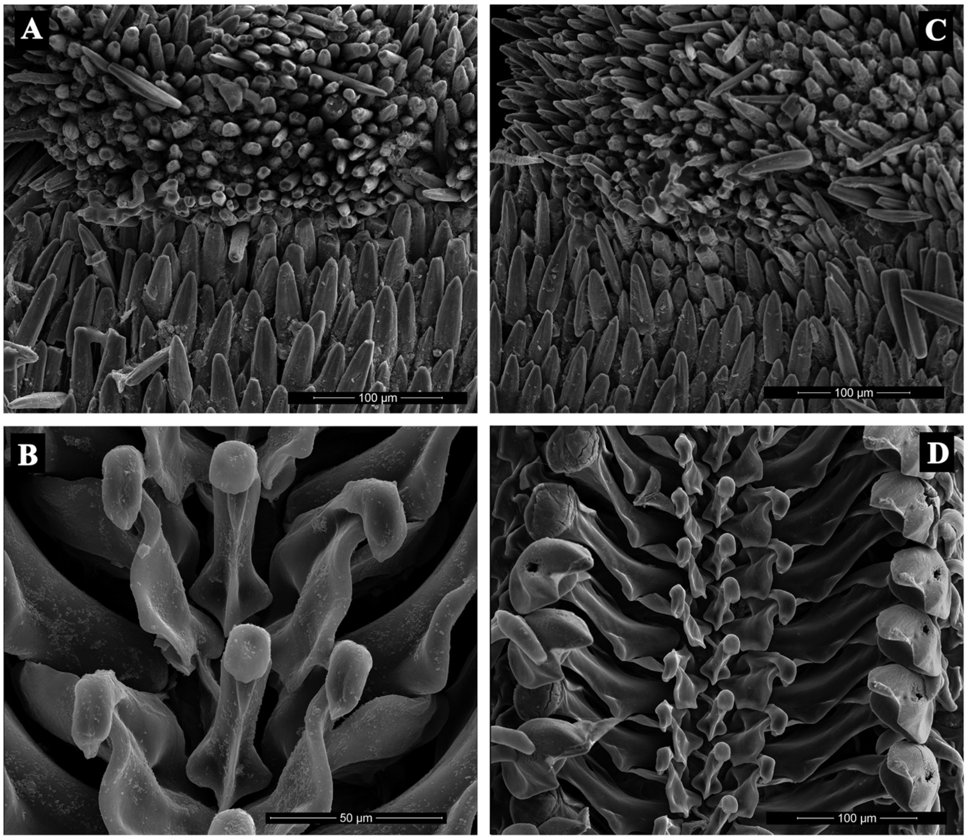

FIG. 27. ***Astrochiton*** *binghami*, Caribbean Sea, off Colombia, (INVEMAR, MOL 2263) BL 7.0 mm. **A.** Dorsal spicules and needles, marginal needles, ventral spicules. **B.** Central and first lateral teeth of radula. **C.** Dorsal spicules, marginal needles and ventral spicules. **D.** Part of radula.

