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Research article

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Genus *Profundiconus* Kuroda, 1956 (Gastropoda, Conoidea): Morphological and molecular studies, with the description of five new species from the Solomon Islands and New Caledonia

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Abstract. The genus *Profundiconus* Kuroda, 1956 is reviewed. The morphological characters of the shell, radular tooth and internal anatomy of species in *Profundiconus* are discussed. In particular, we studied *Profundiconus* material collected by dredging in deep water during different scientific campaigns carried out in the Solomon Islands, Madagascar, Papua New Guinea and New Caledonia. We reconstructed a phylogeny of 55 individuals based on partial mitochondrial *cox1* gene sequences. The phylogeny shows several clades containing individuals that do not match any of the known species of *Profundiconus* based on their shell and radular morphologies, and are introduced here as five new species: *Profundiconus maribelae* sp. nov. from the Solomon Islands; *P. virginiae* sp. nov. from Chesterfield Plateau (New Caledonia); *P. barazeri* sp. nov. from Chesterfield Plateau and the Grand Passage area (New Caledonia); *P. puillandrei* sp. nov. from Norfolk Ridge (New Caledonia), Kermadec Ridge (New Zealand) and possibly Balut Island (Philippines); and *P. neocaledonicus* sp. nov. from New Caledonia. Furthermore, *Profundiconus teramachii* forma *neotorquatus* (da Motta, 1984) is raised to specific status as *P. neotorquatus* (da Motta, 1984).

Keywords. Mitochondrial *cox1* gene, Conoidea, *Profundiconus*, deep-water species, Indo-West Pacific.

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Introduction

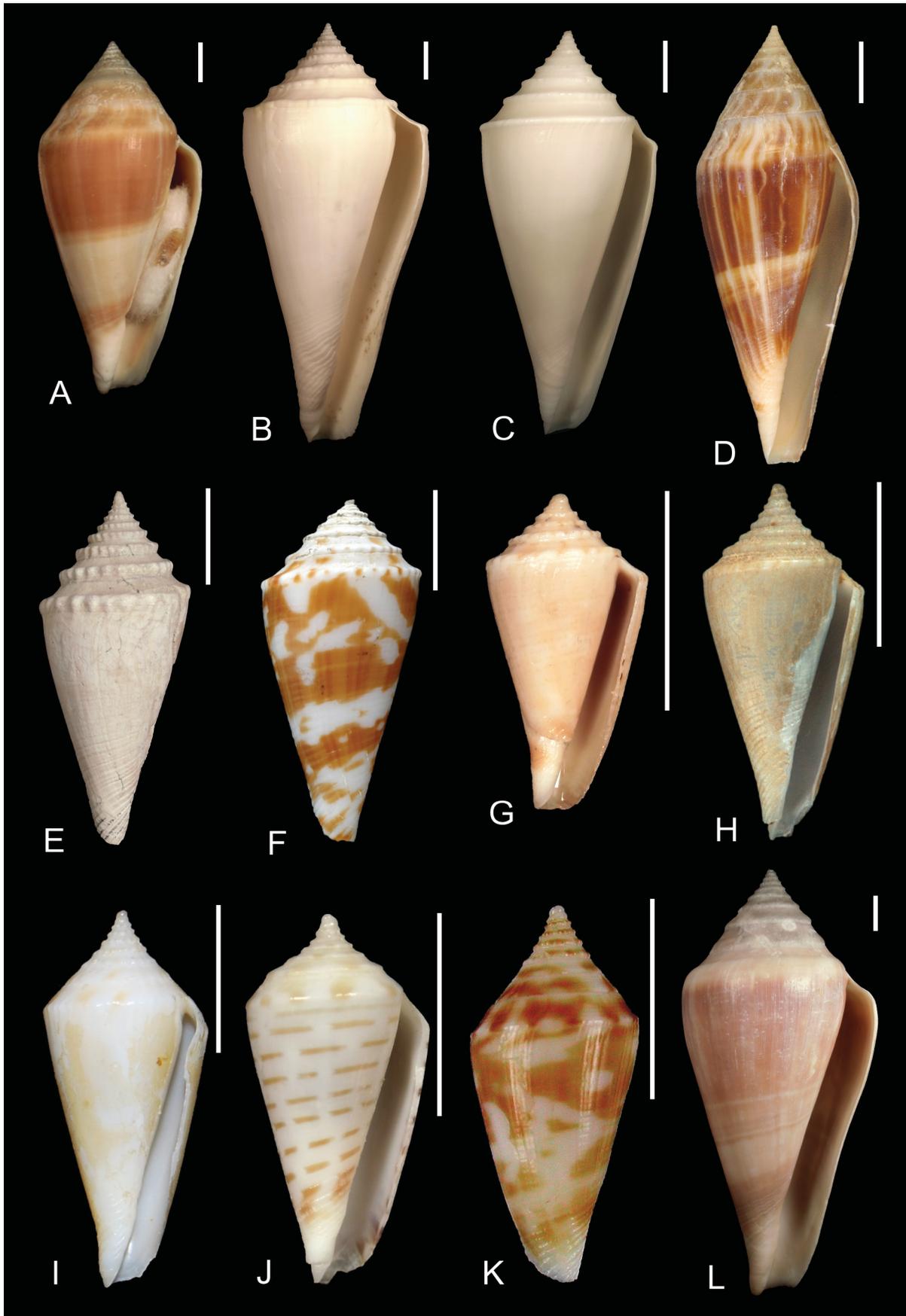
Kuroda (1956) introduced *Profundiconus* as a subgenus of *Chelyconus* Mörch, 1852, a member of the family Conidae Fleming, 1822. *Chelyconus* (?) (*Profundiconus*) *profundorum* Kuroda, 1956 [sic] (Fig. 1A) was originally designated as the type species. *Profundiconus* included simply coloured,

deep-water species of cone snails of a rather large size, but with an extremely thin and elongated shell (Fig. 1). The presence of a rather large operculum with serrated outer margin was considered characteristic of the genus (Tucker & McLean 1993; Tucker & Tenorio 2009). The periostracum was referred to as “rather thickish, somewhat sericeous and very slightly laminated, of olivaceous colouration”. In the same publication, Kuroda also described another large deep-water cone, *Asprella teramachii* Kuroda, 1956 (Fig. 1B), which he placed with a question mark in the subgenus *Endemoconus* Iredale, 1931. This species was at a later date considered as the type for the subgenus *Lizaconus* da Motta, 1991, within the genus *Leptoconus* Swainson, 1849.

In their *Manual of the Living Conidae*, Röckel *et al.* (1995a) treated all species of cone snails as members of one single genus *Conus* Linnaeus, 1758 within the family Conidae. 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. This classification, which was recently revised and updated in Tucker & Tenorio (2013), divides the Holocene cone snails into three families with more than 100 genera. Recently, a large-scale molecular phylogeny including 320 out of the 761 recognized valid species of cone snails was reported (Puillandre *et al.* 2014). The phylogenetic analysis was based on three mitochondrial genes, and revealed four main highly divergent clades. Three of them correspond to reported lineages: one containing only the species *Californiconus californicus* (Reeve, 1844); another is the so called “Small Major Clade” *sensu* Duda & Kohn (2005), roughly equivalent to the Conilithinae *sensu* Tucker & Tenorio (2009), and the third one is the so called “Large Major Clade” *sensu* Duda & Kohn (2005), roughly equivalent to the Conidae *sensu* Tucker & Tenorio (2009). A fourth main clade was found, which included individuals of a number of deep-water Indo-Pacific species belonging to the genus *Profundiconus sensu* Tucker & Tenorio (2009). In the subsequent classification of Conidae proposed by Puillandre *et al.* (2015), based on the molecular phylogeny, generic ranks were given to the four main clades, namely *Conus*, *Conasprella* Thiele, 1929, *Californiconus* Tucker & Tenorio, 2009 and *Profundiconus*, respectively. According to the reconstructed phylogeny of Puillandre *et al.* (2014), *Profundiconus* is the sister-group to all the other cone snails, but this relationship was not statistically supported. The phylogeny is compatible both with the inclusion of *Profundiconus* in the family Conidae *sensu* Puillandre *et al.* (2014) or its placement in a separate family (e.g., Conilithidae, as suggested by Tucker & Tenorio 2009).

According to Tucker & Tenorio (2013), the genus *Profundiconus* includes 16 extant species, to which the recently described *Profundiconus stahlschmidti* Tenorio & Tucker, 2014, *Profundiconus tarava* (Rabil-

Fig. 1. [opposite page] **A.** *Profundiconus profundorum* (Kuroda, 1956) (MJT coll., Okezoko, Kochi Prefecture, Japan, 350 m), 75.0 mm. **B.** *Profundiconus teramachii* (Kuroda, 1956) (MJT coll., South China Sea, trawled in 400 m), 111.3 mm. **C.** *Profundiconus neotorquatus* (da Motta, 1984) (MJT coll., NW coast of Madagascar, dredged in 600–800 m), 78.4 mm. **D.** *Profundiconus smirnoides* Tenorio, 2015 (holotype, MNHN IM-2009-18220, off Ile des Pins, New Caledonia, 480–500 m), 71.8 mm. **E.** *Conilithes antidiluvianus* (Bruguière, 1792), Upper Pliocene, Piacenzian Stage (MJT coll., Pedrera Anna, Molins de Rey, Barcelona, Spain), 35.3 mm. **F.** *Profundiconus emersoni* (Hanna, 1963) (LACM 146906, off Isla Santa Maria (Charles), Galápagos Is., Ecuador, 310 m), 33.7 mm. **G.** *Profundiconus tuberculatus* (Tomlin, 1937) (MJT coll., Miura, Sagami Bay, Kanagawa Prefecture, Japan, 100 m), 13.7 mm. **H.** *Profundiconus loyaltiensis* (Röckel & Moolenbeek, 1995) (holotype, MNHN IM-2000-2545, Ride des Loyauté, New Caledonia, 480 m), 21.8 mm. **I.** *Profundiconus vaubani* (Röckel & Moolenbeek, 1995) (holotype, MNHN IM-2000-3455, Norfolk Ridge, New Caledonia, 435 m), 25.8 mm. **J.** *Profundiconus kanakinus* (Richard, 1983) (MNHN, South New Caledonia, 410–440 m), 19.5 mm. **K.** *Profundiconus cakobau* Moolenbeek *et al.*, 2008 (holotype, MNHN IM-2000-21030, Somo-somo Strait, South of Vanua Levu, Fiji, 426–487 m), 18.9 mm. **L.** *Profundiconus profundorum* (Kuroda, 1956) (MJT coll., South China Sea, trawled in 500–600 m), 109.9 mm. Scale bars = 10 mm.



ler & Richard, 2014), *Profundiconus zardoyai* Tenorio, 2015 and *Profundiconus smirnoides* Tenorio, 2015 (Fig. 1D) must be added. As of November 2015, WoRMS lists 24 records under *Profundiconus*, including one fossil species, *Profundiconus hennigi* Hendricks, 2015, of doubtful assignment to this genus (WoRMS Editorial Board 2015). Two of the listed records, *Conus (Profundiconus) nigrostriatus* Kosuge, 1979 and *Profundiconus soyomaruae* Okutani, 1964, are junior subjective synonyms of *Profundiconus lani* (Crandall, 1979) and *P. profundorum* respectively (Röckel *et al.* 1995a; Tucker & Tenorio 2013). Two of the other listed taxa are now ascribed to other genera: *Profundiconus luciae* (Moolenbeek, 1984) has been placed by Tucker & Tenorio (2013) in the genus *Kurodaconus* Shikama & Habe, 1968 (considered a synonym of *Turriconus* Shikama & Habe, 1968 by Puillandre *et al.* 2015). A study of the radular morphology indicated that *Profundiconus darkini* (Röckel, Korn & Richard, 1993) is actually not a *Profundiconus* but a typical Conidae, and it has tentatively been placed in the genus *Embrikenia* Iredale, 1937 (Tucker & Tenorio 2013). Moreover, recent molecular studies suggest that this species belongs to the same clade as *Kurodaconus luciae* (Puillandre, pers. comm.). Therefore, it is feasible to assume that *darkini* is also a member of the genus *Kurodaconus*.

Apart from the known extant species, the genus *Profundiconus* has a long fossil record ranging from the Cretaceous (*Profundiconus primitivus* (Collignon, 1949)) to the Pliocene (i.e., *Profundiconus yanuyanuensis* (Ladd, 1945)). None of the extant species of *Profundiconus* have been reported as fossils (Tucker & Tenorio 2009). The extant species included in the genus *Profundiconus* occur in the Indo-Pacific region except for *P. emersoni* (Hanna, 1963) (Fig. 1F), which occurs in the East Pacific region (Tucker & McLean 1993; Tenorio *et al.* 2012). However, the inclusion of this species in *Profundiconus* is only provisional (Tenorio *et al.* 2012). The fossil species are known from the Indo-Pacific region and North America.

As their name indicates, species of *Profundiconus* normally live in deep to very deep water. *P. teramachii* has been found at depths of 1134 m (dead) and 977 m (live) (von Martens 1901). However, not all *Profundiconus* are restricted to deep water: Röckel *et al.* (1995a) reported 20–300 m for *P. ikedai* (Ninomiya, 1987) and 75–560 m for *P. lani*. The value of 20 m corresponding to the minimal depth for *P. ikedai* seems too shallow in spite of being quoted in the original description for this species. Okutani (2000) corrected these depth ranges to 250–300 m for *P. ikedai* and 50–560 m for *P. lani*. In general, the deep-sea habitat makes these species difficult to sample. The most commonly collected one is *P. teramachii* (Fig. 1B), which surfaces in the nets of deep-water fishing trawlers. Most of the other species are rare in collections. However, species of *Profundiconus* are not uncommon among the material resulting from dredging carried out by research vessels in deep waters. In this context, the Muséum national d'Histoire naturelle (MNHN) has been carrying out a series of oceanographic expeditions in the deep waters surrounding New Caledonia and beyond since 1980 (Bouchet *et al.* 2008). Many of those research cruises were surveying the seamounts of the Norfolk Ridge (Castelin *et al.* 2011), dredging and trawling from 80 m to a depth of 3000 m. Other areas covered have included the Plateau des Chesterfield and the Grand Passage area. More recently, deep-water surveys have been carried out in the Fiji Islands, Philippines, Vanuatu, Madagascar, Papua New Guinea and other locations, with more missions in preparation. These research cruises produced large lots of deep-water cone snails, both in live and dead condition, with exact depth and locality data. Species of the genus *Profundiconus* are well represented, and their study by an international network of taxonomists has already produced new species (Tenorio 2015a, 2015b; Rabiller & Richard 2014; Moolenbeek *et al.* 2008; Röckel *et al.* 1995b).

