Living species of the genera *Chicomurex* Arakawa, 1964 and *Naquetia* Jousseaume, 1880 (Gastropoda: Muricidae) in the Indo-West Pacific

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ABSTRACT. Twenty-four species of Muricidae are reviewed, 15 assigned to *Chicomurex* Arakawa, 1964 and 9 to *Naquetia* Jousseaume, 1880, two closely related genera. Each species is listed with the author's name(s), the date of description, the synonymy, the chresonymy, the distribution, the description and some comments; the chresonymy is only cited for misidentified figures in recent publications dealing with Muricidae. Each species is illustrated in colour with many specimens, while scanning electron micrographs are provided for the radulae. Photos of the protoconch are provided for most of the species as well as the spiral cord morphology. The type locality and the type material (holotype only) are noted for each name. In addition, a molecular phylogeny of *Chicomurex* is reconstructed from eight species using three mitochondrial genes (cytochrome oxidase *c* subunit I, 12S rRNA, and 16S rRNA). The phylogeny revealed three well-supported clades within the monophyletic *Chicomurex*, the grouping of species being congruent with morphology (*C. laciniatus* complex, *C. superbus* complex, and *C. gloriosus* complex). Species sampled includes three recently described species *C. lani* Houart, Moe & Chen, 2014, *C. globus* Houart, Moe & Chen, 2015, and *C. pseudosuperbus* Houart, Moe & Chen, 2015; the specific status of these were assessed and found to be supported by genetic data.

INTRODUCTION

Vokes (1971) considered *Chicomurex* Arakawa, 1964 a synonym of *Siratus* Jousseaume, 1880 and assigned *C. superbus* (G.B. Sowerby III, 1889) the type species of *Chicomurex*, to the latter (as *Siratus superbus*). She also listed another species, *C. laciniatus* (G.B. Sowerby II, 1841) that she assigned to *Chicoreus*. Fair (1976) listed and illustrated three species, including *C. laciniatus* that she also assigned to *Chicoreus*, as well as *Chicomurex superbus* and *C. elliscrossi* Fair, 1974 both assigned to *Chicomurex* in the text but figured as *Naquetia* in the plate captions. *Chicomurex* was considered a synonym of *Phyllonotus* by Radwin & D'Attilio (1976) who listed the same two species, *C. superbus* and *C. laciniatus*, then in *Phyllonotus*. They neglected *C. elliscrossi* and could not include a fourth species described by Rehder & Wilson (1975), *C. venustulus* (Rehder & Wilson, 1975), since their book was probably already in press at the time, and no longer allowed the addition of further text and images. *Naquetia* Jousseaume, 1880 was accepted by these authors, with the number of accepted, valid species differing among them, with Vokes (1971) listing seven, Fair (1976) listing six, and Radwin & D'Attilio (1976) listing five. Three additional species of *Chicomurex* were then described by Shikama (1977), Lan (1981) and Houart (1981), bringing then the total number of species to seven.

Chicomurex and *Naquetia* were reviewed by Houart (1992) who separated *Chicomurex* and *Naquetia* at genus level and listed two fossil and seven Recent species of *Chicomurex*. The extant species listed were C. elliscrossi, C. laciniatus, C. problematicus (Lan, 1981), C. protoglobosus Houart, 1992, C. superbus, C. turschi (Houart, 1981), and C. venustulus. At that time C. gloriosus (Shikama, 1977) was considered to be a junior synonym of C. venustulus. Naquetia was considered to comprise five extant species in Houart (1992), namely N. barclayi (Reeve, 1848), N. cumingii (A. Adams, 1853), N. fosteri D'Attilio & Hertz, 1987, N. triqueter (Born, 1778), and N. vokesae (Houart, 1986).

Vokes (1996) recognized the genus *Chicomurex* with six or seven valid species and *Naquetia* with five or seven species. Houart (1999) described an additional species of *Chicomurex* from Mozambique – *Chicomurex rosadoi* Houart, 1999. Barco et al. (2010) confirmed *Chicomurex* and *Naquetia* as valid genus-level taxa in a highly supported muricine clade. Finally, Merle et al. (2011: 110) listed three fossil and eight extant species of *Chicomurex* and five extant species of *Naquetia*.

Six new species were subsequently added to *Chicomurex* by Houart (2013) and by Houart et al. (2014, 2015, 2017). These include *C. ritae* Houart, 2013, *C. tagaroae* Houart, 2013, *C. lani* Houart, Moe & C. Chen, 2014, *C. globus* Houart, Moe & Chen, 2015, *C. pseudosuperbus* Houart, Moe & Chen, 2015, and *C. excelsus* Houart, Moe & Chen, 2017. These authors also reviewed the synonymy and the validity of some names, to reach a total of 14 valid Recent Indo-West Pacific species. Houart & Lorenz (2020) added an additional new species from Mauritius, *C. vaulberti* Houart & Lorenz, 2020, increasing this number to 15.

Two additional species of *Naquetia* were described by Houart & Héros (2013) and Houart & Lorenz (2015), including *N. manwaii* Houart & Héros, 2013 and *N. rhondae* Houart & Lorenz, 2015. These authors also reinstated *N. jickelii* as a valid species, increasing the number of *Naquetia* species by three. Finally, *N. annandalei* is here considered as valid and separate from *N. barclayi* on the basis of morphological characters of the shell, bringing the number of valid *Naquetia* species to nine.

The species belonging to both genera live exclusively in the Indo-West Pacific. No extant species has been reported elsewhere.

Material and Methods

The studied and illustrated material is mainly composed of specimens from the collection of the authors, unless labelled otherwise, or photographed during preceding researches and deposited in Muséum national d'Histoire naturelle (MNHN). In addition, the type material of each species was illustrated when available.

Morphological analyses

The characters used here to describe the shell morphology include the maximum size reached by the species, the general aspect, its colour and a brief description of the protoconch, followed by details of the axial and spiral sculptures, the aperture and the siphonal canal.

The description is occasionally more elaborate if the species was described by us or by one of us. In that case, the reviewed original description is usually included, with additional or less details if deemed necessary.

The terminology used to describe the spiral cords follows Merle (2001, 2005). The method used to determine diameter and height, and to count the number of protoconch whorls, follows Bouchet & Kantor (2004), as shown in Fig. 1. Radulae were examined and imaged with scanning electron microscopy (SEM). The morphology of the radula is described starting from the rachidian tooth, followed by the lateral teeth (Fig. 2). The bathymetric ranges given are the inner values of the recorded depths: the deepest minimum and the shallowest maximum of each recorded depth range (Bouchet et al., 2008).



Figure 1. Method for determining diameter, height and counting the number of protoconch whorls. Here exemplified with *Chicomurex rosadoi* Houart, 1999.



Figure 2. Terminology used to describe the radula, here shown using *Chicomurex laciniatus* (G.B. Sowerby II, 1841)

cc: central cusp; **ld:** lateral denticle; **lc:** lateral cusp; **ma:** marginal area; **lt:** lateral teeth (following Kool, 1993)

Molecular analyses

In the present study, a molecular phylogeny of Chicomurex was reconstructed using three genes (mitochondrial COI, 12S rRNA, 16S rRNA). Eight species of Chicomurex were included, including C. superbus (type species of the genus), C. elliscrossi, C. lani, C. pseudosuperbus, C. globus, C. gloriosus, C. protoglobosus, and C. laciniatus. Where possible (i.e., more than one specimen was available for study), COI sequence of two conspecific specimens were sequenced from each species. These included C. lani, C. superbus, C. gloriosus, С. globus, С. pseudosuperbus. For C. gloriosus, one specimen from the Philippines and one from Madagascar, not significantly different in shell morphology, were used. For other species, both specimens came from the same locality.

Genetic work was performed in Japan Agency for Marine-Earth Science and Technology (JAMSTEC). Universal primers used to amplify the sequences included LCO1490 & HCO2198 (Folmer et al., 1994), 12SI (Oliverio & Mariottini, 2001) & 12S-(Bandyopadhyay et al., 2008), and 16Sa & 16Sb (Palumbi et al., 1991). Previously published sequences (Barco et al., 2010; Castelin et al., 2010) were used for C. laciniatus and C. protoglobosus, as well as *Murex pecten* which was used as an outgroup, the other species were sequenced herein. Collection data for newly sequenced specimens are indicated in Figure 3. A previously unpublished COI sequence of C. gloriosus from Madagascar was sequenced and provided by Andrea Barco (Universita di Roma "La Sapienza"), collection data: expedition ATIMO VATAE, south Madagascar, stn DW3530, north of Sainte Luce, 24°35.9'S, 47°32.1'E, 80-86 m.

QIAGEN DNeasy Blood and Tissue Kit (Tokyo, Japan) was used to extract the Genomic DNA. Thermo-cycling for polymerase chain reaction (PCR) was performed using an Applied Biosystems Veriti 200 Thermal Cycler. The protocol was initial denaturation, 95°C, 15 minutes followed by 40 cycles of: [94°C, 45 s; gene-specific annealing temperature, 60 s; 72°C, 60 s]; ending with 72°C, 5 minutes. Annealing temperature used were: COI, 45°C; 12S and 16S, 50°C. Agarose (1%) gel electrophoresis stained with SYBR Safe (Life Technologies; 0.05 µl mL⁻¹) was used to confirm amplification of the desired fragment. PCR products were purified using ExoSAP-IT (Affymetrix/USB) using the manufacturer's protocol. Cyclic sequencing reaction was performed with the BigDye Terminator Kit v3.1 (Applied Biosystems), with products purified using the BigDye XTerminator Kit (Applied Biosystems). Sequences were resolved from precipitated products using an Applied Biosystems 3130xl sequencer.

Forward and reverse sequences were obtained in all cases and these were aligned using Geneious R10 (https://www.geneious.com), highly variable regions were excluded from downstream analyses using the

software Gblocks v0.91b (Castresana, 2000; Talavera & Castresana, 2007). The total final alignment length of 1906bp for the three genes was trimmed to 1240bp after Gblocks. Pairwise genetic distances were calculated using MEGA 6 for COI (Tamura et al., 2013). The most suitable evolutionary model for each gene was selected using the Bayesian Information Criterion in jModeltest v2.1.5 (Darriba et al., 2012). The selected model was GTR+I for COI and HKY+I+G for 12S and 16S genes. Bayesian inference phylogeny analysis was performed using the software MrBayes 3.2 (Ronquist et al. 2012). Metropolis coupled Markov Chain Mote Carlo algorithm was run for two million generations in four differently heated chains, with trees sampled every 1000 generations and the first 25% discarded as 'burn-in'. Convergence of analyses was confirmed by monitoring likelihood values over time in the software Tracer v1.4 (Rambaut & Drummond, 2007).

Abbreviations

Shell structure and terminology (in parentheses: variable feature).

Convex part of the whorl and siphonal canal

P: primary cord; s: secondary cord; t: tertiary cord; ad: adapical (or adapertural); ab: abapical (or abapertural); IP: infrasutural primary cord (primary cord on shoulder); adis: adapical infrasutural secondary cord (shoulder); abis: abapical infrasutural secondary cord (shoulder); P1: shoulder cord; P2-P6: primary cords of the convex part of the teleoconch whorl; s1-s6: secondary cords of the convex part of the teleoconch whorl (example: s1 - secondary cord between P1 and P2; s2 - secondary cord between P2 and P3, etc.); ADP: adapertural primary cord on the siphonal canal; MP: median primary cord on the siphonal canal; ABP: abapertural primary cord on the siphonal canal; ads: adapertural secondary cord on the siphonal canal; ms: median secondary cord on the siphonal canal; abs: abapertural secondary cord on the siphonal canal (example: abs - secondary cord just after ABP).

Aperture

ID: infrasutural denticle; D1 to D6: abapical denticles

Repositories

CC: Collection of Chong Chen

CM: Collection of Chris Moe

IRSNB (RBINS): Royal Belgian Institute of Natural History, Brussels.

JR: Collection of Jose Rosado, Mozambique

KPM: Kanagawa Prefectural Museum, Yokohama, Japan.

MHNG: Muséum d'Histoire Naturelle, Geneva, Switzerland.

MNHN: Muséum national d'Histoire naturelle, Paris, France.

NHMUK: Natural History Museum, London, United Kingdom.

NTM (TMMT): National Taiwan Museum, Taipei, Taiwan.

NMSA: KwaZulu-Natal Museum, Pietermaritzburg, South Africa.

NMW: National Museum of Wales, Cardiff, United Kingdom.

RH: Collection of Roland Houart.

SDNHM: San Diego Natural History Museum, California, U.S.A.

USNM: National Museum of Natural History, Washington, D.C., U.S.A.

ZMB: Museum für Naturkunde der Humboldt Universität zu Berlin, zoologisches Museum, Germany.

ZSI: Zoological Survey of India, Calcutta.

GEOGRAPHICAL DISTRIBUTION (Fig. 3)

The world map is here divided into 19 regions. In the systematic account, the regions are noted in bold at the beginning of each distribution paragraph. A species may, of course, occur in several regions. Antarct.: Antarctic; Arct.: Arctic; C.E.Atl.: Central eastern Atlantic; C.E.Pac.: Central eastern Pacific; C.Pac.: Central Pacific; C.W.Atl.: Central western Atlantic; Indo-W.Pac. (I): Indo-West Pacific (predominantly

Indian Ocean); Indo-W.Pac. (IP): Indo-West Pacific; Indo-W.Pac. (P): Indo-West Pacific (predominantly Pacific Ocean); Med.: Mediterranean Sea; N.E.Atl.: Northeast Atlantic; N.E.Pac.: Northeast Pacific; N.Pac.: Northern Pacific; N.W.Atl.: Northwest Atlantic; N.Z.: New Zealand; S. Af.: South Africa; S.E.Atl.: Southeast Atlantic; S.E.Pac.: Southeast Pacific; S.W.Atl.: Southwest Atlantic.

The Indian Ocean extends for 75 000 000 km². It is limited on the north by India, Pakistan and Iran, to the east by Burma, Thailand, Malaysia, Indonesia and Australia, to the south by the Southern Ocean and to the west by Africa and the Arabian Peninsula. By convention, the Indian Ocean is separated from the Atlantic Ocean by the longitude of Cape Agulhas (South Africa) (20° E), from the Pacific Ocean by the longitude of South West Cape on the island of Tasmania, and from the Southern Ocean by the 60th parallel South (60° S).

In *Chicomurex* and *Naquetia* only four cases are possible:

Indo-W.Pac. (I): Indo-West Pacific (predominantly Indian Ocean).

Indo-W.Pac. (IP): Indo-West Pacific.

Indo-W.Pac. (P): Indo-West Pacific (predominantly Pacific Ocean).

C.Pac.: Central Pacific (here French Polynesia only).



Figure 3. Geographical distribution map (reproduced from Houart, 2014)



Figure 4 — Radulae of *Chicomurex*

A-B. *Chicomurex globus* Houart, Moe & Chen, 2015. Scale bars: A. 100 μm; B. 50 μm (SEM P. Bouchet) (Fig. 6A); **C-D.** *Chicomurex gloriosus* (Shikama, 1977). Scale bars: C. 100 μm; D. 50 μm (SEM P. Bouchet); **E-F.** *Chicomurex laciniatus* (Sowerby II, 1841). Scale bars: 50 μm (SEM P. Bouchet); **G-H.** *Chicomurex lani* Houart, Moe & Chen, 2014. Scale bars: A. 100 μm; B. 50 μm (SEM P. Bouchet).