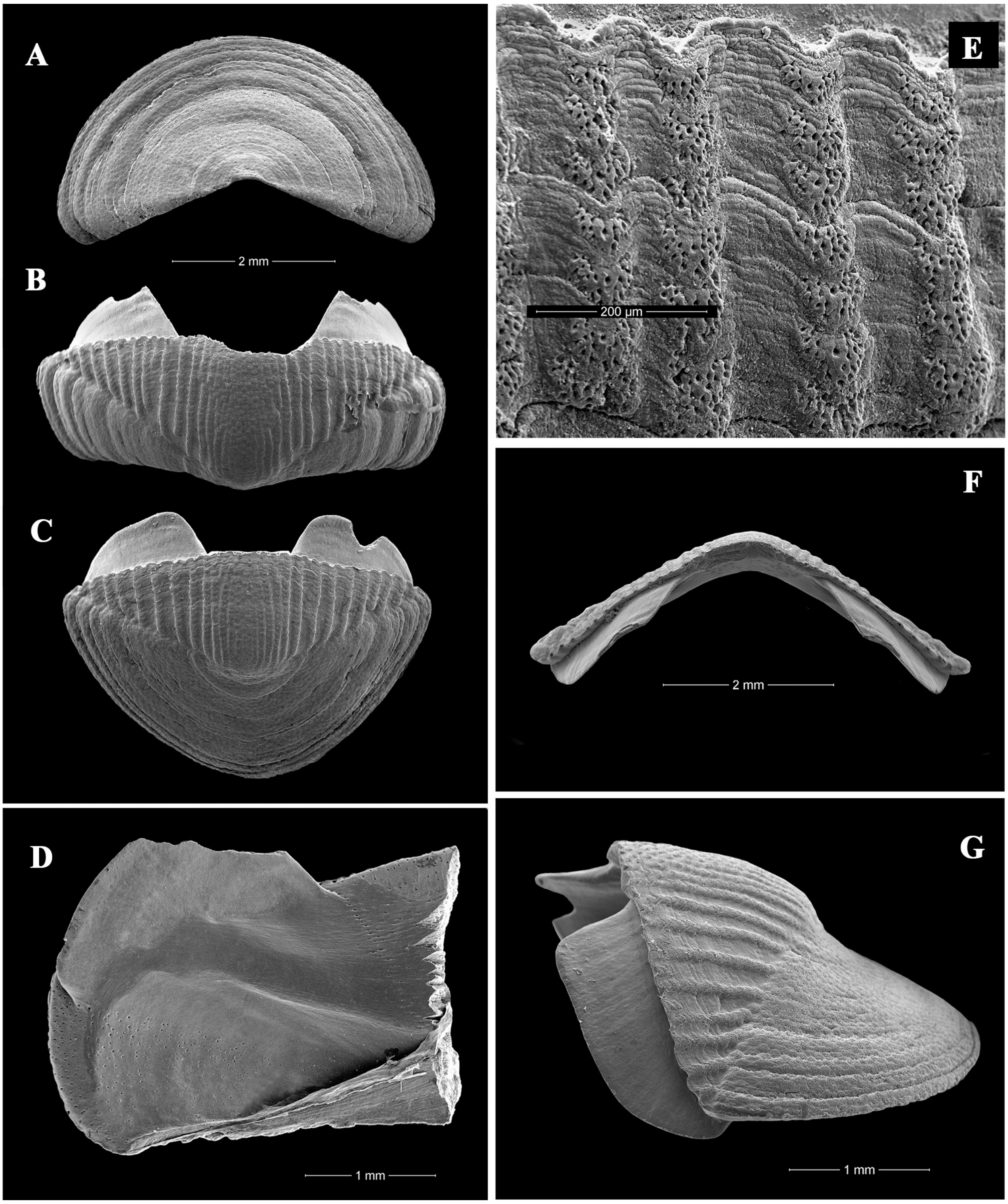

FIG. 28. ***Astrochiton** incongruus*, off Panama, BL 13 mm. **A.** Valve I, dorsal view. **B.** Valve V, dorsal view. **C.** Valve VIII, dorsal view. **D.** Half of valve IV, ventral view. E. Valve V, detail of tegmentum in central area. **F.** Valve V, rostral view. **G.** Valve VIII, lateral view.

three more northern localities in the tropical East Pacific, including the northernmost record from off Manzanillo, Colima, Mexico. Vertical distribution 589–3541 m depth for examined specimens plus two more reported in Ferreira [1979].

Remarks. The study of the radula preparation, performed for examination under a light microscope, showed the similarity of its elements with the teeth of other species of this genus. The studied specimen (BL 13.0 mm) has 16 gills at both sides arranged from valve V to the anus. Tegmentum granules fused into longitudinal ribs on pleural areas have 14–18 pores of aesthetes. Ratio of width of apophyses to width of jugal sinus 1.1. Dorsal spicules with 11–13 longitudinal ribs around it.

This species is closest in the sculpture of the tegmentum to ***A.** binghami* from which it differs in having a smaller number of aesthetes (14–18) (vs 40–45 in ***A.** binghami*), shorter and ribbed dorsal spicules (longer and smooth spicules in ***A.** binghami*).

