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Notes on *Afonsoconus* Tucker & Tenorio, 2013 (Gastropoda, Conidae), with description of a new species from the Southwestern Indian Ocean

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Abstract. Although cone snails are among the most studied group of gastropods, new species are still regularly described. Here, we focus on *Afonsoconus* Tucker & Tenorio, 2013, a lineage that includes only two species from the Indo-Pacific Ocean. The analysis of molecular (partial mitochondrial *cox1* gene sequences) and morphological (shell and radular tooth) characters revealed that the samples collected by dredging in deep water during a recent expedition carried out in the Mozambique Channel are different from the samples collected in the Pacific Ocean. We thus introduce here a new species, *Afonsoconus crosnieri* sp. nov., from the SW Indian Ocean including records from the Mozambique Channel, the Comoros and Glorieuses Islands, Madagascar, South Africa and Reunion Island.

Keywords. Mitochondrial *cox1* gene, Conidae, *Afonsoconus*, South-West Indian Ocean.

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Introduction

During the last decade, no less than 199 new species of cone snails (Gastropoda, Conoidea) have been described, making the 2010's, although still not finished, the most fruitful decade ever in terms of species description for cone snails (WoRMS editorial board 2018). Thus, even though cone snails are among the most studied group of marine molluscs, mainly because their fascinating shell diversity and the deadly venoms they produce have long attracted the attention of shell collectors and toxinologists, it seems

that many species still remain to be discovered, especially in the deep-sea realm. However, as in many other taxa, the dynamism of the taxonomist community has also created a burden of invalid names and synonyms, associated with alternate genus and subgenus allocations, that sometimes led to complicated situations that require careful revision of the literature. As an example of this complex nomenclatural history, we focus on the *Afonsoconus* Tucker & Tenorio, 2013 group from the Indo-Pacific Ocean.

Kuroda (1956) introduced the deep water species *Chelyconus kinoshitai* Kuroda, 1956 (Fig. 1A–B, D), a member of the family Conidae Fleming, 1822 from Kii, Japan. This species was found to be similar to *Pionoconus fulmen* (Reeve, 1843) (Fig. 2A), but the shell differed in its more elongated shape with a less elevated spire, in spire apical whorls lacking the characteristic rose-pink color, and in having a more sharply angular shoulder. Shikama (1973) introduced *Conus* (*Virgiconus*) *tamikoae* Shikama, 1973 (Fig. 1C) from the north Senkaku Islands. Interestingly, the species was referred to as *Conus* (*Virgiconus*) *tamikoana* in the caption to the illustration. Shikama (1979) recognized that his *C.* (*V.*) *tamikoae* was actually a form (and hence a junior synonym) of the taxon *C. kinoshitai* previously described by Kuroda. He re-introduced it under the name *Conus* (*Chelyconus*) *kinoshitai* f. *tamikoana* Shikama, 1973. According to ICZN Article 32.2.1, the correct original spelling is that chosen by the First Reviser. It can be argued that Shikama (1979), as the original author of the taxon, was the First Reviser according to ICZN article 24.2.4 (original authors may be deemed to be First Revisers of spellings), selecting the name *tamikoana*, rather than introducing it as a new name for a form. Hence, the code can be interpreted in a way that retains *C. tamikoana* Shikama, 1973 as a valid name. This name must change its gender to masculine, i.e. *tamikoanum*, in order to be consistent with the gender of the genus name (ICZN Article 34.2). In the same work, Shikama also introduced *Conus* (*Chelyconus*) *kinoshitai* f. *calliginosus* Shikama, 1979 to designate individuals with a pale violet, sparsely patterned shell (Fig. 1E). The name is unavailable according to ICZN articles 45.5 and 45.6 (introduction of form names after 1960), and it is considered a synonym of *C. kinoshitai*. The name *Conus (Strioconus) brontodes* Shikama, 1979 was also introduced for a distinct species in the same work. This name most probably refers to a large subadult specimen of *C. kinoshitai* with an exceptionally low spire and conical shape, and it is therefore considered another junior synonym (Röckel *et al.* 1995; Filmer 2001, 2012; Tucker & Tenorio 2013).

As a result of the dredging carried out by the Royal Danish Research Ship *Galathea* in shallow water (58–85 m) off Raoul Island, Kermadec Islands in 1952 (Powell 1958), a shell of moderate size, rather slender with a narrowly conical spire and carinated at the shoulder was sampled. This was considered a new species, and described with the name *Conus* (*Dauciconus*) *bruuni* Powell, 1958 (Fig. 1F–H).

The original generic or subgeneric placements of the species *kinoshitai* and *bruuni* were solely based on apparent morphological shell similarities with other taxa. This did not necessarily imply a phylogenetic affinity with the respective type species of each genus/subgenus. Röckel *et al.* (1995) treated all species

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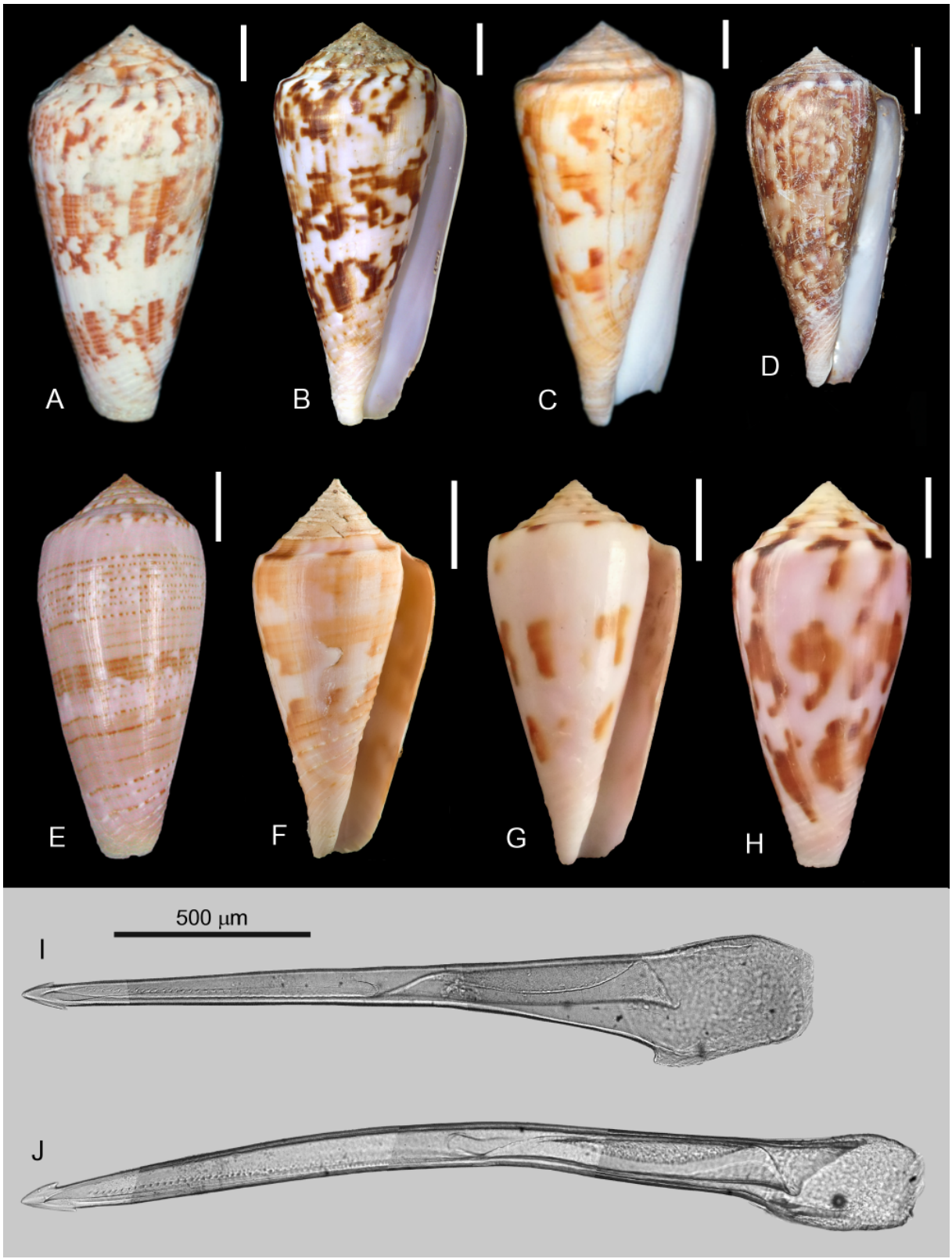
Fig. 1 (opposite page)**. A**. *Chelyconus kinoshitai* Kuroda, 1956, holotype, Kii, Japan, ca 100 fathoms, 71.0 mm (NSMN NC-H329). **B**. *Afonsoconus kinoshitai* (Kuroda, 1956), specimen from Formosa Strait, Taiwan, 78.4 mm (INHS 44626). **C**. *Conus* (*Virgiconus*) *tamikoae* Shikama, 1973, holotype, north of Senkaku Island, Japan, 84.0 mm (KPMY 5602). **D**. *Afonsoconus kinoshitai*, specimen from Taiwan, 51.1 mm (MJT). **E**. *Afonsoconus kinoshitai* f. *calliginosus* (Shikama, 1979), specimen from Philippines, 55.3 mm (EM). **F**. *Conus bruuni* Powell, 1958, holotype, off Raoul Island, Kermadec Islands, 29°13′ S, 177°57′ W, 75–85 m, 43.5 mm (NHMD-91131, previously ZMUC-GAS-808). **G–H**. *Afonsoconus bruuni* (Powell, 1958). **G**. Specimen from south New Caledonia, 223 m, 47.4 mm (MNHN). **H**. Specimen from Banc Cryptélia, Norfolk Ridge, New Caledonia, 180-220 m, 48.3 mm (MNHN). **I**. Radular tooth of *A. kinoshitai* from specimen 1D. **J**. Radular tooth of *A. bruuni*, Atheris voucher specimen from New Caledonia, S_L 68 mm (CP080507AB). Scale bars = 10 mm, unless otherwise stated.