Here, we reconstruct the phylogeny of the genus *Profundiconus*, including a total of 55 individuals for which a fragment of the *cox1* gene was sequenced. The phylogeny, in conjunction with comparative analyses of shell and radula characters, provides useful insights into the taxonomy of *Profundiconus*. The phylogeny shows several clades containing individuals that do not match any of the known species

of *Profundiconus* according to their shell and radular morphologies, and they are introduced here as new species.

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 (2009) with the updates and modifications included in Tucker & Tenorio (2013). Specimens were collected by dredging in deep water during different campaigns carried out by the MNHN in New Caledonia and the Solomon Islands, most of them aboard the R/V *Alis* between 1985 and 2008, at depth ranges of 270 to 1100 m. Some specimens were taken off Curtis Island, Kermadec Ridge and west of northern New Zealand from a depth of 900–1100 m by R/V *Tangaroa* during a dredging campaign by the New Zealand Oceanographic Institute in 1979. Distribution maps were generated using GeoMapApp (<http://www.geomapapp.org>) with the general bathymetric map of the oceans as the default basemap.

We describe shell morphology using the terminology established in Röckel *et al.* (1995a). We also used their procedure for counting the number of protoconch whorls. For morphometric comparisons, adult shells randomly 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 comparisons of shell morphometry, we performed analyses 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, we statistically compared the mean values of S_L using t- and U-tests. Statistical tests were carried out using STATGRAPHICS 5.1 or PAST3 (Hammer *et al.* 2001) once 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). The number of individuals for which the entire radula was examined is indicated in the description of each new taxon. Specimens of shells containing the dried animal inside were digested in concentrated aqueous KOH for 24 h. The contents were flushed out of the shell by injecting distilled water through the aperture of the shell by means of a syringe with an incurved needle. The resulting mixture was then placed in a Petri dish and examined with the binocular microscope. The entire radula was removed with fine tweezers and rinsed with distilled water, then mounted on a slide using Aquatex (Merck) Mounting Medium and examined under the optical microscope. Photos were obtained with a CCD camera attached to the microscope. Samples of individual radular teeth for scanning electron microscopy (SEM) were allowed to dry in the air upon rinsing with distilled water and then mounted on stubs covered with double-sided carbon tape. SEM studies were carried out at the MNCN-CSIC on a FEI Inspect scanning electron microscope, equipped with a secondary and retro-dispersed electron detector, and an Oxford Instruments analytical-INCA integrated analysis system.

Forty-one partial DNA sequences of the mitochondrial *cox1* gene (Folmer *et al.* 1994) were extracted from GenBank (from the study of Puillandre *et al.* 2014; GenBank accession numbers in Table 1). This corresponded to a selection of the DNA sequences of the targeted species of *Profundiconus* as defined by Tucker & Tenorio (2013), which includes members of the “*teramachii/smirna/aff. profundorum/n. sp. g*” complex mentioned in Puillandre *et al.* (2014). An additional set of 14 *cox1* sequences corresponding to *Profundiconus* species were kindly supplied by Dr. Nicolas Puillandre (submitted to GenBank and BOLD) and included in the present study, increasing the number to 55 specimens. Within Conoidea, the sister group of the cone snails is Borsoniidae (Tucker & Tenorio 2009: fig. 16; Puillandre *et al.* 2011, 2014). Consequently, we included in our analyses one member of the family Borsoniidae: *Bathytoma*

Table 1. Species vouchers with GenBank and BOLD accession numbers for the individuals and haplotypes included in the present study. [page 1 of 4]

Species	Voucher	Haplo- type n°	Accession n°		Locality + MNHN Database Link
			GenBank	BOLD	
<i>Bathyconus orbigny</i>	MNHN IM-2007-17921		EU015721	CONO296-08	Bohol Sea, off Balicasag Is., Philippines, 271–318 m, 9°29'24"N, 123°44'23.9928"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-17921
<i>Bathytona neocaledonia</i>	MNHN IM-2007-17857		EU015653	CONO187-08	W Bellona, New Caledonia, 637–650 m, 21°5'56.4036"S, 158°35'1.6296"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-17857
<i>Boucheticonus alisi</i>	MNHN IM-2007-34849		KJ550113	CONO1508-14	Banc Mumida, Norfolk Ridge, New Caledonia, 410–430 m, 22°58'55"S, 168°23'9"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-34849
<i>Conasprella pagoda</i>	MNHN IM-2007-17914		EU015729	CONO313-08	Bohol/Sulu Seas sill, Dipolog Bay, Philippines, 150–163 m, 8°41'18"N, 123°17'48"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-17914
<i>Conus marmoratus</i>	MNHN IM-2007-30653		KJ550367	CONO1004-10	Segond Channel, Vanuatu, 2–7 m, 15°31'21.18"S, 167°9'46.1196"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-30653
<i>Cylinder textile</i>	MNHN IM-2007-30663		KJ550496	CONO1426-14	S Port Benier Bay, E Auré Is., Vanuatu, 15°34'31.998"S, 167°12'17.9892"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-30663
<i>Profundiconus barazeri</i> sp. nov.	MNHN IM-2007-30760	1	KJ550111	CONO1027-10	NW Bellona Reef, Chesterfield, New Caledonia, 333–386 m, 20°25'S, 158°41'E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-30760
<i>Profundiconus barazeri</i> sp. nov.	MNHN IM-2007-30924	2	KJ550112	CONO1084-10	NW Bellona Reef, Chesterfield, New Caledonia, 333–386 m, 20°25'S, 158°41'E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-30924
<i>Profundiconus kanakinus</i>	MNHN IM-2009-18241	3	KJ550314	CONO1526-14	Ile des Pins, New Caledonia, 390–410 m, 22°47'26.412"S, 167°12'20.412"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2009-18241
<i>Profundiconus kanakinus</i>	MNHN IM-2009-18250	4	KJ550315	CONO1524-14	Ile des Pins, New Caledonia, 390–410 m, 22°47'26.412"S, 167°12'20.412"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2009-18250
<i>Profundiconus kanakinus</i>	MNHN IM-2009-18257	4	KJ550316	CONO1525-14	Ile des Pins, New Caledonia, 390–410 m, 22°47'26.412"S, 167°12'20.412"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2009-18257
<i>Profundiconus loyaltiensis</i>	MNHN IM-2007-34857	5	KJ550353	CONO1521-14	Ile des Pins, New Caledonia, 22°51'18"S, 167°15'24.012"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-34857
<i>Profundiconus loyaltiensis</i>	MNHN IM-2007-34871	5	KJ550354	CONO1520-14	Ile des Pins, New Caledonia, 22°51'18"S, 167°15'24.012"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-34871
<i>Profundiconus loyaltiensis</i>	MNHN IM-2007-34972	5	KJ550356	CONO1517-14	Ile des Pins, New Caledonia, 22°51'18"S, 167°15'24.012"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2007-34972
<i>Profundiconus vaubani</i>	MNHN IM-2009-18242	5	KJ550516	CONO1480-14	Banc Stylaster, Norfolk Ridge, New Caledonia, 440–450 m, 23°39'47"S, 167°44'13"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2009-18242
<i>Profundiconus vaubani</i>	MNHN IM-2009-18243	5	KJ550517	CONO1477-14	Banc Stylaster, Norfolk Ridge, New Caledonia, 440–450 m, 23°39'48"S, 167°44'14"E http://colddb.mmhn.fr/catalognumber/mmhn/im/2009-18243

Table 1. Species vouchers with GenBank and BOLD accession numbers for the individuals and haplotypes included in the present study. [page 2 of 4]

Species	Voucher	Haplo- type n°	Accession n°		Locality + MNHN Database Link
			GenBank	BOLD	
<i>Profundiconus vaubani</i>	MNHN IM-2009-18254	5	KJ550519	CONO1481-14	Banc Stylaster, Norfolk Ridge, New Caledonia, 440–450 m, 23°39'9.6"S, 167°43'45.6"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18254
<i>Profundiconus loyaltiensis</i>	MNHN IM-2007-34969	6	KJ550355	CONO1518-14	Ile des Pins, New Caledonia, 22°51'18"S, 167°15'24.012"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34969
<i>Profundiconus maribelae</i> sp. nov.	MNHN IM-2007-30935	7	KJ550352	CONO1370-14	NW Isabel, Solomon Islands, 336–341 m, 7°43'S, 158°29'E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-30935
<i>Profundiconus maribelae</i> sp. nov.	MNHN IM-2007-34878	8	KJ550452	CONO1409-14	Guadalcanal, Solomon Islands, 416–425 m, 9°18'59.3388"S, 160°5'55.518"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34878
<i>Profundiconus maribelae</i> sp. nov.	MNHN IM-2007-34879	9	KJ550453	CONO1410-14	Guadalcanal, Solomon Islands, 416–425 m, 9°18'59.3388"S, 160°5'55.518"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34879
<i>Profundiconus neocaledonicus</i> sp. nov.	MNHN IM-2007-34866	10	KJ550426	CONO1420-14	Ile des Pins, New Caledonia, 468–500 m, 22°54'11.3976"S, 167°15'7.8012"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34866
<i>Profundiconus neocaledonicus</i> sp. nov.	MNHN IM-2009-18225	10	KJ550427	CONO1482-14	Banc Stylaster, Norfolk Ridge, New Caledonia, 440–450 m, 23°39'9.6"S, 167°43'45.6"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18225
<i>Profundiconus neocaledonicus</i> sp. nov.	MNHN IM-2009-18227	10	KJ550428	CONO1493-14	Banc Cryphélia, Norfolk Ridge, New Caledonia, 390–570 m, 23°14'12"S, 168°13'18"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18227
<i>Profundiconus neotorquatus</i>	MNHN IM-2009-15600	11	KJ550479	CONO1637-14	Sud Pointe Barrow, S Madagascar, 821–910 m, 25°35'28.2012"S, 44°15'25.2"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-15600
<i>Profundiconus neotorquatus</i>	MNHN IM-2009-15641	11	KJ550481	CONO1640-14	Sud Pointe Barrow, S Madagascar, 821–910 m, 25°35'28.2012"S, 44°15'25.2"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-15641
<i>Profundiconus neotorquatus</i>	MNHN IM-2009-15667	11	KJ550483	CONO1641-14	Lavanono Sector, S Madagascar, 732–729 m, 25°42'52.7976"S, 44°23'44.9952"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-15667
<i>Profundiconus neotorquatus</i>	MNHN IM-2009-15616	12	KJ550480	CONO1639-14	Sud Pointe Barrow, S Madagascar, 821–910 m, 25°35'28.2012"S, 44°15'25.2"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-15616
<i>Profundiconus neotorquatus</i>	MNHN IM-2009-15665	13	KJ550482	CONO1638-14	Sud Pointe Barrow, S Madagascar, 821–910 m, 25°35'28.2012"S, 44°15'25.2"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-15665
<i>Profundiconus puillandrei</i> sp. nov.	MNHN IM-2007-34865	14	KJ550262	CONO1401-14	Banc Introuvable, Norfolk Ridge, New Caledonia, 555–565 m, 24°40'6"S, 168°39'20"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34865
<i>Profundiconus puillandrei</i> sp. nov.	MNHN IM-2009-18221	15	KJ550484	CONO1469-14	Mont J, Ride des Loyautés, New Caledonia, 660–710 m, 23°48'6.6"S, 169°46'16.8"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18221

Table 1. Species vouchers with GenBank and BOLD accession numbers for the individuals and haplotypes included in the present study. [page 3 of 4]

Species	Voucher	Haplo- type n°	Accession n°		Locality + MNHN Database Link
			GenBank	BOLD	
<i>Profundiconus puillandrei</i> sp. nov.	MNHN IM-2009-31320	16	KT874752	CONO1813-15	Récifs de l'Astrolabe-Nord Ouest, New Caledonia, 608–671, 19°49'42"S, 165°33'6"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-31320
<i>Profundiconus smirmoides</i>	MNHN IM-2009-18220	17	KJ550446	CONO1527-14	Ile des Pins, New Caledonia, 480–500 m, 22°55'31"S, 167°17'6"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18220
<i>Profundiconus smirmoides</i>	MNHN IM-2009-18223	18	KJ550447	CONO1471-14	Banc Jumeau Est, Norfolk Ridge, New Caledonia, 410–440 m, 23°45.04'S, 168°16.31'E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18223
<i>Profundiconus smirmoides</i>	MNHN IM-2009-18244	19	KJ550448	CONO1470-14	Banc Jumeau Est, Norfolk Ridge, New Caledonia, 410–440 m, 23°45'2"S, 168°16'19"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18244
<i>Profundiconus teramachii</i>	MNHN IM-2007-30920	19	KJ550477	CONO1453-14	SE Isabel, Solomon Islands, 487–541 m, 8°16'57.5976"S, 159°59'57.5844"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-30920
<i>Profundiconus teramachii</i>	MNHN IM-2007-34888	19	KJ550478	CONO1411-14	Savo, Solomon Islands, 825–909 m, 9°77'20.12"S, 159°53'58.2216"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34888
<i>Profundiconus teramachii</i>	MNHN IM-2009-18264	19	KJ550485	CONO1539-14	North of Rabaul, Papua New Guinea, 497–500 m, 4°63.6"S, 151°55'40.7784"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18264
<i>Profundiconus teramachii</i>	MNHN IM-2009-18272	19	KJ550486	CONO1556-14	North of Rabaul, Papua New Guinea, 585–601 m, 4°423.9988"S, 151°55'45.6132"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18272
<i>Profundiconus teramachii</i>	MNHN IM-2009-18284	19	KJ550487	CONO1557-14	North of Rabaul, Papua New Guinea, 585–601 m, 4°423.9988"S, 151°55'45.6132"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18284
<i>Profundiconus teramachii</i>	MNHN IM-2013-44602	19	KT874753	CONO1812-15	Continental slope, China Sea, 700–723 m, 20°1'17.0688"N, 115°27.386"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-44602
<i>Profundiconus teramachii</i>	MNHN IM-2013-50257	19	KT874754	CONO1810-15	China Sea, 795–822 m, 20°15'54.8424"N, 116°7'59.2248"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-50257
<i>Profundiconus teramachii</i>	MNHN IM-2009-31391	19	KT874764	CONO1800-15	North of Rabaul, Papua New Guinea, 702–724 m, 4°348.0024"S, 151°49'34.824"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-31391
<i>Profundiconus teramachii</i>	MNHN IM-2013-18481	19	KT874755	CONO1809-15	E Kotakot, Papua New Guinea, 500–510 m, 4°29'21.5988"S, 145°31'21.4104"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-18481
<i>Profundiconus teramachii</i>	MNHN IM-2013-18551	19	KT874757	CONO1807-15	E Kotakot, Papua New Guinea, 800–840 m, 4°26'40.8624"S, 145°34'24.5496"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-18551
<i>Profundiconus teramachii</i>	MNHN IM-2013-19051	19	KT874759	CONO1805-15	NE Sissano, Papua New Guinea, 535–540 m, 2°54'40.14"S, 142°10'46.326"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19051

Table 1. Species vouchers with GenBank and BOLD accession numbers for the individuals and haplotypes included in the present study. [page 4 of 4]