Figure 5 — Radulae of Chicomurex and Naquetia

A-B. *Chicomurex protoglobosus* Houart, 1992. Scale bars: 50 μm (SEM P. Bouchet); **C-D.** *Chicomurex turschi* (Houart, 1981). Scale bars: 50 μm (SEM P. Bouchet); **E-F.** *Naquetia manwaii* Houart & Héros, 2013. E. 100 μm; F. 50 μm (SEM Y. Kantor); **G.** *Naquetia triqueter* (Born, 1778) Scale bar: 50 μm (SEM P. Bouchet).



Figure 6

A. *Chicomurex globus* Houart, Moe & Chen, 2015. New Caledonia, LAGON stn DW542, DW542, 19°06' S, 163°10' E, 49–50 m, MNHN-IM-20125-20902, 45.7 mm (radula illustrated Fig 1A-B); **B–C.** *Chicomurex rosadoi* Houart, 1999, South Mozambique, off Quissico, in lobster traps, 135–140 m, holotype NMSA L4821/T1384 (lost, see remarks), 48.6 mm; D. *Naquetia annandalei* (Preston, 1910), Off Gobalpur, Bay of Bengal, India, holotype ZSI 4708/1, reproduced from D'Attilio & Hertz (1987a).

SYSTEMATICS AND RESULTS

Family **Muricidae** Rafinesque, 1815 Subfamily **Muricinae** Rafinesque, 1815 Genus *Chicomurex* Arakawa, 1964

Type species by original designation: *Murex superbus* Sowerby, 1889, Indo-West Pacific.

DESCRIPTION

Shell broadly ovate, medium or large sized, from 35 to 90 mm in length, spire high with 3 rounded varices on last whorl with short, usually webbed spines; protoconch rounded or conical, with 1.5–3.5 whorls; Spiral sculpture elaborate, consisting of primary and secondary squamous cords, and usually additional tertiary cords between P6 or s6 and ADP. Aperture broadly-ovate; columellar lip smooth or with weak folds with fairly strong, elongate parietal tooth at adapical extremity; outer lip denticulate, with elongate, narrow, split ID, D1–D6 denticles within. Siphonal canal medium sized or long with 2 or 3 short or moderately long, broadly open spines.

Operculum ovate or broadly ovate with apical nucleus. Radula (Figs 2, 4–6) with numerous crowded rows of teeth. Rachidian with a large, broad, triangular central cusp, a small, narrow, triangular lateral denticle and a large, triangular lateral cusp. Marginal area flat, without marginal denticles or marginal cusp. Lateral tooth narrow, sickle shaped.

LIST OF SPECIES

Chicomurex elliscrossi (Fair, 1974) *C. excelsus* Houart, Moe & Chen, 2017 C. globus Houart, Moe & Chen, 2015 C. gloriosus (Shikama, 1977) C. laciniatus (G.B. Sowerby II, 1841) C. lani Houart, Moe & Chen, 2014 C. protoglobosus Houart, 1992 C. pseudosuperbus Houart, Moe & Chen, 2015 C. ritae Houart, 2013 C. rosadoi Houart, 1999 C. superbus (G.B. Sowerby III, 1889) C. tagaroae Houart, 2013 C. turschi (Houart, 1981) C. vaulberti Houart & Lorenz 2020 C. venustulus (Rehder & Wilson, 1975)

> *Chicomurex elliscrossi* (Fair, 1974) Figs 7A-G; 18

Chicoreus elliscrossi Fair, 1974: 1, fig. 2.

Phyllonotus superbus — Radwin & D'Attilio, 1976: 92, in part, pl. 6, fig. 1 (not *Murex superbus* G.B. Sowerby III, 1889).

Type material. Holotype USNM 709574.

Type locality. Kii Peninsula, Japan.

Distribution. Indo-W.Pac (**P**). New Caledonia, Vietnam (Thach, 2005), and south-eastern Japan.

Description. Shell up to 78 mm in length with broadly convex teleoconch whorls. Protoconch unknown.

Axial sculpture of last teleoconch whorl consisting of 3 narrow, moderately high, rounded varices, each with short spines adapically, weakly spinose and webbed abapically. Other axial sculpture of 2 or 3 low intervarical ribs. Spiral sculpture of strong, high primary cords, narrower and lower secondary cords and few tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP and abis followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, P6, s6 and few tertiary cords on convex part of whorl. Primary cords increasing in height and strength abapically.

Aperture broadly ovate. Columellar lip smooth. Outer lip erect, denticulate, with low, elongate denticles within. Siphonal canal moderately long, broad, narrowly open, with 3 moderately long, abapically bent ADP, MP, and ABP spines. ADP strongly dorsally bent.

Whitish or cream with pale orange or brown spots. Aperture white.

Remarks. This species was originally misidentified as *Chicomurex laciniatus* (Sowerby) by Japanese authors; Radwin & D'Attilio (1976: pl. 6, fig. 1) identified a specimen of *C. elliscrossi* as *C. superbus*, but *C. elliscrossi* has a broader shell, with stronger intervarical nodes, a broader aperture, more shouldered and thicker shell, narrower and straighter columellar lip, smaller anal notch, a lower spire and a broader siphonal canal.

Chicomurex excelsus Houart, Moe & Chen, 2017 Figs 7H-K; 8A-G; 18

Chicomurex excelsus Houart, Moe & Chen, 2017: 210, figs 2, 7–17.

Chicomurex venustulus — Merle et al., 2011: 398, pl. 77, fig. 16 (not *Chicoreus venustulus* Rehder & Wilson, 1975).

Type material. Holotype MNHN-IM-2000-33591.

Type locality. Philippines, Bohol Island.

Distribution. Indo-W. Pac. (P). Southern Philippines Islands and Kwajalein Atoll, Marshall Islands, living at 150–200 m.

Description: Shell up to 58.3 mm in length. Lanceolate, angular, broadly ovate, weakly spinose, squamous and nodose.

Spire high with conical protoconch of 2+ whorls (partly broken in a paratype, eroded or broken in other specimens) and up to 7 broad, weakly convex, angular, weakly shouldered, spinose and nodose whorls.

Axial sculpture of teleoconch whorls consisting of low, strong, narrow, rounded, nodose ribs and high, narrow, rounded, weakly spinose varices. Last whorl with 3 narrow, rounded, weakly spinose varices, webbed on abapical part of whorl, webbing extending on siphonal canal. Intervarical sculpture of last whorl consisting of two moderately narrow, high axial ribs with higher node close to preceding varix. Spiral sculpture of primary, secondary and tertiary nodose cords. Primary cords moderately high and broad. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6 on convex part of whorl; P4–P6 slightly broader and higher. Secondary cords narrow, except s6 of similar in strength to P1–P3. Tertiary cords very narrow.

Aperture relatively small, ovate. Columellar lip narrow, smooth abapically, with weak folds adapically and low parietal tooth. Rim partially erect, a small portion adherent at adapical extremity. Anal notch shallow, broad. Outer lip erect, crenulated, with very weak, narrow lirae within.

Siphonal canal long, 40–43% of shell length, broad, weakly dorsally recurved, narrowly open, with dorsally recurved, webbed ADP, (ads), MP, ms, ABP and bs spines, similar in strength to P4–P6; ADP spine occasionally shorter.

Protoconch, with first and second teleoconch whorls light pink. Subsutural ramp to P2 cream or light tan with traces of light brown on spiral cords; orange or dark brown between P2 and P6 or between P2 and ABP; P6 and s6 occasionally white. One paratype creamy white with some orange spots between P2 and s6, s6 light orange; creamy white between s6 and tip of siphonal canal. Aperture white with narrow brown line on outer apertural edge, line often extending on right edge to tip of siphonal canal; ventral left part of siphonal canal white.

Remarks: A paratype of *Chicomurex excelsus* has a partly preserved protoconch with an intact last whorl and a partly intact penultimate whorl. The morphology of these whorls, and the presence of a narrow keel on the abapical part of the last whorl (Fig. 7K) suggest a conical protoconch as observed in a few other species. Chicomurex excelsus is closest to C. gloriosus but consistently differs in having a lower spire in relation to the shell length (approximately 35% of total shell length, as opposed to 38-40% in C. gloriosus) and a longer siphonal canal (40-43% of total shell length compared to 35-40% in C. gloriosus). It also has a less rounded, more angular last teleoconch whorl, narrower axial varices, lower intervarical axial nodes, a less scabrous shell and webbed spines on the siphonal canal whereas these are never webbed in C. gloriosus.

Chicomurex excelsus differs from *C. pseudosuperbus* in having a smaller shell compared to the number of teleoconch whorls, a less rounded teleoconch whorl, a slightly lower spire, and a less scabrous shell with strongly webbed spines on the siphonal canal instead of separate long spines as in *C. pseudosuperbus*.

Chicomurex excelsus further differs from *C. venustulus*, a species currently known only from the Marquesas, in having a larger shell, reaching almost twice the length of an adult *C. venustulus* with a same number of teleoconch whorls. *Chicomurex excelsus*



Figure 7 (scale bar 500 µm)

A–G. *Chicomurex elliscrossi* (Fair, 1974). A–B. Kii peninsula, Japan, holotype USNM 709574, 70.1 mm (photo courtesy USNM); C–D. Japan, off Saeki City, RH, 71.2 mm; E–F. Japan, Wakayama Prefecture, Nada, Gobo city, RH, 73.1 mm; G. Japan, Wakayama Prefecture, Nada, Gobo city, RH, 69.2 mm. **H–K.** *Chicomurex excelsus* Houart, Moe & Chen, 2017, Philippines, Bohol Island, holotype MNHN-IM-2000-33591, 54.8 mm. also has a less rounded last teleoconch whorl, a less scabrous shell and a comparatively longer siphonal canal.

Chicomurex globus Houart, Moe and Chen, 2015 Figs 4A–B; 6A; 8H–N; 9A–E; 18; 29A–B

Chicomurex globus Houart, Moe and Chen, 2015: 3, Figs 1, 3C–D, 4A–L.

Chicoreus superbus — Kaicher, 1973: card 139. *Chicomurex venustulus* — Houart, 1992: 124 (in part); 30, figs 118–119, 170, figs 425–426, 171, fig. 429; Merle et al., 2011: 398, pl. 77, figs 14 & 17.

Type material. Holotype MNHN-IM-2000-27394.

Type locality. Davao Bay, Mindanao, off eastern Samal Island, Philippines, by tangle nets, in 200–300 m.

Distribution. Indo-W. Pac. (P). Okinawa, South China Sea, southern Philippines, Guam, Papua New Guinea, Vanuatu and New Caledonia, living in 18–200 m. *Chicomurex globus* is also known from subfossil beds, off Matupit, near Rabaul, Papua New Guinea.

Description. Shell up to 53 mm in length at maturity. Shell globose, broad, lightly built, spinose and nodose. Spire high with conical protoconch of 2.45 whorls and teleoconch of up to 8 broadly convex, weakly shouldered, spinose and nodose whorls.

Axial sculpture of teleoconch whorls consisting of high, narrow, nodose ribs on two first teleoconch whorls; other whorls with 3 varices, each varix with short, acute, adapically curved, open, primary and secondary spines. Shoulder spine shortest, narrowest, other primary spines increasing in length and breadth abapically. Other axial sculpture of 2 or 3 intervarical ribs or nodes. Last whorl with 3 varices, usually with a strong and high node followed by a weakly lower one. Spiral sculpture of low, narrow, nodose, primary, secondary and tertiary cords and numerous narrow threads. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, and two additional tertiary cords below s6 on convex part of whorl. Varices with short, strongly abaxially and adapically curved spines extending from primary cords and few spinelets from secondary cords. Spines increasing in length abapically, P4, P5, P6 and ADP very strongly curved, webbed, MP slightly straighter and longer, ABP short, narrow, weakly or strongly abapically bent.

Aperture moderately small, roundly ovate. Columellar lip narrow, smooth or covered with small folds or rugae, more obvious abapically; low parietal tooth at adapical extremity; rim partially erect, adherent at adapical extremity. Anal notch shallow, broad. Outer lip erect, crenulated, with weak, elongate denticles within, usually ID split and D1–D6 split. Siphonal canal short, moderately narrow, strongly dorsally recurved at tip, narrowly open.

Creamy white, light tan, tan or chestnut brown, darker coloured below the suture or occasionally on entire subsutural area. Occasionally with two darker coloured spiral bands on P2–s2 and on P6–s6. Other darker spiral band, when present, only obvious on axial varices, covering P3–s3. Tan or brown blotches on axial nodes, on base of varices and on dorsal side of siphonal canal. Shell occasionally entirely white or brown. Aperture glossy white with more or less obvious fine dark brown line along edge of outer apertural lip.

Radula (Fig. 4A–B) typical for *Chicomurex* with numerous crowded rows of teeth and a rachidian with large, broad, triangular central cusp, a smaller, broad, triangular lateral denticle and a slightly larger, triangular lateral cusp. Lateral tooth narrow, sickle shaped.

Remarks. Chicomurex globus was misidentified as C. venustulus auct. (= C. gloriosus) by Hinton (1977) Houart (1992, 2008) and by Merle et al (2011). Chicomurex globus differs from C. gloriosus in having a comparatively smaller shell for a same number of teleoconch whorls. It is also comparatively broader and rounder, and the siphonal canal is shorter compared to the more elongate C. gloriosus which further has a much longer siphonal canal and a more strongly shouldered shell. C. globus also has a very strongly dorsally recurved ADP spine on the siphonal canal as opposed to being only weakly recurved in C. gloriosus. The varical spines are also more strongly dorsally recurved in C. globus, in particular the P5 and P6 spines, while being straight or almost straight in C. gloriosus.

The intervarical ribs or nodes of the last teleoconch whorl are generally lower in *C. globus* and the suture of whorls are less adpressed. The banded form of *C. globus* has the bands covering P2–s2, P6, s6, and, less obvious, on P3–s3. In *C. gloriosus* the colour band is broader, generally covering s2–P5, or s2–S5, or P3–s4.

Chicomurex globus was also confused with *C. superbus* auct. by Kaicher (1973). The shell illustrated as *C. superbus* by many authors was recently described as *C. lani*. It differs markedly from *C. globus* and does not need to be compared here.

Chicomurex globus differs from *C. venustulus* from the Marquesas in having a larger shell relative to the number of teleoconch whorls, in being more globose with a less strongly adpressed suture, a broader aperture and also in having comparatively narrower varices. The position of the coloured spiral bands is also different.



Figure 8 (scale bar 500 µm)

A–G. *Chicomurex excelsus* Houart, Moe & Chen, 2017. A–B. Philippines, Bohol, Balicasag Island, paratype RH, 55.3 mm; C–D. Philippines, Bohol, paratype CM, 58.3 mm; E–F. Philippines, Balut Island, paratype CC, 46.1 mm (photo CC); G. Marshall Islands, Kwajalein Atoll, CM, 43.1 mm (photo CM).
H–N. *Chicomurex globus* Houart, Moe & Chen, 2015. H–I. Philippines, Mindanao, off eastern Samal Island, Davao Bay, 200–300 m, holotype MNHN-IM-2000-27394, 39.7 mm; J–K. Philippines, Mindanao, Surigao straits, paratype CM, 35.0 mm; N. Protoconch, Philippines, Basul Island, Surigao, RH.