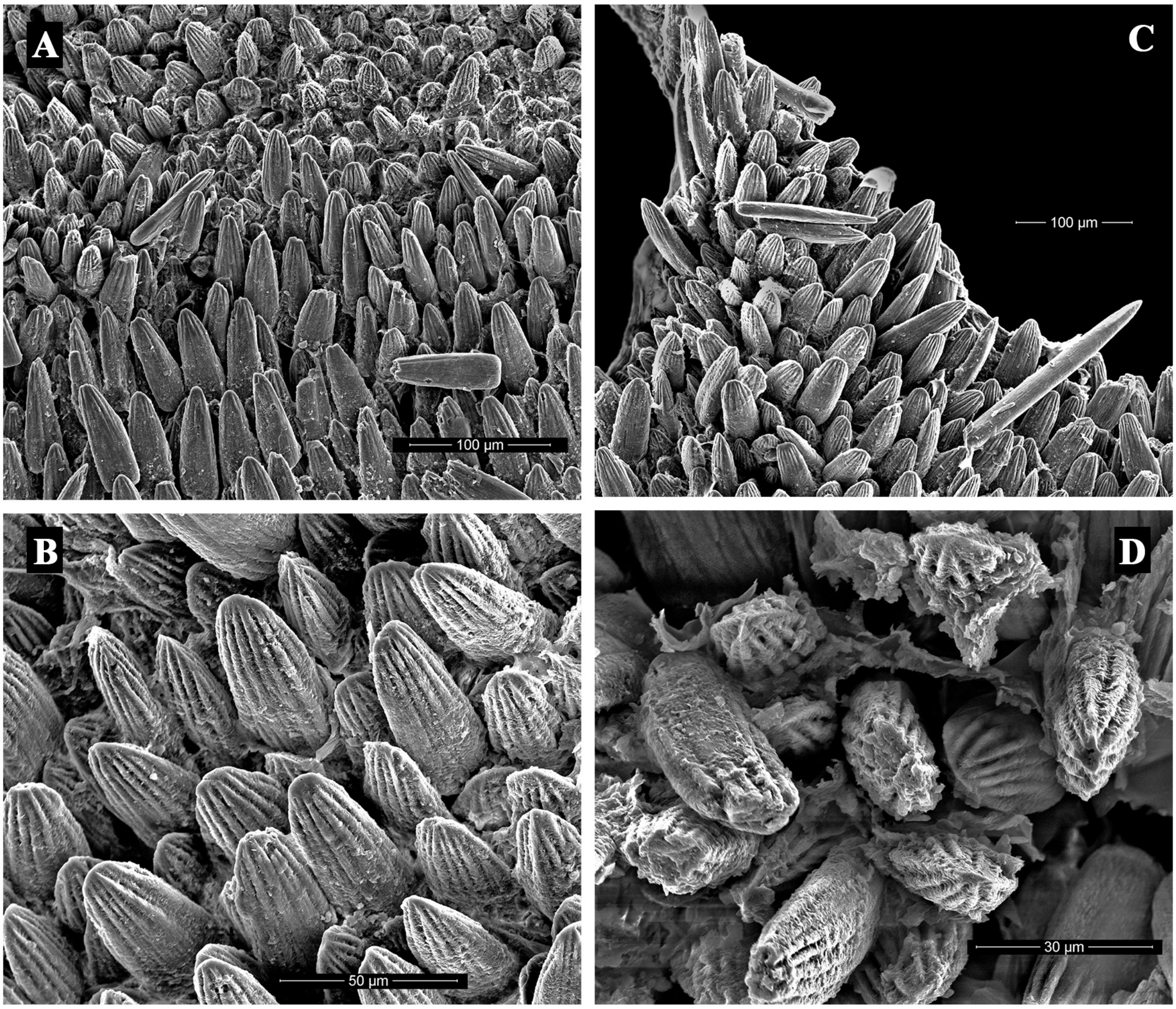

FIG. 29. ***Astrochiton*** *incongruus*, off Panama, BL 13 mm. **A.** Dorsal spicules, marginal needles and ventral spicules. B, **D.** Dorsal spicules. **C.** Dorsal spicules and needles in suture.

A. *incongruus* differs from ***R.*** *vietnamensis* by having wider apophyses, ratio of width of apophyses to width of jugal sinus 1.1 (vs 0 69–0.83 in ***R.*** *vietnamensis*), subcentral mucro (vs anterior mucro in ***R.*** *vietnamensis*), wider interspaces in pleural areas and more numerous longitudinal rows in pleural areas and concentrically rippled head valve, lateral areas of intermediate valves and postmucronal area (vs absence of ripples in tegmentum in ***R.*** *vietnamensis*).

According to the sculpture of the tegmentum, the spicules of the perinotum and the shape of the teeth of the radula, this species is like members of the genus ***Rissochiton*** gen. nov. In addition, the type material, and the sequenced specimen from off Costa Rica, were recovered from sunken wood, and a specimen we dissected had its digestive system filled with brown crushed wood. Together, these observations indicate that this species is xylophagous as documented for other members of the family.