Species	Voucher	Haplo- type n°	Accession n°		Locality + MNHN Database Link
			GenBank	BOLD	
<i>Profundiconus teramachii</i>	MNHN IM-2013-19051	19	KT874759	CONO1805-15	NE Sissano, Papua New Guinea, 535–540 m, 2°54'40.14"S, 142°10'46.326"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19051
<i>Profundiconus teramachii</i>	MNHN IM-2013-19686	19	KT874758	CONO1806-15	N Bagabag Is., Papua New Guinea, 540–580 m, 4°44'24.6012"S, 146°10'41.3832"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19686
<i>Profundiconus teramachii</i>	MNHN IM-2013-19746	19	KT874765	CONO1797-15	N Long Is., Bismarck Sea, Papua New Guinea, 5°10'27.84"S, 147°2'53.8584"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19746
<i>Profundiconus teramachii</i>	MNHN IM-2013-19780	19	KT874760	CONO1804-15	N Long Is., Bismarck Sea, Papua New Guinea, 805–865 m, 5°9'26.82"S, 147°1'35"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19780
<i>Profundiconus teramachii</i>	MNHN IM-2013-19789	19	KT874762	CONO1802-15	N Long Is., Bismarck Sea, Papua New Guinea, 805–865 m, 5°9'26.82"S, 147°1'35"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19789
<i>Profundiconus teramachii</i>	MNHN IM-2013-19790	19	KT874761	CONO1803-15	N Long Is., Bismarck Sea, Papua New Guinea, 805–865 m, 5°9'26.82"S, 147°1'35"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19790
<i>Profundiconus teramachii</i>	MNHN IM-2013-19851	19	KT874763	CONO1801-15	Vitiaz Str., N Cape K. William, Papua New Guinea, 706–715 m, 5°59'50"S, 147°35'35"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19851
<i>Profundiconus teramachii</i>	MNHN IM-2013-19924	19	KT874756	CONO1808-15	SE Tuam Is., Papua New Guinea, 550–575 m, 6°41'17.76"S, 148°11'56.9112"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2013-19924
<i>Profundiconus teramachii</i>	MNHN IM-2009-18286	20	KJ550488	CONO1543-14	S of Lae, Gulf of Huon, Papua New Guinea, 700–740 m, 6°55'30.72"S, 147°8'7.7928"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18286
<i>Profundiconus vaubani</i>	MNHN-IM-2007-34962	21	KJ550513	CONO1519-14	Ile des Pins, New Caledonia, 22°51'18"S, 167°15'24.012"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34962
<i>Profundiconus vaubani</i>	MNHN IM-2009-18236	22	KJ550514	CONO1476-14	Banc Stylaster, Norfolk Ridge, New Caledonia, 440–450 m, 23°39'48"S, 167°44'14"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18236
<i>Profundiconus vaubani</i>	MNHN IM-2009-18237	23	KJ550515	CONO1479-14	Banc Stylaster, Norfolk Ridge, New Caledonia, 440–450 m, 23°39'48"S, 167°44'14"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18237
<i>Profundiconus vaubani</i>	MNHN IM-2009-18245	24	KJ550518	CONO1478-14	Banc Stylaster, Norfolk Ridge, New Caledonia, 440–450 m, 23°39'48"S, 167°44'14"E http://coldb.mnhn.fr/catalognumber/mnhn/im/2009-18245
<i>Profundiconus virginiae</i> sp. nov.	MNHN IM-2007-30854	25	KI550158	CONO1463-14	Plateau des Chesterfield, New Caledonia, 519–522 m, 19°37'S, 158°42'E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-30854
<i>Profundiconus virginiae</i> sp. nov.	MNHN IM-2007-30858	26	KI550159	CONO1461-14	Plateau des Chesterfield, New Caledonia, 431–436 m, 19°37'S, 158°42'E http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-30858
<i>Profundiconus zardoyai</i>	ATHERIS DW080509AO	27	KJ550052	–	Grand Passage, N New Caledonia, 200–400 m, 18°57' to 19°07'S, 163°22' to 163°29'E

neocaledonica Puillandre, Sysoev, Olivera, Couloux & Bouchet, 2010 was selected as the most external outgroup of the targeted species complex. In addition, sequences from GenBank of other species of cone snails from two different clades, namely *Conus marmoreus* Linnaeus, 1758, *Cylinder textile* (Linnaeus, 1758), *Bathyconus orbigny* (Audoin, 1831), *Conasprella pagoda* (Kiener, 1847) and *Boucheticonus alisi* (Moolenbeek, Röckel & Richard, 1995), were selected to form a closer outgroup in order to provide a broader phylogenetic context for the species complex that we were interested in.

The *cox1* gene sequences were translated into amino-acids using MEGA v. 4.0 (Tamura *et al.* 2007) and the invertebrate mitochondrial genetic code to check for stop codons. DNA sequences were aligned using the MUSCLE Server (Edgar 2004). The accuracy of DNA sequence alignment was confirmed by eye. Identical DNA sequences were identified using DnaSP v. 5 (Librado & Rozas 2009) and excluded from posterior analyses. The best-fit nucleotide substitution model (HKY+I+G) for the *cox1* dataset was determined using JModeltest 2 (Guindon & Gascuel 2003; Darriba *et al.* 2012) and the Bayesian Information Criterion (BIC; Posada & Buckley 2004). A maximum likelihood (ML) tree was built using RAxML HPC2 (Stamatakis 2006) on Teragrid v. 7.2.7, implemented in the Cyber Infrastructure for Phylogenetic Research (CIPRES) portal version 3.1 (<http://www.phylo.org/portal2>). The best-scoring ML tree was estimated from 100 independent searches, each starting from distinct random trees. Robustness of nodes was assessed using the rapid bootstrapping algorithm (1000 replicates) (Felsenstein 1985; Stamatakis *et al.* 2008). Bayesian analyses (BA) were performed running two parallel analyses in MrBayes (Huelsenbeck & Ronquist 2001), each consisting of four Markov chains of 5 000 000 generations, each with a sampling frequency of 1 tree each 100 generations. The number of swaps was set to 5, and the chain temperature at 0.05. Convergence and mixing of the chains of each analysis was evaluated using Tracer v. 1.4.1 (Rambaud & Drummond 2007) to check that effective sample size (ESS) values were all greater than 200. A consensus tree was then calculated after omitting the first 25% of trees as burn-in. We considered a clade to be ‘moderately supported’ if it had a bootstrap support value (BP) between 75 and 89% and posterior probability (PP) between 0.95 and 0.97, and ‘highly supported’ when BP \geq 90% and PP \geq 0.98 (Fig. 2).

The following abbreviations are used for museums and institutions:

- CSIC = Consejo Superior de Investigaciones Científicas, Spain
- INHS = Illinois Natural History Survey, Illinois, USA
- LACM = Natural History Museum of Los Angeles County, Los Angeles, USA
- MJT = Manuel J. Tenorio reference collection, Jerez, Spain
- MNCN = Museo Nacional de Ciencias Naturales, Madrid, Spain
- MNHN = Muséum national d’Histoire naturelle, Paris, France
- NIWA = National Institute of Water and Atmospheric Research, Wellington, New Zealand
- NMNZ = Museum of New Zealand Te Papa Tongarewa, New Zealand
- NMP = National Museum of the Philippines, Manila, Philippines

Abbreviations for shell morphometry:

- 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)
- SH = spire height
- S_L = maximum shell length

Abbreviations for radular morphometry:

S_L/T_L	= shell length/radular tooth length
T_L/AP_L	= radular tooth length/anterior portion length
$100B_L/AP_L$	= $100 \times$ blade length/anterior portion length
$100AO_L/AP_L$	= $100 \times$ adapical opening length/anterior portion length

Results

Class Gastropoda Cuvier, 1795
 Subclass Caenogastropoda Cox, 1960
 Order Neogastropoda Wenz, 1938
 Superfamily Conoidea Fleming, 1822
 Family Conilithidae Tucker & Tenorio, 2009

Genus *Profundiconus* Kuroda, 1956

Lizaconus da Motta, 1991 (type species: *Asprella* (*Endemoconus*?) *teramachii* Kuroda, 1956).

Type species

Chelyconus (?) (*Profundiconus*) *profundorum* Kuroda, 1956 (by original designation).

Description

SHELL CHARACTERS (Fig. 1). Conical to narrowly conical shell, usually thin, very small to very large in size; shoulders become rounded in outer whorls, although a ridge is present in some cases; a few cords present on early whorls and become numerous and smaller in outer whorls; nodules obsolete early; anal notch shallow; larval shell either paucispiral or multispiral; operculum large and serrate; periostracum smooth.

RADULAR TOOTH (Fig. 2). Blade and barb present (may be poorly differentiated); blade pointed, moderate in length, up to half length of anterior section of tooth; serrations absent; adapical opening large; a structure that we will refer to as external cusp (non-homologue of a posterior blade) starting at base of adapical opening and extending towards waist; external cusp often laterally expanded and serrated, with several small denticles (Fig. 2C, F); external cusp may appear partially covered by rolled sheet, which conforms to anterior portion of tooth; barb, blade and external cusp arranged in three different planes, which form angle of *c.* 120° between them; waist evident; characteristic fringe composed of closely spaced projections pointing towards apex present immediately below waist (Fig. 2C, F); anterior section of tooth shorter than posterior section; shaft fold present; slanted base with large basal spur.

INTERNAL ANATOMY (Figs 4–5). The internal anatomy of *Profundiconus tuberculosus* (Tomlin, 1937) (Fig. 1G) has been studied in detail by Taki (1937), and can be considered representative for other members of the genus. Taki's work was reviewed by Röckel (1994). Some details of the external anatomy and radular apparatus of several other species of *Profundiconus* are presented in Rolán & Raybaudi-Massilia (1994). We hereby reproduce some of the figures from Taki (1937) (Figs 4–5) to illustrate the details of the internal anatomy in *Profundiconus*.

Taki (1937) remarked that the anatomical features of *P. tuberculosus* indicate in many aspects the ancestral nature of this species. The proboscis sheath (Fig. 3A: RS) has longitudinal folds on the inner side; the inner wall of the respiratory siphon (Fig. 3A–B: SI) is smooth, lacking the furrows or invaginations that have been reported in other species of cone snails; the osphradium (Fig. 3B: OS) is simple and not

divided, with the small lobules arranged like feather banners on both sides of the longitudinal axis; there is only one salivary gland (Fig. 3B: SD), consisting of a multitude of small lobules.

The anterior lobe of the midgut gland (Fig. 4A: L₁, L₂) has a bifurcated excretory duct. The male genitalia (Fig. 4B) have been described in detail. The organs that Bergh (1896) described as testes are considered to be the prostate in the opinion of Taki (1937). The testis consists of two lobes (Fig. 4B: HA, HP), which are spirally coiled and reach the tip of the spire. The prostate (Fig. 4B: PG) is separated into three parts (PGA, PGD, PGS), with irregular shallow grooves on its surface. Both cerebral ganglia (Fig. 4C: C) largely merge with each other and can be distinguished only by a slight constriction in the middle; the right parietal and right visceral nerves (Fig. 4C: PA, V) go together as a single nerve from the subintestinal (IN) ganglion. They separate only after a prolonged course.

Geologic range

Cretaceous to Recent.

Geographic distribution

The Holocene species included in the genus (Table 2) occur in the Indo-Pacific region, except for *Profundiconus emersoni* (Fig. 1F), which occurs in the East Pacific region. Extinct species are known from the Indo-Pacific region and North America (Tucker & Tenorio 2009). For a listing of fossil species placed in the genus *Profundiconus*, see Tucker & Tenorio (2009).

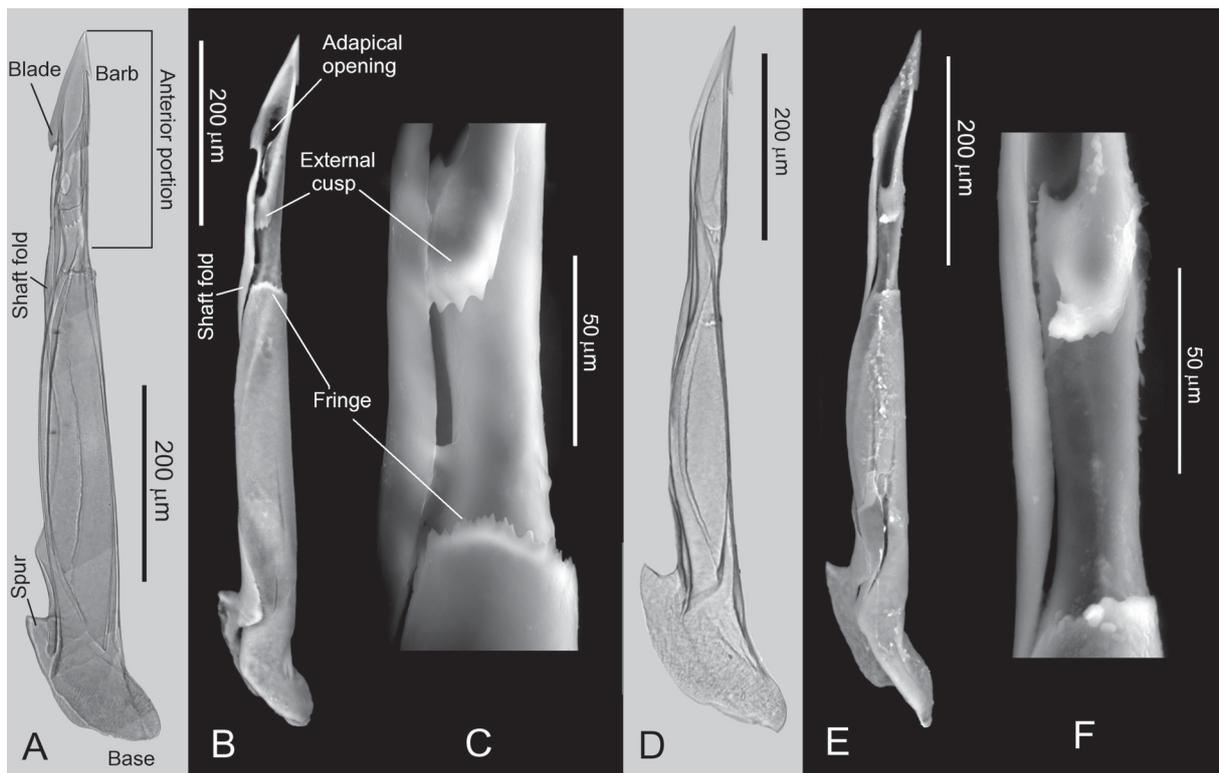


Fig. 2. — A–C. Radular teeth extracted from *Profundiconus vaubani* (Röckel & Moolenbeek, 1995), with major parts and structures labelled. A. Optical photograph (MNHN, uncataloged, S_L 20.6 mm). B. SEM photograph (MNHN, uncataloged, S_L 26.0 mm). C. Enlargement of the middle section of B. — D–F. Radular teeth extracted from *Profundiconus teramachii* (Kuroda, 1956). D. Optical photograph (MNHN IM-2013-44602, S_L 82.7 mm). E. SEM photograph (MNHN IM-2013-50257, S_L 76.7 mm). F. Enlargement of the middle section of E.