Chicomurex gloriosus (Shikama, 1977) Figs 4C–D; 9F–S; 18

Chicoreus gloriosus Shikama, 1977: 14, pl. 2, fig. 8.

Chicomurex venustulus — Houart, 1992: 124 (in part), 30, figs 116–117, 125, fig. 233 (in part), 146, fig. 265, 171, figs 428, 430; Merle et al., 2011: 398, pl. 77, figs 10–13, 15, 18.

Type material. Holotype KPM 3277.

Type locality. Off Cebu Island, Philippine Islands.

Distribution. Indo-W.Pac. (**IP**). Madagascar, Reunion and Mauritius and Nazareth Bank in the Indian Ocean; Philippine Islands, Vietnam, Taiwan, Papua New Guinea, North Queensland, Australia and New Caledonia in the Pacific.

Description. Shell up to 60 mm in length with small, conical protoconch of 3–3.5 whorls with narrow keel abapically and weakly shouldered, broadly convex teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 broad, high, rounded, squamous, varices, each with short, webbed, weakly adapically bent spines on abapical part of varices, extending from P4, P5 and P6 and on siphonal canal from ADP, MP, and ABP. Other axial sculpture of one or two high, conspicuous, nodose intervarical ribs. Spiral sculpture of strong, narrow, high primary and narrower secondary and tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, and one or two tertiary cords on convex part of whorl. Other tertiary cords between primary and secondary cords.

Aperture broadly ovate. Columellar lip with weak folds on its entire length, erect abapically, adherent on a small portion adapically. Outer lip crenulated, with narrow, split, elongate denticles within. Siphonal canal moderately long, narrow, narrowly open, weakly dorsally recurved, with fairly long ADP, MP, and ABP spines. ADP or ADP and MP spines strongly dorsally bent.

Pink or light orange, occasionally with a darker spiral band, usually between s2 and s4 or P5.

Radula (Fig. 4C–D) typical for *Chicomurex* with numerous crowded rows of teeth and a rachidian with large, broad, triangular central cusp.

Remarks. (From Houart et al. 2015) *Chicomurex gloriosus* was first illustrated as *C. venustulus* by Houart (1981) then followed by Springsteen & Leobrera (1986). Houart (1992) classified *C. gloriosus* as subjective junior synonym.

However, after a careful comparison with new material from the Philippines (*C. gloriosus*) and from the Marquesas (*C. venustulus*) it appears that both species has some, permanent, different shell

characters. *C. gloriosus* is larger relative to the number of teleoconch whorls, reaching 60 mm in length *vs* 40.6 mm for *C. venustulus*, it is not as stocky as *C. venustulus* and the siphonal canal is comparatively longer, while the intervarical nodes are generally higher, forming a stronger node on the last whorl. The coloured spiral bands, when present, also differs in being placed on different parts of the last whorl.

Chicomurex laciniatus (G.B. Sowerby II, 1841) Figs 2; 4E–F; 10A–N; 11A–D; 19; 29C–E

Murex laciniatus G.B. Sowerby II, 1841a: pl. 187, fig. 59.

= *Murex scabrosus* G.B. Sowerby II, 1841a: pl. 189, fig. 73; 1841b: 140.

= *Chicoreus filialis* Shikama, 1971: 29, pl. 3, figs 3–4 (as *filiaris* on plate)

Type material. *Murex laciniatus*: Lectotype NHMUK 1974072/1; *Murex scabrosus*: Not located; *Chicoreus filialis*: Holotype KPM 3334.

Type localities. *Murex laciniatus* and *M. scabrosus*: None; *Chicoreus filialis*: Taiwan.

Distribution. Indo-W.Pac. (**IP**). Southern Africa, throughout the Indo-West Pacific, to the Fiji Islands.

Description. Shell up to 77 mm in length with conical protoconch of 2.5–3 whorls and weakly shouldered, broad, teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 narrow, high, rounded, squamous varices, each with short, abaperturally recurved primary spines. Other axial sculpture of 2 or 3 low intervarical ridges. Spiral sculpture of strong, low primary cords and weaker, low secondary cords, both topped with narrow, squamous threads. Spiral sculpture of subsutural ramp of last whorl with t, (t), adis, IP, abis, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, t, (t) on convex part of whorl.

Aperture broadly ovate. Columellar lip smooth, erect abapically, adherent on small portion adapically. Outer lip erect, crenulated, with narrow, split, elongate denticles within. Siphonal canal short or moderately long, broad, narrowly open, strongly dorsally bent at tip, with 3 primary, frondose ADP, MP, and ADP spines. ADP spine weakly dorsally bent.

Light brown, occasionally orange, white, or pale brown, with darker varices. Three paler bands frequently present, most conspicuous on varices. Aperture white, Columellar lip violet or pink.

Radula (Fig. 4E–F) typical for *Chicomurex* with numerous crowded rows of teeth and a rachidian with large, broad, triangular central cusp.

Remarks: *Chicomurex laciniatus* is a highly distinctive species. Some shells, particularly from off



Figure 9 (scale bar 500 µm)

A–E. *Chicomurex globus* Houart, Moe & Chen, 2015. A–B. Philippines, northeastern Mindanao, Surigao, RH, 33.8 mm; C–D. Guam, Agana Bay, RH, 33.5 mm; E. Papua New Guinea, Durangit (Madang Province), Hansa bay, RH, 34.7mm.

F–S. *Chicomurex gloriosus* (Shikama, 1977). F–G. Philippine Islands, off Cebu Id, holotype KPM 3277, 49.5 mm; H–I. South Taiwan strait, RH, 53.4 mm; J. Protoconch, Philippines, Basul Island, RH; K–L. South Madagascar, North of Sainte Luce, MNHN-IM-2009-14511, 50.2 mm; M–N. Philippines, Balut Island, RH, 49.1 mm; O. Papua New Guinea, Durangit (Madang Province), Hansa bay, RH, 27.2 mm; P–Q. Philippines, Samal Id, RH, 47.6 mm; R–S. Philippines, Panglao Id, MNHN-IM-2012-14397, 62.8 mm.



Figure 10 (scale bar 500 µm)

A–N. *Chicomurex laciniatus* (Sowerby II, 1841). A–B. Locality unknown, lectotype NHMUK 1974072, 53.2 mm (photos J.-P. Pointier); C–D. Philippines, Bohol, Balicasag Is, RH, 55.0 mm; E–F. Taiwan, RH, 55.7 mm; G–H. Philippines, Cebu, Sogod, RH, 47.6 mm; I–J. Philippines, Cebu, Sogod, RH, 45.5 mm; K–L. Philippines, Cebu, Sogod, RH, 38.5 mm; M. Philippines, Leyte, RH, 30.5 mm; N. Protoconch, Philippines, RH.

Queensland and the Coral Sea may be paler coloured and more narrowly elongate, but exhibit no other differences. Specimens from off Queensland closely resembles C. *gloriosus* from which they differ in having a larger aperture, lower axial nodes, a narrower columellar lip and a broader siphonal canal.

C. filialis is a synonym that was introduced as the result of confusion between C. *laciniatus* and C. *elliscrossi* by Japanese authors.

Chicomurex lani Houart, Moe & Chen, 2014 Figs 4G–H; 11E–M; 12A–D; 18

Chicomurex lani Houart, Moe & Chen, 2014: 5, figs 2, 4–6, 7–13.

Naquetia superbus — Fair, 1976: 79: 116, pl. 14, fig. 173 (not Murex superbus G.B. Sowerby III, 1889). *Phyllonotus superbus* — Radwin & D'Attilio, 1976:

92 (in part), pl. 6, fig. 2. *Chicomurex superbus* — Houart, 1992: 22, fig. 67, 31, figs 124–125, 117, fig. 227, 122, fig. 231, 170, fig. 424; Merle et al., 2011: 398, pl. 77, figs 1–5.

Type material. Holotype TMMT 201401.

Type locality. Southwest Taiwan, 200 m.

Distribution. Indo-W.Pac. (P). Southern Japan, Taiwan, Vanuatu, Coral Sea, New Caledonia, Northeast Australia, southern Great Barrier Reef, Lady Elliot Is., bathymetric range approximately 40– 300 m for living specimens.

Description. Shell up to 90 mm in length at maturity, lanceolate, broadly ovate, weakly spinose, nodose.

Spire high with 3 protoconch whorls (partially broken in examined specimens) and teleoconch of up to 8 broad, convex, weakly shouldered, spinose and nodose whorls. Suture impressed.

Protoconch (Fig. 11M) small, conical, smooth, glossy, with a narrow, single keel abapically. Terminal lip thin, raised, of sinusigra type.

Axial sculpture of teleoconch whorls consisting of strong, broad, nodose ribs and high, strong, narrow, nodose varices; each varix of last teleoconch whorl with 8 or 9 short, broad, broadly open, blunt, primary and secondary spines; shoulder spine short or moderately long, second short, spines increasing in length abapically. IP spine short. Most abapical spines P5 and P6 longest, s6 weakly shorter, P2-P4 short. Fifth and last whorl with 3 varices and 2, occasionally 3 intervarical, nodose ribs, more conspicuous on shoulder. Spiral sculpture of low, strong, narrow, squamous and nodose primary, secondary and tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6 and some tertiary cords on convex part of whorl. Secondary cord s6 broad,

almost as broad as primary cords, followed abapically by a strong tertiary cord.

Aperture large, broad, roundly ovate. Columellar lip broad, smooth or with 2 or 3 very weak knobs abapically; weak, elongate parietal tooth at adapical extremity. Rim partially erect, adherent at adapical extremity, strongly flaring abapically. Anal notch shallow or moderately deep, broad. Outer lip weakly erect, crenulate, with weak, low denticles within: ID, D1, D2 split, D3 split, D4 split, D5 split, and D6.

Siphonal canal long, broad, tapering abapically, weakly dorsally recurved, narrowly open, with 3 or 4 weakly frondose, long spines extending from ADP, MP, ABP and abs. ADP spine weakly dorsally bent. Pinkish white or creamy white with numerous light

orange to dark brown blotches on and between spiral cords and on axial varices. Aperture glossy white.

Radula (Fig.4G–H) typical for *Chicomurex* with numerous crowded rows of teeth and a rachidian with large, broad, triangular central cusp. The central cusp is slenderer than in the other species and the lateral denticles are attached to its base.

Remarks. Chicomurex lani and C. superbus were very often confused in the past. This confusion is mainly due to the misinterpretation of the original figure of C. superbus (see under C. superbus) because the two species are in fact easily distinguishable. Chicomurex lani is more rounded, less shouldered, with a comparatively higher spire and a broader aperture with broader columellar lip abapically. The primary spiral cords of C. lani are broader, the secondary spiral cords are comparatively lower and narrower, and the axial varices are narrower. The shell of C. lani is also less spinose with less or absent spinelets and less webbed spines; this is more obvious on the abapical part of the varices and on the siphonal canal.

The colour is also different; the spiral cords are obviously less colourful in *C. lani* while they are regularly and usually strongly topped with brown in *C. superbus.*

Chicomurex protoglobosus Houart, 1992 Figs 5A–B; 12E–O; 19

Chicomurex protoglobosus Houart, 1992: 120, figs 72–73, 126–127, 230, 427.

Type material. Holotype MNHN-IM-2000-936.

Type locality. Off SW New Caledonia, 22°46' S, 167°20' E, 300 m.

Distribution. Indo-W. Pac. (P). New Caledonia, in 250–400 m.

Description. Shell up to 49 mm in length with large, rounded protoconch of 1.5 whorls and weakly shouldered, broad teleoconch whorls.



Figure 11 (scale bar 500 μ m)

A–D. *Chicomurex laciniatus* (Sowerby II, 1841). A–B. Australia, Queensland, Lodestone Reef, RH, 56.7 mm; C–D. Australia, Queensland, Lodestone Reef, RH, 50.7 mm.

E–M. *Chicomurex lani* Houart, Moe & Chen, 2014. E–G. Southwest Taiwan, Holotype TMMT 201401, 66.8 mm; H–I. Taiwan, RH, 80 mm; J–K. Southwest Taiwan, paratype RH, 63.5 mm; L. Australia, Queensland, CM, 77 mm; M. Protoconch, Northeast Taiwan, RH.



Figure 12 (scale bar 500 µm)

A–D. *Chicomurex lani* Houart, Moe & Chen, 2014. A–B. New Caledonia, Loyalty Ridge, MNHN-IM-2009-4586, 62.2 mm; C–D. New Caledonia, Loyalty Ridge, MNHN-IM-2009-4591, 34.1 mm (juvenile).
E–O. *Chicomurex protoglobosus* Houart, 1992. E–G. Off SW New Caledonia, 22°46' S, 167°20' E, 300 m, holotype MNHN-IM-2000-936, 30.1 mm (photo MNHN); H–I. New Caledonia, Norfolk Ridge, RH, 39.4 mm; J. North New Caledonia, Grand Passage, MNHN-IM-2009-4864, 39.0 mm; K. North New Caledonia, Grand Passage, MNHN-IM-2009-4863, 44.6 mm; L–M. New Caledonia, South-East Terrasses, MNHN-IM-2009-4578, 44.6 mm; N–O. New Caledonia, Grand Passage, MNHN-IM-2009-4865, 42.7 mm.

Axial sculpture of last teleoconch whorl consisting of 3 narrow, high, rounded, frondose, weakly or moderately webbed varices, each with short, frondose, open primary spines and few, narrower secondary spines. Other axial sculpture of 1 or 2 strongly nodose, high intervarical ribs. Spiral sculpture of strong, high primary cords of approximately same strength and smaller secondary cords. Spiral sculpture of subsutural ramp of last whorl with adis and IP, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6 and additional, tertiary cords and narrow threads.

Aperture broadly ovate. Columellar lip smooth. Outer lip erect, denticulate, lirate within. Siphonal canal moderately long, broad, narrowly open, weakly dorsally bent, with 3 fromdose ADP, MP, and ABP spines. ADP weakly dorsally bent.

Ochre with some brown maculations on shoulder, varices and spiral sculpture.

Radula (Fig. 5A–B) somewhat atypical for a *Chicomurex* species with obviously less crowded rows of teeth.

Remarks. Chicomurex protoglobosus differs from all other species of Chicomurex except C. rosadoi in having a large and globose protoconch, indicating intracapsular larval development. Chicomurex rosadoi is endemic to Mozambique and closely adjacent areas and also has a broad, globose protoconch, denoting the same kind of larval development. Chicomurex turschi has a small, rounded, paucispiral protoconch, and shell with 4.25 teleoconch whorls like the holotype of С. protoglobosus are only 13 or 14 mm in length. Judging from its paucispiral protoconch, C. protoglobosus is probably endemic to the New Caledonian area. It was described from a single. subadult specimen but since its discovery a few adult specimens were collected in 250-400 m.

> Chicomurex pseudosuperbus Houart, Moe & Chen, 2015 Figs 13A–L; 18; 29F–H

Chicomurex pseudosuperbus Houart, Moe and Chen, 2015: 7, Figs 2, 5K–O.

Chicomurex venustulus — Merle et al., 2011: 398, pl. 77, figs 8–9.

Type material: Holotype MNHN-IM-2000-27395.

Type locality: Off Mactan Island, Cebu, Philippines.

