

Classification of the Modulidae (Caenogastropoda, Cerithioidea), with new genera and new fossil species from the Neogene of tropical America and Indonesia

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A revision of the cerithioidean genus *Modulus*, based on shell characters and new fossil material from the Neogene Caribbean and Indonesia, shows the group not to be monogeneric. Several distinct species groups, with restricted geographical distributions, were identified. The genus *Modulus* Gray, 1842, has a geological history starting in the latest Eocene to earliest Oligocene in tropical America, extending to the present day Caribbean and Pacific Panamic faunas, and is found in the early and middle Miocene eastern Atlantic and Mediterranean assemblages, after which there is a gap in its history until the present day, when it is found living off West Africa. *Trochomodulus* gen. nov. is an exclusively tropical American genus, represented from the late-early Miocene to the present day Caribbean and Pacific Panamic faunas. *Laevimodulus* gen. nov. and *Psammmodulus* Collins, 1934, are also

exclusively tropical American genera, with a Miocene-Pliocene fossil record that did not survive to the present day. In the Indo-Pacific, *Indomodulus* gen. nov. first appears in the early Miocene of Indonesia, after which there is no fossil record until the Pleistocene, and is today represented by a single, widely-distributed Indo-Pacific species. *Conomodulus* nov. gen. is restricted to the Miocene of Indonesia.

Six new species were described; from the Caribbean: *Trochomodulus paraguayensis* spec. nov., *Laevimodulus canae* spec. nov., and *Laevimodulus gurabensis* spec. nov.; from Indonesia: *Conomodulus renemai* spec. nov., *Indomodulus pseudotectum* spec. nov., and *Indomodulus miocenicum* spec. nov.

Key words: Modulidae, generic revision, Neogene Caribbean, Neogene Indonesia, new genera, new species, palaeobiogeography.

INTRODUCTION

The rich and diverse Neogene assemblages from the northern Dominican Republic collected as part of the Panama Paleontology Project and now housed in the Naturhistorisches Museum Basel (Switzerland) and the Bernard Landau collections housed in the Naturhistorisches Museum Wien (Austria) continue to provide species as yet unknown to science. Although all these species require formal description, some are more remarkable than others. In this paper we take the opportunity to describe some modulids quite unlike any of those known in the fossil or Recent faunas.

Modulids occur worldwide in tropical waters, but are not speciose, with only about a dozen Recent species known, although some of these may be synonyms. Considering this paucity of species, the family is well represented in the tropical American fossil and Recent faunas, but seemed to be very poorly represented in the Indo-Pacific fossil record. In the course of the preparation of this work, further records for fossil modulids were sought for the Indo-Pacific, and found within the collections of the Naturalis Biodiversity Centre, which houses a superb collection of Indonesian fossil molluscs.

Until now, authors have included all the living species in a single worldwide genus. We are not aware of any molecular phylogenetic work on the genus. However, examination of the shells of “*Modulus*” species, clearly indicates that there are distinct lineages within the family. In this paper we define these modulid lineages based on shell characters, and record four species from the Neogene of the northern Dominican Republic, two of which are new; and a new species from the late-early Miocene Cantaure Formation of Venezuela, and four species from the Miocene of Indonesia, of which three are also new. We stress that unlike working with Recent shells, when working with the fossil record it is not unusual to find species with characters intermediate between genera. This reflects the evolutionary process, and the placement of some species, such as *Indomodulus pseudotectum* spec. nov., remain to some degree subjective and open to alternative representations. This work is not intended to be a monographic treatment of the family at species level, but we take the opportunity of illustrating many of the tropical

American fossil species, placing special attention to the collemellar area. Whilst in the Recent faunas modulids are locally found in large numbers, in the fossil tropical American and Indonesian assemblages they are uncommon. Modulids inhabit rocky and seagrass environments. Rocky environments are known to be poorly represented in the tropical American Neogene record (Vermeij, 2001a), whereas seagrass communities are not. Why modulids should be so uncommon in fossil assemblages is unclear. Nevertheless, this results in a small number of specimens from a large number of widely geographically and stratigraphically separated deposits. The small number of specimens from each assemblage makes intraspecific variability difficult to evaluate. Whenever the shell characters between the fossil populations differed consistently, they were considered distinct species. This might be considered by some to be a rather narrow taxonomic viewpoint, especially with the species here described under the genus *Trochomodulus* gen. nov. (i.e. *T. paraguayensis* spec. nov., *T. vermeiji*, *T. tamanensis*). However, in our experience, at species level, tropical American Neogene faunas tend to have a rapid turnover and be highly endemic, and “splitting” rather than “lumping” turn out to be correct in most cases (Landau et al., 2008).

GEOLOGICAL SETTING

Dominican Republic – The geology and stratigraphy of the Dominican Republic has been extensively studied as part of the Panama Paleontology Project, and its results published by Saunders et al. (1986), and will not be repeated here. Updated stratigraphic charts for the tropical American area can be found in Landau et al. (2012).

Indonesia – The material investigated in this study derives from several different localities in Java and East Kalimantan, Indonesia. Banyunganti is a sampling locality in Yogyakarta, Java, Indonesia, located close to the village Banyunganti. The studied material was collected in unnamed early Burdigalian, fossiliferous beds overlying the marine Jonggrangan Formation (Kadar, 1986). Geology and stratigraphy of the locality are described in detail by Reich et al. (2014). The Javanese material of *Conomodulus preangerensis* Martin, 1905, was collected from unnamed beds in

Cadasngampar and Citalahab (Tji Talahab). The age of both localities is late middle Miocene (Johnson et al., submitted). No further information on the geology or sedimentology of the localities is available.

An overview over the geology of East Kalimantan can be found in Wilson et al., 1999 and in Wilson & Evans (2002). The historical sample locality 114 is situated at the Menkrawit River at the northern Mangkalihhat Peninsula (East Kalimantan, Indonesia). The exact locality is unknown. Sediments at the sampled locality were described as slightly sandy, fossiliferous grey clays in the transition between Tabellar and Menkrawit layers (Beets 1941). The age is middle Miocene based on large benthic foraminifers (Renema, 2007; Lunt & Allen, 2004). Sampling locality 391 (Mangkalihhat, East Kalimantan) is an historical locality with little available information in the proximity of locality 114. It is of middle Miocene age, stratigraphically just above locality 114 (Johnson et al., submitted).

Furthermore, this study includes recently collected material from new sampling localities (TF 102; TF 110, sampled in 2010, and TF 505, referring to the same locality sampled in 2011) in Bontang (East Kalimantan, Indonesia). Bontang is located in the Kutai Basin, the largest Cenozoic sedimentary basin of Kalimantan (Moss & Chambers, 1999). Both localities represent early Tortonian (late Miocene), unnamed beds in marine siliciclastic sediments. Several studies on the sampling localities, their stratigraphy, and associated mollusc faunas have recently been carried out by Renema et al. (submitted); Kusworo et al. (submitted); and Reich et al. (submitted).

MATERIAL AND METHODS

The Caribbean material described here is from the Panama Paleontology Project (PPP) collection, housed in the Naturhistorisches Museum Basel (NMB coll.), Switzerland, and the Bernard Landau collection, now deposited in the Naturhistorisches Museum Wien (NHMW coll.), Vienna, Austria.

All Indonesian material described in this study is housed in the Naturalis Biodiversity Centre, Leiden, The Netherlands (indicated by RGM numbers). The material from East Kalimantan (Indonesia) is largely from collections made by

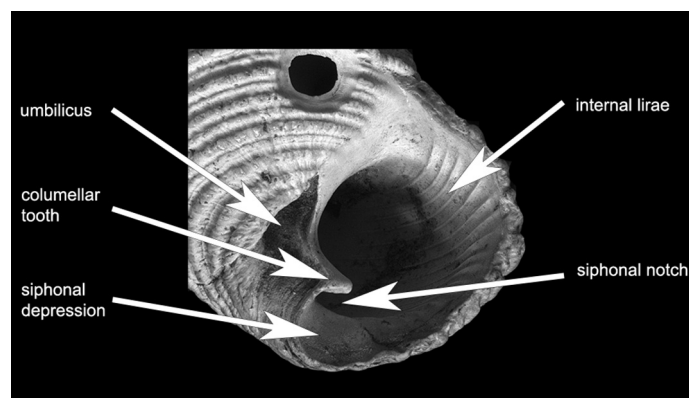


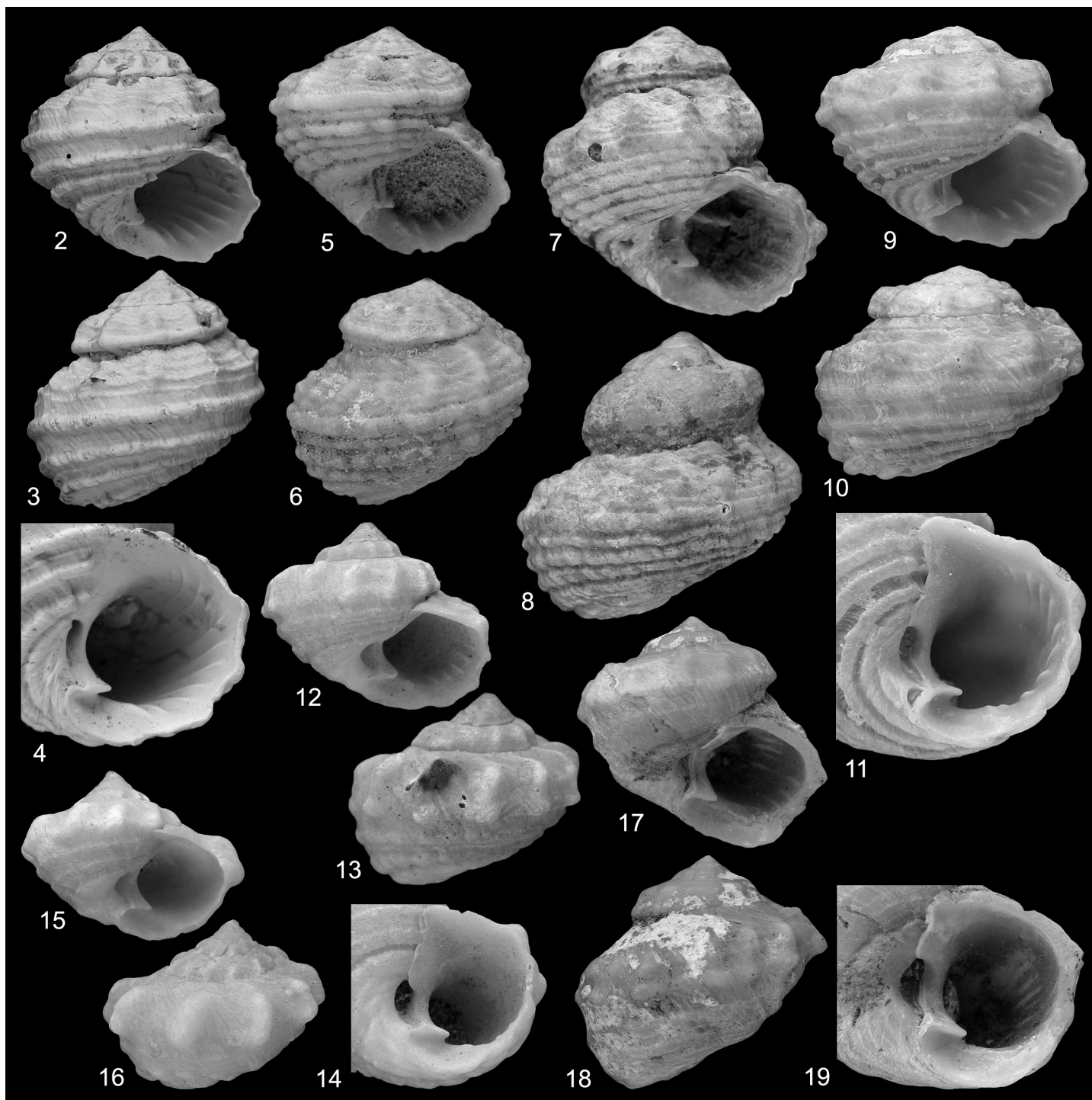
Fig. 1. Apertural features of modiolids; *Conomodulus preanigerensis* (Martin, 1905), holotype RGM.10764, unnamed beds from the late Miocene of Cadasngampar, Java, Indonesia. Height 11.7 mm (specimen tilted posterior to vertical axis to show siphonal structures; photo F. P. Wesselingh).

the Throughflow Project in 2010 and 2011. Only material from localities 114 and 391 (Mangkalihhat Peninsula) is from a collection made by Leopold in the 1920s as part of a survey for the Dienst van het Mijneuzen in Nederlands Oost-Indie. The molluscan fauna from locality 114 is described by Beets (1941). The material from Java includes a holotype from the Martin collection (Leloux & Wesselingh, 2009), a single specimen from Citalahab, and material from the Banyunganti fauna collected in 2006 by F.P. Wesselingh and W. Renema, and described by Reich et al. (2014).

Superfamily Cerithioidea Fleming, 1822

Family Modulidae P. Fischer, 1884

The generic revision proposed herein is based on shell characters. We place particular importance on the apertural characters, especially those of the siphonal area situated immediately below the columellar tooth. The siphon can be marked either by a depression on the columellar callus or by a groove on the medial edge of the columellar callus, or in some modiolid genera a combination of the two (Fig 1).



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TROPICAL AMERICAN AND EASTERN ATLANTIC
MODULID GENERA

Modulus Gray, 1842

Type species. — *Trochus modulus* Linnaeus, 1758, by subsequent designation (J. E. Gray, 1847). Recent, Caribbean.