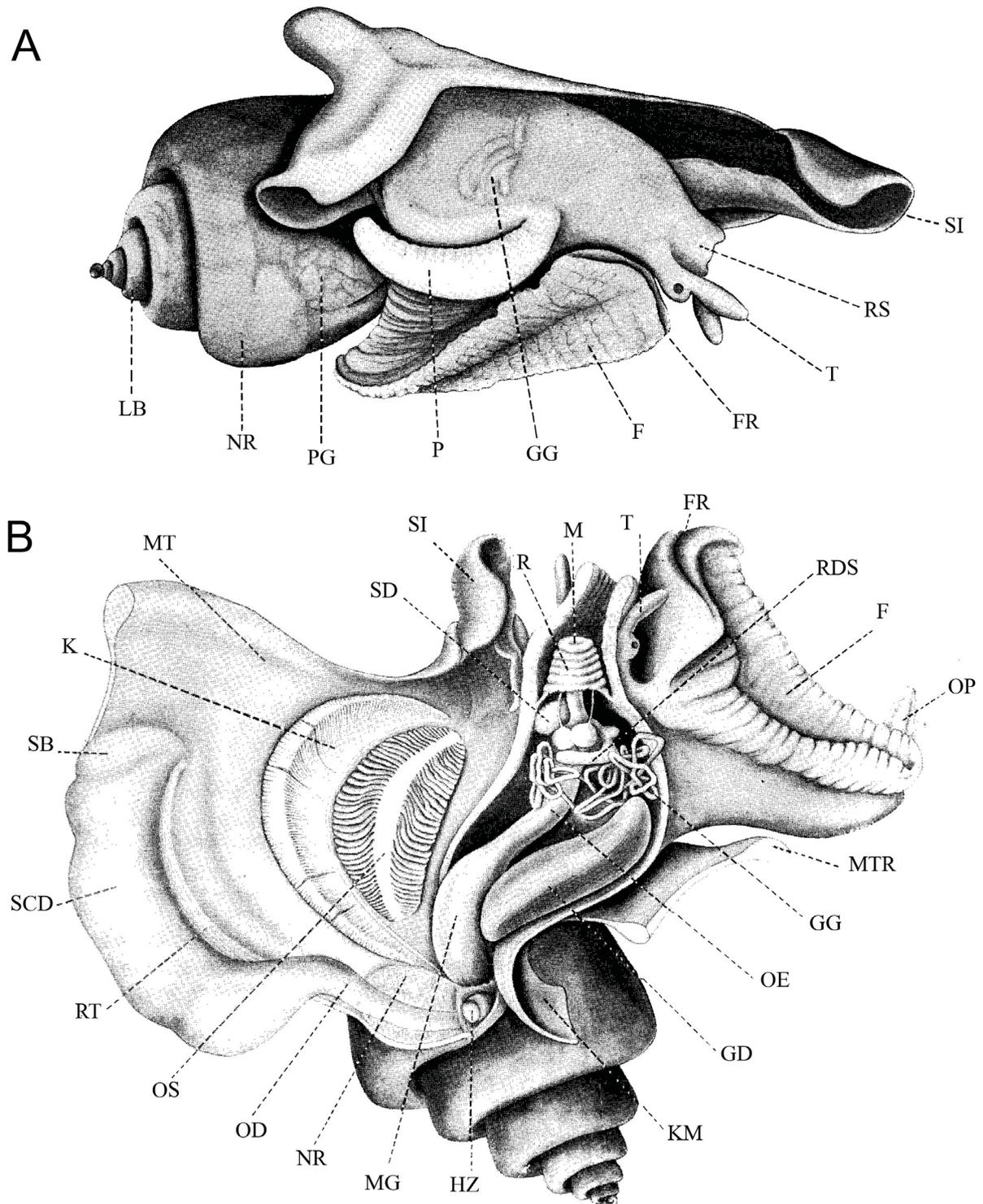


Fig. 3. *Profundiconus tuberculosus* (Tomlin, 1937) (reproduced from Taki 1937, with permission from the Zoological Society of Japan). **A.** External anatomy, male specimen. **B.** Internal anatomy. F = foot; FR = rostrum frontal lobe; GD = venom bulb; GG = venom duct; HZ = heart; K = gill; LB = middle gut; M = mouth; MG = stomach; MT = mantle; MTR = mantle edge; NR = kidney; OD = oviduct; OE = oesophagus; OP = operculum; OS = osphradium; P = penis; PG = prostate; R = rostrum; RDS = radular sac; RT = rectum; SB = receptaculum seminis; SCD = mucous gland; SD = salivary gland; SI = siphon; T = tentacles.

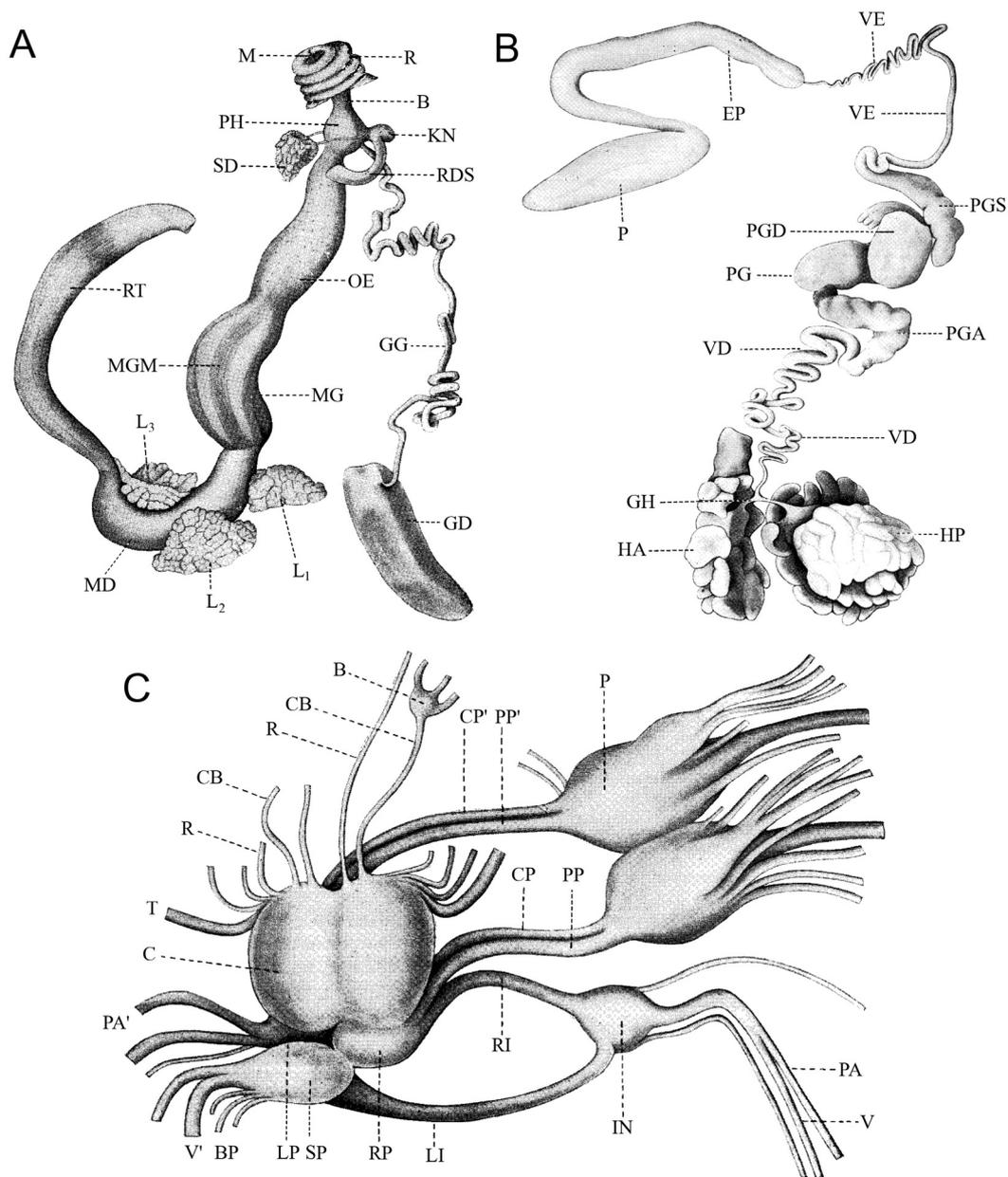


Fig. 4. *Profundiconus tuberculatus* (Tomlin, 1937) (reproduced from Taki 1937, with permission from the Zoological Society of Japan). **A.** Digestive apparatus: A = anus; B = bucal mass; GD = venom bulb; GG = venom duct; KN = caecum of radular sac; L_1 , L_2 , L_3 = liver; MD = middle gut; MGM = stomach muscle; PH = pharynx; R = circular muscles of proboscis; RDS = radular sac; RT = rectum; SD = salivary gland. **B.** Male reproductive apparatus: EP = epiphalus; HA = anterior lobe of testis; HP = posterior lobe of testis; GH = excretory duct of testis; P = penis; PG = prostate; PGA = anterior part of prostate; PGD = posterior part of prostate; PGS = final part of prostate; VD_1 = vas deferens, anterior part; VD_2 = vas deferens, thickened part; VE_1 = vas efferens, posterior part; VE_2 = vas efferens, anterior part. **C.** Nervous system: C = cerebral ganglion; CB = cerebral-buccal connective; CP = right cerebropedal connective; CP' = left cerebropedal connective; IN = subintestinal ganglion; LI = left pleuro subintestinal connective; LP = left pleural ganglion; P = peda-ganglion; PA = right parietal nerve; PA' = left parietal nerve; PP = right pleuropedal connective; PP' = left pleuropedal connective; SP = supra-intestinal ganglion; T = tentacular nerve; V = right visceral connective; V' = left visceral connective.

Table 2. List of Holocene species in the genus *Profundiconus* Kuroda, 1956.

Species (original binomen)	Living species of <i>Profundiconus</i> Kuroda, 1956	Type Locality
<i>Conus cakobai</i> Moolenbeek, Röckel & Bouchet, 2008		Fiji, S of Vanua Levu, Somo-somo Strait, 16°45'S, 179°59.5'E, 426–487 m
<i>Conus dondani</i> Kosuge, 1981		Panglao, Bohol, Philippines
<i>Conus emersoni</i> Hanna, 1963		off Los Frailes, Cape San Lucas, Baja California, Mexico, 300 fathoms
<i>Conus frausseni</i> Tenorio & Poppe, 2004		offshore of Aliquay Island, Philippines
<i>Conus ikedai</i> Ninomiya, 1987		SW of Jogashima Islet, Miura Peninsula, Japan, 20–280 m
<i>Profundiconus jeanmartini</i> Raybaudi-Massilia, 1992		off St. Paul Bay, W coast of Réunion Island, 700 m
<i>Conus kanakinus</i> Richard, 1983		SW of Ile des Pins, New Caledonia, 22°49'S, 167°12'E, 390–395 m
<i>Conus lani</i> Crandall, 1979		off NE Taiwan near Tiao-yu-tai (Uotsuri Shima), 75 m
<i>Conus loyaltiensis</i> Röckel & Moolenbeek in Röckel, Richard & Moolenb., 1995		Loyalty Ridge, New Caledonia, 21°04'S, 167°32'E, 480 m
<i>Conus pacificus</i> Moolenbeek & Röckel, 1996		Bayonnaise Bank, Wallis & Futuna, 12°30.8'S, 176°40.3'W, 597–600 m
<i>Conus teramachii</i> forma <i>neotorquatus</i> (da Motta, 1985)		East Africa
<i>Chelyconus</i> (<i>Profundiconus</i>) <i>profundorum</i> Kuroda, 1956 (type species)		off SW Tosa, Japan, 183 m
<i>Profundiconus scopulicola</i> Okutani, 1972		Hyotanse, Japan, 34°21.5'N, 139°04.5'E, 200 m
<i>Conus smirna</i> Bartsch & Rehder, 1943		near Kauai Island, Hawaii, 257–312 fathoms
<i>Profundiconus smirmoides</i> Tenorio, 2015		off Ile des Pins, New Caledonia, 22°55.5'S, 167°17.1'E, 480–500
<i>Profundiconus stahlschmidti</i> Tenorio & Tucker, 2014		Pasir Tengah Atoll, Togian Is., Sulawesi, Indonesia, 0°26.75'S, 121°39.2'E, 10–12 m
<i>Conus tarava</i> Rabiller & Richard, 2014		Punu Taipu, French Polynesia, 19°16'S, 151°01'W, 683 m
<i>Asprella</i> (<i>Endemoconus</i> ?) <i>teramachii</i> Kuroda, 1956		Tosa, Japan, 200 fathoms
<i>Conus tuberculosus</i> Tomlin, 1937		Sagami Bay, Miyata Zone, Koshiha Zone, Japan
<i>Conus vaubani</i> Röckel & Moolenbeek in Röckel, Richard & Moolenbeek, 1995		S New Caledonia, 23°38'S, 167°43'E, 435 m
<i>Profundiconus zardoyai</i> Tenorio, 2015		Grand Passage, N New Caledonia, 18°57'S, 163°25'E, 325–330 m

Remarks

The shells of species in *Profundiconus* are morphologically related to species included in the fossil genus *Conilithes* Swainson, 1840. Both taxa contain shells with square nodules that are interconnected by carinae on the body whorl, which constitutes a plesiomorphic trait. However, the anal notch is deep in *Conilithes* and shallow in *Profundiconus*. Furthermore, Rolán & Raybaudi-Massilia (1994) have suggested that *Conilithes antidiluvianus* (Bruguière, 1792) (Fig. 1E) and *P. teramachii* (Fig. 1B) are close relatives. Based upon similarities in shell morphology Tucker & Tenorio (2009) placed both genera, *Conilithes* and *Profundiconus*, within the family Conilithidae and separate from Conidae. However, shell traits can be ambiguous. The serrated operculum and the morphology of the radular tooth are more robust proxies for placing a given specimen in *Profundiconus*. The presence on the radular tooth of a laterally widened, often serrated external cusp, along with a characteristic fringe located immediately below the waist composed of closely spaced projections pointing towards the apex in addition to other morphological features (i.e., barb, pointed blade, shaft fold, etc.; see Fig. 2), allow the immediate identification of an individual as a member of *Profundiconus*. The function of the coronated fringe on the tooth in species of *Profundiconus* is unknown, but it resembles a similar structure (collar-shaped band of tubercles) observed on the radular teeth of several members of the genus *Lienardia* Jousseume, 1884, family Clathurellidae, such as *Lienardia tagaroae* Fedosov, 2011, *L. jousseumei* (Hervier, 1896) or *L. cf. rosella* Hedley, 1922 (Fedosov 2011; Bouchet *et al.* 2011).