of cone snails as members of one single genus, *Conus*. Alternatively, Tucker & Tenorio (2009) proposed a new classification for the recent and fossil cone snails based upon shell and radula morphologies and available molecular data. Preliminary examination of the radular teeth of *kinoshitai* and *bruuni* (Rolán & Raybaudi-Massilia 1994a, 1994b) (Fig. 1I–J) suggested a close relationship between these two taxa, which were provisionally placed by Tucker & Tenorio (2009) in the genus *Asprella* Schaufuss, 1869 along with a rather large number of other species. The genus *Asprella* thus defined turned out to be polyphyletic (Puillandre *et al.* 2014). It was split into several genera that were more consistent with the phylogenetic relationships among the different species (Tucker & Tenorio 2013). The species *kinoshitai* and *bruuni* were placed in the new genus *Afonsoconus* Tucker & Tenorio, 2013. In the subsequent classification of Conidae proposed by Puillandre *et al.* (2015) based upon the molecular phylogeny, *Afonsoconus* was given subgeneric rank within *Conus*. According to the reconstructed phylogeny of Puillandre *et al.* (2014), *Afonsoconus* is the sister group to fish-eating species placed in the (sub)genus *Textilia* Swainson, 1840 (Fig. 2B–D), and this relationship was highly supported. Irrespective of its subjective ranking as a genus or a subgenus, the supraspecific taxon *Afonsoconus* includes species that form a monophyletic group. The species in this group exhibit characteristic radular features which can be considered true synapomorphies that allow immediate separation from the species in their sister group *Textilia*.

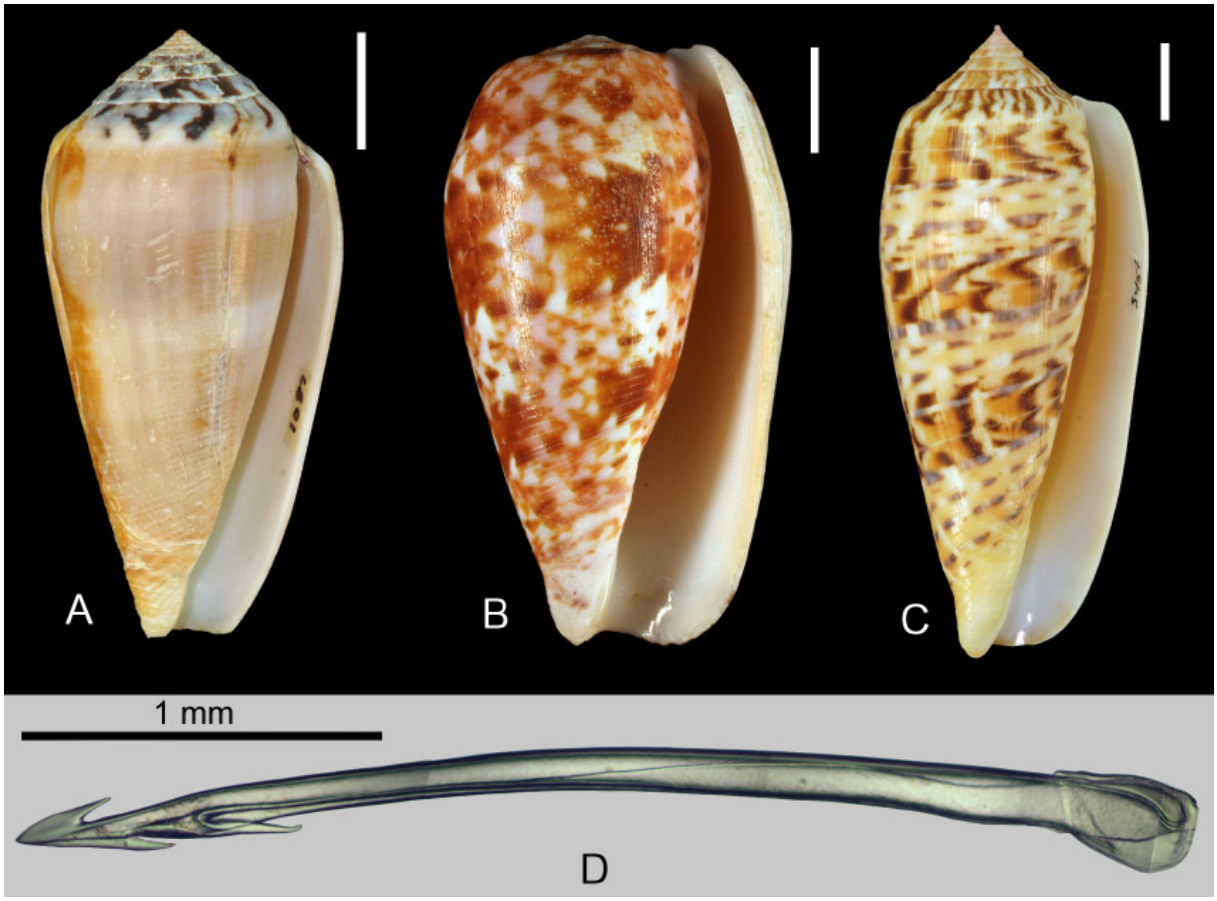


Fig. 2. A. *Pionoconus fulmen* (Reeve, 1843), specimen from Kii Peninsula, Wakayama prefecture, Japan, 51.9 mm (INHS 44603). **B**. *Textilia bullatus* (Linnaeus, 1758), specimen from Ua Huka, Baie Kuiapaku, Marquesas Archipelago, 58.1 mm (MNHN IM-2012-20656). **C–D**. *Textilia dusaveli* (H. Adams, 1872). **C**. Specimen from off Balut Island, Mindanao, Philippines, 260 m, 82.1 mm (INHS 44868). **D**. Radular tooth, specimen from New Caledonia, S_L 67.0 mm (MJT). Scale bars = 10 mm, unless otherwise stated.

According to Tucker & Tenorio (2013) and WoRMS editorial board (2018), the (sub)genus *Afonsoconus* thus includes two extant species, and no species of *Afonsoconus* have been reported as fossils (Tucker & Tenorio 2013). The species included in (sub)genus *Afonsoconus* occur in the Indo-Pacific region, ranging from Japan to New Zealand (Kermadec Islands) through Taiwan, the Philippines, the Solomon Islands and New Caledonia (Röckel *et al.* 1995; Monnier *et al.* 2018). The occurrence of *Afonsoconus kinoshitai* in the Indian Ocean (Mozambique, Madagascar and Reunion Islands) has been cited in the literature (Rolán & Raybaudi-Massilia 1994a; Röckel *et al.* 1995).