Revised description. — Shells medium-sized, solid, turbiniform. Spire depressed in most species. Suture impressed to narrowly canaliculated. Sculpture of broad axial ribs or folds on spire whorls and adapical half of whorl, developed into tubercles at shoulder in most species; spiral cords narrow, rounded, elevated, strongly developed on base, where they are weakly tubercular in some species. Aperture small, circular; outer lip sharp, lirate within. Columellar callus hardly developed, narrow, with a sharp lamella-like columellar tooth abapically. Siphonal depression narrow to absent; siphonal groove, deep. Small umbilical chink present.

Species included. — Recent tropical American: Atlantic; *M. modulus* (Linnaeus, 1758) (Figs 2-8), *M. lindae* Petuch, 1987, *M. kaicherae* Petuch, 1987, *Modulus pacei* Petuch, 1987, *M. bermontianus* Petuch, 1994 (Figs 9-11), *Modulus bayeri* Petuch, 2001, *M.*

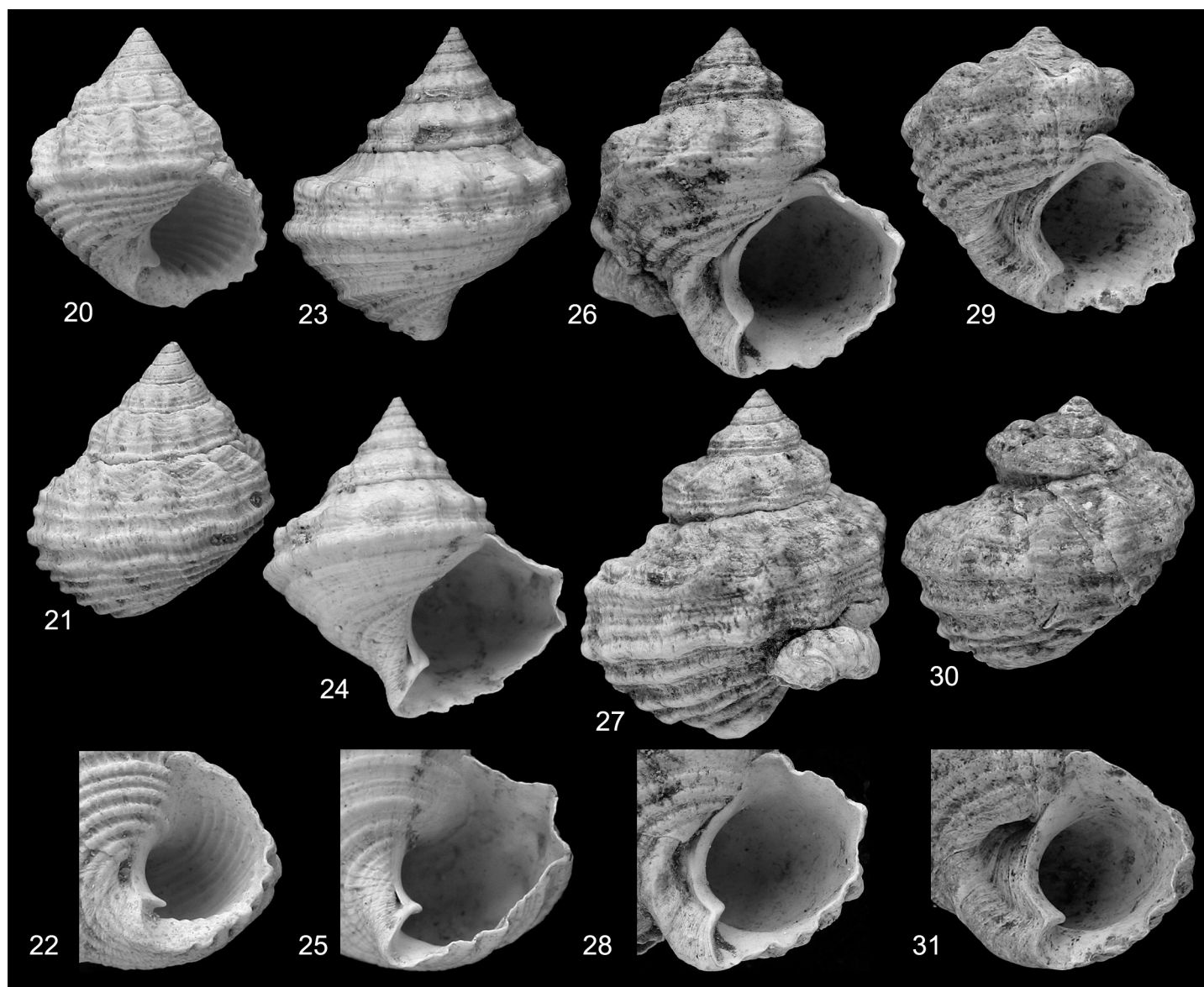
Figs 2-19. *Modulus* species (all photos B. Landau). **2-8**, *Modulus modulus* (Linnaeus, 1758). **2-4**, NHMW 2013/0314/0022 (ex BL coll.), height 13.8 mm, Lantana Road, Palm Beach County, Florida, USA, Fort Thompson Formation, late Pleistocene; **5-6**, NHMW 2013/0314/0045 (ex BL coll.), height 14.1 mm, El Castillo, La Isabella, northern Dominican Republic, La Isabella Formation, late Pleistocene. **7-8**, NHMW 2013/0314/0024 (ex BL coll.), height 17.5 mm, Boca Chica, Margarita Island, Nueva Esparta State, Venezuela, Tortuga Formation, late Pleistocene. **9-11**, *Modulus bermontianus* Petuch, 1994, NHMW 2013/0314/0025 (ex BL coll.), height 9.7 mm, Capeletti Bros. Pit, Dade County, Florida, USA, Belmont Formation, late Pleistocene. **12-16**, *Modulus cerodes* (A. Adams, 1851). **12-14**, NHMW 2013/0314/0026 (ex BL coll.), height 11.6 mm. **15-16**, NHMW 2013/0314/0027 (ex BL coll.), height 10.8 mm, Santa Ines Bay near Mulegé, Baja California Sur, Mexico, late Pleistocene. **17-19**, *Modulus disculus* (Philippi, 1846), “blue house”, Burica Peninsula, Panama, Armuelles Formation, Charco Azul Group, late Pleistocene.

nodosus Macsotay & Campos, 2001. Pacific; *M. cerodes* (A. Adams, 1851) (Figs 12-16), *M. disculus* (Philippi, 1846) (Figs 17-19). Recent eastern Atlantic, West Africa; *M. guernei* Dautzenber, 1900, *M. turbinoides* (Locard, 1897).

Fossil tropical American: *M. liveoakensis* Mansfield, 1937 (latest Eocene-earliest Oligocene: Suwannee Limestone; for age of assemblage see Herbert & Portell, 2002); *M. turbinatus* (Heilprin, 1887) (late Oligocene: Chattian; Silex beds of the Tampa Limestone of Florida); *M. biconicus* Gardner, 1947 (Figs 20-22), *M. compactus* Dall, 1892, and *M. imitatus* Schmelz, 1991 (Figs 23-25) (early Miocene Burdigalian, Chipola Formation of Florida); *M. woodringi* Mansfield, 1930, *M. lindae* Petuch, 1987, *M. caloosahatchiensis* Petuch, 1994, *M. bermontianus* Petuch, 1994 (Figs 9-11) (Plio/Pleistocene of Florida).

Fossil Europe: *M. basteroti* Benoist, 1874 (early-middle Miocene).

Discussion. — *Modulus* is the most species-rich genus of its family in the living fauna. Houbbrick (1980) interpreted the taxon *Modulus modulus* broadly to include populations with direct development, such as the one he studied on the east coast of Florida, as well as populations in which larvae hatch as free-swimming veligers, such as those in Colombia and Bermuda. The species is certainly highly variable in shape and in the height of the spire (Figs 2-8). Contrary to Houbbrick (1980), we suspect that *M. modulus* comprises several species, which are geographically distinct. For example, we note that specimens from Curaçao, Aruba, and the Atlantic coast of Costa Rica (Vermeij collection) differ from more typical *M. modulus* in having obsolete nodes and a high spire; these specimens typically lack lirae on the inner side of the outer lip. Several species within the *M. modulus* species group were erected by Petuch (1987, 1994, 2001) based on small differences of shell morphology. A revision of these species is beyond the scope of this work, but at least some of them are likely to be valid. In the eastern Pacific, the very strongly nodose *M. cerodes* usually lacks lirae (Figs 15-16), although they are present in some specimens (Figs 12-14). Whether *M. cerodes* is truly distinct from the sympatric *M. disculus* (Figs 17-19) is doubtful. Molecular studies will be needed to clarify the taxonomy of living western Atlantic and eastern Pacific species of *Modulus*.



Figs 20-31. *Modulus* species (all photos B. Landau). **20-22**, *Modulus biconicus* Gardner, 1947, NHMW 2013/0314/0028 (ex BL coll.), height 8.7 mm, Tenmile Creek, Calhoun County, Florida, USA, Chipola Formation, upper Burdigalian, early Miocene. **23-25**, *Modulus imitatus* Schmelz, 1991, NHMW 2013/0314/0029 (ex BL coll.), height 16.4 mm, Farley River, Calhoun County, Florida, USA, Chipola Formation, upper Burdigalian, early Miocene. **26-31**, *Modulus basteroti* (Benoist, 1873). Figs **26-28**: NHMW 2013/0314/0030 (ex BL coll.), height 20.2 mm, Moulin de Gamachot, Uzeste. **29-31**, NHMW 2013/0314/0031 (ex BL coll.), height 12.0 mm, Lariey, Saucats, Gironde, France, lower Aquitanian, early Miocene.

Trochomodulus gen. nov.

Type species. — *Modulus catenulatus* Philippi, 1849, designated herein. Recent, Panamic Pacific.

Description. — Shells medium-sized, relatively solid, trochiform. Spire of medium height to moderately depressed, straight-sided to cyrtocooid in profile, whorls straight-sided to concave. Suture impressed. Sculpture of narrow spiral cords, with a single more strongly developed cord at suture, which develops into strong keel-like peripheral cord on last whorl, cords more prominent on base. Aperture small, circular; outer lip sharp, lirate within. Columellar callus weakly thickened and hardly expanded over venter, with a sharp lamella-like columellar tooth abapically. Siphonal depression narrow to absent; siphonal groove, deep. Small umbilical chink may be present or absent.

Species included. — Recent tropical American: Atlantic; *M. carchedonius* (Lamack, 1822) (Fig. 33), *M. calusa* Petuch, 1988 (Figs 34-36). Pacific; *Modulus catenulatus* Philippi, 1849 (Fig. 32).

Fossil tropical American: *M. willcoxi* Dall, 1892 (Figs 37-39) (early Miocene Burdigalian, Chipola Formation of Florida); *M. tamanensis* Maury, 1925 (Figs 40-41) (Brasso Formation, middle Miocene of Trinidad); *M. vermeiji* Landau & Silva, 2010 (Figs 42-44) (Caujarao Formation, late Miocene; and Araya Formation, early Pliocene of Venezuela), *Monodonta basilea* Guppy, 1873 (Figs 45-51) (Baitoa Formation, early Miocene of the Dominican Republic; Bowden Formation, Pliocene of Jamaica; and Caloosahatchee Formation, Pleistocene of Florida).

Etymology. — Name reflecting the trochiform shell shape of this group of modulids. Gender masculine.

Discussion. — Species of *Trochomodulus* are distinguished from those of *Modulus* most importantly by their trochiform rather than turbiniform shell shape, and by their sculpture, which consists of strong spiral cords, with a keel-like periphery and no axial sculpture. The character of the siphonal depression and groove is similar in both genera.

Trochomodulus basileus (Guppy, 1873) (Figs 45-51)

Monodonta basilea Guppy, 1873: 85, pl. 1 fig. 2; Guppy, 1874: 434, pl. 1 fig. 2.

Modulus modulus basileus (Guppy). Woodring; 1928 (in part): 343, pl. 25 fig. 17, pl. 26 figs 1-2 (not figs 3-4 = *Modulus* sp.); Perrilliat, 1972: 46, pl. 14 figs 9-14. Not *Modulus basileus* (Guppy, 1873). Petuch, 1994: 64, pl. 11 fig. E.

Material and dimensions. — Maximum height 11.6 mm, NHMW 2013/0314/0013/1 (ex BL coll.) (Figs 45-47), NHMW 2013/0314/0014/1 (Figs 48-51), NHMW 2013/0314/0015/3, Lopez Section, Río Yaque del Norte, Baitoa Formation, early-middle Miocene.