Distribution. Indo-W.Pac. (P). Japan, Taiwan, Philippine Islands, New Caledonia and Queensland, Australia, living in 60–200 m.

Description. Shell up to 87 mm in length at maturity, lanceolate, broadly ovate, heavy, weakly spinose, squamous and nodose.

Spire high with 2+ protoconch whorls (partially broken in examined specimens). Teleoconch of up to 7 or 8 broad, weakly convex, shouldered, spinose and nodose whorls. Protoconch (Fig. 13L) small, conical. Whorls smooth, with a narrow, single keel abapically. Terminal lip erect, of sinusigera type.

Axial sculpture of teleoconch whorls consisting of low, narrow, nodose ribs on 2 or 3 first whorls and high, narrow, rounded varices and intervarical ribs on other whorls, each varix with short, narrow, open primary and secondary spinelets. Other axial sculpture of 2 low, broad intervarical ribs, broader and higher on penultimate and last whorls. Penultimate and last whorls with 3 varices and 2 strong intervarical ribs or nodes: last whorl usually with a stronger and a weaker node. Spiral sculpture of high, rounded, narrow, squamous, primary, secondary and tertiary cords and weak threads. Spiral sculpture of subsutural ramp of last whorl with adis, IP adis and additional threads, followed abapically by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6 on convex part of whorl; s6 almost similar in strength and height to P6, followed by 2 or 3 strong tertiary cords. Spiral cords ending as short spines on varices. IP-P4 extending as very short, open, slightly adapically curved spines; P4-s6 somewhat longer, increasing in length and width abapically, webbed; ADP strongly dorsally recurved, MP longer, straight or weakly curved, ABP shorter; secondary cords forming short spinelets between primary spines. Aperture large, broadly ovate. Columellar lip moderately broad, flaring, smooth, with 2 or 3 elongate, weak knobs abapically or covered with small rugae; low parietal tooth at adapical extremity. Anal notch broad, moderately deep. Outer lip erect, crenulated, with weak elongate denticles within: ID split and D1-D6 split. Siphonal canal long, broad, weakly dorsally recurved, narrowly open, with 3 frondose, broad, short spines: ADP, MP, ABP and occasional ads.

Creamy white or light tan with numerous dark brown spots on spiral cords, occasionally with brown band covering P2, s2 and s6, t6 and space between these cords. Aperture glossy white, occasionally with fine dark brown, continuous or interrupted, line along outer edge.

Remarks. *Chicomurex pseudosuperbus* was confused with *C. superbus* auct. (= *C. lani*) by Springsteen & Leobrera (1986) and Houart (2008), and with *C. venustulus* auct. (= *C. gloriosus*) by Merle et al (2011). *Chicomurex pseudosuperbus* differs from *C. gloriosus* in having a larger shell relative to the number of teleoconch whorls and a comparatively narrower aperture. Similar to *C. globus*, the colour bands are situated differently on the last teleoconch whorl. In *C. gloriosus* they cover s2–P5 or s2–s5 or P3–s4, while in *C. pseudosuperbus* they cover P2–s2 and s6 plus one or two tertiary cords below s6.

Chicomurex pseudosuperbus differs from *C. superbus* in having a narrower shell with a comparatively higher



Figure 13 (scale bar 500 µm)

A–L. *Chicomurex pseudosuperbus* Houart, Moe & Chen, 2015. A–C. Philippines, Cebu, MNHN-IM-2000-27395, 74.5 mm; D–E. Philippines, Davao, RH, 73.4 mm; F–G. Philippines, S Mindanao, Samal Id, RH, 81.5 mm; H–I. Philippines, Balut Is,, RH, 72.3 mm; J–K. Philippines, Davao, RH, 73.3 mm; L. Protoconch, Philippines (no other data), RH.

spire, less coloured spiral cords and often, less obvious secondary spiral cords. In *C. superbus* the secondary cords are almost as broad and high than the primary cords or weakly smaller, in *C. pseudosuperbus* they are half the size of the primary cords or even less.

Chicomurex pseudosuperbus differs from *C. lani* in having a larger shell relative to the number of teleoconch whorl, a more adpressed suture, a comparatively longer siphonal canal, more obvious axial nodes on the last teleoconch whorl and a more scabrous shell. Also, *C. lani* is not currently confirmed from the Philippines.

Chicomurex pseudosuperbus differs significantly from the two other species with a conical protoconch, *C. globus* and *C. venustulus*, which do not need to be compared here.

Chicomurex ritae Houart, 2013 Figs 14A–I; 19

Chicomurex ritae Houart, 2013: 71, figs 2, 9–13, 23, 26.

Type material. Holotype MNHN-IM-2000-26629.

Type locality. Philippines, Leyte, Sogod, 100–150 m.

Distribution. Indo-W.Pac. (P). Southern Philippines, south Bohol, south Leyte, north and south Mindanao, living at 80–150 m

Description. Shell up to 45 mm in length at maturity. Broadly ovate, heavy, spinose, squamous.

Spire high with 2 protoconch whorls and teleoconch up to 8 broad, weakly angular, shouldered, nodose and squamous whorls, suture impressed. Protoconch small, whorls rounded, smooth. Terminal lip weakly erect, narrow, lightly curved.

Axial sculpture of teleoconch whorls consisting of strong, narrow, nodose ribs and high, narrow, rounded, frondose varices, each varix with short, frondose, narrow, primary and secondary spines, extending from primary and secondary spiral cords. Shoulder spine shortest. Fourth to last whorl with 3 varices and 2 or 3 intervarical ribs or nodes. Last teleoconch whorl with 2, rarely 3 intervarical ribs with strong node at shoulder. Spiral sculpture of high, strong, rounded, squamous or nodose primary, secondary and tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6 and numerous, squamous, tertiary cords and threads on convex part of whorl. Primary cords extending on varices as short, broad, squamous, weakly adapically recurved open spines, increasing in strength and length abapically, P1 shortest, P5 and P6 longest and broadest. Apertural varix broad, ventrally strongly squamous.

Aperture moderately large, broadly ovate. Columellar lip narrow, weakly broader abapically, rim adherent, weakly erect abapically with weak, low parietal tooth at adapical extremity. Anal notch shallow, broad. Outer lip weakly erect, crenulated, with low, narrow lirae within, corresponding to split ID, D1–D6. Siphonal canal relatively short, broad, strongly dorsally bent at tip, narrowly open, with 3 long, frondose ADP, MP, and ABP spines; ADP more or less strongly dorsally bent. Adapical extremity of siphonal canal occasionally with additional, small abs spine.

Orange or light brown, last whorl with darker coloured varices or with dark brown blotches on varices, including siphonal canal, on subsutural area and occasionally on intervarical nodes. Columellar lip light to dark mauve, inside of aperture bluish-white.

Remarks. It is not really difficult to separate *C. ritae* from *C. laciniatus* when the protoconch is intact. In *C. ritae* the protoconch is paucispiral, rounded, consisting of 1.5 to 2 whorls (Fig. 14I), ending with an almost straight lip while in *C. laciniatus* the protoconch is multispiral, conical, consisting of 2.5–3 whorls, of which the last whorl has a narrow keel abapically and ends with a notch of sinusigera type (Fig. 10N).

Chicomurex ritae also differs from *C. laciniatus* in having a higher spire relative to shell length and to the siphonal canal length, the siphonal canal is comparatively shorter, and the last teleoconch whorl is comparatively stockier.

However, given the variation of forms existing in *C. laciniatus* it is extremely difficult, or even impossible, to separate these two sibling species without the examination of the protoconch. The help of the protoconch morphology, or even a part of the last protoconch whorl where a narrow, abapical keel can be seen in *C. laciniatus*, is the best way to distinguish the two species. This is sometimes possible even for some eroded shells. Separation based on other morphological data remains speculative.

Chicomurex rosadoi Houart, 1999 Figs 1, 6B–C; 14J–P; 15A–D; 19

Chicomurex rosadoi Houart, 1999: 128, figs 7-9.

Type material. Holotype NMSA L4821/T1384 (lost, see remarks). Paratype NMSA L8093/T2223

Type locality. South Mozambique, off Quissico, in lobster traps, 135–140 m.

Distribution. Indo-W.Pac. (I). Southern Mozambique, in 135–140 m.

Description. Shell up to 46 mm in length with large, broad and rounded protoconch of 1.5–2 whorls and weakly shouldered, broad teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 narrow, high, frondose, abapically webbed varices, each with short and blunt primary spines. Other axial sculpture of 1 or 2 moderately high intervarical ridges. Spiral sculpture of narrow, high primary cords, weak



Figure 14 (scale bar $500 \,\mu m$)

A–I. *Chicomurex ritae* Houart, 2013. A–B. Philippines, Leyte, Sogod, holotype MNHN-IM-2000-26629, 42.9 mm; C–D. Philippines, N Mindanao, Siargo Is, paratype RH, 39.5 mm; E–F. Philippines, N Mindanao, Siargo Is, paratype RH, 27.8 mm; G–H. Philippines, Mindanao, Surigao, Basul Is, RH, 31.1 mm; I. Protoconch, paratype RH.

J–P. *Chicomurex rosadoi* Houart, 1999. J–L. South Mozambique, trapped, deep water, RH, 46.5 mm; M–N. South Mozambique, Quissico-Zavora, coll. J. Rosado, 27.8 mm, juvenile (photo JR); O–P. South Mozambique, Barra Falsa (Pomene) coll. J. Rosado, 52.1 mm (photo JR).

secondary cords and few tertiary cords and threads. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis and a few threads, followed by P1, (s1), P2, s2, P3, s3, P4, P5, P6, (s6) and few tertiary cords on convex part of whorl.

Aperture broadly ovate. Columellar lip smooth. Outer lip erect, denticulate, lirate within. Siphonal canal moderately long, broad, narrowly open, weakly dorsally bent, with narrow ADP, followed by broader MP and ABP; small gap between s6 and ADP, MP, and ABP extending as small, open spines.

Light tan or tan with darker colored blotches on varices.

Remarks. *Chicomurex turschi*, the only rather similar species, is smaller when at the same number of teleoconch whorls, and has a protoconch half the size of *C. rosadoi*. The intervarical axial ribs are lower, and more numerous in *C. turschi*: 3 or 4 vs 2 or 3 on penultimate whorl, 2 or 3 vs 1 or 2 on last whorl, while the spiral cords on first teleoconch whorls are less numerous, and more irregularly shaped: 3 or 4 vs 5 on first whorl, 4 vs 7 on second, 5 or 6 vs 7 on third, and 5 or 6 vs 8 on fourth.

The original lot of *C. rosadoi* consisted of 5 specimens, the holotype in NMSA and 4 paratypes in private collections, of which one was in RH. The holotype was unfortunately lost with the whole parcel during its transfer from Belgium to South Africa (Linda Davis, in litt.). After that the (damaged) paratype originally in RH collection was sent to the Natal Museum.

The species seems to be very rare and only a few specimens have been collected since its description.

Chicomurex superbus (G.B. Sowerby III, 1889) Figs 15E–M; 16A–D; 18

Murex superbus G.B. Sowerby III, 1889: 565, pl. 28, figs. 10–11.

= Phyllonotus superbus problematicus Lan, 1981: 11, figs 1–4.

Chicomurex problematicus — Houart, 1992: 119, 120, fig. 229, 146, fig. 266; Merle et al., 2011: 398, pl. 77, figs 6–7.

Not *Phyllonotus superbus* — Radwin & D'Attilio (1976: 92, in part, pl. 6, fig. 1 (= *Chicomurex elliscrossi*); pl. 6, fig. 2 (= *Chicomurex lani*).

Not *Chicoreus superbus* — Kaicher, 1973: card 139 (= *Chicomurex globus*).

Not Naquetia superbus — Fair, 1976: 79: pl. 14, fig. 174 (= Chicomurex lani).

Not *Chicomurex superbus* — Houart, 1992: 22, fig. 67, 31, figs 124–125, 117, fig. 227, 122, fig. 231, 170, fig. 424; Merle et al., 2011: 398, pl. 77, figs 1–5 (= *Chicomurex lani*).

Type material. *Murex superbus*: Holotype NMW 1955.158.00016; *Phyllonotus superbus problematicus*: Holotype in NTM, TMMT 198113.

Type localities. *Murex superbus*: Hong Kong; *Phyllonotus superbus problematicum*: Philippines, Cebu, Bohol, 300 m.

Distribution. Indo-W.Pac. (P). Vietnam (Thach, 2005), Philippine Islands and Taiwan, generally associated with corals. Australia: North Queensland and Capricorn Channel, in 80–100 m.

Description. Shell up to 83 mm in length at maturity. Biconical, broadly ovate, heavy, spinose, nodose.

Spire high with 3 protoconch whorls and teleoconch of up to 8 broad, convex, strongly shouldered, spinose and nodose whorls. Protoconch small, conical, last whorl minutely punctate, with a narrow, single keel abapically. Terminal lip thin, raised, of sinusigra type. Axial sculpture of teleoconch whorls consisting of high, broad, rounded ribs and high, strong, narrow, rounded varices; each varix of last teleoconch whorl with 16 or 17 short, frondose, narrow, open, primary and secondary spines and spinelets; subsutural area spinelets short, webbed, shoulder spine weakly longer, followed by small, not webbed, short spines, extending from s1 to s3; P4 spine short, connected to narrow s4; P5 to s6 longest spines, increasing in length and strength abapically, strongly webbed. Spiral sculpture of low, rounded, narrow, squamous, primary, secondary and tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6 and two or three additional, broad, tertiary cords between s6 and ADP. Primary cords flanked by tertiary cords; P1-P4 cords narrow, P5 and P6 broader and higher, s6 broadest and highest cord.

Aperture large, narrow, ovate. Columellar lip broad, with 3 or 4 elongate, weak knobs abapically and a strong parietal tooth at adapical extremity. Rim partially erect, adherent at adapical extremity, strongly flaring abapically. Anal notch shallow or moderately deep, broad. Outer lip weakly erect, crenulate, with very weak, low, elongate denticles within: ID, D1 split, D2 split, D3 split, D4 split, D5 split, and D6 or D6 split.

Siphonal canal moderately long, broad adaperturally, strongly tapering abapically, weakly dorsally recurved, narrowly open, with 3 short, webbed spines extending from ADP, MP, and ABP, occasionally with secondary cords and spinelets. ADP spine weakly dorsally bent.

White or greyish white with primary and secondary cords topped with light or dark brown blotches or lines; some dark brown blotches between axial ribs on subsutural area and light brown or tan between some spiral cords, more obvious on varices. Area between P4 and P6 occasionally lighter colored giving the



Figure 15 (scale bar 500 µm)

A–D. *Chicomurex rosadoi* Houart, 1999. A–B. South Mozambique, Barra Falsa, (Pomene), coll. J. Rosado, 54.0 mm (photo JR); C–D. South Mozambique, Quissico-Zavora, coll. J. Rosado, 49.9 mm (photo JR).
E–M. *Chicomurex superbus* (Sowerby III, 1889). E–G. Hong Kong, holotype NMW 1955.158.00016, 63.7 mm H–I. Philippines, Cebu, Bohol, 300 m, holotype of *Phyllonotus superbus problematicum* Lan, 1981, TMMT 113, 77.8 mm (photo copyright National Taiwan Museum); J, L. Philippines, Balut Is, RH, 72.5 mm; K. Protoconch; Philippines, Bohol, RH; Aperture, Northeast Taiwan, RH.

appearance of a broad, lighter colored spiral band. Aperture white.