Nothing is known about the diet of *Profundiconus* cone snails, nor about the families of conotoxins which might be present in the species of the genus. Whereas most of the toxinological studies on cone snails carried out during the last three decades have focused on species that belong to only a few lineages (Puillandre *et al.* 2012), several lineages remain largely understudied or even not studied at all, as is the case for *Profundiconus* (Puillandre *et al.* 2014). Radular morphology suggests a most likely vermivorous diet. However, Marshall (1981) reported finding the beaks of a small cephalopod in the stomach of an adult specimen of *P. smirnoides* (identified as *smirna*) from Wanganella Bank, New Zealand. This suggests that this species might produce a conotoxin of sufficient potency to rapidly immobilize a fast-moving prey.

Phylogenetic analyses

Ingroup sequences included 657 bp containing 192 variable sites, of which 127 were phylogenetically informative. Excluding redundant sequences, 27 sequences were unique in the ingroup. The ML and BA tree topologies were congruent (Fig. 5) and supported *Profundiconus* as a monophyletic group (PP = 1; BP = 87%). Within *Profundiconus*, several clades corresponding to different species were recovered, although their phylogenetic relationships were poorly resolved (Fig. 5). The individuals belonging to *P. teramachii* were split into two separate monophyletic groups corresponding to different geographic regions, one with specimens from the Indian Ocean (Madagascar) and another with specimens from the Pacific Ocean (China, Papua New Guinea and Solomon Islands). This splitting has previously been reported and discussed by Puillandre *et al.* (2014). The specimens of *P. teramachii* from the Indian Ocean belong to the forma *neotorquatus* da Motta, 1985 (Tucker & Tenorio 2013). In the Indian Ocean this species is widely distributed, from Somalia to South Africa (Natal), including Madagascar. According to the phylogeny and the genetic distances, the specimens from Madagascar deserve specific status, i.e., *Profundiconus neotorquatus* (da Motta, 1984), rather than consideration as a mere form of *P. teramachii*. In spite of the molecular divergence that exists between *P. neotorquatus* and *P. teramachii*, the morphological differences in their shells (Fig. 1B–C) and radulae (Fig. 6) are slight.

The genetic differentiation of *P. smirnoides* and *P. teramachii* was not supported. Moreover, the monophyly of the group was not supported by the ML and BA analyses. Reciprocal monophyly between this group and *P. neotorquatus* was therefore not demonstrated. This is usually the case for recently diverged species, due to the lack of time needed to coalesce (Knowles & Carstens 2007). It is interesting

to note that one of the *cox1* sequences of *P. smirnoides* in GenBank (KJ550448) is essentially identical to that of *P. teramachii*, which represents the haplotype for 18 specimens (Table 1). As the voucher specimen (MNHN IM-2009-18244) seems to be properly identified, this could be due to contamination. However, there also exists the possibility that the *cox1* can simply not separate these two species, which on the other hand can be easily separated based on shell and radular morphologies. There are many examples in the literature of morphologically distinct species having identical or almost identical *cox1* sequences (e.g., Mengual *et al.* 2006; McGuire *et al.* 2007; April *et al.* 2011; Chee 2014). In most cases this has been attributed to hybridization-mediated mitochondrial introgression, as well as incomplete lineage sorting.

Specimens attributed *a priori* to the species *Profundiconus loyaltiensis* (Röckel & Moolenbeek, 1995) based on shell morphology were segregated into two distinct lineages. One of these lineages formed a monophyletic group (PP = 1; BP = 83%) along with specimens assigned to *P. vaubani* (Röckel & Moolenbeek, 1995) and *P. kanakinus* (Richard, 1983). Furthermore, some specimens of *P. vaubani* and *P. loyaltiensis* share the same haplotype. It is not clear at this stage whether this indicates one single polymorphic species, contamination, or simply the failure to separate the three closely related species based upon the *cox1* gene fragment only. All of these specimens come from the same area (Isle of Pines,

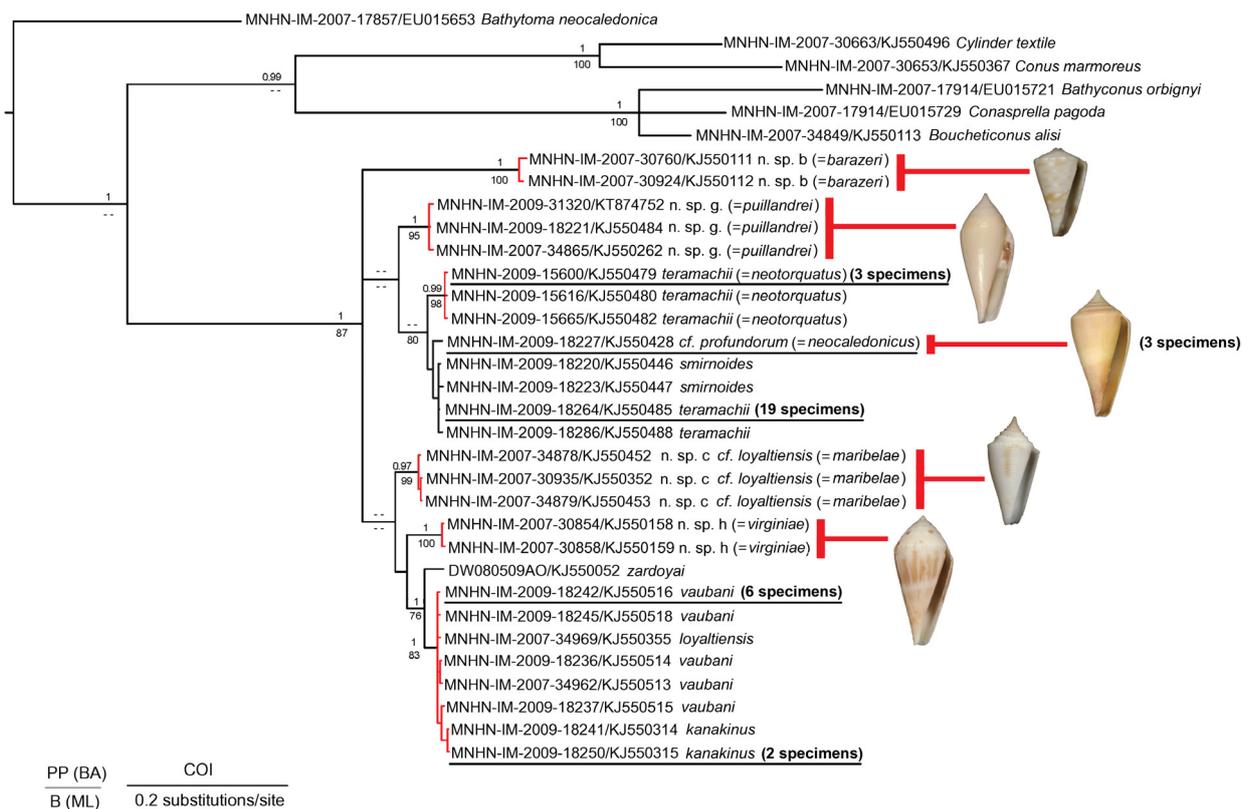


Fig. 5. Likelihood phylogenetic tree of *Profundiconus* Kuroda, 1956 based on a subsample of the mitochondrial *cox1* dataset produced by Puillandre *et al.* (2014). Posterior probabilities and bootstrap values are indicated for each node (when PP \geq 0.95% and BP \geq 75%, respectively). For clarity purposes, external branches of phylogenetically highly supported species are highlighted in red in the consensus tree. *Cox1* sequences are labelled using the MNHN voucher identification number, the Genbank accession number (when available), the species name and the number of specimens (or identical haplotypes) when greater than 1.

South New Caledonia). The group of specimens from the Solomon Islands labelled as “*Profundiconus* n. sp. cf. *loyaltiensis*” was monophyletic and highly supported by BA and ML analyses (PP = 0.97; BP = 99). If we assume that the specimens from New Caledonia are the genuine representatives of a population of the taxon *P. loyaltiensis*, we have to postulate that the specimens from the Solomon Islands belong to a separate group deserving recognition at the species level. The new species is introduced here under the name *P. maribelae* sp. nov. This taxon had previously been labelled as “*Profundiconus* n. sp. c cf. *loyaltiensis*” (Puillandre *et al.* 2014).

There are two groups containing specimens from Plateau des Chesterfield, and one with specimens from Norfolk Ridge and Loyalty Ridge, which do not match any known species of *Profundiconus* described to date. They are respectively introduced here as *P. virginiae* sp. nov., *P. barazeri* sp. nov. and *P. puillandrei* sp. nov. (previously considered in Puillandre *et al.* 2014 as “*Profundiconus* n. sp. h”, “n. sp. b” and “n. sp. g”, respectively). Additionally, we found that in spite of the lack of support at the corresponding nodes in the tree, the specimens (3 individuals sharing identical haplotype) corresponding to *P. cf. profundorum* from Norfolk Ridge exhibit significant conchological differences with the nominal taxon *P. profundorum* known from Japan and China. Based upon these constant differences and the independent branch in the tree, we describe it here as *P. neocaledonicus* sp. nov.

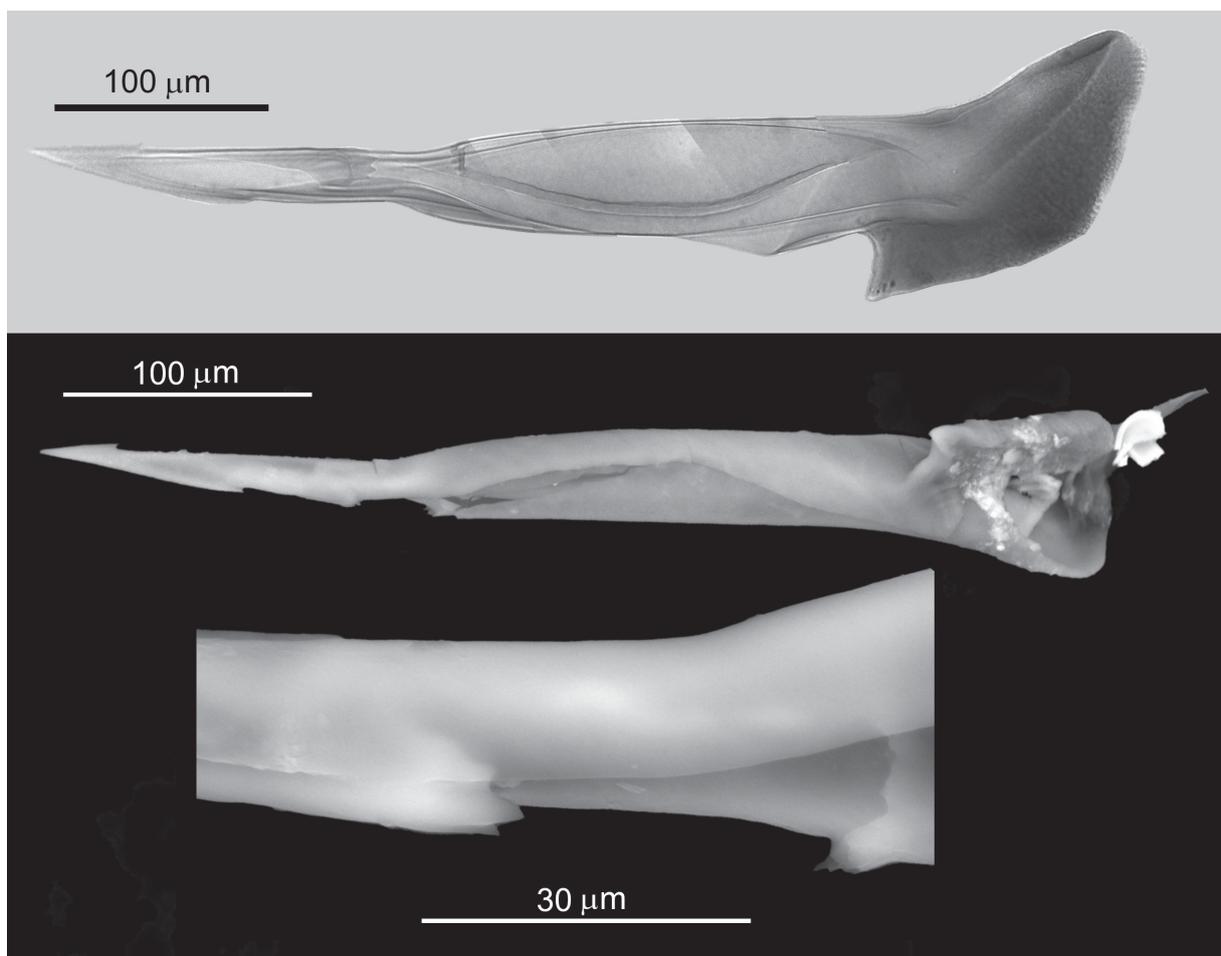


Fig. 6. Radular teeth extracted from *Profundiconus neotorquatus* (da Motta, 1984). **A.** Optical photograph (MJT coll., Mozambique, S_L 68.9 mm). **B.** SEM photograph (MNHN IM-2009-15641, South Madagascar, S_L 48.7 mm). **C.** Enlargement of the middle section of B.

Profundiconus maribelae sp. nov.

urn:lsid:zoobank.org:act:8CAB54B6-D03A-49B7-A289-3F46FCCA9366

Figs 7A–G, 8

Profundiconus n. sp. c. cf. *loyaltiensis* – Puillandre *et al.* 2014: Supplementary Material 1 (unfigured).

Etymology

This species is dedicated to Maribel Albarrán Quintanilla, wife of the first author and a shell-lover, in recognition for her support and constant encouragement to the first author at all times.

Type material examined

Holotype

SOLOMON ISLANDS: 27.5 × 12.6 mm, R/V *Alis*, SALOMONBOA 3 Expedition, st. CP 2767, Guadalcanal, 9°19' S, 160°6' E, 416–425 m (MNHN IM-2007-34878; Fig. 7A; GenBank accession number (*cox1* sequence): KJ550452).

Paratypes

SOLOMON ISLANDS: 30.0 × 12.5 mm, R/V *Alis*, SALOMON 2 Expedition, st. CP 2207, NW Isabel, 7°43' S, 158°29' E, 336–341 m (MNHN IM-2007-30935; paratype 1; Fig. 7B; GenBank accession number (*cox1* sequence): KJ550352); 30.4 × 13.1 mm, R/V *Alis*, SALOMON 2 Expedition, st. CP 2247, NW Isabel, 7°45' S, 156°25' E, 686–690 m (MNHN IM-2007-30338; paratype 2; Fig. 7C); 27.2 × 12.4 mm (broken shell), R/V *Alis*, SALOMONBOA 3 Expedition, type locality, 416–425 m (MNHN IM-2007-34880; paratype 3; Fig. 7E).