In 2017, the Muséum national d'Histoire naturelle (MNHN) carried out the oceanographic expedition BIOMAGLO (https://expeditions.mnhn.fr/campaign/biomaglo) aboard the RV *Antéa*, within the framework of the Tropical Deep Sea Benthos program (Corbari *et al*. 2017). The main objective of the BIOMAGLO campaign was to explore biodiversity and study the deep marine ecosystems of the islands of Mayotte, Glorieuses and Comoros in the Indian Ocean, and to highlight their distinctness or affinities with other regions of the Mozambique Channel. It also pursued the analysis of assemblages of species in relation to the diversity of deep habitats, and the connectivity between the African and north/south coasts of Madagascar to determine the isolation level of the region for selected model species. During this research cruise, the deep benthic fauna in the Mayotte-Glorieuses zone was surveyed, dredging from 80 m to a depth of 1070 m. Several live specimens of a cone snail initially identified as *Conus* (*Afonsoconus*) *kinoshitai* were collected. Several empty shells of apparently the same species had previously been collected in the course of other MNHN expeditions to the Mozambique Channel such as MIRIKY (https://expeditions.mnhn.fr/campaign/miriky), carried out in 2009 to the northwest of Madagascar. Additional specimens had been taken in Banc du Leven in the course of other French dredging campaigns carried out in 1969 and 1973. A number of specimens come from fishermen's nets from different areas in southern Mozambique, South Africa and Reunion Island. Many of these are nowadays in the private collections of amateur shell collectors in Europe. The sequencing of a fragment of the *cox1* gene for the live-collected *kinoshitai* –like individuals from the BIOMAGLO Expedition showed a significant genetic divergence from typical *Afonsoconus kinoshitai* specimens from the Pacific Ocean, and also from *Afonsoconus bruuni* from New Caledonia. The molecular data, in conjunction with comparative analyses of shell and radula characters are consistent with the hypothesis that the members of the *A. kinoshitai* group originating from the SW Indian Ocean actually correspond to a distinct species. Here, we summarize the main morphological features that characterize the members of genus *Afonsoconus*, and introduce the new species from the SW Indian Ocean with the name *Afonsoconus crosnieri* sp. nov.

Material and methods

Most of the material studied here was previously deposited in institutional repositories. Descriptions and measurements are based on shells oriented in the traditional way: spire up with the aperture facing the viewer. The taxonomy used in the present work follows Tucker & Tenorio (2013), with the updates and modifications included in Puillandre *et al.* (2015). Specimens were collected by dredging in deep water during campaigns carried out by the MNHN (expeditions.mnhn.fr) in the Mozambique Channel and northwest Madagascar aboard the RV *Antéa* and *Miriky*, namely BIOMAGLO 2017 and MIRIKY respectively, at depth ranges of 80 to 1100 m. Some specimens were taken in Banc du Leven in the course of other French dredging campaigns carried out in 1969 and 1973. Specimens in private collections come from local fishermen in most cases. Preserved specimens of other cone snail species used in the phylogenetic analyses were collected by the MNHN expeditions EXBODI and TERRASSES in New Caledonia, and SANTO 2006 in Vanuatu. Distribution maps were generated with GeoMapApp (http://www.geomapapp.org), using the general bathymetric map of the oceans as a default basemap.

We describe shell morphology using the terminology established in Röckel *et al.* (1995). We also used the procedure described in Röckel *et al.* (1995) for counting the number of protoconch whorls.

For morphometric comparisons, adult shells selected among available specimens in the collections of the MNHN and other sources (private collections) were measured with a digital caliper, and the measurements rounded to 0.1 millimeter. All the measurements are in a spreadsheet, deposited as electronic supporting information (Appendix). For comparison of shell morphometry, we performed analysis of the covariance (ANCOVA) for different shell parameters, namely maximum diameter (MD), height of the maximum diameter (HMD) and spire height (SH), using species hypotheses as factor and shell length (S_L) as covariate. Additionally, compared the mean values of S_L statistically using t- and U-tests. Statistical tests were carried out using STATGRAPHICS XVII-X64, after all the measurement sets passed the normality tests.

We used the terminology for radular morphology of Tucker & Tenorio (2009), and the abbreviations in Kohn *et al.* (1999) and Rolán & Raybaudi-Massilia (2002). The radular sac was dissected from the cone snail and soft parts were digested in concentrated aqueous potassium hydroxide for 24 hours. The resulting mixture was then placed in a Petri dish and examined with a binocular microscope. The radular teeth were removed with fine tweezers, rinsed with distilled water, then mounted on a slide using Aquatex (Merck) Mounting Medium, and examined under a compound microscope. Figure photos were obtained with a CCD camera attached to the microscope.

DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturers' recommendations. A fragment of the cytochrome oxidase subunit I (*cox1*) was amplified using universal primers LCO1490/HCO2198 (Folmer *et al.* 1994). PCR reactions were performed in 25 µl, containing 3 ng of DNA, 1 × reaction buffer, 2.5 mM $MgCl_2$, 0.26 mM dNTP, 0.3 mM of each primer, 5% DMSO, and 1.5 units of Qbiogene Q-Bio Taq. Amplification consisted of an initial denaturation step at 94°C for 4 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 50°C for *cox1*, followed by extension at 72°C for 1 min. The final extension was at 72°C for 5 min. PCR products were purified and sequenced by the Eurofins sequencing facility. Specimens are registered in the MNHN collections and sequences were deposited in BOLD and GenBank (Table 1).

Additional sequences from the *Afonsoconus* clade and from closely related species (*Textilia*), as well as one sequence of *Fraterconus distans* (Hwass in Brugière, 1792), used as outgroup, were downloaded from GenBank (Table 1). As no indels were detected, *cox1* sequences were aligned manually. A phylogenetic tree was reconstructed using MrBayes 3.2 (Huelsenbeck & Ronquist 2001), with two runs, each consisting of three Markov chains of 10 000 000 generations each, with a sampling frequency of one tree each 1000 generations. Each codon position of the *cox1* gene was treated as an unlinked partition, each following a GTR model, with a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites. Convergence of each analysis was evaluated using Tracer 1.7 (Rambaut *et al.* 2018) to check that ESS values were all greater than 200. A consensus tree was then calculated after omitting the first 25% of trees as burn-in. Kimura 2-parameter (K2P) genetic distances were calculated using MEGA 6 (Tamura *et al*. 2013).

Collection acronyms

CR = Christophe Roux reference collection, Vitry-sur-Seine, France
EM = Eric Monnier reference collection, Paris, France
FP = Fabrice Prugnaud reference collection, Suresnes, France
GH = Guy Hoarau collection [to be accessioned by the Muséum d'Histoire Naturelle de Saint Denis], La Réunion
INHS = Illinois Natural History Survey, Brighton, Illinois, USA
KPMY = Kanagawa Prefectural Museum, Yokohama, Japan
MJT = Manuel J. Tenorio reference collection, Jerez, Spain
MNHN = Muséum national d'Histoire naturelle, Paris, France

Table 1. Species vouchers with GenBank and BOLD accession numbers for the individuals included in the present study.

MNHN Voucher ID	Status	BOLD ID	Country	Expedition	Station	Species	GenBank Accession Number
			New Caledonia			*Afonsoconus bruuni*	KJ550020
			New Caledonia			*Afonsoconus bruuni*	KJ550021
MNHN-IM-2009-18219		CONO1485-14	New Caledonia	TERRASSES	DW3069	*Afonsoconus bruuni*	KJ550151
MNHN-IM-2009-18222		CONO1486-14	New Caledonia	TERRASSES	DW3069	*Afonsoconus bruuni*	KJ550152
MNHN-IM-2009-18226		CONO1490-14	New Caledonia	TERRASSES	DW3072	*Afonsoconus bruuni*	KJ550153
MNHN-IM-2009-18228		CONO1492-14	New Caledonia	TERRASSES	DW3075	*Afonsoconus bruuni*	KJ550154
MNHN-IM-2009-18229		CONO1472-14	New Caledonia	TERRASSES	CP3054	*Afonsoconus bruuni*	KJ550155
MNHN-IM-2009-18239		CONO1474-14	New Caledonia	TERRASSES	DW3056	*Afonsoconus bruuni*	KJ550156
MNHN-IM-2009-31355		CONO2133-18	New Caledonia	EXBODI	DW3857	*Afonsoconus bruuni*	MH777769
MNHN-IM-2009-31356		CONO2134-18	New Caledonia	EXBODI	DW3855	*Afonsoconus bruuni*	MH777768
MNHN-IM-2013-62924	Paratype	CONO2135-18	Mayotte-Glorieuses	BIOMAGLO	DW4809	*Afonsoconus crosnieri* sp. nov.	MH777767
MNHN-IM-2013-62925	Paratype	CONO2136-18	Mayotte-Glorieuses	BIOMAGLO	DW4809	*Afonsoconus crosnieri* sp. nov.	MH777766
MNHN-IM-2013-62927	Holotype	CONO2137-18	Mayotte-Glorieuses	BIOMAGLO	DW4838	*Afonsoconus crosnieri* sp. nov.	MH777765
MNHN-IM-2013-62932	Paratype	CONO2138-18	Mayotte-Glorieuses	BIOMAGLO	DW4838	*Afonsoconus crosnieri* sp. nov.	MH777764
MNHN-IM-2013-62933	Paratype	CONO2139-18	Mayotte-Glorieuses	BIOMAGLO	DW4838	*Afonsoconus crosnieri* sp. nov.	MH777763
			Philippines			*Afonsoconus kinoshitai*	FJ937341.1
			Philippines			*Afonsoconus kinoshitai*	KJ550543
						aff. *tamikoanus*	
MNHN-IM-2007-30695		CONO1372-14	Vanuatu	SANTO_2006	DB63	*Textilia bullatus*	KJ550157
			Philippines?			*Textilia cervus*	KJ549886
			Philippines?			*Textilia dusaveli*	KJ549899
MNHN-IM-2007-30646		CONO999-10	Vanuatu	SANTO_2006	FR04	*Fraterconus distans*	KJ550204