Remarks. *Chicomurex superbus* (Sowerby III, 1889) was described from a single specimen collected in Hong Kong. The original figure illustrates a shell with a high spire, a long, broad siphonal canal and a relatively broad, shouldered shell.

In 2014 it was noted (Houart et al. 2014) that the holotype of C. superbus figured by the National Museum of Wales on its website: http://naturalhistory.museumwales.ac.uk/, was probably the same species recently described by T.C. Lan (1981) as Phyllonotus superbus problematicum. It obviously differed from other specimens illustrated afterwards by several authors as C. superbus. The holotype in the National Museum of Wales, when compared to Sowerby (1889: pl. 38, figs 10, 11), has a seemingly lower spire and the siphonal canal is badly broken (Fig. 15E–G).

After a correspondence with Harriet Wood of the National Museum of Wales it became certain that the specimen in their collection was indeed the holotype of *C. superbus* and that the siphonal canal was broken after the illustration by Sowerby III (1889). The spire is also slightly lower than the original drawing but this kind of exaggeration in drawings is often seen in older publications.

After examination of the holotype it became obvious that the shell described afterwards by Lan (1981) as *P. superbus problematicum* was in fact the true *Chicomurex superbus* and that the species illustrated by several authors, including Lan (1981) as *C. superbus* remained unnamed. It was described as *C. lani* by Houart et al. (2014), see above. *Phyllonotus superbus problematicum* is rendered a junior synonym of *C. superbus*.

Chicomurex tagaroae Houart, 2013 Figs 16E–L; 19

Chicomurex tagaroae Houart, 2013: 70, figs 1, 3–8, 21–22, 26.

Type material. Holotype MNHN-IM-2000-26628.

Type locality. Philippines, Mindanao, Surigao, Mabua, trawled in 80–100 m, 2013.

Distribution. Indo-W.Pac. (P). Southern Philippines, north of Mindanao, living at 80–100 m.

Description. Shell small sized for the genus, up to 44.5 mm in length at maturity. Biconical, broadly ovate, heavy, squamous and nodose.

Spire high with 1.5–2 protoconch whorls (Fig. 16L) and teleoconch of up to 7 or 8 relatively broad, strongly convex, more or less shouldered, weakly spinose, nodose whorls.

Axial sculpture of teleoconch whorls consisting of low, narrow, nodose ribs and high, strong, narrow, frondose varices, each with short, frondose, narrow spines extending from primary and secondary spiral cords. Last whorl with 3 varices and 2, rarely 3, more or less conspicuous intervarical nodes. Last (apertural) varix broadest and large. Additional axial sculpture of squamous growth lamellae. Spiral sculpture of moderately high, rounded, primary, secondary and tertiary cords. Subsutural ramp of last teleoconch whorl with adis, IP, abis, and additional tertiary cords, followed by P1, t, s1, t, then P2 on shoulder margin; convex part of whorl with s2, P3, s3, P4, (s4), P5, s5, P6, s6, occasionally followed by one or two tertiary cords. Siphonal canal with ADP, MP, ABP. P2–P6 spines crowded, very close from each other, joined by varical flange, forming ventrally squamous varix.

Aperture broad, roundly ovate. Columellar lip narrow with low parietal tooth at adapical extremity, otherwise smooth; rim weakly erect. Anal notch narrow, shallow. Outer lip erect, crenulated, with narrow lirae within, extending into aperture, corresponding to split ID, D1– D6. Siphonal canal short, broad, strongly dorsally recurved at tip, narrowly open, with adapically curved ADP, MP, and ABP spines. ADP spine more or less dorsally bent.

Light tan, brown or light orange with weakly or strongly darker coloured axial varices on last teleoconch whorl, or uniformly coloured with occasional additional dark blotches on varices and subsutural ramp. Spire whorls occasionally pinkish. Columellar lip light pink to dark mauve, aperture white or bluish-white.

Remarks. Small or subadult shells of *Chicomurex tagaroae* could be confused with *C. turschi* (Houart, 1981). However, small specimens of *C. tagaroae* are stouter than *C. turschi* with a comparatively lower spire, lower and relatively broader whorls and narrower, more numerous intervarical ribs. The siphonal canal is shorter with more crowded ADP, MP, and ABP spines, and the columellar lip is light to darker mauve in *C. tagaroae* while always white in *C. turschi*.

Chicomurex tagaroae may also be compared with *C. rosadoi* (Houart, 1999) from Mozambique, but *C. tagaroae* has lower, more numerous teleoconch whorls relative to its shell length, a shorter siphonal canal, less obvious intervarical nodes. Importantly, *C. tagaroae* has a very different protoconch which is almost 3 or 4 times smaller than that of *C. rosadoi*, which has a voluminous protoconch denoting intracapsular larval development.

The other *Chicomurex* species, all occurring in the Indo-West Pacific and some in the Philippines, are not easily confused and do not need to be compared here.

Chicomurex turschi (Houart, 1981) Figs 5C–D; 16M–Q; 17A–E; 19

Chicoreus (Chicomurex) turschi Houart, 1981: 186, figs. 1-6.

Not *Chicomurex turschi* — Merle et al., 2011: 400, pl. 78, figs 11–14 (= *Naquetia vokesae*).



Figure 16 (scale bars 500 µm)

A–D. *Chicomurex superbus* (Sowerby III, 1889). A–B. Philippines, North Mindanao, RH, 82.4 mm; C–D. Northeast Taiwan, RH, 55.3 mm.

E–L. *Chicomurex tagaroae* Houart, 2013. E–F, I. Philippines, Mindanao, Surigao, Mabua, holotype MNHN-IM-2000-26628, 36.6 mm; G–H. Philippines, Surigao, Basul Is, paratype RH, 32.8 mm; Philippines, Mindanao, Surigao Delsur, RH, 44.5 mm; L. Protoconch, Philippines, Mindanao, Surigao, Basul Is, RH.

M–Q. *Chicomurex turschi* (Houart, 1981). M–N. Papua New Guinea, Hansa Bay, off Durangit, holotype IRSNB IG 26178/MT 374, 30.0 mm; O–P. Papua New Guinea, Hansa Bay, off Durangit, paratype RH, 35.6 mm; Q. Protoconch, Papua New Guinea, Hansa Bay, off Durangit, paratype RH.

Type material. Holotype IRSNB IG 26178/MT 374.

Type locality. Papua New Guinea, Hansa Bay, off Durangit, 45–60 m.

Distribution. Indo-W. Pac. (IP). Zululand, South Africa (?), Madagascar (?), the Philippines (?), Papua New Guinea, south of New Caledonia, Fiji and Tonga, in 45–79 m (see remarks).

Description. Shell up to 40 mm in length with small, rounded protoconch of 1.5 whorls (Fig. 16Q) and weakly shouldered teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 narrow, high, rounded, weakly frondose varices, each with very small, open, primary spines adapically; abapical spines webbed. Other axial sculpture of 2 or 3 low nodose ribs. Spiral sculpture of low primary and secondary cords and few threads. Spiral sculpture of subsutural ramp of last whorl of adis, IP, abis, and few threads, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, (s5), P6, s6 and 2 or 3 tertiary cords between s6 and ADP.

Aperture broadly ovate. Columellar lip smooth. Outer lip erect, denticulate, lirate within. Siphonal canal short or moderately long, narrow, narrowly open, weakly dorsally recurved, with 3 or 4 abapically or weakly abapically bent spines: ADP, MP, and ABP; ADP slightly dorsally recurved.

Cream or light brown with 3 darker bands, more apparent on varices, brown spots on suture and occasionally on axial ridges. Occasionally entirely white or orange. Aperture bluish white.

Radula (Fig. 5C–D) typical for *Chicomurex* with numerous crowded rows of teeth and a rachidian with large, broad, triangular central cusp.

Remarks. This species is clearly distinguishable from the other *Chicomurex* species. Only one specimen was collected in the Philippines (coll. J. Colomb). It is illustrated in Houart (1992: fig. 432) and in Merle et al. (2011, pl. 78, fig. 6). No other records have been confirmed. Other specimens from the Philippines illustrated in Merle et al. (2011, pl. 78, figs 11–12) are another species, probably *Naquetia vokesae* which would mean a geographical extension for that species (see further information under *N. vokesae* below). The other specimens illustrated in Merle et al. (2011, pl. 78, figs 13–14) from Madagascar are also specimens of *N. vokesae*.

The records of a juvenile specimen of *C. turschi* from Madagascar in Houart (1992: 123, fig. 433) and from South Africa have not been yet confirmed by additional material.

Specimen from Fiji and Tonga were reported by Houart & Héros (2008: 446).

Chicomurex vaulberti Houart & Lorenz, 2020 Figs 17F–J; 19

Chicomurex vaulberti Houart & Lorenz, 2020: 24, pl. 1, fig. A–H.

Type material. Holotype MNHN-IM-2000-35213.

Type locality. Northern Mauritius, dredged in 100 m.

Distribution. Indo-W. Pac. (I). Known only from the type locality to date.

Description of the holotype. Shell medium sized for the genus, 35.0 mm in length. Globose, biconical, heavy, spinose, squamous and weakly nodose. Subsutural ramp narrow, weakly sloping, lightly convex.

Spire low, acute. Teleoconch of 6 broad, broadly convex, weakly shouldered, spinose and nodose whorls. Protoconch partially broken (Fig. 17I), consisting of rounded, smooth, glossy whorls. Terminal lip thin, weakly prosocline.

Axial sculpture of teleoconch whorls consisting of low, narrow ribs from first to third whorl and of rounded varices and intervarical ribs from fourth to last whorl. Apertural varix very broad and ventrally squamous. Last teleoconch whorl starting with a varix and 3 ribs, followed by a second varix, a broader rib and a narrower one between antepenultimate varix and penultimate one, and a single, broad rib with obvious node between penultimate and apertural varix. Varices increasing in strength and height abaperturally. Spiral sculpture of moderately high, rounded, squamous, primary and secondary cords topped with squamous, narrow lirae. Spiral sculpture of subsutural ramp of last whorl with adis, IP, P1, followed by s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, and two threads on convex part of whorl. Spiral cords increasing in strength abapically, ending as short, acute, open spines on apertural varix. ADP and MP spines strongly dorsally recurved, ABP abapically bent.

Aperture broad, roundly ovate. Columellar lip narrow, smooth with strong, narrow, elongate parietal tooth at adapical extremity; rim partially broken. Anal notch deep, narrow. Outer lip crenulate, with low, split D1–D6 denticles within. Siphonal canal moderately long, 38% of total shell length, broad, strongly dorsally bent at tip, narrowly open, with acute, short ADP, MP, and ABP spines.

White with small brown blotches on axial varices of last whorl, more particularly on apertural varix, between P1 and P2, P4 and P5, and on s6, most obvious on ventral side of varix. Additional small blotch on subsutural area of last whorl.



Figure 17 (scale bars 500 µm)

A–E. *Chicomurex turschi* (Houart, 1981). A–B. Papua New Guinea, Hansa Bay, off Durangit, RH, 31.6 mm; C–D. Papua New Guinea, off Matupit, near Rabaul, semi-fossil beds, RH, 38.1 mm; E. Papua New Guinea, Hansa Bay, off Durangit, paratype RH.

F–J. *Chicomurex vaulberti* Houart & Lorenz, 2020. N Mauritius, dredged 100 m, holotype MNHN-IM-2000-35213, 35.0 mm.

K–R. *Chicomurex venustulus* (Rehder & Wilson, 1975). K–L. Off SW Coast of Tahuta, 36–39 fms (66–71 m), Marquesas Islands, holotype UNSM 707241, 40.6 mm (photo USNM); M. Marquesas Islands, Nuku Hiva, MNHN-IM-2012-20898, 38.4 mm; N, R. Marquesas Islands, Nuku Hiva, RH, 32.4 mm; O. Protoconch, Marquesas Islands, Nuku Hiva, Haao Fupa, RH; P–Q. Marquesasa Islands, Nuku Hiva, MNHN-IM-2018-5226, 34.9 mm.



Figure 18. Chicomurex species: Comparative overview 1



Figure 19. Chicomurex species: Comparative overview 2

Remarks. Four species of *Chicomurex* live in the western Indian Ocean, namely *Chicomurex laciniatus*, *C. gloriosus*, *C. rosadoi*, and probably *C. turschi*. Of these four species, *C. laciniatus* and *C. gloriosus* have a conical, multispiral protoconch denoting planktotrophic larval development as opposed to the rounded protoconch whorls in *C. vaulberti*, denoting lecithotrophic development. Their shell characters are also very different.

Chicomurex turschi, described from Papua New Guinea was also recorded from the Philippines, New Caledonia, Madagascar and South Africa by Houart (1992), but differs in many ways, in having a narrower, less squamous and more colourful shell with narrower axial varices, lower intervarical ridges, a higher spire and a narrower siphonal canal.

Chicomurex rosadoi is also different, having a broad, large, rounded protoconch denoting intracapsular larval development, a broad, more angular, more colourful shell with a much higher spire and comparatively narrower, less squamous, axial varices on the last teleoconch whorl.

Another species with broad, paucispiral, rounded protoconch is *Chicomurex protoglobosus* Houart, 1992 living in the New Caledonia area, which also differs in having a broader protoconch, denoting intracapsular laval development and *ipso facto* probably geographically endemic to that region. *Chicomurex protoglobosus* also has a more angular shell with a higher spire, narrower and less squamous varices on the last teleoconch whorl and straight spines on the siphonal canal, either not at all or much less bent dorsally.

Chicomurex venustulus (Rehder & Wilson, 1975) Figs 17K–R; 19

Chicoreus (Chicomurex) venustulus Rehder & Wilson, 1975: 7, figs. 4, 5.

Not *Chicomurex venustulus* — Merle et al., 2011: 398, pl. 77, fig. 16 (= *Chicomurex excelsus*).

Not *Chicomurex venustulus* — Houart, 1992: 124 (in part); 30, figs 118–119, 170, figs 425–426, 171, fig. 429; Merle et al., 2011: 398, pl. 77, figs 14 & 17 (= *Chicomurex globus*).

Not *Chicomurex venustulus* — Houart, 1992: 124 (in part), 30, figs 116–117, 125, fig.233 (in part), 146, fig. 265, 171, figs 428, 430; Merle et al., 2011: 398, figs 10–13, 15, 18 (= *Chicomurex gloriosus*).

Not *Chicomurex venustulus* — Merle et al., 2011: 398, figs 8–9 (= *Chicomurex pseudosuperbus*).

Type material. Holotype USNM 707241.

Type locality. Off SW Coast of Tahuta, 36–39 fms (66–71 m), Marquesas Islands.

Distribution. C.Pac. The species is apparently endemic to the Marquesas Islands, living at 54–109 m.

Description. Shell up to 40.6 mm in length (holotype), with small, conical protoconch of 3 whorls, with narrow keel abapically (Fig. 17O) and weakly shouldered, broad, convex teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 broad, high, frondose and squamous varices, occasionally with very short, primary P1 spine and webbed, short P5–P6 spines. Other axial sculpture of 2 or 3 strong, moderately high, nodose, intervarical ribs. Spiral sculpture of narrow, strong, high primary cords, strong, narrower secondary and few tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis, followed by P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, and 2 strong tertiary cords on convex part of whorl.