Type locality

SOLOMON ISLANDS: Guadalcanal, 9°19' S, 160°6' E, 416–425 m (SALOMONBOA 3 st. CP 2767).

Other material examined

SOLOMON ISLANDS: 31.5 × 14.4 mm, R/V “*Alis*”, SALOMONBOA 3 Expedition, type locality (MNHN IM-2007-34879; Fig. 7F; GenBank accession number (*cox1* sequence): KJ550352). Note: This specimen was photographed (<http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34879>) and sequenced, but the shell was destroyed in the process and is no longer available.

Description

Morphometric parameters: $S_L = 27\text{--}32$ mm; $RD = 0.55\text{--}0.62$; $RSH = 0.21\text{--}0.26$; $PMD = 0.89\text{--}0.93$.

Shell moderately small. Maximum length 31.5 mm. Shell profile conical, with straight to very slightly convex sides and spire moderate to high. Spire profile straight, stepped. Paucispiral protoconch with 1.5–1.75 whorls, brownish, glossy and translucent (Fig. 7D). Teleoconch whorls stepped, ridged with small but strong nodules which persist in shoulder in most cases. Sutural ramp concave, with subsutural ridge and 3 to 4 strong spiral cords crossed by thin radial threads. Shoulder carinated, most often covered with small nodules along shoulder angle. Early teleoconch whorls pure white. Late teleoconch whorls in vicinity of shoulder area may exhibit some small, irregular brown blotches. Last whorl with grooves forming flat spiral ribbons, which may extend from shoulder to base. In some specimens sculpture of grooves and flat spiral ribbons in last whorl reduced to subshoulder area and basal half. Ground colour white overlaid with sparse brown, axially arranged flammules or blotches. White ground colour predominates in all specimens studied. Columella and aperture white. Anal notch shallow. Periostracum yellow-brown, thin and translucent. Operculum present, serrated on left border.

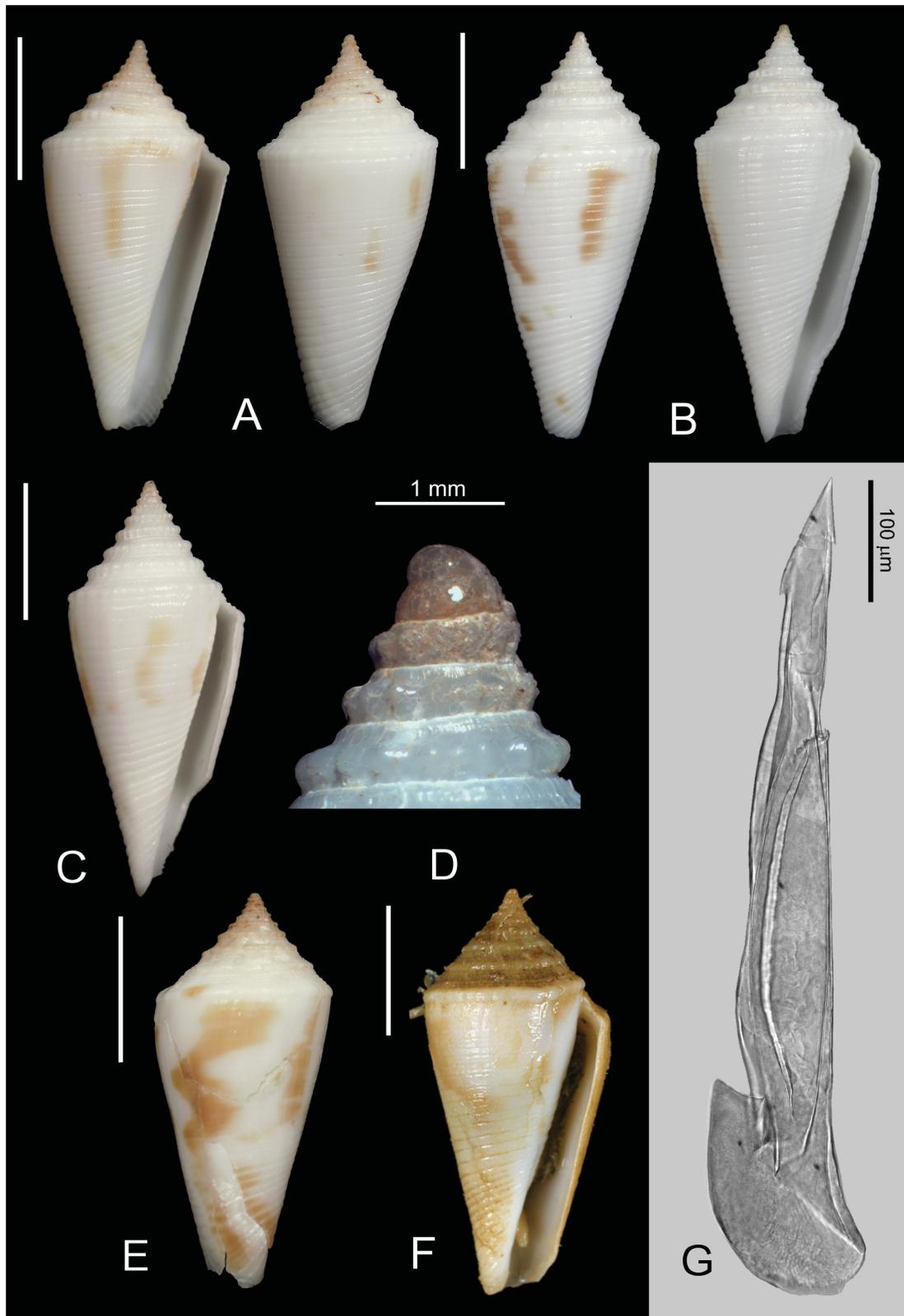


Fig. 7. *Profundiconus maribelae* sp. nov. **A.** Holotype, 27.5 × 12.6 mm. **B.** Paratype 1, 30.0 × 12.5 mm. **C.** Paratype 2, 30.4 × 13.1 mm. **D.** Paratype 2, enlargement of the spire. **E.** Paratype 3 (broken shell), 27.2 × 12.4 mm. **F.** Sequenced specimen (MNHN IM-2007-34879), 31.5 × 14.4 mm. **G.** Radular tooth from paratype 1. Scale bars = 10 mm unless otherwise indicated.

Radular teeth examined in paratype 1 (Fig. 7G). 38 teeth in radular sac. Radular tooth medium-sized, its total length relative to shell length $S_L/T_L = 45$. Anterior portion much shorter than posterior section of tooth ($T_L/AP_L = 3.43$). With one barb and pointed, well-defined blade which covers 50% of anterior portion of tooth. With external cusp located at approximately lower quarter of anterior portion of tooth, extending between 75% and 90% of length of anterior portion of tooth. External cusp laterally expanded and serrated, with 5 small denticles. Immediately below waist with characteristic fringe composed of closely spaced projections pointing towards apex. Shaft fold present. Large and prominent basal spur present on top of slanted base of tooth.

Distribution and habitat

Known from the Solomon Islands, including the New Georgia Group (Vella Lavella Island), Santa Isabel and Guadalcanal, at depths between 336 and 690 m (Fig. 8).

Remarks

The specimens of *P. maribelae* sp. nov. from the Solomon Islands form a monophyletic group supported by BI and ML analyses. *P. maribelae* sp. nov. was initially referred to as *P. cf. loyaltiensis* in the phylogenetic analysis, given the resemblance of its shell to that of *P. loyaltiensis*, a species known only from New Caledonia (Fig. 1H). However, the shell of *P. maribelae* sp. nov. attains a larger size (27–32 mm for *maribelae* vs. 21.5–26 mm for *loyaltiensis*). The spire outline in *P. maribelae* sp. nov. is straight rather than deeply concave as occurs in *P. loyaltiensis*. The sculpture of flat spiral ribbons in the last whorl is much more developed in *P. maribelae* sp. nov. than in *P. loyaltiensis*. The most evident difference between the two species is that the shell of *P. loyaltiensis* is white and patternless, whereas the shell of *P. maribelae* sp. nov. exhibits a pattern of sparse, axially arranged brown flammules or blotches. The morphology of the radular teeth of *P. maribelae* sp. nov. and *P. loyaltiensis* is very similar, but they

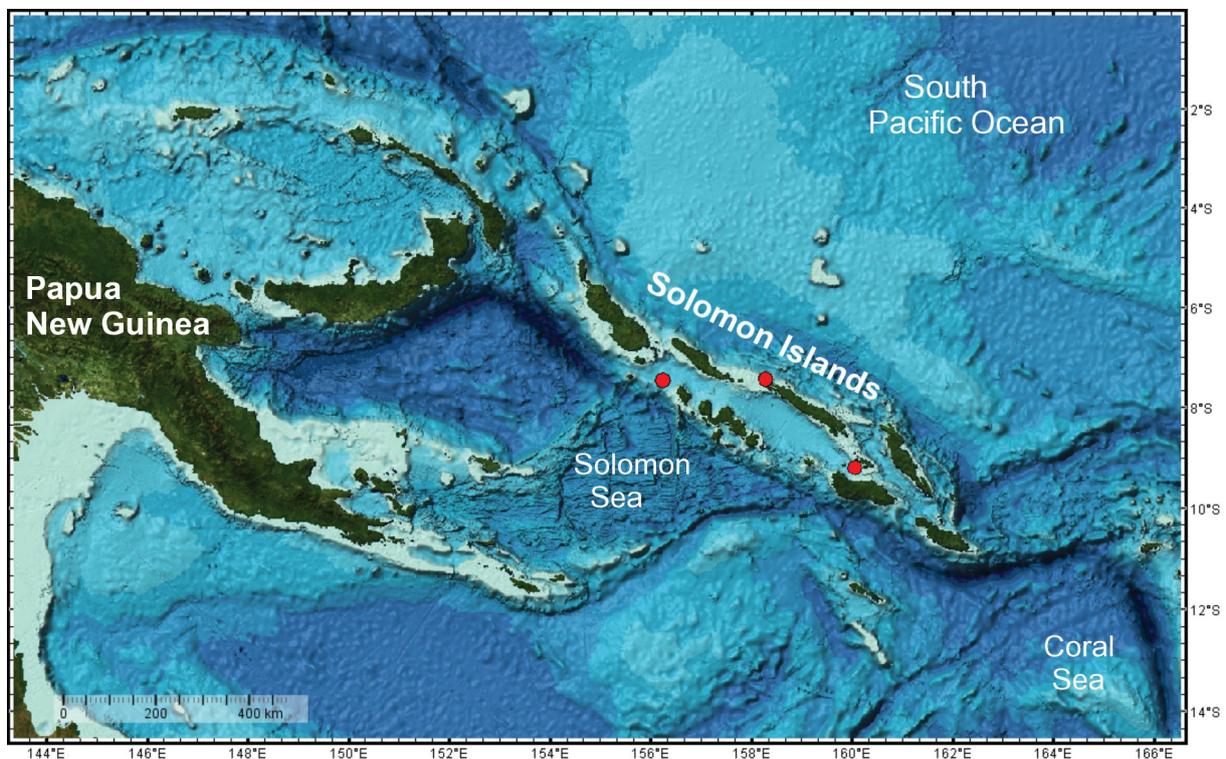


Fig. 8. Distribution map for *Profundiconus maribelae* sp. nov. Red circles indicate the points where the species has been collected.

differ in their relative sizes, being larger in *P. loyaltiensis* ($S_L/T_L = 30\text{--}37$; versus 45 for *P. maribelae* sp. nov.). The shell of *P. teramachii* (Fig. 1B) is easily separated from that of *P. maribelae* sp. nov. by its much larger size, its pale, straw-yellow, patternless shell, smooth sculpture of the last whorl, usually much less developed nodules, absence of strong cords on the sutural ramp, and by its multispiral instead of paucispiral protoconch. *P. maribelae* sp. nov. is distantly related to both *P. loyaltiensis* and *P. teramachii* in the phylogeny presented here.

***Profundiconus virginiae* sp. nov.**

[urn:lsid:zoobank.org:act:1785F28A-89FA-40FC-B28A-68E828B3F0A9](https://doi.org/10.1785F28A-89FA-40FC-B28A-68E828B3F0A9)

Figs 9A–D, G, 10

Profundiconus n. sp. h – Puillandre *et al.* 2014: Supplementary Material 1 (unfigured).

Profundiconus cf. *cakobau* – Tenorio 2015a: 37 (unfigured; non *Conus cakobau* Moolenbeek, Röckel & Bouchet, 2008).

Etymology

This species is dedicated to Virginie Héros, assistant curator of molluscs at the Muséum national d'Histoire naturelle of Paris (MNHN) and an experienced member of the numerous collecting expeditions carried out by this institution. Her contribution to our knowledge of the New Caledonian deep-water cones is recognised by naming this remarkable new species of *Profundiconus* after her.

Material examined

Holotype

NEW CALEDONIA: 42.5 × 19.4 mm, R/V *Alis*, EBISCO Expedition, st. DW 2613, Plateau des Chesterfield, 19°37' S, 158°42' E, 519–522 m (MNHN IM-2007-30854; Fig. 9A; GenBank accession number (*cox1* sequence): KJ550158).

Paratypes

NEW CALEDONIA: 33.3 × 16.5 mm, R/V *Alis*, EBISCO Expedition, type locality, 431–436 m (MNHN IM-2007-30858; paratype 1; Fig. 9B; GenBank accession number (*cox1* sequence): KJ550159); 16.3 × 13.0 mm, R/V *Alis*, EBISCO Expedition, st. DW 2610, Plateau des Chesterfield, 19°34' S, 158°41' E, 486–494 m (MNHN IM-2000-30789; paratype 2; Fig. 9D; fragment of the spire, well preserved).

Type locality

NEW CALEDONIA: Coral Sea, Plateau des Chesterfield, 19°37' S, 158°42' E, 519–522 m (EBISCO st. DW 2613).

Description

Morphometric parameters: $S_L = 33\text{--}43$ mm; $RD = 0.59\text{--}0.63$; $RSH = 0.21\text{--}0.23$; $PMD = 0.82\text{--}0.83$.