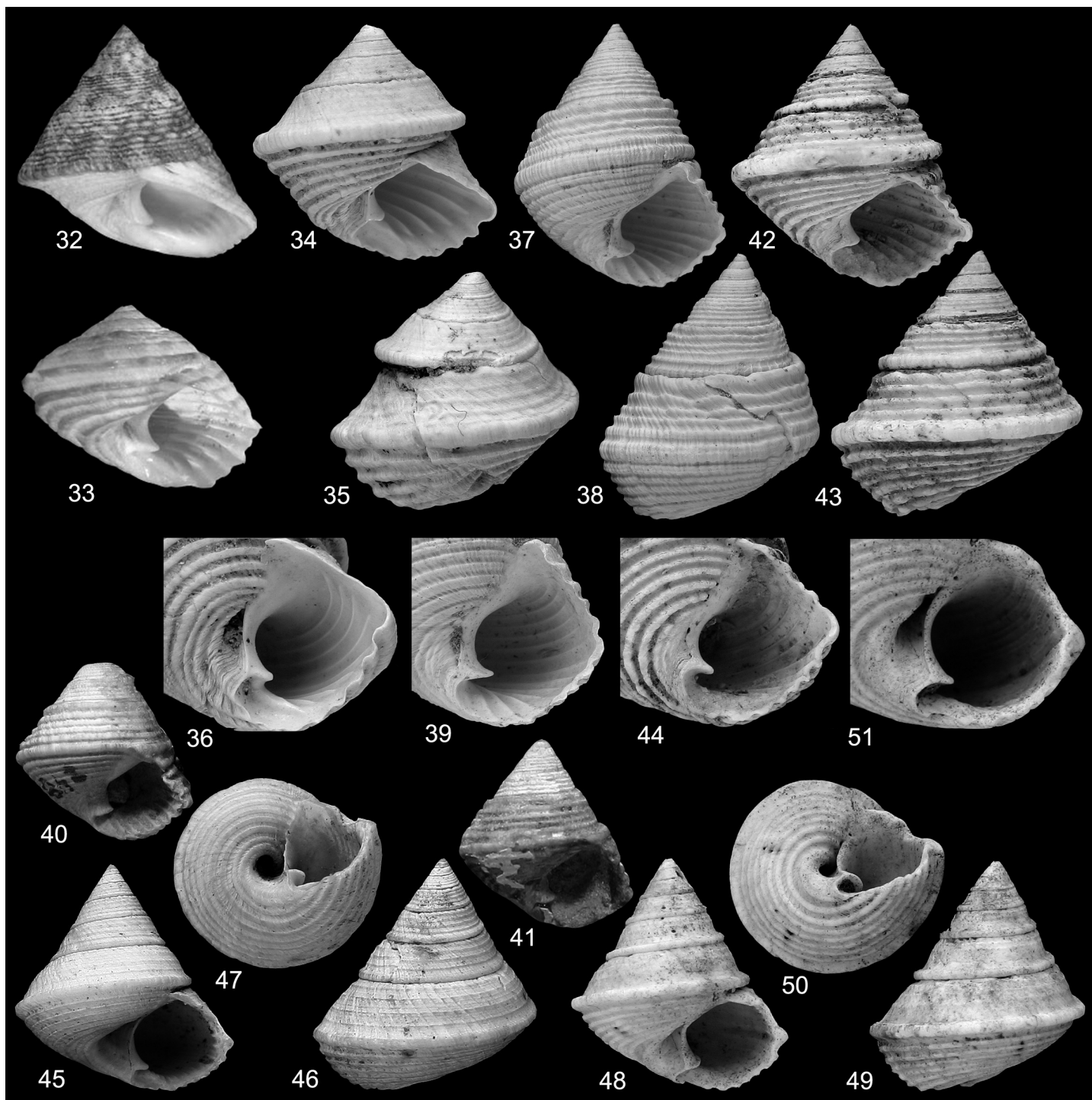
Discussion. — *Trochomodulus basileus* (Guppy, 1873) is somewhat variable in respect to the strength of the spiral sculpture and the carina is coarsely tubercular in some specimens, as shown by the specimens illustrated here from the Dominican Republic (Figs 45-51), those from the late Pliocene Piacenzian Agueguexquite Formation of Mexico (Perrilliat, 1973, pl. 14 figs 9-14), and those from the Pliocene Bowden Formation of Jamaica (Woodring, 1928, pl. 25 fig. 17, pl. 26 figs 1-2). However, some of the specimens figured by Woodring (1928, pl. 26 figs 3-4) with axial sculpture are not this species, but a species of *Modulus*. The shell illustrated by Petuch (1994, pl. 11 fig. E) as *Modulus basileus* from the early Pleistocene Caloosahatchee Formation of Florida has very weak spiral sculpture on the spire whorls and above the keel on the last whorl, and in our opinion is more likely to represent *Trochomodulus calusa* (Petuch, 1988).

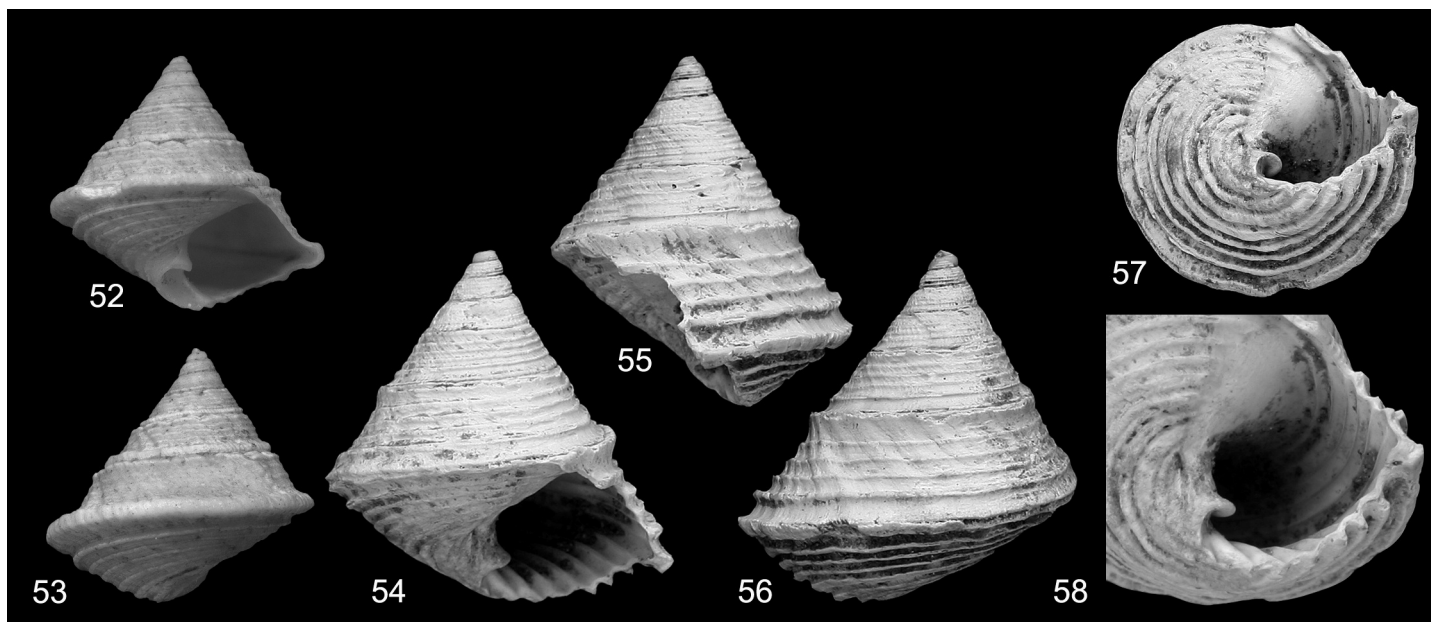
Trochomodulus willcoxi (Dall, 1892) from the early Miocene Burdigalian Chipola Formation of Florida, *T. tamanensis* (Maury, 1925) from the middle Miocene Brasso Formation of Trinidad and *T. vermeiji* (Landau & Silva, 2010) from the late Miocene Caujarao Formation and early Pliocene Araya Formations of Venezuela all differ from *T. basileus* in having no umbilicus present.

Distribution. — Early-middle Miocene: Baitoa Formation, Dominican Republic (this paper); Pliocene, Bowden Formation, Jamaica (Woodring, 1928); late Pliocene: Agueguexquite Formation, Mexico (Perrilliat, 1973).

Trochomodulus sp. (Figs 52-53)

Material and dimensions. — NMB H20204 (Figs 12-13), one juvenile specimen height 3.7 mm, width 3.9 mm.





(opposite page)

Figs 32-51. *Trochomodulus* species (all photos B. Landau unless indicated). **32**, *Trochomodulus catenulatus* (Philippi, 1849), NMR 44212, height 16 mm, Mexico, Recent (NMR collection). **33**, *Trochomodulus carchedonius* (Lamarck, 1822), NMR 44157, height 14 mm, Sanibel Island, Florida, USA, Recent (NMR collection). **34-36**, *Trochomodulus calusa* (Petuch, 1988), NHMW 2013/0314/0032 (ex BL coll.), height 9.9 mm, Davies Pit, Okeechobee County, Florida, USA, Caloosahatchee Formation, late Pleistocene. **37-39**, *Trochomodulus willcoxi* (Dall, 1892), NHMW 2013/0314/0033 (ex BL coll.), height 37.0 mm, Tenmile Creek, Calhoun County, Florida, USA, Chipola Formation, upper Burdigalian, early Miocene. **40-41**, *Trochomodulus tamanensis* (Maury, 1925). **40**, Syntype PRI 1069, height 17.5 mm. **41**, Syntype PRI 1070, height 15.0 mm, Machapoorie, Samana, Trinidad, early-middle Miocene (Photos courtesy of PRI). **42-44**, *Trochomodulus vermeiji* (Landau & Silva, 2010), Holotype NHMW 2010/0038/0007 (ex BL coll.), height 15.5 mm, Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela, Araya Formation, Cubagua Group, early Pliocene. **45-51**, *Trochomodulus basileus* (Guppy, 1873), Lopez Section, Río Yaque del Norte, Baitoa Formation, early-middle Miocene. **45-47**, NHMW 2013/0314/0013 (ex BL coll.), height 11.6 mm, width 10.6 mm. **48-51**, NHMW 2013/0314/0014 (ex BL coll.), height 11.7 mm, width 10.7 mm.

Figs 52-58. *Trochomodulus* species (all photos B. Landau).

52-53, *Trochomodulus* sp., NMB H20204, NMB locality 17814, east coast of Cayo Agua, just south of Punta de Nispero, Bocas del Toro, Panama, Cayo Agua Formation, Zanclean, Early Pliocene, height 3.7 mm. **54-58**, *Trochomodulus paraguayensis* spec. nov., holotype NHMW 2013/0314/0023, Casa Cantaure, Paraguaná Peninsula, Falcón State, Venezuela, upper shell bed, Cantaure Formation (early Miocene; Burdigalian), height 15.3 mm.

Locality. — NMB locality 17814, east coast of Cayo Agua, just south of Punta de Nispero, Bocas del Toro, Panama.

Stratum. — Cayo Agua Formation, Zanclean, Early Pliocene.

Discussion. — A single small specimen of a *Trochomodulus* species from the Early Pliocene, Zanclean Cayo Agua Formation of Bocas del Toro is present in the NMB collections. It may represent a strongly keeled specimen of *T. basileus*, but it does not have the umbilicus as strongly developed. The specimen is too juvenile to determine with certainty.

Trochomodulus paraguanensis spec. nov. (Figs 54-58)

Type material and dimensions. — Holotype NHMW 2013/0314/0023, height 15.3 mm, width 14.7 mm (Figs 54-58); paratype 1 NMB H20231, height 14.0 mm, width 13.1 mm, NMB locality 17516.

Other material. — Known only from type material.

Type locality. — 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela (= locality GS-6-PGNA of Gibson-Smith & Gibson-Smith, 1979).

Type stratum. — Upper shell bed, Cantaure Formation (early Miocene; Burdigalian).

Etymology. — From geographic area in which it is found — the Paraguaná Peninsula, Falcón State, Venezuela. Gender masculine.

Diagnosis. — A *Trochomodulus* species with a medium-sized shell, with six narrow spiral cords on spire whorls, the abapical cord slightly more strongly developed, a narrowly canalculated suture, axial sculpture of collabral growth lines on early adult whorls, base moderately depressed, bearing ten spiral cords, and a deep siphonal groove with no siphonal depression.

Description. — Shell medium-sized, trochiform. Teleoconch of six weakly concave whorls. Suture impressed, very narrowly canalculated. Protoconch and early teleoconch whorls somewhat abraded. Fourth to last whorl with six narrow spiral cords, abapical cord slightly stronger and more distant from others, forming periphery. Strongly prosocline collabral growth lines present on early whorls, giving them finely reticulate appearance, growth lines obsolete, or almost so, from fourth whorl. Last whorl acutely an-

gled at peripheral cord. Base moderately depressed, bearing ten spiral cords, widening towards centre. Umbilicus almost closed. Aperture subquadrate, outer lip sharp, angled at peripheral cord, strongly and deeply lirated within; anal canal not developed; siphonal notch deep, narrow; siphonal depression not developed. Columella excavated in mid-portion, with strong, sharp, sub-horizontal columellar tooth. Columellar callus weakly developed.

Discussion. — *Trochomodulus paraguanensis* spec. nov. is represented by only two specimens, but it is distinctive enough to warrant description. It clearly belongs to the genus *Trochomodulus* gen. nov., characterised by its rather biconic shell, predominantly spiral sculpture, much reduced axial sculpture, and by its very sharp, keel-like periphery.

Trochomodulus paraguanensis is most similar to *Trochomodulus tamanensis* (Maury, 1925) from the Middle Miocene Brasso Formation of Trinidad. Six specimens of *T. tamanensis* in the Basel collections (NMB lot 10434 [sic] from Caparo River) differ from the Cantaure specimen in having a more elevated shell and a less angular periphery. Moreover, the spire whorls have five spiral cords as opposed to six in *T. paraguanensis*. *Trochomodulus vermeiji* (Landau & Silva, 2010) from the late Miocene Caujarao Formation and early Miocene Araya Formation of Venezuela is also similar, but has a narrower shell, with a less depressed base, and wider and fewer spiral cords. *Trochomodulus basileus* (Guppy, 1873) (discussed above) differs in the same characters, of a narrower shell with fewer spiral cords, but also has a wide umbilicus, which is almost absent in *T. paraguanensis*. This new species differs from the Recent tropical American Atlantic *T. carchedonius* (Lamack, 1822) and Pacific *T. catenulatus* Philippi, 1849 in having a much narrower and sharper peripheral keel and spiral cords.

Distribution. — Early Miocene: Cantaure Formation, Falcón State, Venezuela (this paper).

Laevimodulus nov. gen.