Molecular Results

Our combined-gene phylogenetic estimate (Fig. 30 is based on 42 total specimens, 14 from Nierstraszellidae, with all but one having both 16S and *cox1* sequences available (Table 1, Supplementary Table S1). Our broad selection of chiton outgroup specimens helped with rooting within Nierstraszellidae and support this grouping as one of multiple basal lineages within Lepidopleurida, but its deep affinities within the order are not well resolved. The included outgroup species for our combined-gene analysis belong to other chiton orders and three Lepidopleurida genera: *Leptochiton* Gray, 1847, *Hanleyella* Sirenko, 1973, and *Belknapchiton* Sirenko, Saito et Schwabe, 2022. Lepidopleurida includes about 175 extant species accepted in MolluscaBase [2025]. Most (about 153) species of the suborder are currently placed within Leptochitonidae Dall, 1889, dominated by about 122 species of *Leptochiton*, both family and genus now regarded as polyphyletic assemblages united only by plesiomorphic features, and often superficially similar in appearance. Our combined-gene maximum likelihood analysis supports the monophyly of Nierstraszellidae, found in 100 percent of our bootstrap replicates. This is the first time this broad grouping of species has been grouped as members of Nierstraszellidae. This family, as proposed by Sirenko [1992], at first included only *Nierstraszella lineata* and later a second species, *Lepidopleurus andamanicus*, was revived from synonymy and added as *N. andamanica* [Sigwart, 2009; Sigwart, Sirenko, 2012]. Our preliminary molecular analyses of species treated here, following our January 2018 DNA extractions and sequencing of specimens at MNHN, revealed that these species were part of a well-supported monophyletic grouping, corresponding to Nierstraszellidae as recast here (but with some included species still lacking sequences). These species also share a tendency for a xylophagous diet. We also realized that *N. lineata* was relatively distant from *N. andamanica*, which grouped instead with various "*Leptochiton*" species that had similar morphology to it. Besides *N. lineata*, the remaining Indo-West Pacific species in the family are herein re-assigned to ***Rissochiton*** gen. nov., with the oldest species name, ***R.*** *rissoi*, designated as the type species. The clear morphological similarities we have found among all included members of ***Rissochiton*** are reinforced by our molecular result, with *N. lineata* and ***Rissochiton*** each supported as monophyletic in 100 percent of our bootstrap replicates (Fig. 30). Likewise, we support the monophyly of a third genus, ***Astrochiton*** gen. nov. with 100 percent bootstrap support (Figs. 30, 31B). The included two species have a neotropical distribution, one in the vicinity of the Caribbean and one in East Pacific (with only *cox1* sequences from Seid *et al.*, 2025). Together, ***Astrochiton*** is supported as sister lineage to the other two Indo-West Pacific genera, *Nierstraszella* and ***Rissochiton***, which group with 88 percent bootstrap support (Fig. 30); this likely reflects an ancient disjunct distribution within Nierstraszellidae. Our 16S-only (Fig. 31A) and *cox1*-only (Fig. 31B) results have substantially expanded the number of examined specimens that we could include from Nierstraszellidae with emphasis on specimens with both gene sequences available.

Another striking molecular result that influenced our decision to place *Lepidopleurus binghami* Boone, 1928 in ***Astrochiton*** gen. nov., was its basal position within Nierstraszellidae. Although ***A.*** *binghami* shares some features with *N. lineata*, our combined-gene and *cox1*-only molecular phylogenetic estimates (Figs. 30, 31B) suggest that these morphological similarities are more likely to be plesiomorphic for the family, and to include ***A.*** *binghami* within *Nierstraszella* instead would have made that genus paraphyletic. Our result is also consistent with a deep biogeographic separation between the Caribbean ***A.*** *binghami* and all the species of the family that are restricted to the Indo-West Pacific. The more recent availability of a *cox1* sequence from "*Leptochiton*" *incongruus* [Seid *et al.*, 2025; D.J. Eernisse and A. Draeger, in prep.] revealed that this tropical East Pacific species is supported as sister species to ***A.*** *binghami* (Figs. 30, 31B), leading us to group it as ***A.*** *incongruus*. This has expanded the distribution of the genus, and has implications for a deep biogeographic separation between neotropical and Indo-West Pacific species groups.

Some previously reported sequences in GenBank that we have resolved as members of Nierstraszellidae are likely to be based on misidentifications or possible contamination because they were identified as species from other genera. For example, *cox1* sequences reported by Sigwart *et al.* [2011] to represent *Leptochiton juvenis* (HQ907863) and *L. satoi* (HQ907870) could not have been those species because these sequences group firmly within ***Rissochiton*** (Fig. 31B) despite very different morphological features for those species. In the case of *L. saitoi*, we have included sequences from verified specimens of that species as part of our outgroup (Fig. 30).

Our 16S-only result (Fig. 31A) for specimens initially identified as ***R.*** cf. *rissoi* implies that they have closer affinities to ***R. quincuncialis*** sp. nov. (with 70 percent bootstrap support) than to ***R.*** *rissoi*. The two specimens identified as ***R.*** cf. *rissoi* were from 1218–1252 m depth, within the range (753–1449 m) of the other nine sequenced specimens identified as ***R.*** *rissoi*, and only slightly deeper than the five sequenced specimens identified as ***R. quincuncialis*** sp. nov. (842–1022 m), whereas the lectotype of ***R.*** *rissoi* was collected at 2,053 m depth about midway between the sampled Papua New Guinea and Philippines localities. Pending further study, we have retained the provisional status of ***R.*** cf. *rissoi* based on preliminary morphological identification but the results indicate that these two specimens are unlikely to be conspecific with what we have identified as ***R.*** *rissoi*.