Shell moderately small to medium sized. Maximum length 42.5 mm. Shell profile ventricosely conical, with spire moderate to high. Spire profile sigmoid. Multispiral protoconch with 3–3.5 whorls, white, glossy and translucent (Fig. 9C). Early 4–5 teleoconch whorls stepped, ridged with small nodules which tend to disappear after fifth whorl. Sutural ramp flat to slightly concave, with 3 to 6 fine spiral cords becoming obsolete in late spire whorls. Shoulder subangulate, forming characteristic ridge, covered with axial costae on last whorl. Early teleoconch whorls creamy white with brown spiral band on periphery, extending over row of nodules. On later whorls, this brown band interrupted by white areas. Spire creamy white with sparse, small brown blotches in areas near suture. Last whorl smooth or with very fine striae and with spiral ribs on basal third. Ground colour creamy white overlaid with orange-brown

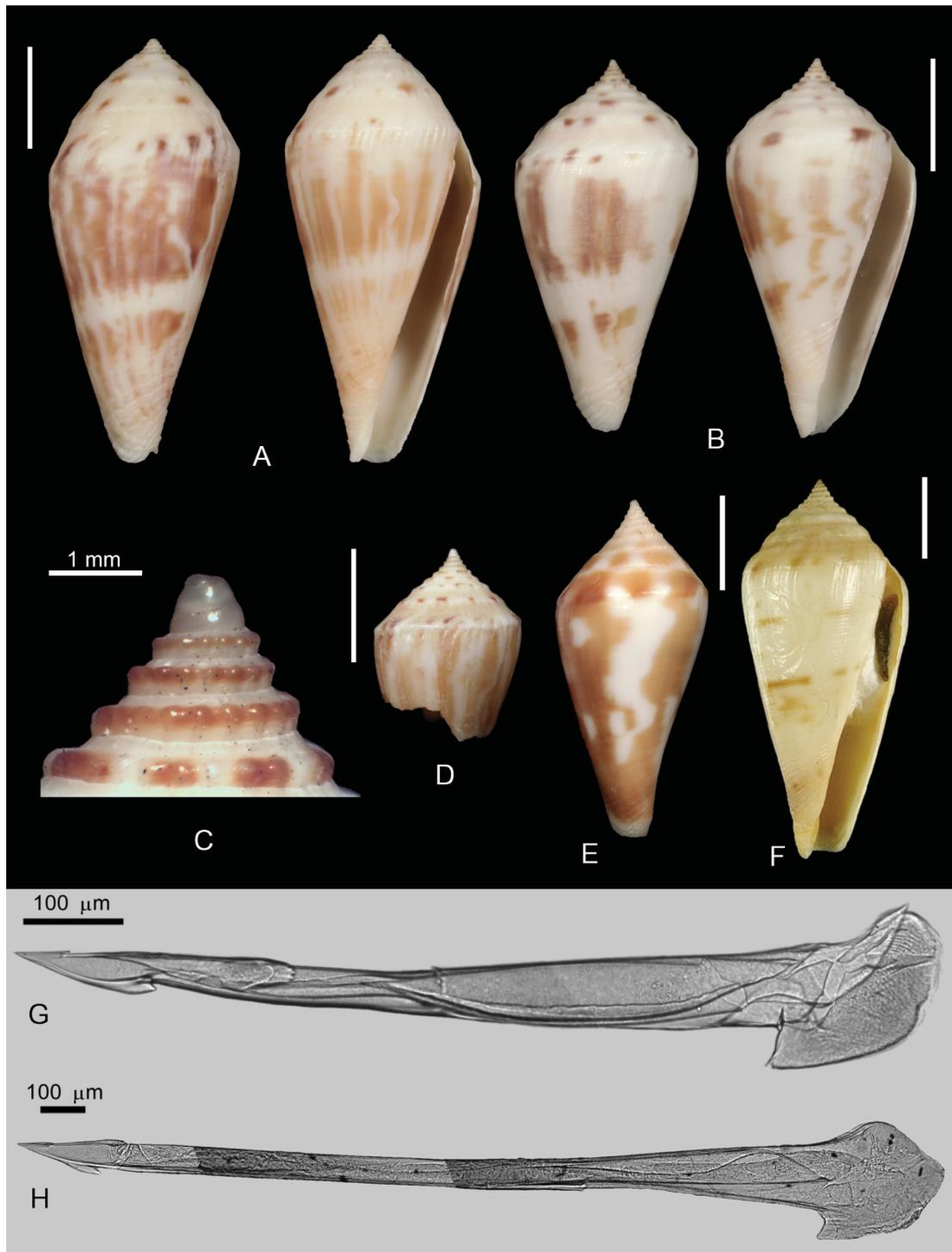


Fig. 9. — **A–D.** *Profundiconus virginiae* sp. nov. **A.** Holotype, 42.5 × 19.4 mm. **B.** Paratype 1, 33.3 × 16.5 mm. **C.** Paratype 1, enlargement of the spire. **D.** Paratype 2 (fragment), 16.3 × 13.0 mm. — **E.** *Profundiconus* cf. *cakobau* Moolenbeek *et al.*, 2008 (MJT coll., Balut Is., Mindanao, Philippines, 450–500 m), 35.8 × 16.3 mm. — **F.** *Profundiconus fraussen* (Tenorio & Poppe, 2004) (holotype, NMP, Aliguay Island, Philippines, 100–150 m), 47.0 × 21.0 mm. — **G.** Radular tooth of *Profundiconus virginiae* sp. nov. from the holotype. — **H.** Radular tooth, *Profundiconus smirnooides* Tenorio, 2015 (MNHN IM-2000-30058, Norfolk Ridge, New Caledonia), S_L 81.4 mm. Scale bars = 10 mm unless otherwise indicated.

to purplish brown, irregular blotches or axially arranged flammules, interrupted by ground-colour band at midbody. Columella white. Aperture creamy white. Anal notch shallow. Periostracum and operculum not observed.

Radular teeth examined in holotype (Fig. 9G) and in paratype 1. 48 to 53 teeth in radular sac. Radular tooth medium to large-sized, its total length relative to shell length $S_L/T_L = 37\text{--}45$, rather elongated. Waist poorly defined. Anterior portion shorter than posterior section of tooth ($T_L/AP_L = 2.61\text{--}2.70$). With one barb and pointed, well-defined blade which covers 40–43% of anterior portion of tooth. With external cusp located at approximately lower third of anterior portion of tooth, extending between 60% and 81% of length of anterior portion of tooth. External cusp laterally expanded and serrated, with 5–6 small denticles. With characteristic fringe of closely spaced projections pointing towards apex located immediately below waist. Shaft fold present. Large and prominent basal spur on top of slanted base of tooth.

Distribution and habitat

Only known from the Coral Sea, Plateau des Chesterfield area, New Caledonia (Fig. 10).

Remarks

Profundiconus virginiae sp. nov. was initially misidentified as *P. smirnoides* (Fig. 1D). The latter has a fusiform shell, larger in size ($S_L = 52\text{--}98$ mm; versus 33–43 mm), more slender ($RD = 0.46\text{--}0.56$; versus 0.59–0.63) and with a higher spire ($RSH = 0.25\text{--}0.36$; versus 0.21–0.23) than *P. virginiae* sp. nov. The shell of *P. smirnoides* has a pattern consisting of a brown spiral band on each side of centre, interrupted by creamy white axial streaks, but lacks the axial costae on the ridge. The radular teeth of *P. virginiae* sp. nov. and *P. smirnoides* also differ. The latter has a very elongated radular tooth (Fig. 9H), with the

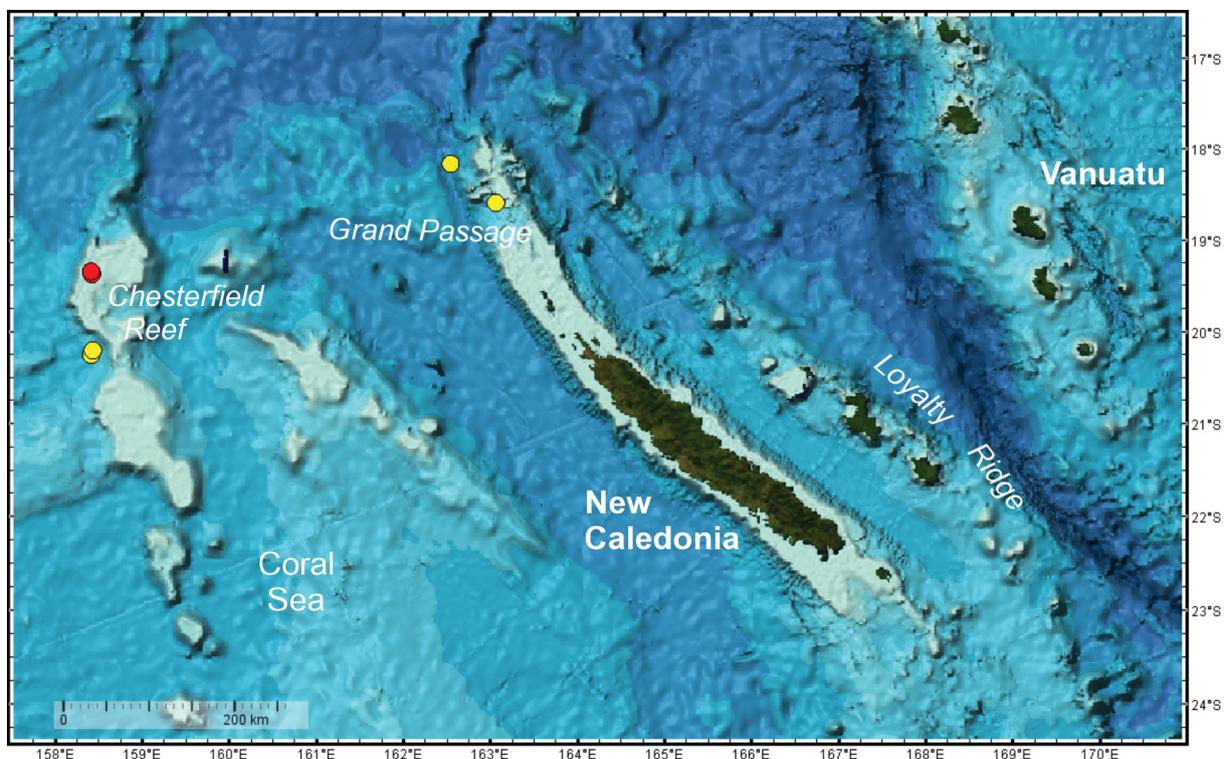


Fig. 10. Distribution map for *Profundiconus virginiae* sp. nov. (red circles) and *P. barazeri* sp. nov. (yellow circles). Symbols indicate the points where each of the species have been collected.

anterior and posterior sections difficult to separate (Tenorio 2015b). Still, the anterior section of the tooth in adult *P. smirnoides* is longer than the posterior section ($T_L/AP_L = 1.7-1.8$). The strongly pointed blade covers less than 25% of the anterior section. The external cusp is pointed, not expanded laterally and is not serrated, in contrast to *P. virginiae* sp. nov. Interestingly, in *P. smirnoides* the external cusp occupies a very high position in the anterior section, extending from 20 to 30% of its length (i.e., almost the same position as the blade, but with a different orientation).

P. virginiae sp. nov. resembles no other species of *Profundiconus*. Although only two live-taken specimens and the spire of a broken shell of this species have been examined, their shell and radula features, as well as the phylogenetic analysis, warrant its description as a new species. Apart from *P. smirnoides*, *P. virginiae* sp. nov. can be compared to *P. vaubani* from New Caledonia (Fig. 1I), and to *P. cakobau* from the Fiji Islands (Fig. 1K) and *P. cf. cakobau* (Fig. 9E) from the Philippines. *P. vaubani* also has axial costae and brown elements on the shell pattern. However, its paucispiral protoconch readily separates this species from *P. virginiae* sp. nov., which has a multispiral protoconch and appears rather distant from *P. vaubani* on the tree shown in Fig. 5. *P. cakobau* and *P. cf. cakobau* exhibit a shell pattern similar to that of *P. virginiae* sp. nov., including the brown spiral band on the periphery of the early teleoconch whorls extending over the row of nodules. However, both have a paucispiral protoconch instead of multispiral, and both lack the characteristic axial costae present in *P. virginiae* sp. nov. at the shoulder ridge. The elusive species *P. frausseni* (Tenorio & Poppe, 2004) (Fig. 9F), known only from a few specimens collected in the Philippines, has a protoconch and early teleoconch resembling that of *P. virginiae* sp. nov. However, the multispiral protoconch is white in *P. virginiae* sp. nov., but cream-coloured in *P. frausseni* (Tenorio & Poppe 2004). The latter is lower spired (RSH = 0.19–0.21; versus 0.21–0.23) and more conical (PMD = 0.87–0.89; versus 0.82–0.83) than *P. virginiae* sp. nov. Cords on the teleoconch whorls of *P. frausseni* are more developed, whereas they become obsolete on the late whorls in *P. virginiae* sp. nov. The shoulder in *P. frausseni* is rounded (subangulate in juvenile specimens), whereas in *P. virginiae* sp. nov. it is subangulate and ridged, covered with axial costae which are absent in *P. frausseni*. The scarce number of specimens of *P. virginiae* sp. nov. available prevented any statistical comparison of shell morphometry among different taxa. The two individuals of *P. virginiae* sp. nov. form a monophyletic group in the phylogeny that is the sister group of *P. zardoyai*, *P. vaubani*, *P. loyalti* and *P. kanakinus*.

***Profundiconus barazeri* sp. nov.**

[urn:lsid:zoobank.org:act:3D0659AE-4433-41C4-B03A-BFED9523E1EE](https://doi.org/10.3896/BI.2015.523E1EE)

Figs 10, 11A–G, K

Profundiconus n. sp. b – Puillandre *et al.* 2014: Supplementary Material 1 (unfigured).

Etymology

At the request of Prof. Philippe Bouchet from MNHN, this new species is named after Captain Jean-François Barazer, first captain on IRD's research vessel *Alis*, in recognition of his dedication to, and expertise in, deep-sea exploration in the South and West Pacific. Many new species have been discovered during the cruises that he has skilfully commanded.

Material examined

Holotype

NEW CALEDONIA: 11.6 × 7.0 mm, R/V *Alis*, EBISCO Expedition, st. DW 2564, NW Bellona Reef, Plateau des Chesterfield, 20°25' S, 158°41' E, 333–386 m (MNHN IM-2007-30760; Fig. 11A; GenBank accession number (*cox1* sequence): KJ550111).

Paratypes

NEW CALEDONIA: 14.5 × 8.6 mm, collecting data as for holotype (MNHN IM-2007-30924; paratype 1; Fig. 11B; GenBank accession number (*cox1* sequence): KJ550112); 16.5 × 9.9 mm, R/V *Alis*, EBISCO Expedition, st. DW 2576, N Bellona Reef, Chesterfield, 20°20' S, 158°43' E, 390–394 m (MNHN IM-2000-30790; paratype 2; Fig. 11C); 10.3 × 6.2 mm, R/V *Alis*, CONCALIS Expedition, st. DW 2985, Grand Passage, Northern New Caledonia, 18°59' S, 163°06' E, 277–289 m (MNHN IM-2000-30791; paratype 3; Fig. 11D); 10.6 × 5.5 mm, collecting data as for preceding (MNHN IM-2000-30792; paratype 4; Fig. 11E); 10.5 × 5.6 mm, R/V *Alis*, CONCALIS Expedition, st. DW 2979, Grand Passage, N New Caledonia, 18°16' S, 162°54' E, 350 m (MNHN IM-2000-30777; paratype 5; Fig. 11G).