Type species. — *Laevimodulus canae* spec. nov., designated herein. Late Miocene, Dominican Republic.

Description. — Shells small, of medium-thickness, low-turbiniiform. Spire depressed, whorls convex. Suture deeply

impressed. Sculpture inconspicuous on spire whorls and apical half of last whorl, consisting of weak spiral cords and collabral growth lamellae, base with conspicuous spiral cords. Aperture small, circular; outer lip sharp, lirate within. Columellar callus hardly developed, with a sharp lamella-like columellar tooth abapically. Siphonal depression relatively large, very deep, narrow; siphonal groove, deep. Umbilicus narrow, deep.

Species included. — *Laevimodulus canae* spec. nov. (late Miocene, Cercado Formation, Dominican Republic), *Laevimodulus gurabensis* spec. nov. (middle-late Miocene, Gurabo Formation, Dominican Republic).

Etymology. — Latin *laevis* = smooth. Reflecting the rather smooth surface sculpture seen in this group of modulids. Gender masculine.

Discussion. — Species of *Laevimodulus* differ from the other modulid genera discussed in being smaller and lighter-shelled. *Psammmodulus* species are even smaller, but more solid-shelled. Moreover, *Psammmodulus* species differ in having a tall spire and display the tendency to agglutinate grains of sand, which is not seen in any other modulid genus. *Laevimodulus* species also differ from other modulid genera in having a narrow, but relatively deep umbilicus, whereas the umbilicus in other modulid genera is usually reduced to a small chink.

The absence of strong sculpture separates it from *Modulus* and *Tectomodulus*.

Laevimodulus canae spec. nov. (Figs 59-70)

Type material and dimensions. — Holotype NHMW 2013/0314/0001 (ex BL coll.), height 9.5 mm, width 10.3 mm (Figs 59-63); paratype 1 NHMW 2013/0314/0002 (ex BL coll.), height 8.9 mm, width 9.2 mm (Figs 64-67); paratype 2 NHMW 2013/0314/0003 (ex BL coll.), height 8.3 mm, width 8.9 mm (Figs 68-70); paratype 3 NHMW 2013/0314/0004 (ex BL coll.), height 9.0 mm, width 9.4 mm; paratype 4 NHMW 2013/0314/0005 (ex BL coll.), height 6.8 mm, width 6.9 mm.

Other material. — 16 specimens lot NHMW 2013/0314/0006 (ex BL coll.). 5 juveniles NMB collection unnumbered, NMB locality 16844.

Type locality. — Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, (Saunders et al., 1986, text-figure

15; Landau et al., 2012, chart 5).

Type stratum. — Cercado Formation (late Miocene, Messinian).

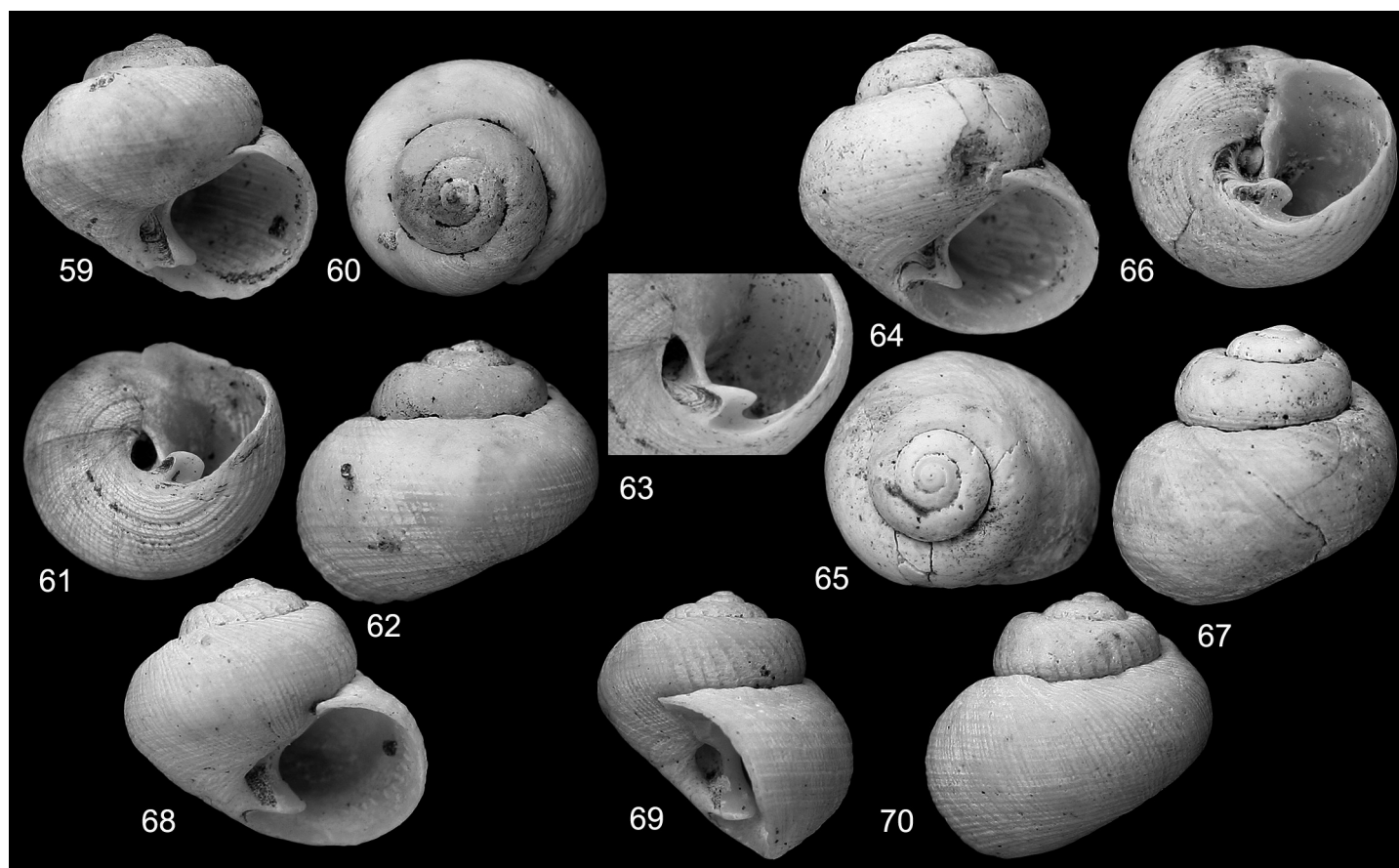
Etymology. — Named after the type locality of Río Cana in the northern Dominican Republic. Gender masculine.

Diagnosis. — A small *Laevimodulus* species, with a depressed turbiniform shell, strongly convex whorls, sculpture of very weak spiral cords, axial sculpture absent or in some specimens consisting of close-set collabral growth lamellae, a rounded aperture, a sharp columellar tooth, a deep, narrow siphonal depression, narrow siphonal groove, and a narrow, deep umbilicus.

Description. — Shell small, turbiniform, spire depressed. Protoconch, probably of two depressed whorls. Teleoconch of five strongly convex whorls. Suture deeply impressed, linear. Sculpture of very fine, subobsolete, narrow spiral cords and collabral growth lamellae, the lamellae subobsolete in most specimens (Figs 59-63), conspicuous in some (Figs 68-70). Last whorl strongly and regularly convex. Base not clearly delimited, bearing indistinct, narrow spiral cords. Umbilicus narrow, relatively deep. Aperture ovate, outer lip sharp, strongly prosocline in lateral view, regularly rounded, irregularly and weakly lirate within; anal canal not developed; siphonal canal represented by deep narrow groove in columellar callus below columellar tooth. Columella deeply excavated in mid-portion, with strong, sharp, abapical columellar tooth. Columellar callus hardly developed, very narrow.

Discussion. — *Laevimodulus canae* spec. nov. is characterised by its turbiniform shell, very convex whorls, weak spiral sculpture and lack of axial rugae or tubercles. The only comparable species is *Laevimodulus gurabensis* spec. nov., see below. The protoconch in the new species is abraded in all specimens, but seems to be composed of about two whorls, similar to that of the Recent *Modulus modulus* (Houbrick, 1980).

Modulus species in Recent Caribbean faunas are associated with shallow-water seagrass habitats (Houbrick, 1980) and those in the Panamic Pacific on mud flats (Keen, 1971). The presence of this species, together with numerous specimens of *Smaragdia viridis* (Linnaeus, 1758), strongly suggest this assemblage represents a seagrass community, as *Smaragdia* provides a proxy for seagrass beds in the fossil



Figs 59-70. *Laevimodulus* species (all photos B. Landau). *Laevimodulus canae* spec. nov. Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, Cercado Formation (late Miocene, Messinian). **59-63**, holotype NHMW 2013/0314/0001 (ex BL coll.), height 9.5 mm, width 10.3 mm. **64-67**, paratype 1 NHMW 2013/0314/0002 (ex BL coll.), height 8.9 mm, width 9.2 mm. **68-70**, paratype 2 NHMW 2013/0314/0003 (ex BL coll.), Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, Cercado Formation (late Miocene, Messinian), height 8.3 mm, width 8.9 mm.

(opposite page)

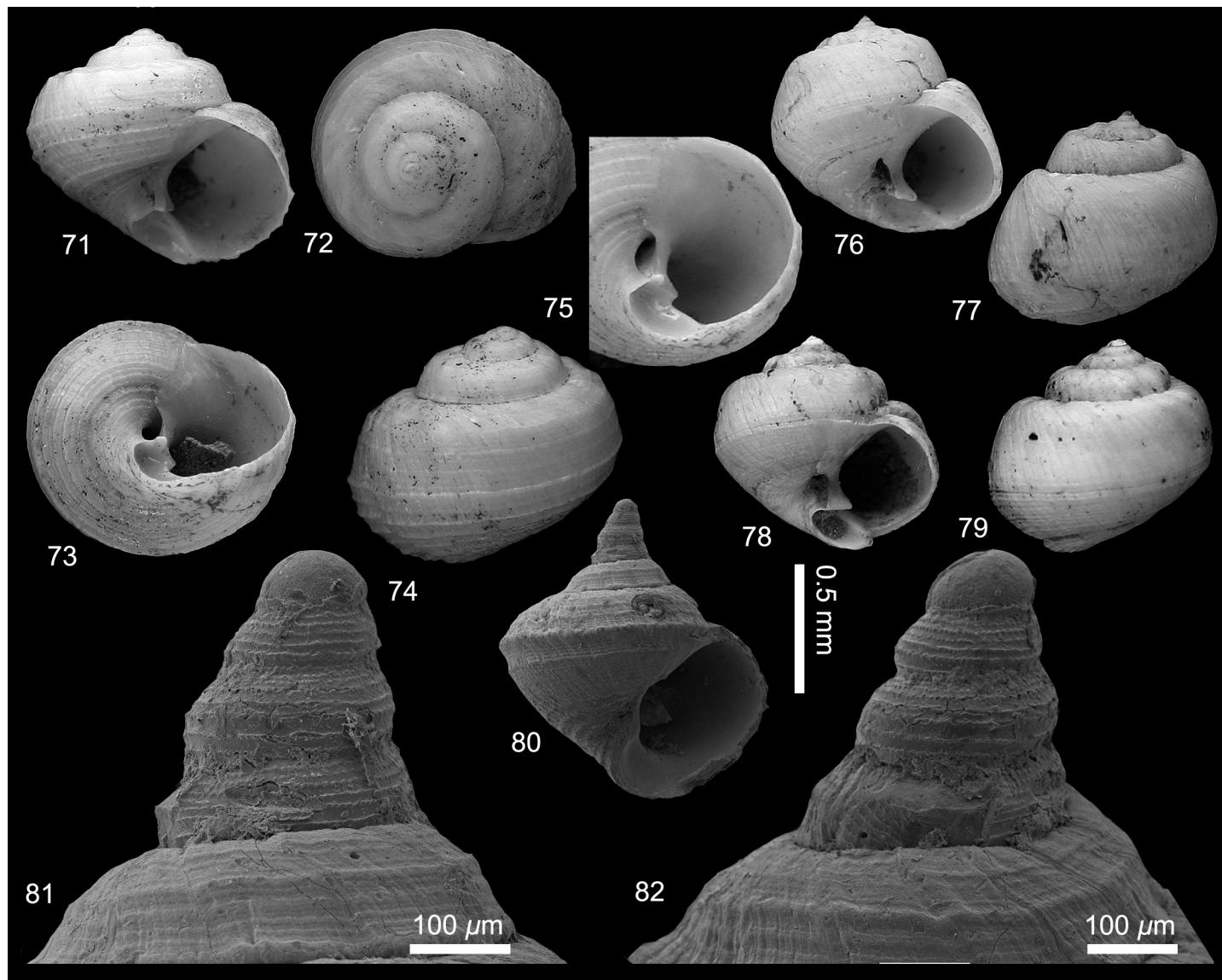
Figs 71-82. *Laevimodulus* species (all photos B. Landau). *Laevimodulus gurabensis* spec. nov. **71-75**, holotype NHMW 2013/0314/0007 (ex BL coll.), height 8.0 mm, width 9.1 mm. **76-77**, paratype 1 NHMW 2013/0314/0008 (ex BL coll.), height 6.7 mm, width 7.3 mm. **78-79**, paratype 2 NHMW 2013/0314/0009 (ex BL coll.), height 5.7 mm, width 6.1 mm. **80-82**, paratype 5 NMB H20219 (juvenile illustrating protoconch), NMB locality 16811 (area within TU 1215) SEM photographs.

record (Costa et al., 1998). Interestingly, *Indomodulus tectum* (Gmelin, 1791), which is widespread in the Indo-Pacific, lives under coral rock (Healy & Wells, 1998) and *M. guernei* Dautzenberg, 1900 from the eastern Atlantic Cape Verde Archipelago lives on rocky bottoms (Rolán, 2005).