NHMD = Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark (previously ZMUC)
NSMN = Nishinomiya Shell Museum, Nishinomiya, Japan
SV = Stephan Veldsman reference collection, Pretoria, Rep. South Africa

Shell morphometry abbreviations

AH = aperture height
HMD = height of the maximum diameter
MD = maximum diameter
PMD = relative position of the maximum diameter (= HMD/AH)
RD = relative diameter (= MD/AH)
RSH = relative spire height (= SH/S_L)
S_L = maximum shell length
SH = spire height

Radular morphometry abbreviations

S_L/T_L = shell length/radular tooth length
T_L/AP_L = radular tooth length/anterior portion length
$100B_L/AP_L$ = 100 × blade length/anterior portion length

Results

Morphological characterization of Afonsoconus

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Neogastropoda Wenz, 1938
Superfamily Conoidea Fleming, 1822
Family Conidae Fleming, 1822

Genus ***Afonsoconus*** Tucker & Tenorio, 2013

Type species

Chelyconus kinoshitai Kuroda, 1956, by original designation.

Diagnosis

Shell (Fig. 1A–H). Elongated conical to cylindrical shell; spire low and conical in shape; posterior notch deep and cords present on whorl tops; columella twisted, but without anterior notch; shell and spire coloration variable; operculum small, ovate-shaped; periostracum thin and translucent, with multiple fine spiral rows of small tufts.

Radular tooth (Fig. 1I–J). Narrow and elongated, with a large to medium relative size; waist indistinct; anterior section equal or slightly longer than the posterior section; tooth serrated with a fairly long row of small serrations; terminating cusp small; barb and blade very short; blade barely twice as long as barb; base large; basal spur present; basal ligament present (not shown in Fig. 1I–J).

Geographic distribution

The species included in the genus occur in the Indo-Pacific region.

Geologic range

Recent.

Remarks

Afonsoconus is here treated as a genus, following Tucker & Tenorio (2013) and Monnier *et al*. (2018), but Puillandre *et al*. (2014) ranked it as a subgenus within *Conus*.

There are currently two species included in genus *Afonsoconus* (WoRMS editorial board 2018). A number of taxon names associated with *A. kinoshitai* are considered synonyms (forms). These are *tamikoanus* Shikama, 1973, *calliginosus* Shikama, 1979 and *brontodes* Shikama, 1979, and were already presented in the Introduction (vide supra). The name *Conus* (*Chelyconus*) *wistaria* Shikama, 1970 has occasionally been associated to *A. kinoshitai* especially among amateur shell collectors, but the name actually applies to a color form of *Pionoconus fulmen* (Röckel *et al*. 1995; Filmer 2012; Tucker & Tenorio 2013).

The food habits of the species in *Afonsoconus* are not known, but the radular morphology (Fig. 1I–J) suggests that they prey on worms. Based upon conotoxin analysis, it has been inferred that *A. kinoshitai* is a piscivorous species (Bulaj *et al.* 2005; Puillandre *et al.* 2010). However, this is not supported by direct observation of prey capture (Olivera *et al.* 2015). In analogous fashion, other species of Conidae in the genera *Embrikena* Iredale, 1937 and *Asprella* have been considered piscivorous based upon the presence of certain conotoxins in their chemical repertoire (Olivera *et al.* 2015). However, this assumption is not supported either by direct observation of prey capture nor by the morphology of the respective radular teeth of these species, which are more consistent with a vermivorous feeding mode (Tucker & Tenorio 2013). Several conotoxins have been identified for *A. kinoshitai*, most notably the μ-conotoxin μ-KIIIA (Bulaj *et al.* 2005; Zhang *et al.* 2007; Khoo *et al.* 2009). This conotoxin blocks mammalian neuronal tetrodotoxin (TTX) resistant voltage-gated sodium channels (VGSCs) and is a potent analgesic (Bulaj *et al.* 2005; Zhang *et al.* 2007; McArthur *et al.* 2011).

Phylogenetic analyses

Afonsoconus is recovered as a monophyletic group with high support (Posterior Probability PP = 1) (Fig. 3). The *Afonsoconus* clade is sister to the *Textilia* clade (Puillandre *et al.* 2014), which contains fish-eating species characterised by their polished and shining subcylindrical to cylindrical shells (Fig. 2), and by their harpoon-shaped radular teeth (Fig. 2). *Afonsoconus* is clearly split in three subclades, each of them fully supported (PP = 1), and with high genetic distances between them (> 8%). Conversely, genetic distances within each subclade are all < 1%, except between the two samples of *kinoshitai*, with a genetic distance of 5.4%. The three subclades correspond to different geographic regions, one with specimens from the Philippines, another with specimens from New Caledonia, and a third one containing the specimens from the Mozambique Channel (BIOMAGLO expedition). The specimens from the Philippines and New Caledonia correspond respectively to the species *A. kinoshitai* and *A. bruuni*. According to the phylogenetic relationships and the genetic distances, the specimens from the Mozambique Channel deserve specific status, and this new species is hereby introduced. It is interesting to note that the observed p-distance between the two specimens of *A. kinoshitai* from GenBank (sequences FJ937341.1 and KJ550543.1) is consistent with a separation at the species level, as found for other species of cone snails (e.g., Duda *et al*. 2008; Puillandre *et al*. 2011). Both specimens come from the Philippines, and one of them (sequence KJ550543.1) appears labelled in GenBank as *Conus kinoshitai tamikoae* (= *tamikoanus*). Given the fact that the *tamikoanus* from Japan/China is a synonym (form) of *A. kinoshitai*, as recognised by its author in Shikama (1979), the results of the phylogeny actually suggest that there may be at least two different species of *Afonsoconus* in the Philippines. If we accept that the specimen associated with the sequence FJ937341.1 is *A. kinoshitai*, the other one would be a putative new species, morphologically similar to the form *tamikoanus* according

to its label. The specimens from the Philippines labelled as *tamikoanus* are treated as a subspecies of *A. bruuni* in Raybaudi-Massilia (2008), or as a full species in Monnier *et al.* (2018). It is likely that the *tamikoanus*-like specimen in GenBank is a representative of the taxon featured in Raybaudi-Massilia (2008) and in Monnier *et al.* (2018). Unfortunately, no voucher specimen or photo thereof is associated with the GenBank sequence KJ550543.1, so any further taxonomical claim on this matter would be merely speculative at this stage.

Description of new species

Afonsoconus crosnieri sp. nov.
urn:lsid:zoobank.org:act:BE37EA7A-7F2A-4F32-82BA-8E8D6205154D
Figs 4A–H, 5A–L

Afonsoconus aff. *kinoshitai* – Monnier *et al.* 2018: 638, figs 1–5.