Aperture broadly ovate. Columellar lip with numerous weak or strong folds on its whole length, weakly erect abapically, adherent on small portion adapically. Outer lip crenulated, with elongate denticles within. Siphonal canal short or moderately long, narrow, narrowly open, weakly dorsally bent, with short, abapically bent, webbed, ADP, MP, and ABP spines, occasionally with additional median secondary cord (ms).

Cream or light tan with broad or narrow, light brown spiral bands.

Remarks. The name *Chicomurex venustulus* was used by Houart et al. (2015) only for the species from the Marquesas Islands and the taxon *C. gloriosus* was then reinstated as a valid and available name.

After a careful comparison with material from the Philippines (*C. gloriosus*) and from the Marquesas (*C. venustulus*) it appeared that both species has some consistently different shell characters. *Chicomurex gloriosus* is larger relative to the number of teleoconch whorls, reaching 60 mm in length as opposed to 40.6 mm for *C. venustulus*, it is not as stocky as *C. venustulus* and the siphonal canal is comparatively longer, while the intervarical nodes are generally higher, forming a stronger node on the last whorl. The coloured spiral bands, when present, also differs in being placed on different parts of the last whorl.

The genetic evaluation of *C. venustulus* specimens has not been possible to date, due to a lack of appropriately fixed specimens.

Molecular phylogenetics

A Bayesian phylogeny was reconstructed for eight species of *Chicomurex* with materials available, including *C. superbus*, *C. elliscrossi*, *C. lani*, *C. pseudosuperbus*, *C. globus*, *C. gloriosus*, *C. protoglobosus*, and *C. laciniatus*. The COI barcoding fragment was successfully sequenced for every specimen and species of *Chicomurex* included in the analysis, but this was not the case for the other two genes. The 12S gene could not be amplified for *Chicomurex globus* and *C. superbus*, and 16S could not be obtained from *C. globus*. For the *C. gloriosus* specimen from Madagascar only COI was available as the material was not available directly to the authors, but all three genes were obtained for the Philippines specimen.

The reconstructed Bayesian phylogeny (Fig. 20) was well resolved. Within *Chicomurex* two wellsupported major clades were recovered (Bayesian posterior probability, BPP = 1), one containing the species pair *C. protoglobosus* and *C. laciniatus* and another containing other included *Chicomurex* species. Within the latter clade, *C. elliscrossi* was recovered basal with good support (BPP = 0.97). *Chicomurex globus* and *C. gloriosus* were recovered as sisters most closely related to a clade containing *C. lani*, *C. superbus*, and *C. pseudosuperbus* with moderate support (BPP = 0.78). In that clade, *C. superbus* and *C. pseudosuperbus* were closer related to each other than *C. lani* (BPP = 1).

Table 1 shows percentage pairwise distances of a 502bp alignment of COI sequences among the *Chicomurex* specimens used in this study. The average distances between morphologically identified and described species was 11.12% (range 7.71-14.13%), while distances between morphologically identified conspecifics averaged at 1.07% (range 0-3.08%), the highest value coming from the two *Chicomurex gloriosus* specimens sampled from distant localities.

From the percentage pairwise divergence of COI (Table 1), the average intraspecific divergence was much lower (1.06%) compared to interspecific divergences (11.12%). Even the highest pairwise distance within species (3.08%) recorded in *C. gloriosus* was much lower than lowest between species (7.71%), indicative of a clear barcoding gap corresponding to the gap between intraspecific and interspecific variation. This is higher than the 4% intraspecific COI divergence commonly seen across Gastropoda (Meyer & Paulay, 2005). The genetic data therefore agrees well with morphologically identified species in genus *Chicomurex*, at least those eight species sampled in the present study.

The relatively high divergence found between *C. gloriosus* from the Philippines and Madagascar may be indicative of the long geographic distances between the two sampling localities which effectively represent the two ends of its very wide distribution, and the two populations are unlikely to directly interbreed and instead has many stepping-stone populations inbetween. In such cases a relatively high genetic divergence may be expected. Future studies of more specimens from each locality and further localities sampled in between the two extremes would help paint a better picture of connectivity within *C. gloriosus*.

The phylogenetic reconstruction presented here generally agrees with morphological characteristics of the Chicomurex species, with morphologically similar species being grouped together. For example, C. superbus, C. pseudosuperbus have been confused until very recently (Houart et al., 2015) and they were recovered as sister species in the tree. Chicomurex lani is also a similar species to C. superbus as is clear from the fact that T. C. Lan described C. problematicus as a subspecies of C. superbus when he thought the name C. superbus referred to C. lani (Lan, 1981), and this is congruent with the phylogeny where C. lani falls sister to the C. superbus - C. pseudosuperbus pair. gloriosus and C. globus Chicomurex are morphologically similar among the genus (Houart et al., 2015) along with C. venustulus, and they are also recovered as sisters. Unfortunately, C. venustulus could not be sampled in the present study.

protoglobosus Chicomurex stands out in Chicomurex for having a very large, bulbous paucispiral protoconch (indicating intracapsular development; Houart, 1992), a feature it shares only with C. rosadoi from Mozambique. The fact that C. protoglobosus was not recovered as basal among *Chicomurex* on the phylogeny is indicative that this large, bulbous pausispiral protoconch is likely a derived character, although this requires improved taxon sampling to confirm. A related topic of particular interest to explore in the future is the relationships between C. ritae Houart, 2013 with the superficially similar C. laciniatus, as they too are mainly differentiated by the protoconch, with C. ritae having a rounded, paucispiral protoconch and C. laciniatus having a conical, multispiral one.

Species	ies	GenBank	1.1	1.2	2.1	2.2	3	4.1	4.2	5	6.1	6.2	7.1	7.2	8
1.1	1.1 Chicomurex globus (#1)	MN985822	,												
1.2	Chicomurex globus (#2)	MN985823 0.20%	0.20%	,											
2.1	Chicomurex gloriosus (Philippines)	MN985825 10.03%	10.03%	9.80%											
2.2	Chicomurex gloriosus (Madagascar)	MN985824 8.88%	8.88%	8.65%	3.08%	1									
С	Chicomurex laciniatus	GU575369 11.46%	11.46%	11.70%	11.24%	11.25%									
4.1	Chicomurex lani (#1)	MN985826 11.30%	11.30%	11.06%	12.27%	11.79% 12.96%	12.96%								
4.2	Chicomurex lani (#2)	MN985827 10.35%	10.35%	10.12%	11.32%	11.08%	12.24%	1.62%	1						
5	Chicomurex protoglobosus	GU439804	12.38%	12.62%	12.12%	12.38%	9.93%	12.04%	12.33%	,					
6.1	Chicomurex pseudosuperbus (#1)	MN985828 10.86%	10.86%	11.10%	11.09%	11.84%	11.90%	8.82%	8.15%	10.80%					
6.2	Cnicomurex pseudosuperous (#2)	MN985829 10.86%	10.86%	11.10%	11.09%	11.84%	11.90%	8.82%	8.15%	10.80%	0.00%				
7.1	Chicomurex superbus (#1)	MN985830 11.07%	11.07%	11.31%	12.10%	11.62%	14.13%	9.08%	9.10%	12.34%	7.71%	7.71%			
7.2	Chicomurex superbus (#2)	MN985831	11.07%	11.31%	12.10%	11.62%	14.13%	9.08%	9.10%	12.34%	7.71%	7.71%	0.00%		
8	Chicomurex elliscrossi	MN985821 11.41%	11.41%	11.17%	12.43%	12.43% 12.97% 12.82%	12.82%	13.09%	13.09% 12.36% 12.41% 12.63%	12.41%		12.63%	12.63% 12.63%	12.63%	ĩ

Table 1. Pairwise distances of COI sequences (502bp) between each *Chicomurex* species and specimens used in this study. In all cases #1 refer to the specimen used in three-gene sequencing, and #2 a supplementary specimen with only COI sequenced. The average intraspecific distance was 1.07% (range 0-3.08%), while the average interspecific distance was 11.12% (range 7.71-14.13%).

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Figure 20. Bayesian phylogeny of genus *Chicomurex* reconstructed using a combination of COI, 12S, and 16S genes (1906bp, trimmed to 1240bp by Gblocks). Node values denote Bayesian posterior probabilities. The specimens figured are the exact specimens sequenced, with their collection localities shown. NCBI GenBank accession numbers are shown for each gene successfully sequenced in each individual.

Genus Naquetia Jousseaume, 1880

Type species by original designation: *Murex triqueter* Born, 1778, Indo-W. Pac.

Description

Shell medium or large sized, up to 134 mm in length, spire high with 3 wing-like or rounded varices on last whorl; protoconch rounded or conical, with 1.5–3.5 whorls; spiral sculpture elaborate, consisting of primary and secondary cords, and usually additional tertiary cords. Aperture ovate or broadly-ovate; columellar lip smooth with fairly strong, elongate parietal tooth at adapical extremity; outer lip denticulate or smooth, with elongate, narrow, split ID, D1–D6 denticles within. Siphonal canal medium sized or long with 3 short or moderately long, broadly open, webbed spines.

Radula similar to *Chicomurex*, with numerous crowded rows of teeth. Rachidian with a large, broad, triangular central cusp, a small, narrow, triangular lateral denticle, shorter than lateral cusps, and a large, triangular lateral cusp. Marginal area flat, without marginal denticles or marginal cusp. Lateral tooth narrow, sickle shaped.

REMARKS

As was noted in a previous publication (Houart & Héros, 2013), *Naquetia* and *Chicomurex* are two muricine genera with strongly similar shell morphology, with an average height of 40–90 mm in *Naquetia* and 30–70 mm in *Chicomurex*. The protoconch is paucispiral, consisting of 1.5–2 whorls, or conical of sinusigera type, with 3–3.5 glossy whorls, then usually with a narrow keel abapically. Each teleoconch whorl bears three rounded, squamous varices from the second or third whorl, with short, broadly open spines connected by a squamous webbing. The radula is similar in both genera *Chicomurex* and *Naquetia*, consisting of usually crowded rows of teeth with a rachidian bearing a large, broad, triangular central cusp.

The type species of *Chicomurex*, *C. superbus*, differs from the type species of *Naquetia*, *N. triqueter*, in having a broader and more globose shell, a comparatively lower spire and a proportionally larger and broader aperture. Within these two genera, all species exhibit this distinction more or less consistently.

LIST OF SPECIES

Naquetia annandalei (Preston, 1910) N. barclayi (Reeve, 1858) N. cumingii (A. Adams, 1853) N. fosteri D'Attilio & Hertz, 1987 N. jickelii (Tapparone Canefri, 1875) N. manwaii Houart & Héros, 2013 N. rhondae Houart & Lorenz, 2015 N. triqueter (Born, 1778) N. vokesae (Houart, 1986)

> Naquetia annandalei (Preston, 1910) Figs 6D; 21A–J; 28

Pteronotus (sic) annandalei Preston, 1910: 119, fig. 3.

Naquetia barclayi — Radwin & D'Attilio, 1976: 80, pl. 15, fig. 8; Houart, 1992: 21, fig. 58, 125 (in part), 126, fig. 236, 127, fig. 237 (in part), 171, fig. 434; Merle et al., 2011: 404, pl. 80, figs 5–10 (not *Murex barclayi* Reeve, 1858).

Not *Naquetia annandalei* — Fair, 1976: 21 (in part), pl. 14, fig. 171; Radwin & D'Attilio, 1976: 80, pl. 15, figs 9–10 (= *Naquetia fosteri*).

Type material. Holotype ZSI 4708/1, illustrated by D'Attilio & Hertz (1987a).

Type locality. Off Gobalpur, Bay of Bengal, India.

Distribution. Indo-W. Pac. (IP); C. Pac. The Bay of Bengal, Vietnam (Thach, 2005), the Philippine Islands, Taiwan, South Japan, Queensland, Australia, and the Marquesas.

Description. Shell up to 134 mm in length with small, abapically keeled, conical protoconch of 3.25–3.5 whorls (Fig. 21J) and weakly shouldered, broad, convex teleoconch whorls. Length/width ratio 2.3–2.4. Axial sculpture of last teleoconch whorl consisting of 3 narrow, high, webbed varices. Other axial sculpture of 2 or 3 weak or moderately strong, low, nodose ribs, with low or moderately high node on shoulder. Spiral sculpture of strong, moderately high, primary cords, with additional, narrower, occasionally of same strength secondary cords and few, narrow, tertiary cords.

Spiral sculpture of subsutural ramp of last whorl with, adis, IP followed by P1, s1, P2, P3, s3, P4, s4, P5, s5, P6, s6 on convex part of whorl. Primary cords P1–P3 of same strength, P4–P6 increasing in strength abapically. Secondary cords s1, s3, s4, and s6 broader than other secondary cords. Tertiary cords narrower or approximately equal to secondary cords. Juvenile of one teleoconch whorl (Fig. 21E) clearly supports only IP, P1–P6, s6, ADP, MP, ABP.

Aperture broadly ovate. Columellar lip smooth, with strong partietal tooth adapically, erect abapically, adherent on small portion adapically. Outer lip smooth with several, split, low elongate denticles within. ID denticle strongest. Siphonal canal long, narrow, ventrally narrowly open, 39–43% of total shell length, with abapically bent, webbed, ADP, MP, and ABP spines.

Tan or light brown with darker blotches on and between spiral cords. Ventral side of siphonal canal lighter coloured. Aperture glossy white.

Remarks. Two similar taxa, namely *Naquetia annandalei* from Bay of Bengal to Pacific Ocean and *N. barclayi* from the Western Indian Ocean, have been considered synonyms by many authors including Houart, 1992, while others such as D'Attilio & Hertz (1987a) considered them separate species.

After having examined carefully several shells, including now juvenile specimens and using the new methodology including both the description of the spiral sculpture and the counting of the cords, the two taxa are formally separated as distinct species herein with their differences outlined as follows.

The protoconch of N. annandalei (Fig. 21J) is more acute with a narrower first whorl, having a width of 1.1 to 1.5 mm as opposed to 2.1 to 3.0 mm in N. barclavi from the Western Indian Ocean (Fig. 21M). Naquetia annandalei also has obviously narrower primary and secondary spiral cords on the convex part of the teleoconch whorl except s1 and s2 which are broader than in N. barclayi, and on the siphonal canal, but the tertiary cords are larger and wider than in N. barclayi (Figs. 21B and 22D). The s4 spiral cord is broad and conspicuous in N. annandalei while it is missing or very narrow in N. barclayi. The siphonal canal in N. annandalei is also comparatively narrower and longer. These differences are observed in both juvenile and adult specimens (Figs 21H-I; N-O). Furthermore, N. annandalei is also generally narrower and less shouldered, but this is not consistent. The length/width ratio in N. annandalei is 2.3-2.4 as opposed to 1.8-2.0 in N. barclayi.

An exceptionally large specimen of *N. annandalei* of 134 mm in length, from Queensland, Australia, was illustrated by Wilson & Gillett (1971: 83, pl. 56).

Naquetia barclayi (Reeve, 1858) Figs 21K–O; 22A–D; 28

Murex barclayi Reeve, 1858: 209, pl. 38, fig. 2.

Not *Naquetia barclayi* — Radwin & D'Attilio, 1976: 80, pl. 15, fig. 8; Houart, 1992: 21, fig. 58, 125 (in part), 126, fig. 236, 127, fig. 237 (in part), 171, fig. 434; Merle et al., 2011: 404, pl. 80, figs 5–10 (= *Naquetia annandalei*).