Distribution. — Late Miocene: Cercado Formation, Dominican Republic (this paper).

Laevimodulus gurabensis spec. nov. (Figs 71-82)

Type material and dimensions. — Holotype NHMW 2013/0314/0007 (ex BL coll.), height 8.0 mm, width 9.1 mm (Figs 71-75); paratype 1 NHMW 2013/0314/0008 (ex BL coll.), height 6.7 mm, width 7.3 mm (Figs 76-77); paratype 2 NHMW 2013/0314/0009 (ex BL coll.), height 5.7 mm, width 6.1 mm (Figs 78-79); paratype 3 NHMW 2013/0314/00010 (ex BL coll.), height



5.8 mm, width 6.3 mm; paratype 4 NHMW 2013/0314/0011 (ex BL coll.), height 5.6 mm, width 5.7 mm; paratype 5 NMB H20219 (juvenile illustrating protoconch, Figs 80-82), NMB locality 16811 (area within TU 1215). Other material. — 16 specimens lot NHMW 2013/0314/00012 (ex BL coll.).

Type locality. — Rio Gurabo, locality TU 1215 (Landau et al., 2012, chart 5).

Type stratum. — Gurabo Formation (early Pliocene, Zanclean).

Etymology. — Named after the type locality of Río Gurabo in the northern Dominican Republic.

Diagnosis. — A small *Laevimodulus* species, with a tall, multispiral, sculptured protoconch, a depressed turbiniform shell, weakly angular whorls, sculpture of poorly developed axial ribs on intermediate whorls only, very weak spiral sculpture, a rounded aperture, smooth outer lip, a prominent, sharp abapical columellar tooth, a deep siphonal depression on the columellar callus below the columellar tooth and a small umbilicus.

Description. — Shell small, turbiniform, depressed. Protoconch tall, multispiral of about 3.5-4 whorls sculptured by 6-7 granular spiral cordlets. Junction with teleoconch sharply delimited. Teleoconch of 4.5 convex whorls, with narrow, horizontal subsutural ramp, roundly shouldered, convex below, with periphery at abapical suture. Suture deeply impressed, canaliculate in subadult shells. Axial sculpture of very weak, broad ribs, present only on second and third whorls in most, but not all specimens, ribs not elevated, forming an undulating suture on these intermediate whorls. Fine collabral growth lamellae present in most specimens. Spiral sculpture of very fine, weak, irregular narrow spiral cords, obsolete in some specimens. Last whorl with almost horizontal sutural ramp, roundly shouldered a short distance below suture, whorl convex below. Base delimited by weak angulation, bearing distinct, irregular spiral cords and a deep groove delimiting the siphonal fasciole. Umbilicus narrow. Aperture ovate, outer lip sharp, strongly prosocline in lateral view, regularly rounded, smooth within; anal canal not developed, siphonal canal represented by deep concavity in the columellar callus below columellar tooth, with a small groove at its inner side. Columella deeply excavated in mid-portion, with strong, sharp, abapical columel-

lar tooth. Columellar callus thin, weakly developed, narrow.

Discussion. — *Laevimodulus gurabensis* spec. nov. although similar in size and shape to *Laevimodulus canae* spec. nov., both having rather depressed spire whorls, axial sculpture greatly restricted or absent and a very weak spiral sculpture, the apertural characters of the two species are quite different. *Laevimodulus gurabensis* is quite unlike any of the other fossil or Recent tropical American modulids in having a smooth inner aspect to the outer lip and in having a deep, spoon-like siphonal depression below the columellar tooth bearing a small siphonal notch at its medial edge. This depression is also seen in *L. canae*, but is much wider and more prominent (compare figs 63 and 75). These characters are reminiscent of the monotypic *Indomodulus* nov. gen., which also has a smooth outer lip and a siphonal depression below the columellar tooth, but in *Laevimodulus gurabensis* this siphonal depression is far deeper and more clearly delimited than in *I. tectum* (Gmelin, 1791). Moreover, *Indomodulus* does not have an umbilicus, or at most a small umbilical chink, whereas the umbilicus is clearly developed in *L. gurabensis*. Apart from these apertural differences, *L. gurabensis* has shouldered spire whorls and axial ribs weakly developed on the intermediate whorls in some, but not all specimens, whereas *L. canae* has regularly convex whorls and no axial ribs in any specimens. *Laevimodulus gurabensis* has a deep groove on the base delimiting the siphonal fasciole, absent in *L. canae*.

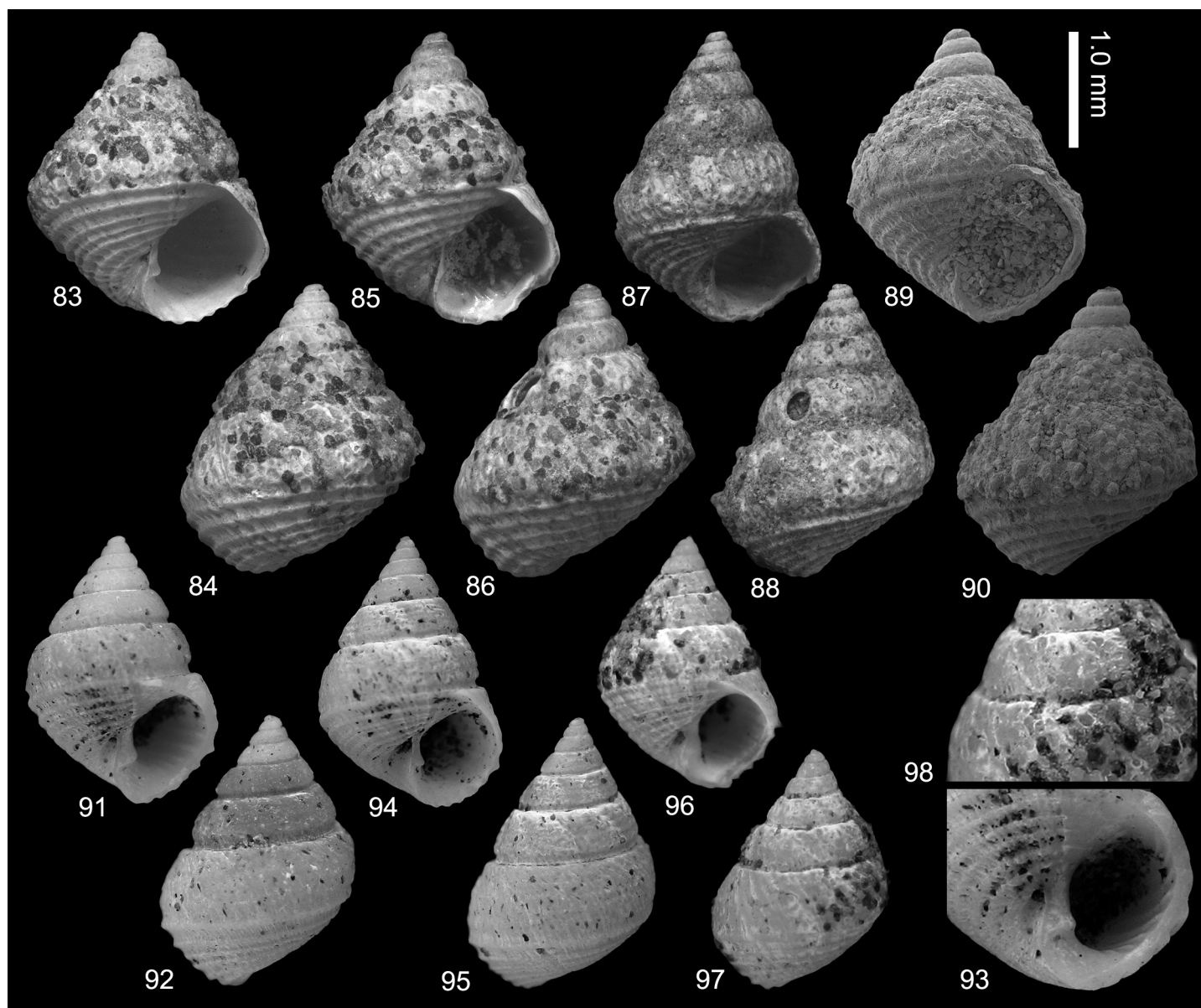
Distribution. — Early Pliocene: Gurabo Formation, Dominican Republic (this paper).

Psammmodulus Collins, 1934

Type species. — *Psammmodulus mexicanus* Collins, 1934, by monotypy. Late Pliocene, Agueguexquite Formation, Mexico.

Revised description. — Shells very small, turbiniform. Spire moderately tall, whorls convex. Sculpture absent, except for cords on base. Aperture small, circular; outer lip sharp, lirate within. Columellar callus hardly developed, with a sharp lamella-like weak columellar tooth abapically; siphonal groove, shallow. Coarse grains of sand adherent on surface of spire and adapical half of last whorl. Umbilicus closed.

Species included. — Monotypic.



Figs 83-98. *Psammmodulus* species (photograph 83-88 S. Reich; 89-93 B. Landau). **83-90,** *Psammmodulus mexicanus* Collins, 1934 NMB H20210, Figs 83-84: NMB H20211, NMB locality 18477, southwest of Punta Piedra Roja, Cayo Agua, Bocas del Toro, Panama, Cayo Agua Formation, Zanclean, early Pliocene. **85-86,** NMB H20214, NMB locality 18677, northwest coast of Escudo de Veraguas, Bocas del Toro, Panama, Escudo de Veraguas Formation, Piacenzian-Gelasian, late Pliocene-early Pleistocene. **87-90,** NMB H20202, NMB locality 18602, northeast coast of Isla Popa, about 1 km southeast of coal mine, Serravallian, middle Miocene. **91-98,** *Psammmodulus* cf. *mexicanus* Collins, 1934, mouth of Arroyo Bajón, Río Mao, Cercado Formation, late Miocene. **91-93,** NHMW 2013/0314/0016 (ex BL coll.), height 5.3 mm. **94-95,** NHMW 2013/0314/0017 (ex BL coll.), height 4.8 mm. **96-98,** NHMW 2013/0314/0017 (ex BL coll.), height 4.2 mm.

Psammodulus mexicanus Collins, 1934 (Figs 36-43)

Psammodulus mexicanus Collins, 1934: 128, pl. 13 fig. 4.

Psammodulus mexicanus Collins. Perrilliat, 1973: 47, pl. 15 figs 1-9.

Type material and dimensions. — NMB H20210 (Figs 83-84), NMB H20211 (Figs 85-86), NMB locality 18477, southwest of Punta Piedra Roja, Cayo Agua, Bocas del Toro, Panama, Cayo Agua Formation, Zanclean, early Pliocene; NMB H20214 (Figs 87-88), NMB locality 18677, northwest coast of Escudo de Veraguas, Bocas del Toro, Panama, Escudo de Veraguas Formation, Piacenzian-Gelasian, late Pliocene-early Pleistocene; NMB H20202 (Figs 89-90), NMB locality 18602, northeast coast of Isla Popa, about 1 km southeast of coal mine, Serravallian, middle Miocene; NMB H20203 (1) + 1 unnumbered specimen, NMB locality 17862, northeast coast of Isla Popa 1100 m northeast of Cerro Popa; 2 unnumbered specimens NMB locality 18379, Deer Island; 1 unnumbered specimen, NMB locality 18716, Cayo Patterson, south side of Valiente Peninsula, Valiente Formation, Serravallian, middle Miocene. 1 unnumbered specimen NMB locality 17819, east coast of Cayo Agua, south of Nispero Point; 1 unnumbered specimen, NMB H17811, east coast of Cayo Agua, west of Punta de Tiburón, Cayo Agua Formation, Zanclean, early Pliocene.

Discussion. — *Psammodulus* Collins, 1934, was described for the very unusual *Psammodulus mexicanus* Collins, 1934. This strange shell from the Agueguexquite Formation of Mexico, now considered late Pliocene, Piacenzian (Cotton, 1999; Landau et al., 2012), differs from the *Modulus* and *Trochomodulus* in having a high turbiniform shell shape, without any sculpture, except for spiral cords on the base of the last whorl, and in agglutinating grains of sand to its shell surface in a pattern of collabral lines on the spire whorls and adapical half of the last whorl (Collins, 1934, pl. 13 fig. 4; Perrilliat, 1972, pl. 15 figs 1-9).

Psammodulus mexicanus Collins, 1934, is also widely distributed in the Bocas del Toro assemblages, and found in deposits varying in age from middle Miocene to late Pliocene-early Pleistocene. The Bocas shells are comparable to those figured by Collins (1934) and Perrilliat (1972) from the Agueguexquite Formation of Mexico.

Agglutinating foreign object onto the shell surface for camouflage is well known amongst xenophorid gastropods, but has also evolved sporadically in other groups, such as

the Caribbean Neogene turritellid genus *Springvaleia* (Woodring, 1958).

Distribution. — Middle Miocene: Serravallian, Valiente Formation, Bocas del Toro, Panama (this paper); early Pliocene: Zanclean, Cayo Agua Formation, Bocas del Toro, Panama (this paper); late Pliocene: Agueguexquite Formation, Mexico (Perrilliat, 1973); late Pliocene-early Pleistocene: Piacenzian-Gelasian, Escudo de Veraguas Formation, Bocas del Toro, Panama (this paper).

Psammodulus cf. *mexicanus* Collins, 1934 (Figs 91-98)

Material and dimensions. — Maximum height 5.3 mm, NHMW 2013/0314/0016/1 (ex BL coll.) (Figs 91-93), NHMW 2013/0314/0017/1 (ex BL coll.) (Figs 94-95), NHMW 2013/0314/0018/1 (ex BL coll.) (Figs 96-98), NHMW 2013/0314/0019/6 (ex BL coll.), mouth of Arroyo Bajón, Río Mao.