Etymology

This new species is named after Alain Crosnier, oceanographer at Office de la Recherche Scientifique et Technique d'Outre-Mer (ORSTOM – which later became IRD, Institut de Recherche pour le Développement). In the early 1970s, while he was based in Nosy Bé, Alain Crosnier used the RV *Vauban* to conduct surveys of the benthic fauna in the Mozambique Channel, which resulted in the discovery of many new species of marine invertebrates – including the first specimens of the present new cone. Later in the 1970s–1980s, Alain Crosnier was instrumental in launching the MUSORSTOM expeditions ('Campagnes MUSORSTOM'), initially also on the RV *Vauban*, and the resulting volumes of scientific results – initially as *Résultats des Campagnes MUSORSTOM*, which later became *Tropical Deep-Sea Benthos*. Alain Crosnier was himself a specialist of penaeid shrimps.

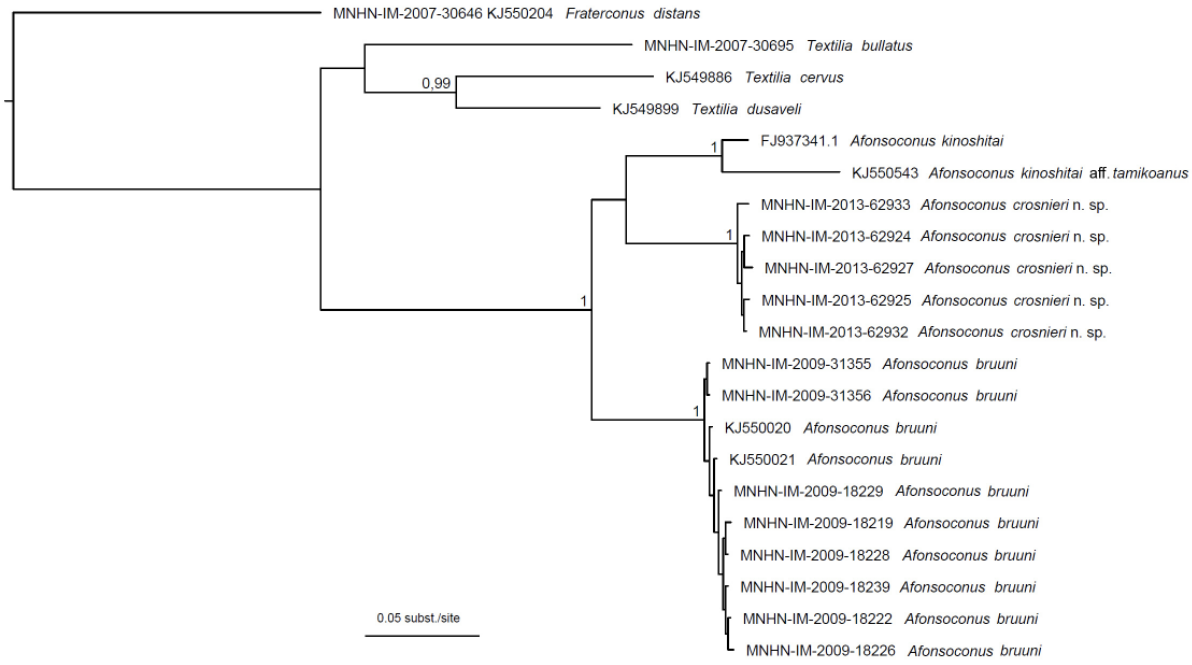


Fig. 3. Bayesian phylogenetic tree. Posterior probabilities (above 0.95) are indicated for each node. Sequences are labelled with the MNHN registration number or the GenBank accession number, and the species name.

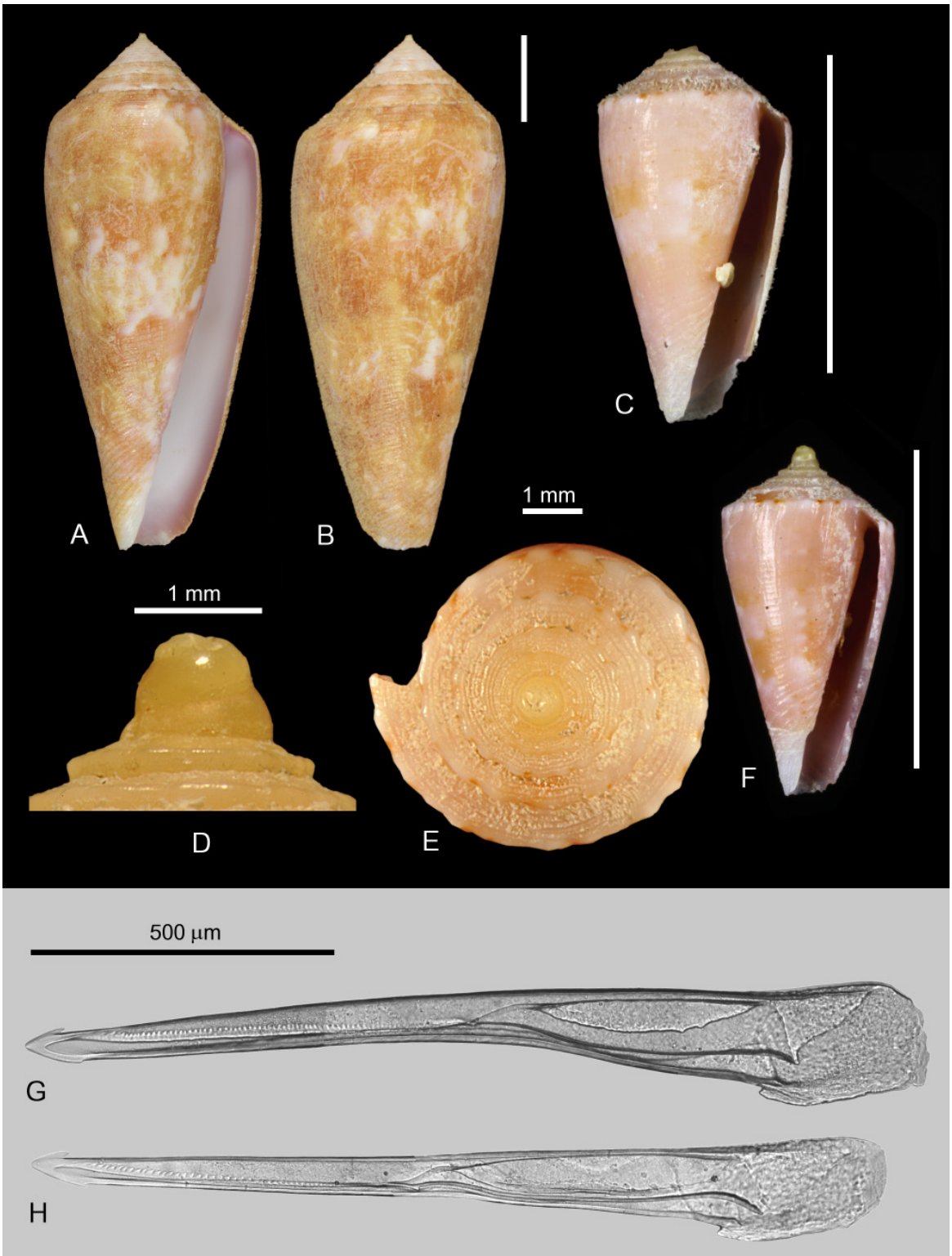
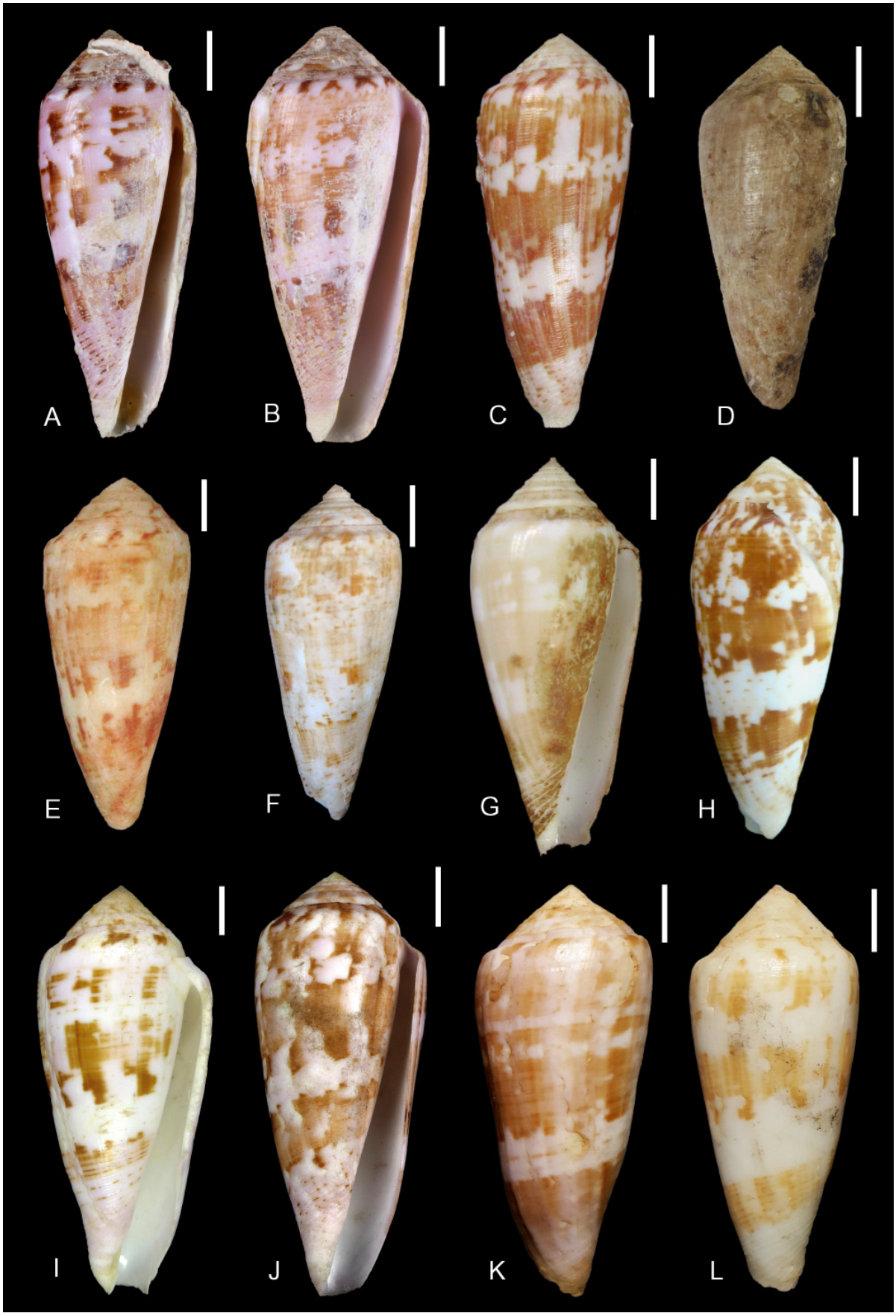