Our revision returns *Nierstraszella* to the status of a monotypic genus, but the situation is far from resolved. Our presented combined gene analysis (Fig. 30), with no missing data for 41 of 42 specimens, and our separate gene analyses (Fig. 31A, B), imply phylogeographic or cryptic species distinctions within *N. lineata* populations from Japan, the Philippines, and Papua New Guinea. Our *cox1*-only results (Fig. 31B) that included Vanuatu specimens with only *cox1* sequences [Duperron *et al.,* 2013] added a fourth geographic region for *N. lineata* that is genetically distinct. This result is consistent with mere phylogeographic separation, although the extent of genetic separation is more substantial than is

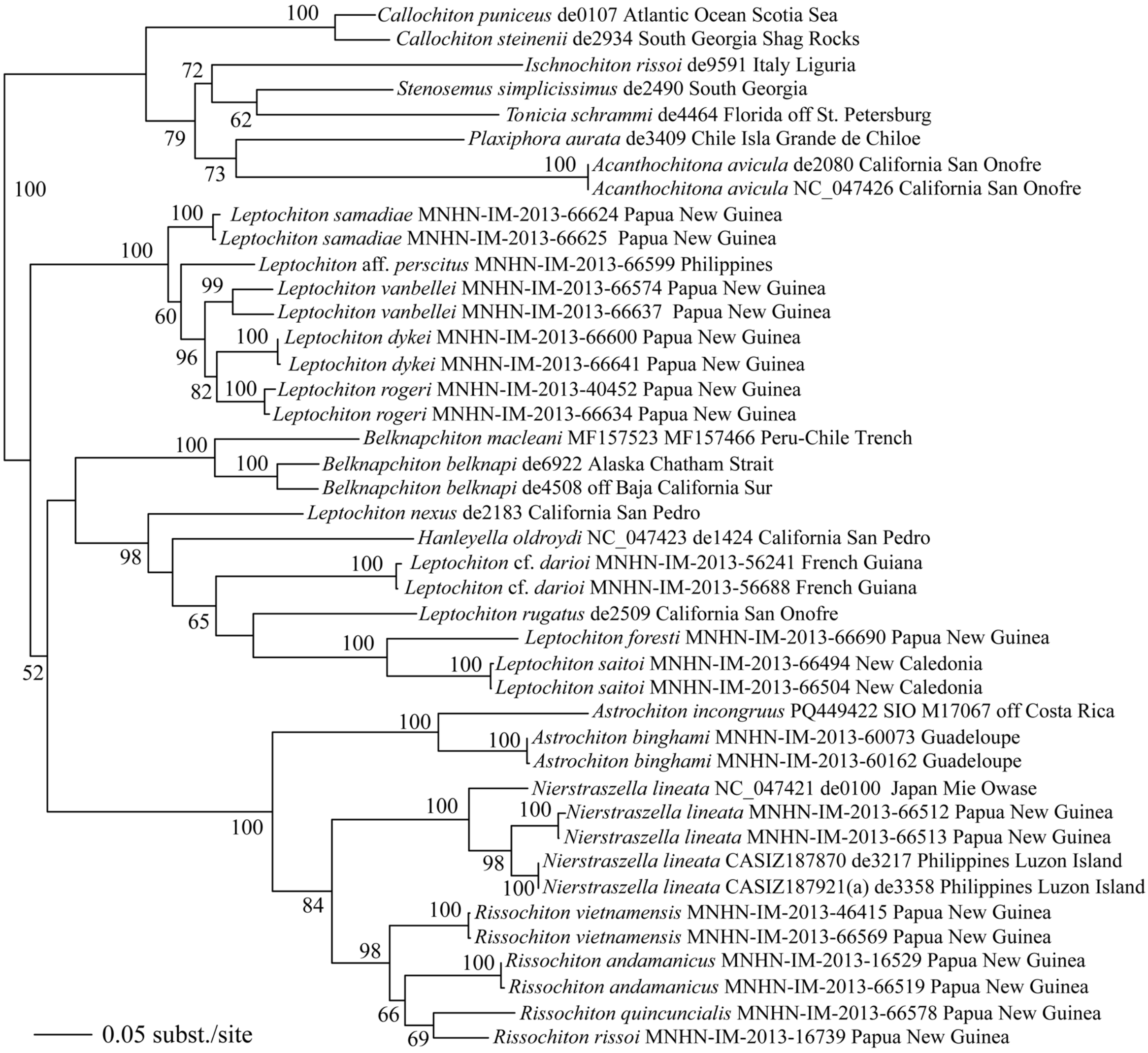

FIG. 30. Best maximum likelihood tree for the combined mitochondrial 16S + *cox1* gene sequence data set. Only specimens with both 16S and cox1 have been included except for a single sequenced specimen (*cox1* only) of ***A.** incongruus*, identified by DE, from Seid *et al.* [2025]. Multiple outgroups include representatives of non-Lepidopleurida taxa: Callochitonida, Chitonida: Chitonina, and Chitonida: Acanthochitonina. Table 1 and Supplementary Table S1 present more details of the specimens and their localities for this analysis, and for additional specimens included only in single-gene results (Fig. 31A, B). Numbers at nodes are the percentage of 400 bootstrap replicates for which the corresponding node was observed. Nodes without values had <50% bootstrap support.

typically reported in phylogeographic studies (see below). However, *N. lineata* from Japan grouped with a 16S-only specimen from Papua New Guinea, well apart from a group of all other Papua New Guinea specimens with 16S sequence (Fig. 31A). In contrast, *N. lineata* from Japan grouped with a *cox1*-only specimen from the Philippines, well apart from a group of other Philippine specimens with *cox1* sequence (Fig. 31B). These results imply that *N. lineata* specimens with divergent haplotypes co-occur within Papua New Guinea the Philippines, and Japan, which is unexpected if our results were reflecting only phylogeographic separation. It is more consistent with a cryptic species complex that overlaps broadly in distribution. We have yet to discover corresponding morphological distinctions within what appears to be the single morphospecies we treat as *N. lineata*. Because mitochondrial markers are not suited for assessing the extent of current reproductive connectivity within a potential cryptic species complex, this pattern could be consistent with either microallopatric speciation followed by resumed overlapping distribution [Kelly, Eernisse, 2008] or else incomplete allopatric speciation.