Type material. Lectotype NHMUK 1962077.

Type locality. St. Brandon Shoal, near Mauritius.

Distribution. Indo-W. Pac. (I). Off Durban, South Africa, Mozambique, Mauritius and Reunion.

Description. Shell up to 105 mm in length with small, conical protoconch of 3.15 whorls (Fig. 21M) and weakly shouldered, broad, convex teleoconch whorls. Length/width ratio 1.8–2.0.

Axial sculpture of last teleoconch whorl consisting of 3 narrow, high, nodose and webbed varices. Other axial sculpture of 2 or 3 weak or moderately strong, high, nodose intervarical ribs with stronger shoulder nodes at crossing of axial ribs with P1 and P2 spiral cords. Spiral sculpture of weak, low or moderately high primary cords, small, narrow secondary cords and few tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP followed by P1, s1, P2, s2, P3, t, s3, t, P4, s4, P5, P6, s6, ADP, MP, ABP on convex part of shell and siphonal canal. Primary cords and s3 higher and broader on axial varices. P6 broadest cord, occasionally with P1 and P5. P2, P3, P4, and s3 of same strength; s6 weakly narrower. ADP, MP, and ABP broad, approximately of same strength. Other secondary and tertiary cords low and narrow.

Aperture broadly ovate. Columellar lip smooth, with strong partietal tooth adapically, erect abapically, adherent on small portion adapically. Outer lip smooth with several, split, low elongate denticles within. ID denticles strongest. Siphonal canal monderately long, broad, ventrally narrowly open, weakly dorsally bent, 39–43% of total shell length, with abapically bent, webbed, ADP, MP, and ABP spines.

Light tan, orange or light brown with darker blotches on axial varices and spiral cords. Siphonal canal occasionally lighter coloured ventrally.

Remarks. See under N. annandalei.

Naquetia cumingii (A. Adams, 1853) Figs 22E–R; 28

Murex trigonulus Lamarck, 1822: 167 (non Lamarck, 1816).

= *Murex cumingii* A. Adams, 1853: 270; Sowerby, 1879, fig. 115.

= *Murex* (*Chicoreus*) *triqueter* var. *amanuensis* Couturier, 1907: 142.

Naquetia trigonulus — Kaicher, 1973: card 166 (Not *Murex trigonulus* Lamarck, 1822).

Naquetia trigonulus (Lamarck, 1816) — Fair, 1976: 83, pl. 14, fig. 179 (Not Murex trigonulus Lamarck, 1816).

Naquetia trigonula (Lamarck, 1816) — Radwin & D'Attilio, 1976: 81, pl. 15, fig. 12 (Not Murex trigonulus Lamarck, 1816).

Not *Naquetia cumingii* — Houart, 1992: 128 (in part), 129, fig. 238 (in part), 173, fig. 445; Merle et al., 2011: 402, pl. 79, fig. 18 (= *Naquetia jickelii*).



Figure 21. (scale bars 500 µm)

A–J. *Naquetia annandalei* (Preston, 1910). A–B. Bohol, Philippines, RH, 98.8 mm; C–D. Philippines, Balut, RH, 94.5 mm; E. Philippines, Bohol Island, RH, 2.7 mm; F–G. Taiwan, North Keelung, RH, 87.9 mm; H–J. Philippines, Cebu, RH, 17.2 mm.

K–O. *Naquetia barclayi* (Reeve, 1858). K–L. St Brandon Shoal, near Mauritius, on shore after a hurricane, lectotype NHMUK 196277, 83.1 mm (photos J.-P. Pointier); M–O. Mozambique, RH, 19.5 mm.
Type material. *Murex cumingii*: Lectotype NHMUK 1963.817; *Murex trigonulus*: Lectotype MHNG 1099/35; *Murex triqueter* var. *amanuensis*: not located.

Type locality. *Murex cumingii*: Philippine Islands; *Murex trigonulus*: Unknown; *Murex triqueter* var. *amanuensis*: Amanu, Tuamotu, French Polynesia.

Distribution. Indo-W. Pac. (IP); C. Pac. From southwestern Madagascar eastwards throughout the Indian and Pacific oceans, with Tuamotu Archipelago as the eastern limit.

Description. Shell up to 66 mm in length with small, shouldered protoconch of 2–2.25 whorls (Fig. 22R) and weakly convex teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 rounded, frondose and weakly webbed varices. Other axial sculpture of 2 or 3 intervarical nodose cords. Spiral sculpture of strong, broad, low primary, secondary and tertiary cords. Spiral sculpture of subsutural ramp of last whorl with abis, IP followed by P1, s1, P2, s2, P3, t, s3, t, P4, s4, P5, P6, s6, ADP, MP, ABP, (abs) on convex part of shell and siphonal canal.

Aperture ovate. Columellar lip smooth. Outer lip with split, elongate, narrow denticles within. Siphonal canal short, broad, ventrally narrowly open, with 3 or 4 webbed spines, ABP, MP, ABP and abs.

Yellowish to pale brown with 2 or 3 brown spiral bands on last whorl and numerous brown blotches on shell surface. Aperture white.

Remarks. This species was previously known as *Naquetia trigonulus* (Lamarck, 1816), but this name is actually a junior synonym of *Naquetia triqueter* (Born, 1778).

Lamarck (1822) realized that the *Murex trigonulus* he described in 1816 was a synonym of *N. triqueter*. Then, in 1822, considering that this name was no longer used and once again available, he used the same name *Murex trigonulus* in a description for this species. A lectotype (Fig. 22G–H) was designated by Finet and Houart (1989). This second *Murex trigonulus* is a junior homonym of the first 1816 name and is therefore invalid.

As such, the first available and valid name for this species is *Murex cumingii* A. Adams, 1853. See Finet & Houart (1989) for a detailed history.

Naquetia fosteri D'Attilio & Hertz, 1987 Figs 23A–L; 28

Naquetia fosteri D'Attilio & Hertz, 1987b: 190, fig. 1–6.

Naquetia annandalei — Fair, 1976: 21 (in part), pl. 14, fig. 171; Radwin & D'Attilio, 1976: 80, pl. 15, figs 9–10 (not *Pteronotus annandalei* Preston, 1910).

Type material. Holotype SDNHM 91996.

Type locality. Red Sea, Gulf of Aqaba, off Eilat.

Distribution. Indo-W. Pac. (I). Red Sea, Northern end of the Gulf of Aqaba.

Description. Shell narrow, up to 94.5 mm in length with small, rounded protoconch of 1.5 whorls (Fig. 23G) and weakly convex teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 narrow, high varices with abapical varical flange extending on the siphonal canal. Other axial sculpture of 3–5 narrow, nodose, intervarical ridges. Spiral sculpture of narrow, high, primary cords, narrower secondary cords and few tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP, abis followed by P1, s1, P2, s2, P3, t, s3, t, P4, s4, P5, P6, s6, ADP, MPm and ABP on convex part of shell and siphonal canal.

Aperture ovate. Columellar lip smooth. Outer lip erect, with split, narrow, elongate denticles within. Siphonal canal moderately long, ventrally narrowly open, weakly dorsally bent, with 3 broad, webbed, open spines, ADP, MP, and ABP.

First teleoconch whorls pink or pale orange, teleoconch whorls light brown with 2 darker brown bands on last whorl, more obvious on axial varices and brown blotches on and between ridges.

Remarks. *Naquetia fosteri* has long been confused with *N. barclayi*, largely due to the shell variability in Muricidae. Nevertheless, it differs from both species *N. barclayi* and *N. annandalei* by its narrower and elongate shell, by its numerous intervarical ridges, and by its paucispiral protoconch consisting of 1.5 whorls compared to the conical and multispiral protoconch in both *N. barclayi* and *N. annandalei*.

Naquetia jickelii (Tapparone Canefri, 1875) Figs 24A–L; 28

Murex jickelii Tapparone Canefri, 1875: 582, pl. 19, fig. 6.

Naquetia cumingii — Houart, 1992: 128 (in part), 129, fig. 238 (in part), 173, fig. 445; Merle et al., 2011: 402, pl. 79, fig. 18 (no *Murex cumingii* A. Adams, 1853).

Type material. Holotype ZMB/Moll-37370.

Type locality. Red Sea, Sudan, Suakin, on madrepores.

Distribution. Indo-W. Pac. (I). Red Sea, Sudan (Suakin and Port Sudan), Saudi Arabia (Jeddah) and the Dahlak Archipelago.

Description. Shell up to 66 mm in length with a



Figure 22 (scale bar 500 µm)

A–D. *Naquetia barclayi* (Reeve, 1858). A–B. S. Mozambique, fish traps, 91.6 mm, coll. & photos Travis Payne; C–D. Mozambique, RH, 87.3 mm.

E–R. *Naquetia cumingii* (A. Adams, 1853). E–F. Philippine Islands, lectotype NHMUK 1963.817, 58.1 mm (photo G. Dajoz, MHNG); G–H. Locality unknown, lectotype of *Murex trigonulus*, MHNG 1099/35/1, 37.4 mm (photo G. Dajoz, MHNG); I–J. N. Mozambique, Nacala Bay, RH, 47.2 mm; K–L. Madagascar, Tulear, RH, 59 mm; M. Vanuatu, Port Vila, RH, 62 mm; N. Guam, Apra Harbour mouth, RH, 22.2 mm (juvenile); O–P. Guam, near Neye Island, RH, 59.2 mm; Q. Guam, North of Alutom Is., Agat Bay, RH; R. Protoconch (see Fig. N).



Figure 23 (scale bar 500 µm)

A–L. *Naquetia fosteri* D'Attilio & Hertz, 1987. A–C. Red Sea, Gulf of Aqaba, off Eilat, holotype SDNHM 91996, 92.2 mm (photo SDNHM); Egypt, Sinai, Oa'hah, RH, 68.5 mm; H. Israel, Eilat (crabbed), RH, 70.7 mm; I–L. Israel, Eilat, 30 m, CM; I–J. 90.4 mm; K–L. 88.1 mm (photos Dave Lum).

protoconch of undetermined nature and weakly shouldered, broad, convex teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 broad, low or moderately high, rounded, nodose varices. Other axial sculpture of a single or 2 strong, high, nodose intervarical ridges, with high node at crossing with P3, s3 and P4 spiral cords. Spiral sculpture of strong, high primary cords, lower and narrower secondary cords, except broader s3 and few, narrow tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP followed by P1, s1, P2, P3, t, s3, t, P4, s4, P5, s5, P6, (s6), t, on convex part of shell; s3 broader than other secondary cords and P6 narrow.

Aperture broadly ovate. Columellar lip smooth, almost completely adherent to shell. Outer lip crenulated, with narrow, elongate, split denticles on a short distance within, ID, D1–D6, all split. Siphonal canal short, broad, ventrally narrowly open, strongly dorsally bent at tip, with abapically bent ADP, MP, ABP, and abs.

Greyish brown or tan with darker coloured spiral bands at shoulder, periphery and above siphonal canal.

Remarks. *Naquetia jickelii*, formerly treated as a synonym of *N. cumingii* by Houart (1992: 128) and by Merle et al. (2011: 113), was later rehabilitated a valid species by Houart & Lorenz (2015), occurring only in the Red Sea. Prior to that, this species was already considered valid by Kaicher (1973: card 167), Fair (1976: 51), and Houart (1985: 10). Vokes (1978: 396) also retained it as valid, but she mixed the broad east African form of *N. cumingii* with the typical *N. jickelii* from the Red Sea. Radwin & D'Attilio (1976: 89) incorrectly synonymized *N. jickelii* with *Chicomurex laciniatus*.

Naquetia jickelii differs from *N. cumingii* in having lower spire whorls, a broader, less shouldered, last teleoconch whorl, a broader aperture, stronger intervarical ridges, a lower spire, and a comparatively shorter siphonal canal.

Naquetia manwaii Houart & Héros, 2013 Figs 5E–F; 24M–O; 25A–E; 28

Naquetia manwaii Houart & Héros, 2013: 510, figs 1B, 3B, 4G–J, 7G, 8A, B.

Type material. Holotype MNHN-IM-2000-26506, sequenced as IM-2009-14457.

Type locality. South Madagascar, West of Lavanono, 25°23.1–2'S, 44°51.4–6'E, 20–23 m.

Distribution. Indo-W. Pac. (I). South Madagascar, living at 20–21 m

Description. Shell small for the genus, up to 34 mm in length. Broadly biconical, weakly spinose, lightly

built, squamous. Subsutural ramp narrow, weakly sloping, concave or straight.

Spire high with 1.15–1.5 protoconch whorls (Fig. 24O) and teleoconch up to 6 broad, strongly convex, shouldered, squamous and nodose whorls. Protoconch large, broad, whorls rounded, smooth. Terminal lip delicate, broad, erect, weakly curved.

Axial sculpture of teleoconch whorls consisting of moderately high, broad, rounded ribs and high, narrow, rounded, squamous varices. Other axial sculpture of low growth lamellae, more apparent on spiral cords, giving a squamous appearance to surface. Last whorl with 3 varices and 3 intervarical elongate knobs or 2 knobs with a third reduced one. Apertural varix broadest, ventrally strongly squamous. Spiral sculpture of low, rounded, primary, secondary and tertiary cords. Last whorl with adis, IP, abis, P1, s1, t, P2, s2, P3, t, s3, t, P4, s4, P5, P6, s6, (t), ADP, MP, ABP, (abs); s1 larger than P1 on penultimate and last whorls. P4-P6 broadest cords. Primary and secondary cords giving rise to very short, broadly open spines. P1 spine slightly longer. All spines connected by frilly webbing.

Aperture large, broad, broadly ovate. Columellar lip narrow with weak knob abapically, 2 or 3 weak folds and low but obvious parietal tooth at adapical extremity. Lip weakly erect abapically, otherwise adherent. Anal notch moderately deep, narrow. Outer lip weakly erect, denticulate, with weak, low, narrow lirae or elongate denticles within: ID split, D1-D4 split, D5, D6. Presence of secondary split lirae between D1 and D2. Siphonal canal short, broad, strongly dorsally bent at tip, narrowly open, with three frondose, webbed, short spines at ADP, MP, and ABP. Grevish-brown. Protoconch and two or three first teleoconch whorls pink or pinkish-brown. Subsutural ramp with a narrow dark brown band below suture, varices of last teleoconch whorl with dark brown blotches, extending on the siphonal canal. Occasionally dark brown, narrow, incomplete spiral bands on last whorl. Aperture white or bluish-white.

Radula (Fig. 5E—F) with crowded rows of teeth with a broad, long, triangular, acute central cusp, short, narrowly triangular lateral denticles and broad, long, triangular, lateral cusps. Lateral tooth sickle shaped, broad.

Remarks. Naquetia manwaii was included in Naquetia despite the slightly broader shell relative to its length compared to other Naquetia species and its relatively low spire. However, it differs from Chicomurex in having a short, broad, squamous siphonal canal, relatively shorter varical spines and a more strongly triangular outline, which are typical characters of Naquetia.

Naquetia cumingii is less squamous, reaching a larger size relative to the number of teleoconch whorls and chiefly in having a very different, smaller protoconch, consisting of 2–2.15 whorls with a strongly keeled first whorl.