Fig. 4. *Afonsoconus crosnieri* sp. nov. **A–B**. Holotype, ventral and dorsal views, 59.6 × 24.8 mm (MNHN IM-2013-62927). **C–G**. Paratypes. **C**. Juvenile, 11.9 × 6.0 mm (MNHN IM-2013-62933). **D–F**. Juvenile, 11.5 × 5.7 mm (MNHN IM-2013-62932). **D**. Enlargement of the spire. **E**. Apical view of the spire. **F**. Shell. **G–H**. Radular teeth. **G**. Specimen of 71.0 × 27.4 mm (MNHN IM-2013-62925). **H**. Holotype. Scale bars = 10 mm, unless otherwise indicated.



Type material

Holotype

COMOROS: 59.6 × 24.8 mm, Mozambique Channel, S of Grande Comore, stn BIOMAGLO DW4838, 11°59′ S, 43°31′ E, 185–267 m (MNHN IM-2013-62927; GenBank accession number (*cox1* sequence): MH777765) (Fig. 4A–B).

Paratypes

COMOROS: 1 juv., 11.9 × 6.0 mm, same data as for the holotype (MNHN IM-2013-62933; GenBank accession number (*cox1* sequence): MH777764) (Fig. 4C); 1 juv., 11.5 × 5.7 mm, same data as for the holotype (MNHN IM-2013-62932; GenBank accession number (*cox1* sequence): MH777763) (Fig. 4D–F).

MOZAMBIQUE: 1 ex., 81.5 × 34.6 mm, S Mozambique, 180–250 m (EM) (not figured); 1 ex., 65.5 × 26.4 mm, same data as for the preceeding (EM) (Fig. 5H); 1 ex., 83.8 × 34.8 mm, S Mozambique, off Quissico (CR) (Fig. 5I); 1 ex., 70.9 × 28.3 mm, S Mozambique, off Inhambane, 180–200 m (FP) (Fig. 5J).

MADAGASCAR: 1 ex., 64.2 × 25.3 mm, Banc du Leven, off Nosy Bé, RV *Miriky*, expedition MIRIKY, stn DW3211, 12°32′ S, 47°52′ E, 244–300 m (MNHN IM-2000-33924) (Fig. 5C); 1 ex., 51.5 × 21.4 mm, Cap St. André, Majunga, RV *Miriky*, expedition MIRIKY, stn DW CP3260, 15°35′ S, 45°45′ E, 179–193 m (MNHN IM-2000-33925) (Fig. 5D); 1 ex., 67.5 × 27.4 mm, NW Madagascar, East of Banc du Leven, 12°43′ S, 48°16′ E, 245–255 m, coll. Crosnier (MNHN IM-2000-33926) (Fig. 5E); 1 ex., 54.6 × 22.2 mm, NW Madagascar, East of Banc du Leven, 12°41′ S, 48°16′ E, 308–314 m, coll. Crosnier (MNHN IM-2000-33927) (Fig. 5F).

FRANCE: 1 ex., 71.0 × 27.4 mm, Mozambique Channel, Iles Glorieuses, RV *Antéa*, expedition BIOMAGLO, stn DW4809, 11°30′ S, 47°29′ E, 293–301 m (MNHN IM-2013-62925; GenBank accession number (*cox1* sequence): MH777766) (Fig. 5A); 1 ex., 73.1 × 31.3 mm, same data as for the preceeding (MNHN IM-2013-62924; GenBank accession number (*cox1* sequence): MH777767) (Fig. 5B); 1 ex., 65.2 × 27.1 mm, Réunion Island (GH) (Fig. 5G).

SOUTH AFRICA: 1 ex., 71.2 × 30.0 mm, S KwaZulu-Natal, off Park Rynie, 110 m (SV) (Fig. 5K); 1 ex., 65.3 × 27.2 mm, same data as for the preceeding (SV) (Fig. 5L).

Description

Morphometric parameters. S_L = 52–84 mm; RD = 0.45–0.51; RSH = 0.13–0.18; PMD = 0.86–0.94.

Shell. Moderately large. Maximum length: 83.8 mm. Shell profile narrowly conical, with convex sides adapically, and straight below. Spire of moderate height, of straight or very slightly convex outline. Multispiral protoconch with about three whorls, yellowish, glossy and translucent (Fig. 4D). First four teleoconch whorls weakly tuberculated (Fig. 4E), with tubercles becoming obsolete on fifth whorl, being absent in later whorls. Occasionally, the tubercles may fuse together forming a ridge over the

Fig. 5 (opposite page)**.** *Afonsoconus crosnieri* sp. nov. Paratypes. **A**. 71.0 × 27.4 mm (MNHN IM-2013-62925). **B**. 73.1 × 31.3 mm (MNHN IM-2013-62924). **C**. 64.2 × 25.3 mm (MNHN IM-2000-33924). **D**. 51.5 × 21.4 mm (MNHN IM-2000-33925). **E**. 67.5 × 27.4 mm (MNHN IM-2000-33926). **F**. 54.6 × 22.2 mm (MNHN IM-2000-33927). **G**. 65.2 × 27.1 mm (GH). **H**. 65.5 × 26.4 mm (EM). **I**. 83.8 × 34.8 mm (CR). **J**. 70.9 × 28.3 mm (FP). **K**. 71.2 × 30.0 mm (SV). **L**. 65.3 × 27.2 mm (SV). Scale bars = 10 mm.

suture, producing a spire with a slightly stepped aspect. Sutural ramp flat or slightly concave, with five increasing to eight spiral cords. Shoulder subangulate to rounded.

Teleoconch. Early teleoconch whorls white or yellowish. Late teleoconch whorls white with light brown irregular blotches and flecks. Ground colour white, pale yellow or pale violet. Last whorl overlaid with brown flammules or blotches, often fused forming spiral bands. There are two broad white, sparsely patterned spiral bands immediately above and below mid-body. Basal quarter and shoulder area also predominantly white and sparsely patterned. In addition, reddish-brown fine interrupted spiral lines and dots present in variable amounts, more evident in sparsely patterned areas. Columella white, callous and twisted. Aperture white or pale purplish, rather narrow adapically, widening abapically. Posterior notch rather deep. Periostracum yellow-brown, thin and translucent, with fine spiral rows of small tufts. Small and ovate operculum present.