This at least partly geographic pattern accounts for the relatively high 8.8 percent *cox1* sequence divergence within *N. lineata* (Table 3), based on an average pairwise percentage difference. A similar high average (6.8 percent) was observed for ***Rissochiton** andamanicus* when the *cox1* sequence

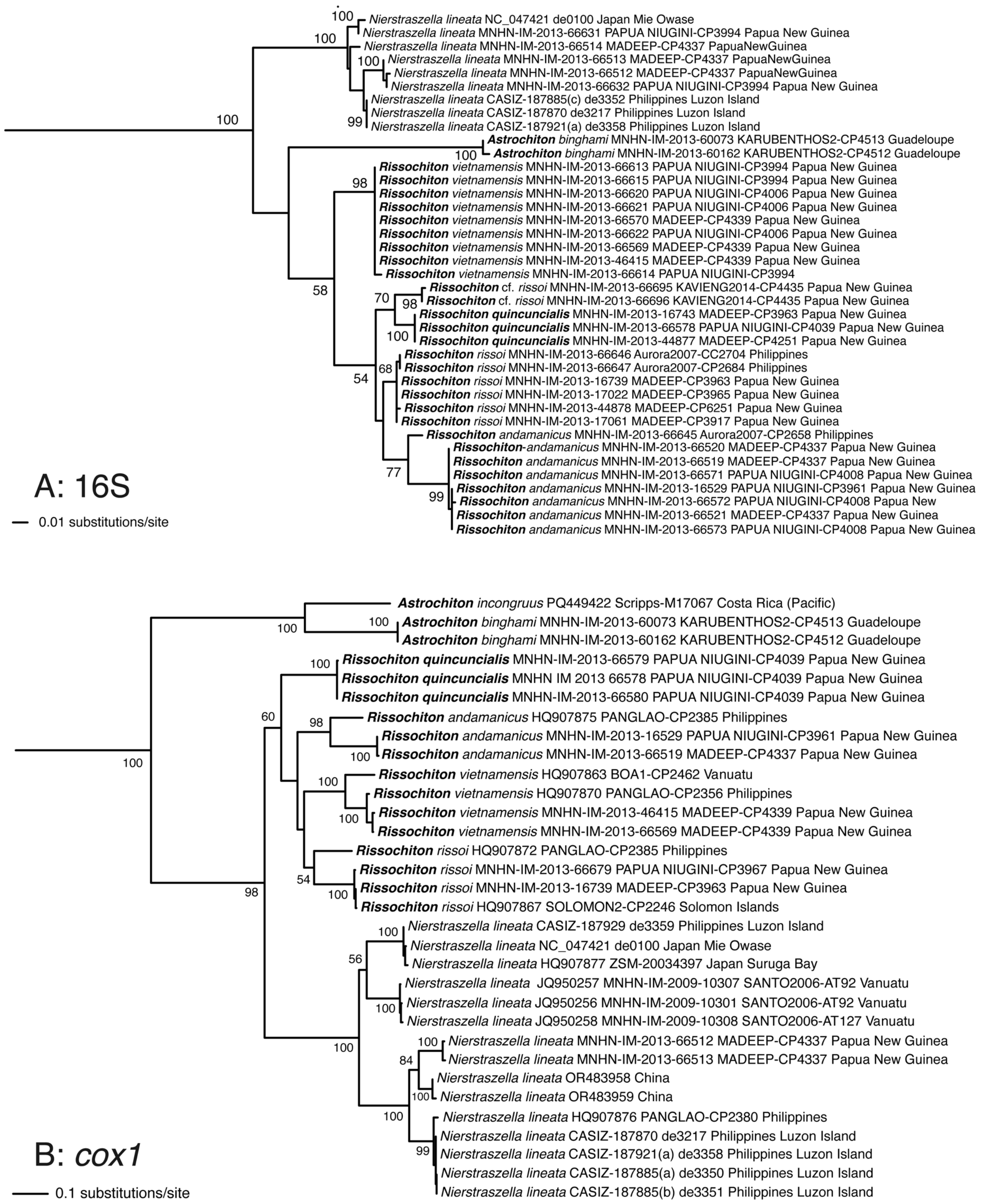

FIG. 31. Best maximum likelihood trees for separate (**A**) 16S and (**B**) *cox1* gene data sets. Table 1 lists all specimens that have at least 16S or *cox1* available. The estimates based on 16S (**A**) and *cox1* (**B**) included the same selection of outgroups for rooting the ingroup as in Figure 30, but these have been trimmed from the figures to highlight relationships within Nierstraszellidae. Other details are as in Figure 30.