Locality. — mouth of Arroyo Bajón, Río Mao.

Stratum. — Cercado Formation, late Miocene.

Discussion. — Specimens of a *Psammodulus* species very similar, if not conspecific with *Psammodulus mexicanus* were found in the late Miocene Cercado Formation of the Dominican Republic, where it is found in deposits at the mouth of Arroyo Bajón on the Río Mao. The specimens are all small (maximum height 5.3 mm), similar in size as those found in Mexico (maximum height 4.2 mm; Perrilliat, 1973: 47), but differ in being slightly more slender, although there is some variability in this feature, and most importantly in having a canaliculated suture. The number of cords on the base and shape of the columellar tooth is similar to that of *P. mexicanus*, to which we refer these Dominican specimens with some doubt. The Dominican shells have lost most of their agglutinated sand grains, but on Fig. 98 the scars of where grains were agglutinated are clearly visible.

Distribution. — Late Miocene: Cercado Formation, Dominican Republic (this paper).

INDO-PACIFIC MODULID GENERA

Conomodulus gen. nov.

Type species. — *Modulus preangerensis* Martin, 1905, desig-

nated herein. Late middle Miocene, Cadasngampar, Java.

Description. — Shells medium-sized, solid, turbiniform to biconic. Spire relatively tall. Suture impressed. Sculpture of axial folds not forming tubercles at shoulder, subobsolete in some species; spiral sculpture of prominent narrow cords. Last whorl weakly angular at periphery; axial sculpture not extending onto base. Aperture ovate; outer lip not flared, lirate within. Columellar callus narrow and not expanded over venter, erect abapically, with sharp lamella-like columellar tooth abapically. Prominent, deep siphonal groove present below columella. Umbilicus relatively broad, bordered medially by erect columellar wall.

Species included. — *Modulus preangerensis* Martin, 1905 (unnamed beds, late middle Miocene, Java; unnamed beds, late Miocene, early Tortonian, Kalimantan), *C. renemai* spec. nov. (unnamed beds, early Miocene, early Burdigalian, Java).

Etymology. — Name reflecting the conical spire seen in shells of this group of modulids. Gender masculine.

Discussion. — *Conomodulus* gen. nov. differs from all other modulid genera in the character of the siphonal groove placed below the columellar tooth, which is wider and deeper than in any other genus within the family. In shell shape *Conomodulus* is most like *Trochomodulus* nov. gen., but members of *Trochomodulus* have a more evenly conical spire, the periphery of the last whorl is sharply angular and axial sculpture is absent. In *Conomodulus* the axial sculpture can be much reduced, as in the type species *C. preangerensis* (Martin, 1905), but it is well developed in other species, such as *C. renemai* spec. nov.

Conomodulus preangerensis (Martin, 1905) (Figs 1, 99-108)

Modulus preangerensis Martin, 1905: 221, pl. 46 fig. 671; Martin, 1928: 127.

Modulus preangerensis Martin. Van der Vlerk, 1931: 252; Ladd, 1972: 24, pl. 5 figs 19-21.

Modulus spec. nov. — Beets, 1941: 37.

Modulus preangerensis Martin, 1905. Dharma, 2005: 306, pl. 118 fig. 15; Leloux & Wesselingh, 2009: 142, pl. 275 figs 14, 15.

Type material and dimensions. — Holotype RGM.10764, height 11.4 mm, width 10.5 mm (Figs 1, 99-100).

Other material. — Maximum height 12.0 mm, 12 specimens from

TF 110 (sample TF 110_SR38, RGM.794.178); 13 specimens from TF 505 (sample TF 505FWJT_1: 1 specimen, RGM.794.179 (Figs 101-102); 12 specimens, RGM.794.180); 1 specimen from locality 391, RGM.312.287 (Figs 103-104); 5 specimens from TF 102 (1 specimen, sample 102_SR45, RGM.794.175 (Figs 105-106); 4 specimens, sample TF 102SR_53, RGM.794.176; single specimen, sample TF 102_SR54, RGM.794.177); 1 specimen from Citalahab (RGM.92181, Figs 107-109).

Discussion. — The holotype of *Conomodulus preangerensis* (Martin, 1905) from the late middle Miocene of Cadasngampar (Figs 99-100) is the only specimen from Java in the Naturalis collections with relatively strong spiral sculpture. The shell illustrated by Ladd (1972, pl. 5 figs 19-21) from the late Miocene of Palau is similarly strongly sculptured. Further specimens in the Naturalis collections (Figs 101-102) from the early Tortonian (late Miocene) of Bontang, East Kalimantan (locality TF 110), share the same sculptural elements as the holotype, but the spiral cords are far more weakly developed. Moreover, the shape of the last whorl varies from rounded (Figs 103-104) to weakly angular (locality TF 102; Figs 105-106). It is possible that these sculptural differences reflect difference in palaeoenvironment. The specimens from TF 110 represent a seagrass meadow, whilst the specimens from TF 102 (6 in collection) represent a coral carpet habitat (Reich et al., submitted; Kusworo et al., submitted).

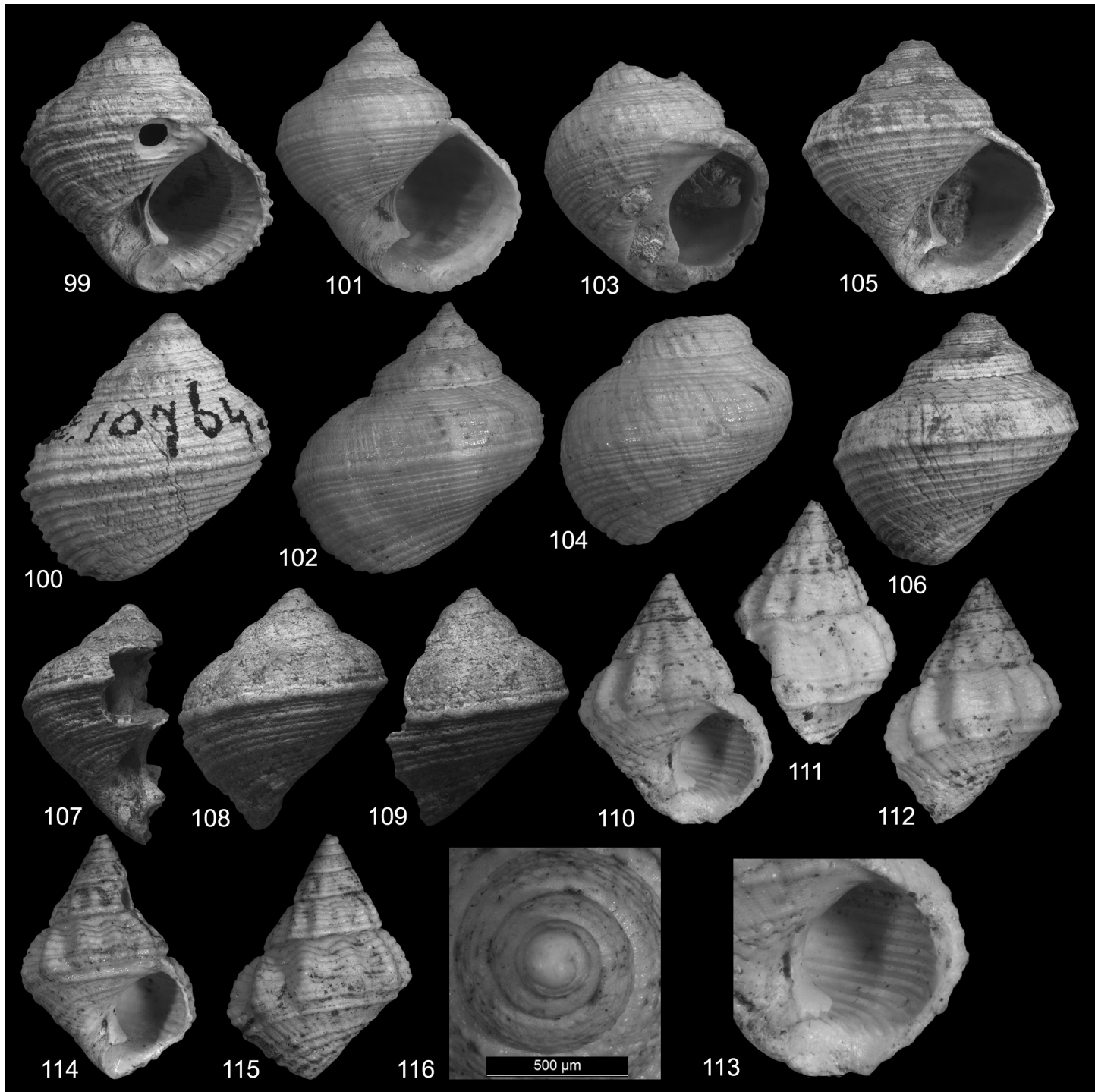
The single specimen from Citalahab, although abraded, shows an ornament similar in strength to the specimens from TF 102, although it is less angular. It is the only available specimen of this species having weak axial folds (Figs 107-109).

Modulus spec. nov. Beets, 1941, is also identified as *C. preangerensis*. The informal holotype of the species from locality 114 is lost, but a specimen informally assigned as paratype is available from locality 391. The specimen agrees well with *C. preangerensis* from TF 110.

Distribution. — Middle Miocene: Kalimantan (Beets, 1941); late middle Miocene: Java (Martin, 1905); late Miocene: Palau (Ladd, 1972), Kalimantan (new data, Throughflow Project).

Conomodulus renemai spec. nov. (Figs 110-116)

Modulus sp. 1 — Reich et al., 2014: 21, pl. 4 fig. 11.



Type material and dimensions. — Holotype RGM.784.794, height 6.8 mm, width 5.3 mm (Figs 110-113); paratype 1 RGM.794.186, height 5.5 mm, width 3.9 mm (Figs 114-115); paratype 2 RGM.794.187, height 3.5 mm, width 2.4 mm (incomplete, Fig. 116).

Other material. — 10 specimens RGM.784.795.

Type locality. — Banyunganti, Java.

Type stratum. — Unnamed formation, early Miocene, early Burdigalian.

Etymology. — In honour of Dr. W. Renema (Naturalis Biodiversity Centre) and his important contribution to the better understanding of the Indonesian localities mentioned in this study. Gender masculine.

Diagnosis. — A medium-sized *Conomodulus* species, with a biconic shell, straight-sided spire whorl, sculpture of broad, strong axial ribs and narrow spiral cords, a roundly angular last whorl, with axial sculpture restricted to adapical half of whorl, an umbilicus present, outer lip lirate within, and a broad, deep siphonal groove.

Description. — Shell medium-sized, biconic; spire relatively tall, regularly conical. Protoconch paucispiral, of about two whorls with large nucleus. Teleoconch of five straight-sided whorls. Suture deeply impressed, undulating. Axial sculpture of up to 13 orthocline, rounded ribs, equal in

width to their interspaces. Spiral sculpture of six narrow rounded cords, which overrun axial sculpture. Last whorl roundly angular at periphery, axial sculpture well developed on abapical half of whorl, stops abruptly at periphery. Base straight-sided, bearing collabral axial growth lines; spiral sculpture of one narrow cord just below periphery, four cords abapically, and fine spiral threads in interspaces. Umbilicus moderately wide, shallow. Aperture ovate, outer lip damaged, likely sharp, prosocline in lateral view, regularly rounded, strongly and deeply lirate within; anal canal not developed; siphonal canal represented by broad, deep, rounded groove in columellar callus placed below columellar tooth. Columella deeply excavated in mid-portion, with strong, sharp, abapical columellar tooth. Columellar callus hardly developed, very narrow.

Discussion. — *Conomodulus renemai* spec. nov. is easily separated from *Conomodulus preangerensis* (Martin, 1905) in having a biconic rather than turbiniform shell shape, in having straight-sided spire whorls instead of weakly angular whorls seen in *C. preangerensis*, and in having axial sculpture that persists onto the abapical half of the last whorl.

Distribution. — Early Miocene, Burdigalian, Java.

Conomodulus aff. *renemai* (Figs 117-118)

Material and dimensions. — Single incomplete specimen, RGM.794.181, height 8.2 mm, width 7.2 mm (Figs 117-118).

Locality. — Bontang, East Kalimantan, Borneo, Indonesia; locality TF 505

Stratum. — Unnamed formation from early Tortonian, late Miocene.

Discussion. — A single shell from the early Tortonian of Bontang (East Kalimantan, Borneo, Indonesia; locality TF 505) differs from *Conomodulus renemai* spec. nov. in having a shorter spire and a wider shell, with slightly more convex spire whorls. The only specimen available is abraded and incomplete, and it is possible that it represents a squatter form of *C. renemai*, as the sculptural elements are similar. More material is needed to clarify the status of this form.

Distribution. — Late Miocene, early Tortonian, Bontang, East Kalimantan, Indonesia (locality TF 505).

Figs 99-116. *Conomodulus* species (all photos S. Reich). **99-109**, *Conomodulus preangerensis* (Martin, 1905). **99-100**, Holotype RGM.10764, unnamed beds from the late middle Miocene of Cadasngampar, Java, Indonesia (pl. 46, fig. 671 in Martin, 1905). Height 11.7 mm. **101-102**, RGM.794.179, late Miocene, early Tortonian of Bontang, East Kalimantan, Indonesia (locality TF 505). Height 12.0 mm. **103-104**, RGM.312.287, middle Miocene, lower Menkrawit beds, East Kalimantan, Indonesia (locality 391). Height 5.0 mm (incomplete). **105-106**, RGM.794.175, early Tortonian of Bontang, East Kalimantan, Indonesia (locality TF 102). Height 9.3 mm (incomplete). **107-109**, RGM.92181, early middle Miocene of Citalahab, Java, Indonesia. Height 9.7 mm. **110-116**, *Conomodulus renemai* spec. nov., early Miocene, early Burdigalian, Banyunganti, Java, Indonesia. **110-113**, Holotype RGM.784.794, height 6.8 mm. **114-115**, Paratype 1 RGM.794.186, height 5.5 mm. **116**, Paratype 2 RGM.794.187, height 3.5 mm (incomplete).