Figure 24 (scale bars 500 μ m)

A–L. *Naquetia jickelii* (Tapparone Canefri, 1875). A–C. Red Sea, Sudan, Suakin, on madrepores, holotype ZMB/Moll-37370, 48 mm (photo ZMB); D–E. Red Sea, Eritrea, Dahlak Archipelago, RH, 40.1 mm; F–H. Red Sea, Saudi Arabia, Jeddah, RH, 57.9 mm; I–J. Red Sea Ethiopia, 30 m, CM, 66.2 mm (photo Dave Lum); K–L. Socotra Island, CM, 57. 6 mm (photo Dave Lum).

M–O. *Naquetia manwaii* Houart & Héros, 2013. Southern Madagascar, West of Lavanono, holotype MNHN-IM-2000-26506, 34.0 mm.

Naquetia vokesae differs in having a relatively narrower shell with a higher spire (height/width ratio 2.1-2.3 vs 1.9-2.0 in *N. manwaii*), an almost three times smaller protoconch, the penultimate and last teleoconch whorls with 3 or 4 narrow intervarical, narrow, axial ridges vs 2 or rarely 3 elongate, broad knobs in *N. manwaii*, and in having a narrower aperture.

Due to the superficially similar shells, two species of *Chicomurex* were also compared by Houart & Héros (2013): *C. turschi* (Houart, 1981) and *C. rosadoi* Houart, 1999, from Papua New Guinea and Mozambique, respectively.

Chicomurex turschi differs from *N. manwaii* in having a more slender and higher spire with narrower teleoconch whorls, a comparatively smaller aperture, a more slender, longer siphonal canal and a smaller protoconch, more than half the size of *N. manwaii*.

Chicomurex rosadoi described from south Mozambique has a broader, more globose protoconch, probably denoting intracapsular larval development, broader spire whorls, a broader, globose last whorl, and a narrower siphonal canal.

The spiral cords morphology in Houart & Héros (2013: fig. 3B) is slightly modified (Fig. 25E) to adopt the same pattern used here in the other *Naquetia* species and after careful re-examination of the specimens.

Naquetia rhondae Houart & Lorenz, 2015 Figs 25F–P; 28

Naquetia rhondae Houart & Lorenz, 2015: 44, text figs 1–3, pl. 1, figs A–D; pl. 2, fig. I.

Type material. Holotype MNHN-IM-2000-27724.

Type locality. Red Sea, Gulf of Aqaba, 50 km off Sharm el-Sheikh, 27°48' N, 33°55' E at 25–28 m.

Distribution. Indo-W. Pac. (I). North of Red Sea, From Sharm el-Sheikh to the north of Ras Banas (Egypt), living at 20 to 25 m.

Description. Shell medium sized for the genus, up to 59.2 mm in length at maturity. Biconical, heavy, strongly nodose. Subsutural ramp narrow, strongly sloping, almost straight.

Spire high with 2+ protoconch whorls (Fig. 25O) and teleoconch up to 6 moderately broad, convex, weakly shouldered, nodose whorls. Suture slightly adpressed. Protoconch small with broad, rounded last whorl and narrow, small, rounded first whorl; tip somewhat damaged. Terminal lip eroded.

Axial sculpture of teleoconch whorls consisting of high, narrow, rounded, nodose varices and high, nodose intervarical ribs. Last whorl with 2 uneven, nodose ribs. Spiral sculpture of rounded, narrow, weakly squamous cords. Last teleoconch whorl with IP, abis, P1, s1, P2, s2, P3, s3, P4, s4, P5, P6, (s6), ADP, MP, ABP and a few additional tertiary cords and threads. Primary spiral cords approximately similar in size and strength except quite smaller P6. Secondary cords very narrow, except s3 almost as large as primary cords, forming large gap between P3 and P4. Primary cords extending on axial varices, forming very short, broadly open, webbed spines.

Aperture small, ovate. Columellar lip narrow, weakly flaring, smooth, with narrow, low, parietal tooth at adapical extremity; rim partially erect, adherent at adapical extremity. Anal notch deep, broad. Outer lip erect, crenulated, with 13 or 14 weak, elongate denticles within: ID–D5 split and D6 occasionally split. Siphonal canal moderately long, broad, dorsally bent at tip, narrowly open, with 3 broad, webbed spines: ADP, MP, and ABP.

Light tan with a few darker colored spots on primary spiral cords and darker spiral bands between P1–P2, P3–P4, and P5–ADP, more obvious on axial varices. Other brown spots occasionally on shoulder ramp. Aperture white.

Remarks. *Naquetia rhondae* differs from the closely resembling *N. cumingii* in having a different morphology of the protoconch whorls and axial sculpture of the teleoconch whorls. The protoconch of *N. cumingii* consists of a very small, narrow, more or less shouldered or carinate first whorl (Fig. 22R) and a weakly broader last whorl with a straight outline and a narrow keel abapically vs. a rounded, small, first whorl and a broad, rounded, last whorl in *N. rhondae* (Fig. 25O).

The spiral sculpture of *N. cumingii* is identical to *N. rhondae*, consisting of broad, strong, primary cords, narrow, weak, secondary cords and very small tertiary cords and threads. However, the intervarical axial sculpture differs in being shallower, consisting of 2 or 3, occasionally 4 axial ridges on penultimate and last whorls in *N. cumingii* vs 2 broad ridges on penultimate whorl and one broad node with an additional, lower, node in *N. rhondae*. The second node even becomes obsolete on the last portion of the whorl, between penultimate and the last varix.

Naquetia jickelii has a stouter and broader shell, occasionally also with broad intervarical axial nodes on the last whorl, but bearing 2 or 3 ridges on penultimate whorl. It also has broader and stronger secondary spiral cords, a broader shell with a comparatively broader aperture, a lower spire and a shorter siphonal canal.

Naquetia vokesae is also a species with paucispiral protoconch (Fig. 27H, O) consisting of 2 whorls, but with broader, more rounded whorls. The teleoconch morphology is also quite different from *N. rhondae*, having a higher spire, a more scabrous sculpture, narrower varices and 3 to 5, low, rounded, nodose, intervarical ridges.



Figure 25 (scale bars 500 µm)

A–E. *Naquetia manwaii* Houart & Héros, 2013. A–B. South Madagascar, West of Lavanono, paratype RH (crabbed), 34.7 mm; C–D. South Madagascar, Sud-Est Faux-Cap, 25°38' S, 45°57' E, paratype MNHN-2000-26510, 23.0 mm; E. South Madagascar, West of Lavanono, holotype MNHN-IM-2000-26506.
F–P. *Naquetia rhondae* Houart & Lorenz, 2015. F–G, P. Red Sea, Gulf of Aqaba, 50 km off Sharm el-Sheikh, Holotype MNHN-IM 2000-27724, 50.5 mm; H–I, O. Red Sea, Egypt, north of Ras Banas, Rafa Sataya, paratype F. Lorenz, 50.3 mm; J–K. Red Sea, Gulf of Aqaba, Shaab Sharm in Wadi Gamal, paratype RH, 51.6 mm; L. Northern Gulf of Aqaba, 50 km off Sharm el-Sheikh (dd), RH, 41.2 mm; M–N. Egypt, Hurghada, Manawish Island, CM, 59.3 mm (photo Dave Lum).

Naquetia triqueter (Born, 1778) Figs 5G; 26A-R; 28; 29I-J

Murex triqueter Born, 1778: 288 (ref. to Martini fig. 1038).

- = Purpura cancellata Roding, 1798: 143.
- = Purpura variegata Roding, 1798: 143.
- = *Triplex flexuosa* Perry, 1811: pl. 7, fig. 4.

= *Murex trigonulus* Lamarck, 1816: pl. 417, fig. 4 (not 1822).

= *Murex roseotinctus* G.B. Sowerby II, 1860: 429, pl. 49, fig. 6.

Not *Naquetia trigonulus* (Lamarck, 1816) — Fair, 1976: 83, pl. 14, fig. 179 (= *Naquetia cumingii*).

Not Naquetia trigonula (Lamarck, 1816) — Radwin & D'Attilio, 1976: 81, pl. 15, fig. 12 (= Naquetia cumingii).

Not *Naquetia triqueter* — Kaicher, 1973: card 164 (in part); Radwin & D'Attilio, 1976: 82 (in part), pl. 15, fig. 11; Merle et al., 2011: 79 (in part), pl. 79, fig. 3 (probably) (= *Naquetia vokesae*).

Type material. *Murex triqueter*: Shell figured in Martini (1777: fig. 1038), lectotype designation by Vokes (1974); *M. roseotinctus*: Lectotype NHMUK 1974100, indirect designation by inference of holotype by Finet & Houart (1989). No other material.

Type locality. *Murex triqueter*: East Indies and Tranquebar, restricted to Tranquebar, India by Vokes (1974); *M. roseotinctus*: Philippines.

Distribution. Indo-W. Pac. (IP); C. Pac. Andaman Islands (Subba Rao, 2003), Christmas Is, Indian Ocean (Wells et al., 1990); Straits of Makassar, the Moluccas, Vietnam, The Philippine Islands, Okinawa, Japan, Papua New Guinea and other localities in the Pacific Ocean with the Tuamotus as the eastern limit. A specimen from Reunion Island was illustrated by Merle et al. (2011: pl. 79, fig. 3) but to our knowledge that species was never recorded from the western Indian Ocean.

Description. Shell up to 70 mm in length, with a conical protoconch of 3.5 whorls (Fig. 26E) and weakly shouldered, convex teleoconch whorls.

Axial aculpture consisting of 3 broad, rounded varices, more developed abapically. Other axial sculpture of 2–4 narrow, nodose, intervarical ridges. Spiral sculpture of squamous primary, secondary and tertiary cords. Spiral sculpture of subsutural ramp of last whorl with adis, IP, (abis) followed by P1, s1, P2, s2, P3, t, s3, t, P4, s4, P5, P6, s6, t, ADP, MP, ABP, (abs), t on convex part of shell and siphonal canal.

Aperture ovate. Columellar lip smooth, rim adherent. Outer lip denticulate, with narrow, elongate denticles within. Siphonal canal short, broad, narrowly ventrally open, weakly dorsally bent, with 3 or 4 short, squamous ADP, MP, ABP, and abs spines. White or pale brown with darker bands, especially visible on varices and darker blotches on axial ridges. Ventral side of siphonal canal lighter coloured. Aperture white.

Radula (Fig. 5G) with crowded rows of teeth with a broad, long, triangular, acute central cusp, short, narrowly triangular lateral denticles and broad, long, triangular, lateral cusps. Lateral tooth sickle shaped, broad.

Remarks. *Naquetia triqueter* is difficult to separate from *N. vokesae* except by using its conical protoconch morphology consisting of 3.5 whorls, ending with a sinusigera terminal lip attesting to a planktotrophic larval development (Fig. 26E), compared to a lecithotrophic, rounded and paucispiral protoconch of 1.5 to 2 whorls in *N. vokesae* (Fig. 27H, O).

Merle et al. (2011: pl. 79, fig. 3) illustrated a specimen from Reunion but we know of no other records of *N. triqueter* in the Western Indian Ocean. All specimens (or lot of specimens) from the eastern African coast in which a protoconch, or a partial protoconch could be observed proved to be *N. vokesae*. We therefore remain dubious about the presence of *N. triqueter* in the Western Indian Ocean.

> Naquetia vokesae (Houart, 1986) Figs 27A–O; 28

Chicoreus (Naquetia) triquiter (sic) vokesae Houart, 1986: 95, figs. 1–2.

Naquetia triqueter — Kaicher, 1973: card 164 (in part); Radwin & D'Attilio, 1976: 82 (in part), pl. 15, fig. 11; Merle et al., 2011: 79 (in part), pl. 79, fig. 3 (probably).

Chicomurex turschi — Merle et al., 2011: 400, pl. 78, figs 11–14.

Type material. Holotype NMSA H213.

Type locality. Northern Mozambique, southeast Nacala Bay, 9 m.

Distribution. Indo-W. Pac. (IP). South Africa, N Zululand and Natal; Mozambique; Madagascar; Comoros Is; Tanzania and S Zanzibar in the western Indian Ocean and probably the Philippines, in the Pacific Ocean.

Description. Shell up to 78 mm in length, with rounded protoconch of 1.5–2 whorls (Fig. 27H, O) and weakly convex teleoconch whorls.

Axial sculpture of last teleoconch whorl consisting of 3 narrow, high, rounded, nodose varices. Other axial sculpture of 3–5 strong, narrow, low or moderately high, intervarical ridges. Spiral sculpture of strong, narrow, low, primary, secondary and tertiary cords. Spiral sculpture of subsutural ramp of last whorl with



Figure 26 (scale bars 500 µm-

A–R. *Naquetia triqueter* (Born, 1778). A–B. Papua New Guinea, Rabaul, Nodup, RH, 58.4 mm; C–D. Thailand, Phuket, RH, 52.3 mm; E–H. Guam, Orote Point, juv., RH, 15.9 mm; I–J. Philippines, Palawan, RH, 50.8 mm; K–L. Indonesia, Sulawesi, RH, 53.4 mm; M–N. Kwajalein Atoll, Marshall Islands, RH, 39.3 mm; O–P. Tahiti, Faaone, RH, 30.7 mm; Q–R. *Murex roseotinctus* Sowerby II, 1860, Philippines, lectotype NHMUK 1974.100, 35.1 mm.



Figure 27 (scale bars 500 µm)

A–O. *Naquetia vokesae* (Houart, 1986). A. Northern Mozambique, southeast Nacala Bay, 9 m, holotype NMSA H213, 66 mm (photo KwaZulu-Natal Museum); B–C. Mozambique, N Conducia Bay, S.E. Quissingula Is, paratype RH, 63.4 mm; D–E. South Zanzibar, Ras Kízimkazí, RH, 58 mm; F–H. Philippines, Palawan, Balabac Island, RH, 46.5 mm; I–J. Zanzibar, West of Stone Own, RH, 38.9 mm; K–L. Madagascar, Tulear, RH, 52.7 mm; M–O. Mozambique, Nacala, RH, 36.6 mm.



Figure 28. Naquetia species: Comparative overview



Figure 29. Living specimens (all New Caledonia, photos David Massemin)

A–B. Chicomurex globus Houart, Moe & Chen, 2015; C–E. Chicomurex laciniatus (Sowerby II, 1841); F–H. Chicomurex pseudosuperbus Houart, Moe & Chen, 2015; I–J. Naquetia triqueter (Born, 1778)

adis, IP, (abis) followed by P1, s1, P2, s2, P3, t, s3, t, P4, s4, P5, P6, t, s6, ADP, MP, ABP, (abs) on convex part of shell and siphonal canal.

Aperture ovate or broadly ovate. Columellar lip smooth. Outer lip denticulate, with narrow, elongate denticles within. Siphonal canal short, broad, weakly dorsally bent, with 3 or 4 squamous spines.

Cream, light or dark brown with darker, narrow spiral bands, most obvious on axial varices. Axial ridges with dark brown blotches. Ventral side of siphonal canal lighter coloured. Aperture white.

Remarks. See under *Naquetia triqueter*. Specimens of *N. vokesae* have been recently recorded from the Philippine Islands, a noteworthy range extension.

No significant differences could be detected between specimens from the Indian Ocean and those from the Philippines. The protoconch is also identical (Figs 27H, O). A genetic analysis would be welcome to confirm the conspecificity of these populations.

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