from a Philippines specimen that was identified as this species [Sigwart *et al.,* 2011] is contrasted with sequences from our two Papua New Guinea specimens. Two other moderately high *cox1* intraspecific contrasts likewise involve geographic contrasts, whereas two others from a single locality have < 1 percent sequence difference. Although some of these averages are high even for the rapidly evolving *cox1* gene, they are still much less than the range of high, even for shallow-water chitons, interspecific sequence divergences (12.7– 22.3 percent) observed across the family for *cox1*. For our larger 16S data

Table 3. Comparison of average sequence percentage pairwise differences for *cox1* (top) and 16S (bottom).

cox1	n	Abi	Nli	Ran	Rqu	Rri	Rcfri	Rvi
Astrochiton *binghami* (Abi)	2	0.0						
Nierstraszella lineata (Nli)	13	22.3	8.8					
Rissochiton *andamanicus* (Ran)	3	21.7	17.4	6.8				
Rissochiton quincuncialis sp. nov. (Rqu)	3	20.5	16.5	14.3	0.1			
Rissochiton *rissoi* (Rri)	4	22.1	17.5	13.1	12.7	5.4		
Rissochiton cf. *rissoi* (Rcfri)	0	-	-	-	-	-	-	
Rissochiton *vietnamensis* (Rvi)	4	22.2	17.2	14.0	14.2	13.0	-	4.4
Total	29							
16S	n	Abi	Nli	Ran	Rqu	Rri	Rcfri	Rvi
Astrochiton *binghami* (Abi)	2	0.4						
Nierstraszella lineata (Nli)	10	12.0	1.7					
Rissochiton *andamanica* (Ran)	8	12.6	12.3	0.9				
Rissochiton quincuncialis sp. nov. (Rqu)	3	11.4	12.7	5.6	0.0			
Rissochiton *rissoi* (Rri)	6	11.1	11.7	4.6	3.4	0.2		
Rissochiton cf. *rissoi* (Rcfri)	2	10.9	12.3	5.6	2.9	3.6	0.2	
Rissochiton *vietnamensis* (Rvi)	9	10.9	10.8	6.7	6.0	5.1	6.7	0.1
Total	40							

set, a maximum of 1.7 percent intraspecific sequence divergence was observed, contrasted with greater (2.9–12.7 percent) interspecific divergence.

When our larger 16S data set was analyzed with ABGD software [Puillandre *et al.,* 2012] for objectively estimating species delineation patterns, ABGD provided partition sets resulting from four different settings of prior maximal distance (P). The setting resulting in the fewest partitions (P=2.15e-02) produced grouped sequences that corresponded nearly exactly to our morphology-based species identifications with two exceptions. First, a specimen from the Philippines (MNHN-IM-2013-66645; AURORA 2007; no *cox1* available) was identified as ***R.*** *andamanicus* based on morphology, but was in its own ABGD partition, apart from the other seven ***R.*** *andamanicus* specimens with 16S from Papua New Guinea. Second, two specimens with only 16S were earlier identified as ***R.*** cf. *rissoi* (KAVIENG 2014) based on their morphology were separated together in their own partition, apart from multiple samples of ***R.*** *rissoi* that included some others from Papua New Guinea (multiple expeditions) but also from New Caledonia (EXBODI) and the Philippines (Aurora 2007). Neither of these situations is simple. Compared with ***R.*** *andamanicus* from Papua New Guinea, the ***R.*** *andamanicus* specimens from the Philippines (including a separate specimen with only *cox1* sequence discussed earlier) were both collected at a great distance from the type locality for the species in the Bay of Bengal southeast of India so it is impossible to predict whether either corresponds to future topotype sequencing of *R. andamanicus*. For the two specimens separated as ***R.*** cf. *rissoi*, their morphology remains to be examined in more detail to determine whether there might be subtle differences from other ***R.*** *rissoi*.

Discussion

As a result of our revision and expansion of the family Nierstraszellidae, we found that it includes three morphologically similar genera *Nierstraszella*, ***Rissochiton*** gen. nov., and ***Astrochiton*** gen. nov. All species of these three genera are distinguished by the high similarity of the sculpture and aesthete pore distribution of the tegmentum, the armament of the perinotum, and the teeth of the radula. Our phylogenetic estimates from combined and separate 16S or *cox1* sequence analyses produced results that are congruent with our arrangement that is largely based on microscopic features as imaged with SEM. It is likely that all members of the family are also united by their preferred habitat of deep-sea sunken wood, and this could explain their similarity to other taxa with a similar xylophagous habitat. For example, the normally ribbed dorsal spicules of the girdle and long smooth needles scattered over the perinotum are very similar to those of species of the genus *Ferreiraella* Sirenko, 1988, and it is likely that they perform similar sensory functions. But *Ferreiraella* differs substantially in its morphology and belongs to a different family, Abyssochitonidae Dell'Angelo et Palazzi, 1989 (formerly Ferreiraellidae Dell'Angelo et Palazzi, 1991). The similarity in the disjunctive distribution of Nierstraszellidae and Abyssochitonidae is also striking. Both families are comprised of xylophages that have a very similar geographical distribution, indicating their likely shared presence in more ancient seas.