Indomodulus gen. nov.

Type species. — *Trochus tectum* Gmelin, 1791, designated herein. Recent, East Africa, Indo-Pacific.

Description. — Shells large, solid, turbiniform. Spire very depressed, whorls rapidly expanding. Suture superficial. Sculpture of axial folds, obsolete over sutural ramp, swollen at shoulder; spiral sculpture subobsolete. Last whorl greatly inflated, axial cords strongly opisthoclinal and elevated at shoulder, with second row of weaker tubercles at base. Aperture large; outer lip flared, smooth or very weakly lirate within. Columellar callus moderately thickened and expanded over venter, with sharp lamella-like columellar tooth abapically. Siphonal depression present below columellar tooth, shallow, poorly delimited, hardly grooved. Umbilicus not present, or developed as a small umbilical chink.

Species included. — *Trochus tectum* Gmelin, 1791 (Pleistocene-Recent, Pacific), *Indomodulus pseudotectum* spec. nov. (middle Miocene, Kalimantan), *Indomodulus miocenicum* spec. nov. (middle Miocene, Indonesia).

Etymology. — Name reflecting the Indo-Pacific distribution of this group of modulids. Gender masculine.

Discussion. — *Indomodulus* gen. nov. differs from all other modulid genera in being much larger, in having by far the highest whorl expansion rate, and the last whorl being far more globose than in any tropical American or West African modulid species. Although there are differences in sculpture, the most important differences between this group of Indo-Pacific modulids and the rest is in apertural characters; the outer lip in *Indomodulus* is strongly flared, the inner aspect is smooth or weakly lirate as opposed to strongly lirate in *Modulus*, *Trochomodulus*, *Psammomulus* and *Laevimodulus*, the columellar callus is distinct and expanded over the medial side of the venter, whereas in the other modulid genera the columellar callus is very narrow or hardly developed, and the siphon forms a depression on the aperture below the columellar tooth in *Indomodulus*, and a small groove, whereas in the other modulid genera a distinct and usually deep narrow groove is formed below the columellar tooth.

Indomodulus pseudotectum spec. nov. (Figs 119-121)

Modulus tectum (Gmelin). Beets, 1941: 37 (in part).

Type material and dimensions. — Holotype RGM.794.182, height 8.7 mm, width 9.1 mm (Figs 119-121).

Other material. — Known only from holotype.

Type locality. — Menkrawit River, northern Mangkalihat Peninsula, East Kalimantan, Indonesia (locality 114).

Type stratum. — Unnamed formation from middle Miocene.

Etymology. — Name reflecting the superficial similarity of this species to *Indomodulus tectum* (Gmelin, 1791). Gender masculine.

Diagnosis. — A medium-sized *Indomodulus* species, with a globular shell, low spire, a sculpture of flattened axial ribs developed only on sutural platform of last whorl, very reduced spiral sculpture, present only on base of last whorl, a globose last whorl, umbilicus present, outer lip lirate within, and a broad, deep siphonal groove.

Description. — Shell medium-sized, globular; spire very low. Protoconch not preserved. Teleoconch of four whorls, spire whorls very depressed, weakly angular at shoulder. Suture deeply impressed, linear. Last whorl globose, sutural ramp shallow, shoulder rounded, whorl profile convex below, very weakly constricted at base. Sculpture consisting of about 12 low, rounded, axial ribs, only present on the sutural ramp, lacking on first two whorls and weakening towards the lip, spiral ornament weakly developed and abraded, consisting of about four narrow cords on the sutural ramp and 4-5 poorly-defined narrow cords on the base, more close-set towards umbilicus, with 1-2 weak spiral threads in the interspaces. Umbilicus round edged, relatively wide and deep. Aperture ovate, outer lip sharp, prosocline in lateral view, smooth within; anal canal not developed; siphonal canal represented by broad, deep, rounded groove in columellar callus placed below columellar tooth. Columella deeply excavated in mid-portion, with strong, sharp, abapical columellar tooth. Columellar callus hardly developed, narrow, erect abapically, forming medial border of umbilicus.

Discussion. — Generic placement of *Indomodulus pseudotectum* spec. nov. is problematic. Its globose shell shape and low spire place it in the genus *Indomodulus* gen. nov. However, the umbilicus is more strongly developed than is usual for the genus and the siphonal area in typical *Indomodulus* species is represented by a wide, shallow depression on the columella, and a very small siphonal groove, whereas in *I. pseudotectum* a broad, deep, rounded siphonal groove is present below the columellar tooth. These features are reminiscent of the genus *Conomodulus* gen. nov. (see above), and it is likely that this species represents an intermediate stage in the evolution between *Conomodulus* and *Indomodulus*. Despite the siphonal groove being deeper in the new species, the overall shape of the siphonal area and tooth are similar (compare Figs 121 and 124).

The shell shape of *I. pseudotectum* spec. nov. is also reminiscent of the tropical American and tropical eastern Atlantic genus *Modulus* Gray, 1842, but in these species the siphonal area below the columellar tooth is represented by an elongated depression in the columella and a deep but narrow siphonal groove.

Distribution. — Middle Miocene, Kalimantan.

Indomodulus tectum (Gmelin, 1791) (Figs 122-133, 142-145)

Trochus tectum Gmelin, 1791: 3569.

Modulus candidus nobis. Petit de la Saussaye, 1853: 132, pl. 5 fig. 11.

Modulus tectum (Gmelin). Ladd, 1972: 24.

Discussion. — Although Tröndlé (1989) argued that *M. candidus* Petit de la Saussaye (1853) was a distinct species, most subsequent authors (Wilson, 1993; Healy & Wells, 1998; Bouchet, 2012), but not all (Dharma, 2005), have not followed this opinion and consider there to be a single modiolid in the Recent Pacific, *Indomodulus tectum* (Gmelin, 1791).

This species is widely distributed today in the Pacific from East Africa, through the Philippines to Australia. According to Ladd (1972) it is widespread in the Holocene Indo-Pacific and has been found in the Pleistocene of Guam (Ladd, 1972) and the Red Sea (Beets, 1941). The species is recorded in the Naturalis collection from the Quaternary of Kaju Ragi (Sulawesi, Indonesia), but the material is missing.

Records of the species from older deposits (i.e. Beets, 1941) are based on misidentifications, and therefore the occurrence of this species before the Pleistocene cannot be confirmed.

Indomodulus tectum is indeed a highly variable species in relation to sculpture. Specimens from a single locality in the Red Sea Pleistocene of Hurghada, Egypt (NHMW coll.) show both strongly sculptured (Figs 131-133) and almost completely smooth forms (Figs 122-124), although the two extremes are linked by an endless series of intermediate forms (Figs 125-130). Some specimens even develop a second row of low tubercles mid-whorl (129-130). The inner aspect of the outer lip varies from completely smooth (Figs 125, 127, 129) to very finely and weakly lirate (Figs 124, 133). However, the columellar characters are constant (Figs 124, 133).

Indomodulus miocenicum spec. nov. (Figs 134-141)

Modulus tectum (Gmelin). Beets, 1941: 37 (in part).

Type material and dimensions. — Holotype, RGM.312.286, height 3.1 mm, width 3.4 mm (Figs 134-135); Paratype 1 RGM.794.183, height 7.0 mm, width 7.2 mm (Figs 136-137); paratype 2 RGM.794.184, height 4.7 mm (incomplete, Figs 138-139), width 6.0 mm; paratype 3 RGM.794.185, height 5.1 mm, width 5.9 mm (Figs 140-141).

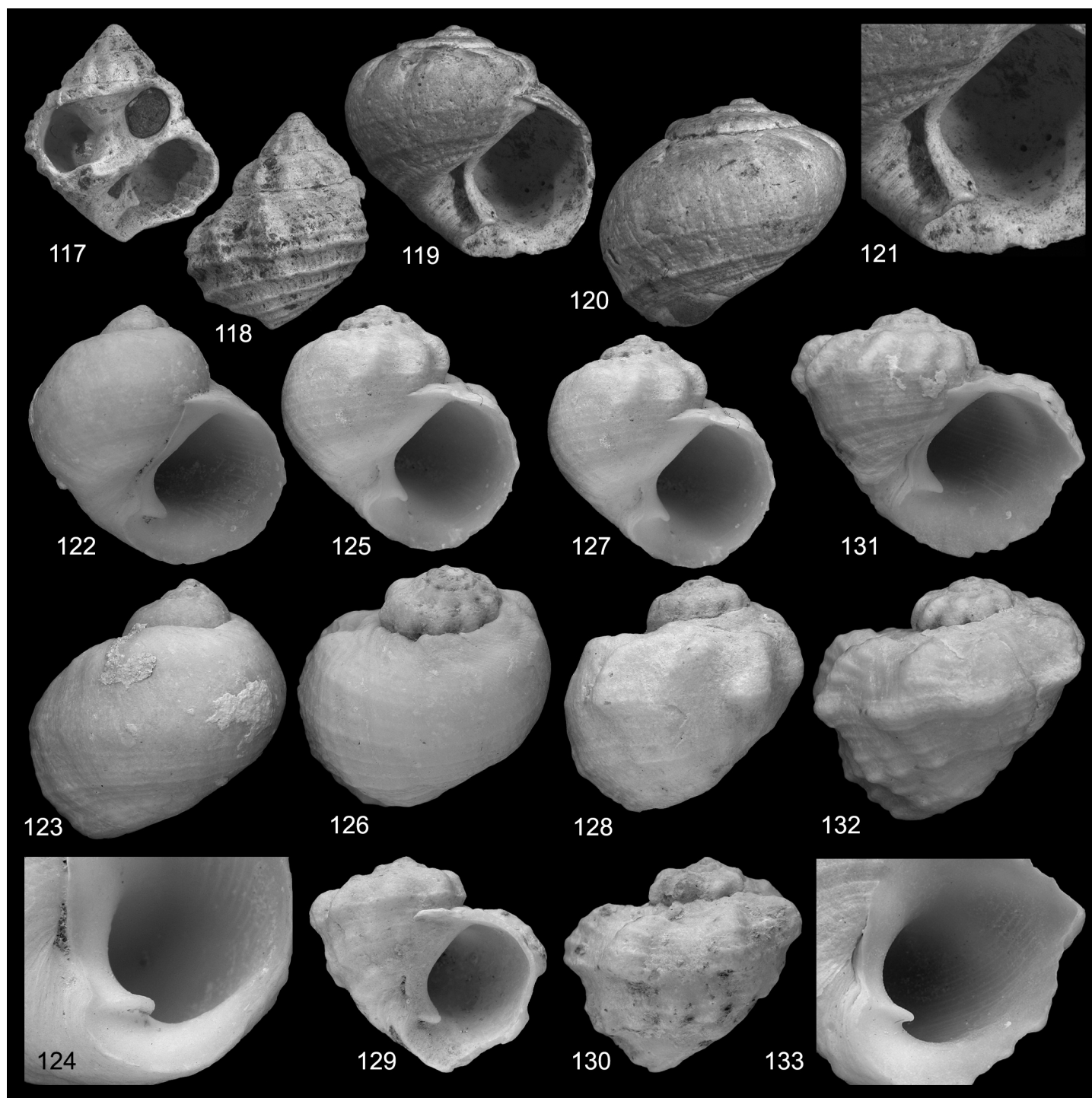
Other material. — Known only from type material.