Radular teeth (examined in holotype (Fig. 4H) and in paratype MNHN IM-2013-62925 (Fig. 4G)). 35 to 45 teeth in radular sac. Radular tooth medium-sized: its total length relative to shell length S_L/T_L = 42–48. Waist indistinct. Anterior portion equal to or slightly longer than posterior section of tooth (T_L/AP_L= 1.8–2.0). With one barb opposed to a pointed, very short blade, which covers 12–14% of anterior portion of tooth. Blade only slightly larger than barb, which covers 8–9% of anterior portion. Tooth serrated, with one long row composed of 40–60 small denticles, ending in a small, pointed terminating cusp. Base large, with small but prominent sharp spur pointing upwards. Basal ligament present (not shown in Fig. 4G–H).

Distribution and habitat

Known from the Mozambique Channel including the Comoros, Iles Glorieuses, southern Mozambique, South Africa (Kwazulu-Natal coast) and NW Madagascar, between 180 and 314 m depth. Also present in Réunion Island (Fig. 6).

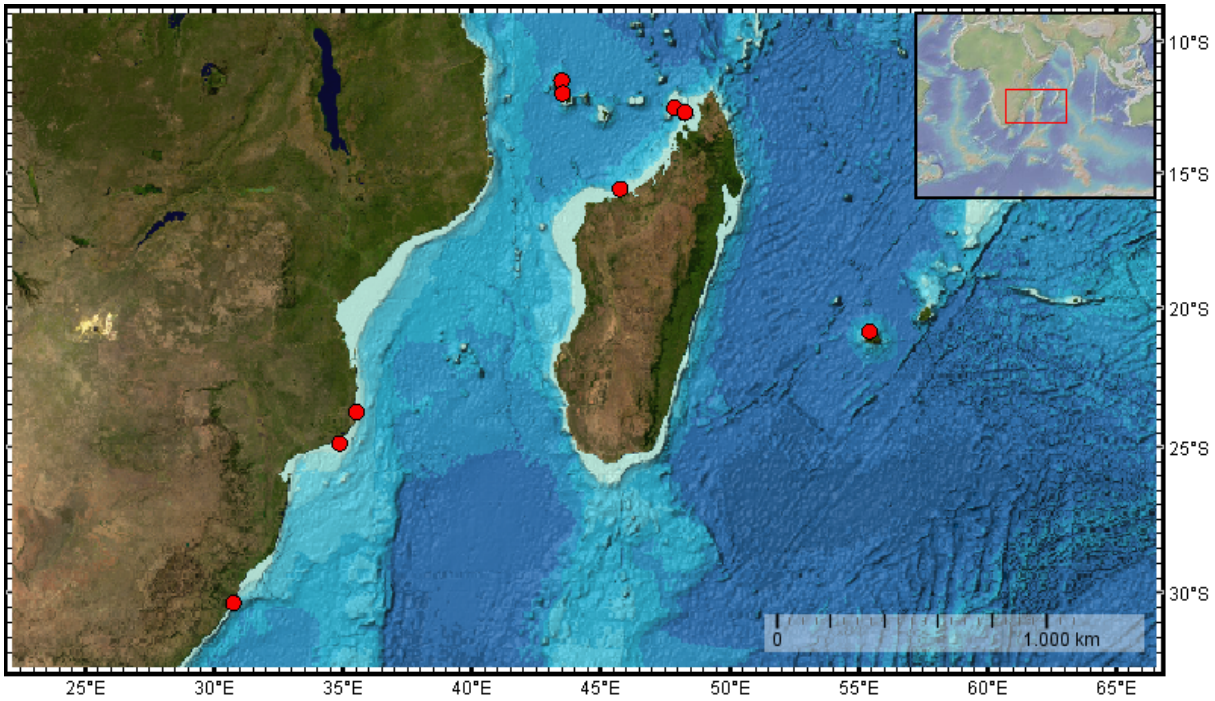


Fig. 6. Distribution map for *Afonsoconus crosnieri* sp. nov. Red circles indicate the points where the species has been collected.

Table 2. Comparison between morphometric parameters for *Afonsoconus crosnieri* sp. nov. (N = 14) and *A. kinoshitai* (Kuroda, 1956) (N = 18): Least-squares (LS) means and ANCOVA results. [1] ANOVA results. For the pairwise comparison of mean S_L: t = 1.788, p = 0.084; U = 75.0, p = 0.055.

Trait	LS mean values (mm) for		F	p
	A. crosnieri sp. nov (Type series)	*A. kinoshitai* (China/Philippines)		
MD	26.4	29.6	51.84	0.0000
HMD	48.3	46.1	13.14	0.0011
SH	10.2	7.9	21.29	0.0001
S_L [1]	67.5	62.5	3.20	0.0838

Remarks

The specimens of *A. crosnieri* sp. nov. form a monophyletic group, with large genetic distances with respect to the two other species, *A. kinoshitai* and *A. bruuni* (Fig. 3). Despite the overall similarities in shell characters, *A. crosnieri* sp. nov. can be separated from its sister species by shell morphometry. Thus, *A. crosnieri* sp. nov. and *A. kinoshitai* do not exhibit significant differences in shell length, but they do differ in RD, PMD and RSH. Analysis of the covariance (ANCOVA) for the shell parameters MD, HMD and SH, using species hypotheses as factor and shell length (S_L) as covariate, yielded statistically significant results (Table 2). In the case of *A. bruuni*, there are statistically significant differences in mean shell length with *A. crosnieri* sp. nov. There are no differences in PMD or RSH, but these two species do differ in RD: ANCOVA for MD, using species hypotheses as factor and S_L as covariate indicates statistically significant differences (Table 3). Thus, *A. crosnieri* sp. nov. is narrower-bodied and has a higher spire than the conoid-cylindrical *A. kinoshitai*, whereas *A. bruuni* has a shell which is usually smaller in length and broader at the shoulder, with a more conical appearance. A discriminant function analysis (DFA), performed with shell length (S_L) and the shell morphometric parameters MD, HMD and SH as variables and species hypotheses as factor, correctly classified 100% of the specimens in the sample (Fig. 7). According to the standardized coefficients, discriminant function 1 (DF1) represents mainly decrease in S_L and increase in MD, whereas discriminant function 2 (DF2) represents mainly decrease in S_L and increase in HMD, with a smaller contribution of increasing SH. These results indicate that *A. crosnieri* sp. nov. can be separated with a high degree of certainty from *A. kinoshitai* and *A. bruuni* based on significant differences in size and shell shape. The radular teeth of the three species show similar morphological characters. In spite of these similarities in the general aspect of the radular teeth, there are differences in their relative sizes. Thus, the radular teeth of *A. kinoshitai* and *A. bruuni* exhibit rather large relative sizes, with S_L/T_L in the range of 25 to 30. The radular teeth examined for *A. crosnieri* sp. nov. are clearly smaller, with S_L/T_L in the range of 42 to 48. This difference might indicate radular tooth adaptation to a specific type of prey, most likely a particular group of worms, and constitutes another useful trait for the separation of *A. crosnieri* sp. nov. from its sister species.

Discussion

The introduction of the new taxon *A. crosnieri* sp. nov. elevates to three the number of species in *Afonsoconus*. However, it seems likely that the number of species in this group is actually understimated, and that there is a hidden biodiversity yet to be studied and properly identified. We have remarked upon the fact that the taxon *A. kinoshitai* from the Philippines most likely comprises two species at least, but additional preserved material with reliable locality data is necessary to accomplish the task of identification. There is firm evidence for the expansion of the range of *Afonsoconus* species to the

Southern Pacific. Moolenbeek *et al.* (2008) figured a heavily damaged specimen (fragment) of a species identified as *A. kinoshitai* from Fatu Hiva, Marquesas Islands. This represents a new record for the Marquesas Archipelago and a range extension to this part of the Pacific. Furthermore, examination of the inventory of specimens of cone snails gathered during the MNHN BENTHAUS campaign (https://expeditions.mnhn.fr/campaign/benthaus) to the Austral islands and surrounding underwater seamounts yielded a number of records corresponding to empty shells cataloged as *A. kinoshitai* and *A. bruuni*. This represents a very significant expansion of the range of *Afonsoconus* species, which covers large areas in the Pacific. There are also some records from Fiji and Tonga (MNHN expeditions BORDAU1 and 2). The question remains open about whether the identity of these specimens of *Afonsoconus* species from the Southern Pacific can be verified. In the same fashion as the specimens from the SW Indian Ocean have turned out to be members of a new species, it is possible that the specimens collected in the remote Austral Islands might actually correspond to undescribed taxa within the genus. These specimens are currently under study, and will probably require the acquisition of further preserved material for a solid specific identification.