Sirenko [1997] proposed that the family Abyssochitonidae occurred at the end of the Paleozoic, but this has not been supported by available molecular comparisons of the extant members of *Ferreiraella*; these have resolved them not as a basal divergent lineage but as nested within Lepidopleurida [Sigwart *et al.,* 2011; Eernisse, Irisarri, 2019]. For Nierstraszellidae, extant members of the family exhibit highly similar sculpture of the tegmentum, also found in the Jurassic species ***Rissochiton*** *shapovalovi*. Further study might lead to the conclusion that the Jurassic fossil is not included within Nierstraszellidae. The present disjunct distribution found between two species of ***Astrochiton*** is likely much more ancient than the vicariant land barrier arising between the Pacific and proto-Caribbean Sea during the Pliocene [Burke, 1988; Neill *et al.,* 2014].

Species of all three genera of the family Nierstraszellidae are characterized by the presence of a very large number of pores of aesthetes (from 6 up to 45) in each aesthete group, and often with a strong size (age) intraspecific variability of this number of pores, which is unusual for many species of the genus *Leptochiton*. Apparently, a strong increase in the number of pores of aesthetes and the expansion of apophyses are the main trends in the evolution leading to the last common ancestor shared by members of Nierstraszellidae within Lepidopleurida.

As in members of Abyssochitonidae, the armament of the girdle and the shape of the teeth of the radula are highly conserved, reflecting adaptation to life at great depths with a general dependence on a sunken-wood substrate for their supply of food in the form of cellulose or else associated microbes and detritus. The highly similar morphological features of the perinotum and radula contrast with much more variable tegmentum sculpture, even varying within the same species, and this seems to be true for all species of Nierstraszellidae. Such close similarity of morphological features can lead to errors in determining the taxa of generic and species ranks, and therefore the use of molecular methods is desirable.

Conclusions

The chiton genus, *Nierstraszella*, is returned to monotypic status, represented only by its type species, *N. lineata*. However, the family it represents, Nierstraszellidae, is substantially expanded by this study, adding two new genera that accommodate a total of seven extant species. Besides *N. lineata*, all five other Indo-West Pacific species, including two that are new, are herein grouped as ***Rissochiton*** gen. nov. The family also includes two additional neotropical species assigned to ***Astrochiton*** gen. nov. and, in our molecular analyses (Figs. 30, 31B), the neotropical (***Astrochiton*** gen. nov.) and Indo-West Pacific (*Nierstraszella* + ***Rissochiton*** gen. nov.) groupings are supported as reciprocally monophyletic. The type species of ***Astrochiton***, ***A.*** *binghami*, is a relatively common deep-water Caribbean and Gulf of Mexico species, and the morphologically distinct, ***A.*** *incongruus*, is found in the tropical East Pacific.

This study continues a recent trend in systematic revisions of the most diverse order of chitons in the deep sea, Lepidopleurida. We employ SEM examination to reveal diagnostic features of the aesthete sensory system, radula, and girdle elements, as supplemented with molecular analysis, to support species and higher-level taxonomic classification. As in other recent studies for Lepidopleurida, this study reassigns species that have been uncomfortably grouped in the large polyphyletic genus, *Leptochiton*, introducing new species and genera and a new concept for Nierstraszellidae. The species we include in this family are also united by their xylophagous microhabitat and dietary specialization on deep-water sunken wood. A combined-gene analysis of mitochondrial 16S and *cox1* further supports the morphological species concepts, and supports the monophyly of Nierstraszellidae, a basal biogeographic split within the family, and the monophyly of each genus. Our study has also revealed complex phylogeographic pattern within at least *N. lineata*, and this implies a lack of genetic connectivity within the vast Indo-West Pacific deep sea region.

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Conflict of Interest

The authors declare there is no conflict of interest associated with this contribution.

Authors' Contributions

BS completed early draft manuscript based on his SEM-based study of deep-water specimens from MNHN and other sources and contributed to the writing in all subsequent manuscript revisions. DE was responsible for all molecular analyses based on sequencing at MNHN and CSUF, for studying associated molecular vouchers to ensure the accuracy of identification, writing portions of the manuscript, and as corresponding author assumed primary responsibility for manuscript revisions.

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Supplementary materials

Supplementary Table S1. Details for specimens used in molecular analyses, incliuding Genbank accession numbers for 16S and *cox1* sequences.

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