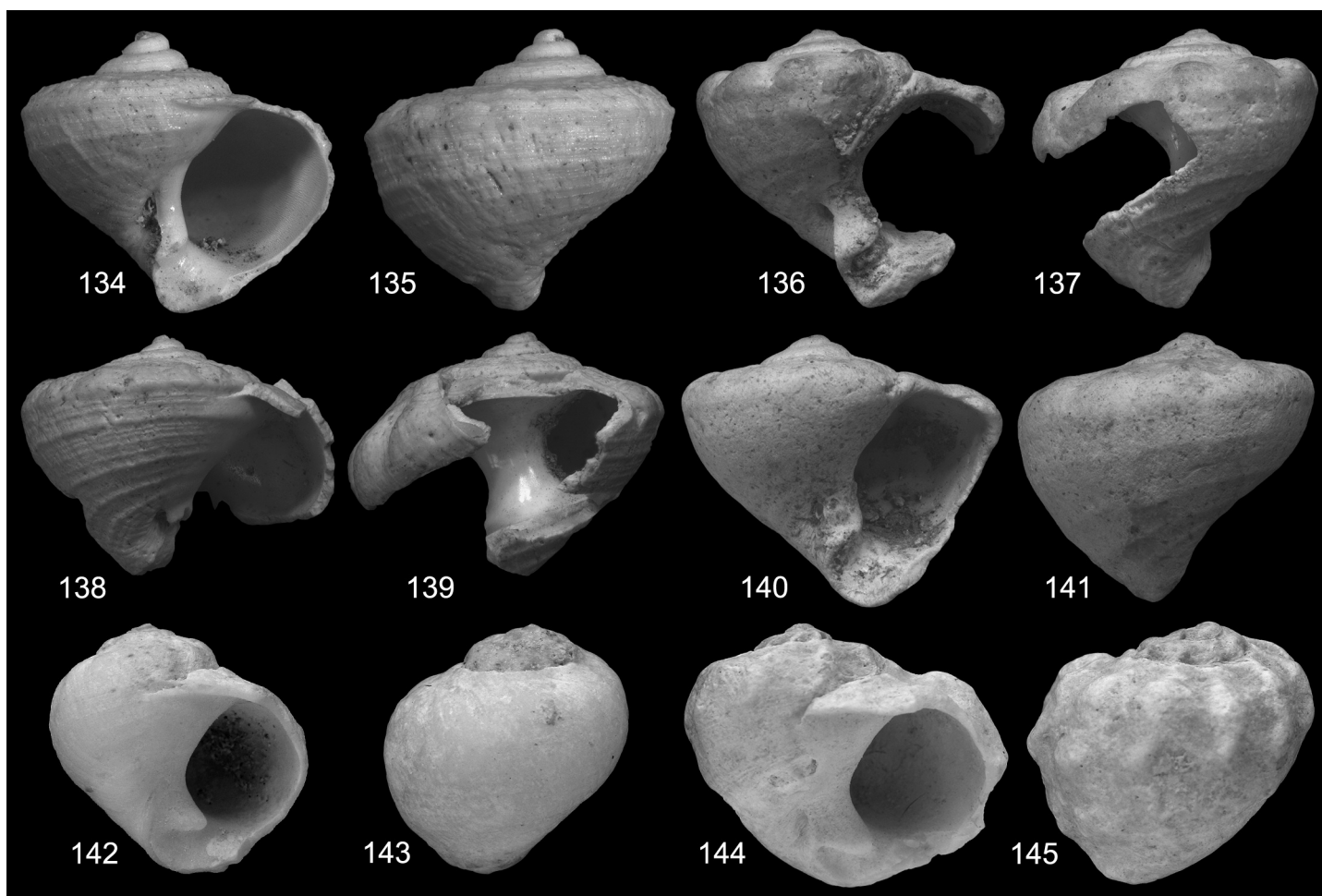
Type locality. — Menkrawit River, northern Mangkalihat Peninsula, East Kalimantan, Indonesia (locality 114).

Type stratum. — Unnamed formation from the middle Miocene.

Etymology. — Name reflecting Miocene age in which it is found. Gender masculine.

Diagnosis. — A small-sized *Indomodulus* species, with a globular shell, a low pointed spire, an axial sculpture of tubercles developed only at the shoulder of the last whorl, a spiral sculpture of weak irregular cords, a roundly angular last whorl, with a very shallow sutural ramp, a small umbilical chink present, outer lip smooth within, a shallow, broad, siphonal depression extending abapically, with almost no siphonal groove and a very weak columellar tooth.





Figs 134-145. *Indomodulus* species (photos 134-141 S. Reich; 142-145 B. Landau). **134-141**, *Indomodulus miocenicum* spec. nov., middle Miocene, Menkrawit River, northern Mangkalihat Peninsula, East Kalimantan, Indonesia (locality 114). **134-135**, Holotype RGM.312.286, height 3.1 mm. **136-137**, Paratype 1 RGM.794.183, height 7.0 mm. **138-139**, Paratype 2 RGM.794.184, height 4.7 mm (incomplete). **140-141**, Paratype 3 RGM.794.185, height 5.1 mm. **142-145**, *Indomodulus tectum* (Gmelin, 1791), Excavations around Hurghada, Red Sea, Egypt, late Pleistocene. **142-143**, NHMW 2013/0314/0037 (ex BL coll.), smooth form (juvenile), height 10.0 mm. **144-145**, NHMW 2013/0314/0038 (ex BL coll.), sculptured form (juvenile), 12.0 mm.

(opposite page) **Figs 117-133.** *Conomodulus* and *Indomodulus* species (photos 117-121 S. Reich; 122-133 B. Landau). **117-118**, *Conomodulus* aff. *renemai* spec. nov., RGM.794.181, late Miocene, early Tortonian of Bontang, East Kalimantan, Indonesia (locality TF 505). Height 8.2 mm. **119-121**, *Indomodulus pseudo-tectum* spec. nov., holotype RGM.794.182, middle Miocene, Menkrawit River, northern Mangkalihat Peninsula, East Kalimantan, Indonesia (locality 114). Height 8.7 mm. **122-133**, *Indomodulus tectum* (Gmelin, 1791), Excavations around Hurghada, Red Sea, Egypt, late Pleistocene. **122-124**, NHMW 2013/0314/0020 (ex BL coll.), smooth form, height 24.1 mm. **125-126**, NHMW 2013/0314/0034 (ex BL coll.), intermediate form, height 24.0 mm. **127-128**, NHMW 2013/0314/0035 (ex BL coll.), intermediate form, height 20.4 mm. **129-130**, NHMW 2013/0314/0036 (ex BL coll.), intermediate form with tubercles mid-whorl on last whorl, height 22.6 mm. **131-133**, NHMW 2013/0314/0021 (ex BL coll.), strongly sculptured form, 24.0 mm.

Description. — Shell small, turbiniform; spire low, pointed. Protoconch not preserved. Teleoconch of three whorls, spire whorls low, rounded, with periphery at abapical suture. Suture impressed, linear. Last whorl globose, sutural ramp wide, very shallow, shoulder placed high, rounded, whorl profile convex below, hardly constricted at base. Sculpture consisting of about 10-12 poorly-developed axial ribs, obsolete at first whorl, poorly developed at second whorl, best developed at shoulder of last whorl, where they form rounded tubercles of variable strength; spiral ornament weakly developed and abraded, consisting of about 4-6 narrow cords on the sutural ramp and 4-5 poorly-defined narrow cords on the base, more close-set towards umbilicus, with up to 4 weak spiral threads in the interspaces. Umbilicus absent or represented by small, narrow chink. Aperture ovate, outer lip damaged, smooth within; anal canal not developed; siphonal canal represented by a broad shallow, rounded depression in the columellar callus, placed below columellar tooth, which extends abapically. Columella shallowly excavated in mid-portion, with very weak columellar tooth. Columellar callus hardly developed adapically; somewhat thickened, erect abapically, forming medial border of umbilical chink.

Discussion. — Several specimens from the middle Miocene of Menkrawit River (northern Mangkaliah Peninsula, East Kalimantan, Indonesia; locality 114) present in the Naturalis collections represent the stratigraphically oldest member of the genus *Indomodulus* gen. nov. Although most of the material available is in a poor state of preservation, the shells are characteristic enough to warrant description. *Indomodulus miocenicum* spec. nov. is characterised by its greatly inflated last whorl, its very wide aperture; the outer lip is smooth within, and the siphonal area is marked by a wide, shallow depression in the columellar callus abapically, and no siphonal groove is developed. Uncharacteristically for the family, the columellar tooth is hardly developed. A small umbilicus is present in some specimens, which can also be seen in some subadult specimens of *Indomodulus tectum* (Gmelin, 1791). The sculpture of this new species is somewhat variable, as some specimens have almost no axial sculpture (Figs 134-135, 140-141), whilst others have well-developed tubercles at the shoulder of the last whorl (Figs 136-

137), with intermediates present (138-139).

Indomodulus miocenicum differs from *I. tectum* in having a smaller shell with a more pointed spire and in having the shoulder on the last whorl narrower and more acute. The axial sculpture is far more restricted in *I. miocenicum*, although in some specimens of *I. tectum* the axial sculpture is almost completely lacking. However, these smoother forms of *I. tectum* tend to have a rather rounded last whorl (Figs 122-123, 125-126) as opposed to the strongly-shouldered last whorl seen in *I. miocenicum*. The apertural characters of the two species are similar, except that the columellar tooth is much weaker in *I. miocenicum*, the siphonal groove is almost absent, and the siphonal depression more elongated abapically. An umbilical chink is present in most specimens of *I. miocenicum*, whereas a well-developed umbilicus is uncommon in adult shells of *I. tectum*. We have compared the Indonesian fossil shells to juvenile specimens of *I. tectum* of both the smooth and sculptured varieties (Figs 142-145). At the same size *I. tectum* is thicker shelled, and even at the juvenile stage, the columellar tooth is more strongly developed than in *I. miocenicum* and the siphonal depression does not show the abapical extension typical of the new species.

It is likely that *I. miocenicum* is a predecessor of the Pleistocene to Recent *I. tectum*.

Distribution. — Middle Miocene: Kalimantan.

HISTORICAL BIOGEOGRAPHY OF THE MODULIDAE

The Modulidae is a small but highly distinctive family of shallow water marine cerithioidean gastropods with a continuous fossil record extending back to the latest Eocene or earliest Oligocene. Bandel (2006) suggested a much earlier origin for the family when he proposed the genus *Modulostylina* from the Cassian Formation (Late Triassic) of northern Italy. This genus is separated by more than 150 million years from the first undoubted modulid (see below). Bandel (2006) also suggested that the Eocene genus *Conocerithium* Sacco, 1895, might be a modulid, but gave no supporting arguments.

The oldest undoubted modulid is *Modulus liveoakensis* Mansfield, 1937, from the Suwannee Limestone of Florida.

Although this formation has usually been regarded as of early Oligocene age, Herbert & Portell (2002) place it in the latest Eocene or earliest Oligocene, with a radiometric age of 36 Ma. The next oldest species is *M. turbinatus* (Heilprin, 1887) from the Silex beds of the Tampa Limestone (Late Oligocene) of Florida. The record of the family is thus continuous from earliest Oligocene time onward.

The family Modulidae is unusual among tropical marine molluscan clades on two counts. First, it is exceptionally low in species diversity, with only 12 to 15 living species known thus far. Second, the group is much more diverse in the Atlantic-East Pacific (AEP) realm than in the Indo-West Pacific (IWP). 2 or 3 species are known from the eastern Pacific, 9 or more in the western Atlantic, 1 or 2 in the eastern Atlantic, and only 1 in the IWP. As noted in the discussion of the genus *Modulus*, the western Atlantic taxon *M. modulus* may well consist of two or more separate species, further accentuating the high diversity of the family in the western Atlantic. This biogeographic pattern, with a peak diversity in the AEP, is similar to that in several other gastropod clades including Fissurellinae (Aktipis et al., 2011), Calyptraeidae (Collin, 2003), Ocenebrinae (Vermeij, 1996), and Fasciolarinae (Snyder et al., 2012). The Pseudolividae is still another example, although living species in the AEP are known only in the eastern Pacific and West African tropics (Vermeij, 1998). Why these clades have diversified so little in the IWP, which is the center of diversity for most shallow-water animal groups, remains a biogeographical mystery.

The fossil record strongly indicates a tropical American origin for the Modulidae. After a slow Oligocene beginning, the family diversified during the Early Miocene with six known species belonging to two distinct lineages, *Modulus* and *Trochomodulus*. By the Late Miocene to Early Pliocene, there are 7 western Atlantic species, representing the genera *Modulus*, *Trochomodulus*, *Laevimodulus*, and *Psammmodulus*. The two last-named genera became extinct after the Pliocene. In the eastern Pacific, the only fossil modulids known are *Modulus cerodes* from the Late Pliocene of the Gulf of California (Durham, 1950; Emerson & Hertlein, 1968). We do not know when *Modulus* and *Trochomodulus* first appeared there, but an Early Pliocene or earlier dispersal of the two groups is certain in view of the open Central

American seaway through which their populations would have dispersed westward.

The earliest modulid lineage outside tropical America is *Modulus basteroti*, an eastern Atlantic species from the earliest Miocene (Aquitanian) of southern Europe and from the early to middle Miocene of southern Europe and Paratethys. This record therefore implies that the eastern Atlantic and Indo-West Pacific realms were colonized by modulids from the west. Similar eastward expansion from tropical America was noted for many other gastropod clades including Neritidae (*Nerita*), Bursidae, Vasidae, Fasciolarinae, Rapaninae, Coralliophilinae, and Nassariinae, among others (Vermeij, 2001b; Frey & Vermeij, 2008; Claremont et al., 2013). Just when this expansion took place is uncertain, but all the groups mentioned, including Modulidae have late Eocene origins in tropical America, implying that the spread eastward might have occurred during the Oligocene. How the eastern Atlantic modulids are related phylogenetically to the Indo-West Pacific lineage is not yet known.

Only a single lineage of Modulidae, likely derived from *Trochomodulus*, entered the IWP realm. The oldest known IWP species is *Conomodulus renemai* spec. nov., recorded from the Early Miocene (Burdigalian) of Java. Two species of *Conomodulus*, including *C. renemai*, are known from the Early to Middle Miocene of the inner IWP realm. The lineage of *Conomodulus* split in the Late Miocene, giving rise to the last species of that genus (*C. preangerensis*) and the earliest member of *Indomodulus*. The characters of *I. pseudotectum* strongly indicate that this species was transitional between *Conomodulus* and *Indomodulus*.

Despite its enormous range, from the Red Sea to southeast Polynesia and Hawaii, the single living IWP modulid (*Indomodulus tectum*) has an exceptionally sparse fossil record. This species is only known fossil from the Pleistocene of the northern Red Sea and from the Pleistocene Mariana Limestone of Guam (Ladd, 1972). *Indomodulus tectum* is unique among living modulids and the only species other than the Middle Miocene *Conomodulus preangerensis* in that it occupies shallow-water coral-reef environments. The other IWP modulids, all now extinct, appear to have been associated with seagrasses.

Although the magnitude of extinction of molluscan lineages

seems to have been lower in the IWP than elsewhere in the Neogene tropics, it is intriguing that many of the largest, most iconic taxa that did become extinct there in the Late Miocene to Early Pleistocene interval thrived in seagrass habitats. Examples may be found among ampullinids, campanilids, strombids, cypraeids, melongenids, and clavilithine fascioliids. The susceptibility of seagrass ecosystems and their occupants to disruption even in a region as rich and biodiverse as the inner IWP is well worth a closer look.

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