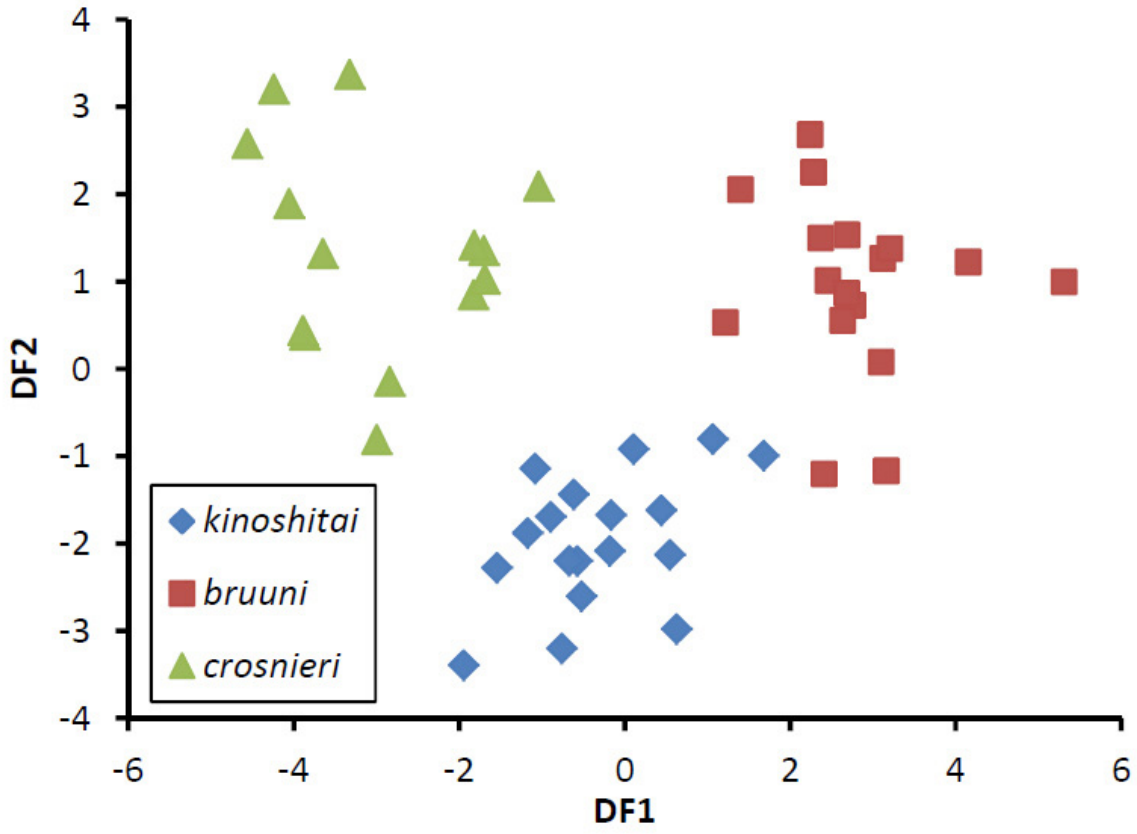


Fig. 7. 2D Scatter plot of the discriminant function analysis (DFA) for the species *A. kinoshitai* (Kuroda, 1956), *A. bruuni* (Powell, 1958) and *A. crosnieri* sp. nov. The analysis was performed using shell length (S_L) and the shell morphometric parameters MD, HMD and SH as variables, and species hypotheses as factor. Both DF1 and DF2 are statistically significant at the 95% probability level (DF1: 69.9 % relative percent, Wilks lambda = 0.0449, χ^2 = 138.085, df = 8, p = 0.0000; DF2: 30.1 % relative percent, Wilks lambda = 0.2946, χ^2 = 54.38, df = 3, p = 0.0000).

Table 3. Comparison between morphometric parameters for *A. crosnieri* sp. nov. (N = 14) and *A. bruuni* (Powell, 1958) (N = 17): Least-squares (LS) means and ANCOVA results. [1] ANOVA results. For the pairwise comparison of mean S_L: t = -4.68, p = 6.19×10^{-5}; U = 211.0, p = 2.80×10^{-4}.

Trait	LS mean values (mm) for		F	p
	A. crosnieri sp. nov. (Type series)	*A. bruuni* (New Caledonia)		
MD	23.2	30.1	111.5	0.0000
HMD	43.7	43.9	0.03	0.8668
SH	9.4	8.5	1.65	0.2090
S_L [1]	67.5	51.5	21.91	0.0001

Acknowledgements

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Appendix. Measurements of shell parameters (see Material and methods).

Species	L (mm)	MD (mm)	AH (mm)	HMD (mm)	SH (mm)
kinoshitai	78.4	37.6	68.5	56.3	9.9
kinoshitai	71.0	31.0	62.4	49.1	8.6
kinoshitai	70.0	32.7	60.6	49.6	9.4
kinoshitai	66.0	29.5	58.1	47.5	7.9
kinoshitai	64.0	29.7	59.2	47.5	4.8
kinoshitai	64.5	28.8	56.2	45.8	8.3
kinoshitai	63.0	28.8	56.2	44.9	6.8
kinoshitai	63.0	26.4	53.4	41.9	9.6
kinoshitai	61.0	26.4	52.4	42.9	8.6
kinoshitai	60.2	28.9	54.6	43.1	5.6
kinoshitai	59.0	27.3	51.0	41.0	8.0
kinoshitai	59.5	28.5	53.8	43.6	5.7
kinoshitai	58.0	25.7	51.3	40.9	6.7
kinoshitai	55.0	24.3	49.1	40.2	5.9
kinoshitai	53.0	22.6	46.3	36.2	6.7
kinoshitai	51.1	24.3	45.3	37.6	5.8
kinoshitai	69.2	32.7	59.6	49.8	9.6
kinoshitai	59.5	29.4	51.6	42.5	7.9
bruuni	40.4	19.4	33.1	30.1	7.3
bruuni	65.2	36.1	56.2	49.8	9.0
bruuni	43.6	21.3	35.4	29.6	8.2
bruuni	42.3	20.5	35.0	32.5	7.3
bruuni	38.0	19.1	31.5	27.3	6.5
bruuni	70.6	36.5	59.6	52.2	11.0
bruuni	56.8	29.9	49.8	40.7	7.0
bruuni	47.4	24.0	40.8	35.0	6.6
bruuni	56.7	27.8	48.6	44.2	8.1
bruuni	42.1	21.7	36.7	30.7	5.4
bruuni	39.7	19.8	34.1	29.5	5.6
bruuni	51.3	30.5	46.2	41.1	5.1
bruuni	52.3	27.8	45.4	40.5	6.9
bruuni	57.4	28.9	46.7	40.7	10.7
bruuni	65.3	33.5	55.1	48.8	10.2
bruuni	50.9	24.5	44.7	38.9	6.2
bruuni	55.8	28.4	49.0	40.1	6.8
crosnieri sp. nov.	59.6	24.8	49.9	44.0	9.7
crosnieri sp. nov.	71.0	27.4	58.5	53.3	12.4
crosnieri sp. nov.	73.1	31.3	63.3	54.5	9.8
crosnieri sp. nov.	64.2	25.3	56.1	49.1	8.1
crosnieri sp. nov.	51.5	21.4	43.1	39.1	8.4
crosnieri sp. nov.	67.5	27.4	58.3	52.2	9.2
crosnieri sp. nov.	54.6	22.2	46.4	41.3	8.2
crosnieri sp. nov.	65.2	27.1	53.2	45.6	12.0
crosnieri sp. nov.	81.5	34.6	69.6	64.9	11.9
crosnieri sp. nov.	65.5	26.4	54.9	51.6	10.6
crosnieri sp. nov.	83.8	34.8	68.8	61.1	15.0
crosnieri sp. nov.	70.9	28.3	59.9	51.7	11.0
crosnieri sp. nov.	71.2	30.0	61.9	52.3	9.3
crosnieri sp. nov.	65.3	27.2	52.7	45.2	12.6
crosnieri sp. nov. (juv.)	11.9	6.0	10.8	9.1	1.1
crosnieri sp. nov. (juv.)	11.5	5.7	9.6	8.7	1.9