Type locality

NEW CALEDONIA: Coral Sea, NW Bellona Reef, Plateau des Chesterfield, 20°25' S, 158°41' E, 333–386 m (EBISCO st. DW 2564).

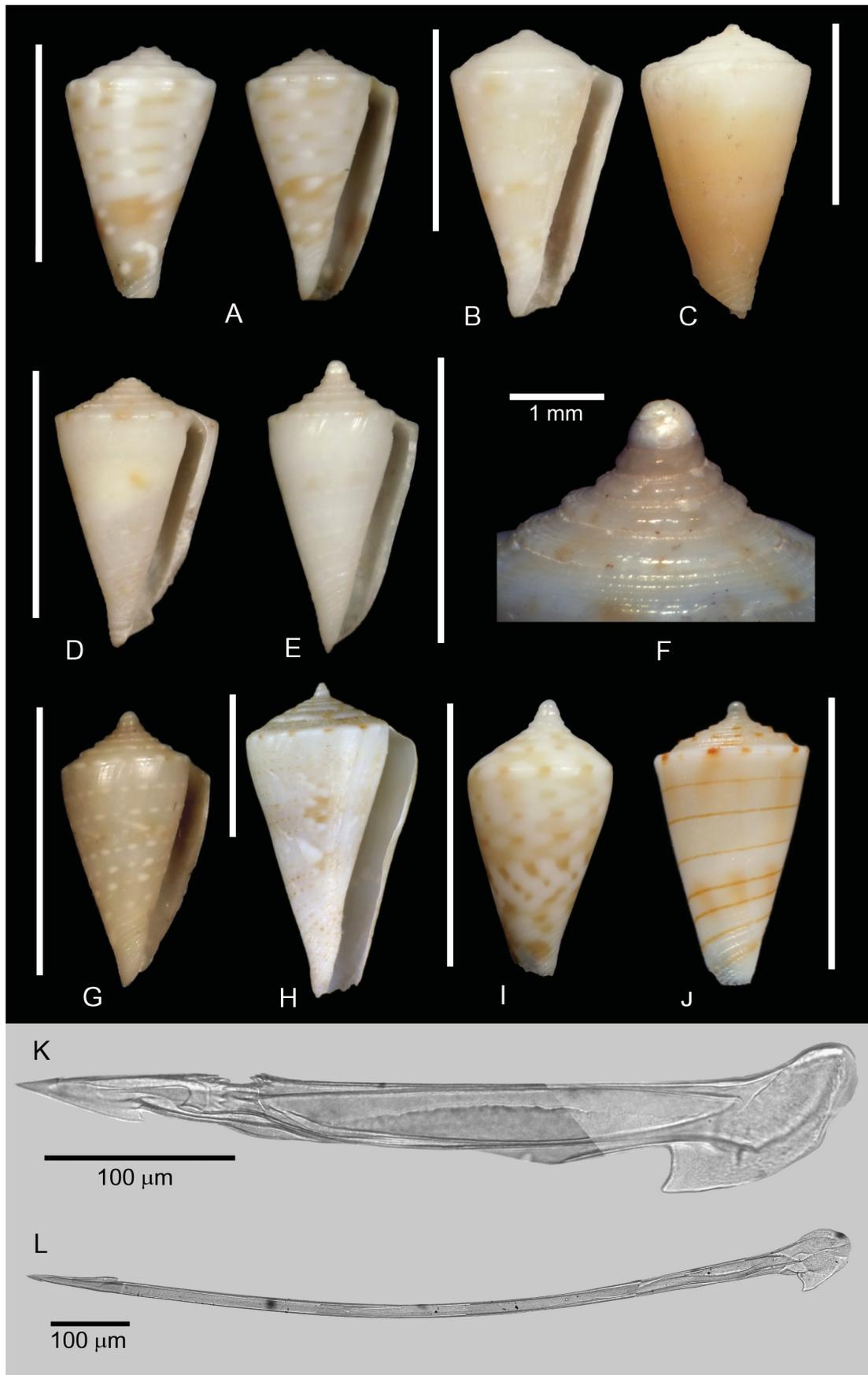
Description

Morphometric parameters: $S_L = 10\text{--}15$ mm; $RD = 0.63\text{--}0.69$; $RSH = 0.11\text{--}0.19$; $PMD = 0.90\text{--}0.95$.

Shell very small (maximum length 16.5 mm). Shell profile conical, with spire low to moderate in height. Spire profile straight. Shoulder angulated, with distinct rim. Last whorl with straight sides, smooth, with some grooves in basal quarter, which appears slightly deflected to the left. Protoconch white, porcellaneous, with 1.5 whorls (Fig. 11F). Early teleoconch whorls with small nodules which are lost after whorl 3. Sutural ramp flat to slightly concave, slightly stepped, bearing 3–5 strong cords, with smooth ridge above suture. Spire white, with yellow-brown blotches on ridge above suture. Ground colour pale orange-brown to creamy white. Last whorl with pattern of pure white dashes and dots arranged in spiral lines, often alternating with dashes of orange-brown. Sparse small, diffuse rounded, orange-brown spots occasionally present. Holotype just below midbody with orange-brown narrow band overlaid with white dashes arranged in spiral, absent in other specimens examined, some of which are patternless. Columella and aperture white.

Radular tooth examined in holotype (Fig. 11K) and paratype 1. 45 teeth in radular sac. Radular tooth of rather large relative size: its total length relative to shell length $S_L/T_L = 26\text{--}30$. Anterior portion much shorter than posterior section of tooth ($T_L/AP_L = 3.7\text{--}3.8$). With one barb and pointed, well-defined blade, which covers 48–61% of apical portion of tooth. External cusp present, extending between 80 and 96% of length of anterior portion of tooth. External cusp laterally widened and serrated, with 7–9 small denticles. Large adapical opening occupying most of anterior portion of tooth ($100AO_L/AP_L = 64\text{--}70$). With characteristic fringe of closely spaced projections pointing towards the apex located immediately below waist. Shaft fold present. Large and prominent basal spur on top of slanted base of tooth.

Fig. 11. [opposite page]—**A–G.** *Profundiconus barazeri* sp. nov. **A.** Holotype, 11.6 × 7.0 mm. **B.** Paratype 1, 14.5 × 8.6 mm. **C.** Paratype 2, 16.5 × 9.9 mm. **D.** Paratype 3, 10.3 × 6.2 mm. **E.** Paratype 4, 10.6 × 5.5 mm. **F.** Paratype 5, enlargement of the spire. **G.** Paratype 5, 10.5 × 5.6 mm. — **H.** *Boucheticonus alisi* (Moolenbeek *et al.*, 1995) (holotype, MNHN IM-2000-2588, Norfolk Ridge, New Caledonia, 330–367 m), 22.2 mm. — **I.** *Profundiconus zardoyai* Tenorio, 2015 (holotype, MNHN IM-2000-28206, Grand Passage, New Caledonia, 325–330 m), 10.5 mm. — **J.** *Continuconus estivali* (Moolenbeek & Richard, 1995) (holotype, MNHN IM-2000-2566, Plateau des Chesterfield, New Caledonia, 400 m), 10.5 mm. — **K.** Radular tooth of *Profundiconus barazeri* sp. nov. from the holotype. — **L.** Radular tooth, *Boucheticonus alisi* (Moolenbeek *et al.*, 1995) (Atheris voucher DW080502AD, New Caledonia), S_L 19.0 mm. Scale bars = 10 mm unless otherwise indicated.



Distribution and habitat

Specimens from two separate populations in New Caledonia are known: from NW Bellona Reef, Plateau des Chesterfield (type locality), and from the Grand Passage area; at depths from 277 to 350 m (Fig. 10).

Remarks

P. barazeri sp. nov. resembles in general aspect a small specimen of *Boucheticonus alisi* (Fig. 11H). The latter has a larger shell, variably patterned, with a multispiral protoconch, which exhibits a characteristic brown blotch. The protoconch is paucispiral in *P. barazeri* sp. nov. These two species are phylogenetically distant (Fig. 5) and have very different radular morphologies. In contrast to the tooth of *P. barazeri* sp. nov., the radular tooth of *B. alisi* (Fig. 11L) is very large and elongated, with an extremely long anterior section that is more than four times longer than the posterior section of the tooth. It has a small and indistinct barb opposite a blade, which is enlarged and widened laterally. *P. barazeri* sp. nov. shows some similarities to *P. zardoyai* (Fig. 11I) and to *Continuconus estivali* (Moolenbeek & Richard, 1995) (Fig. 11J). The scarce specimens available of the latter species come from the Chesterfield Reef area. *C. estivali* is also characterized by its small size and conical shape. However, the pattern of *C. estivali* is quite constant and consists of 6 to 8 fine brown spiral lines on a white background. The shoulder in *C. estivali* is sharply angulated to carinate instead of angulated, and the teleoconch whorls on its stepped spire are concave. *P. barazeri* sp. nov. lacks the large, globose protoconch of about 2 whorls, which constitutes one of the most relevant features of *C. estivali*. The species *P. zardoyai*, recently described from Grand Passage, North New Caledonia, has a similar size and ground colour, with a variable pattern. However, its shell usually has a higher spire (RSH = 0.14–0.23 versus 0.11–0.19 for *barazeri*) of sigmoid profile rather than straight. Although their radular teeth look superficially similar, the tooth of *P. barazeri* sp. nov. (Fig. 11K) has a larger relative size ($S_L/T_L = 26\text{--}30$ versus $33\text{--}40$ for *zardoyai*) and bears more denticles in the laterally widened external cusp (7–9 in *barazeri* sp. nov. versus 5–6 in *zardoyai*). *P. zardoyai* and *P. barazeri* sp. nov. are phylogenetically distant (Fig. 5).

Profundiconus puillandrei sp. nov.

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Figs 12A–J, 13A–D, 14

Conus ikedai – Poppe 2008: pl. 615, fig. 1a–b (non *C. ikedai* Ninomiya, 1987).

Conus smirna – Marshall 1981: 499, fig. 3j (non *C. smirna* Bartsch & Rehder, 1943).

Conus sp. C – Röckel *et al.* 1995b: 585, fig. 49.

Profundiconus n. sp. g. – Puillandre *et al.* 2014: Supplementary Material 1 (unfigured).

Etymology

This new species is dedicated to Dr. Nicolas Puillandre, mollusc curator at the MNHN. Dr. Puillandre has a long and outstanding trajectory in the study of the phylogeny of the Conoidea. The naming of the new species after him recognises his important contributions to the taxonomy of Conoidea at the molecular level.

Type material examined

Holotype

NEW CALEDONIA: 43.2 × 18.0 mm, R/V *Alis*, NORFOLK 1 Expedition, st. DW 1707, Banc Jumeau Est, Norfolk Ridge, 23°43' S, 168°16' E, 381–493 m (MNHN IM-2000-30771; Fig. 12A).

Paratypes

NEW CALEDONIA: 39.6 × 17.3 mm, R/V *Alis*, NORFOLK 2 Expedition, st. DW 2072, Banc Aramis, Norfolk Ridge, 25°21' S, 168°57' E, 1000–1006 m (MNHN IM-2000-30772; paratype 1; Fig. 12B);

40.7 × 16.8 mm, R/V *Alis*, NORFOLK 2 Expedition, st. DW 2077, Banc Zorro, Norfolk Ridge, 25°21' S, 168°19' E, 666–1000 m (MNHN IM-2000-30773; paratype 2; Fig. 12C); 35.0 × 15.5 mm, R/V *Alis*, NORFOLK 2 Expedition, st. DW 2068, Banc Porthos, Norfolk Ridge, 25°20' S, 168°57' E, 680–980 m (MNHN IM-2000-30774; paratype 3; Fig. 12D); 31.7 × 13.2 mm, R/V *Alis*, NORFOLK 2 Expedition, st. DW 2066, Banc Athos, Norfolk Ridge, 25°17' S, 168°55' E, 834–870 m (MNHN IM-2000-30775; paratype 4; Fig. 12E, H); 43.6 × 18.1 mm, R/V *Alis*, NORFOLK 2 Expedition, st. DW 2074, Banc Zorro, Norfolk Ridge, 25°24' S, 168°20' E, 623–691 m (MNHN IM-2000-30776; paratype 5; Fig. 12F); 57.3 × 24.6 mm, R/V *Alis*, EXBODI Expedition, st. DW 3907, Récifs de l'Astrolabe-Nord Ouest, 19°50' S, 165°33' E, 608–671 m (MNHN IM-2009-31320; paratype 6; Fig. 12G; GenBank accession number (*cox1* sequence): KT874752); 45.2 × 18.5 mm, R/V *Alis*, NORFOLK 2 Expedition, st. DW 2054, Banc Jumeau Est, Norfolk Ridge, 23°40' S, 168°15' E, 736–800 m (MNHN IM-2000-30778; paratype 7; Fig. 12I); 44.8 × 18.2 mm, R/V *Alis*, BATHUS 3 Expedition, st. DW 776, Loyalty Ridge, 24°44' S, 170°08' E, 770–830 m (MNHN IM-2000-30779; paratype 10); 49.9 × 21.6 mm, R/V *Alis*, TERRASSES Expedition, st. DW 3045, Mont J, Ride des Loyautés, 23°48' S, 169°46' E, 660–710 m (MNHN IM-2009-18221; paratype 11; GenBank accession number (*cox1* sequence): KJ550484); 37.0 × 17.2 mm, R/V *Alis*, BATHUS 3 Expedition, st. DW 776, Loyalty Ridge, 24°44' S, 170°08' E, 770–830 m (MNCN 15.05/60171; paratype 12).

NEW ZEALAND: 38.9 × 17.5 mm, R/V *Tangaroa*, st. K861, Kermadec Ridge, 30°36.5' S, 178°22.5' W, 1030 m (NIWA 99587; paratype 8; Fig. 12J); 44.9 × 19.5 mm, R/V *Tangaroa*, st. K831, Kermadec Ridge, 29°51.5' S, 178°10.5' W, 965 m (NIWA 99588; paratype 9).

Type locality

NEW CALEDONIA: Banc Jumeau Est, Norfolk Ridge, 381–493 m, 23°43' S, 168°16' E (NORFOLK 1 st. DW1707).

Other material examined

NEW CALEDONIA: 33.2 × 14.8 mm, R/V “Alis”, NORFOLK 2 Expedition, st. DW 2057, Banc Introuvable, Norfolk Ridge, 24°40' S, 168°39' E, 555–565 m (MNHN IM-2007-34865; GenBank accession number (*cox1* sequence): KJ550262). Note: This specimen, matching the holotype, was photographed (<http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-34865>) and sequenced, but the shell was destroyed in the process and is no longer available.

Additionally, we examined 31 more specimens from 15 uncataloged MNHN lots collected at several stations in Norfolk Ridge and Loyalty Ridge, New Caledonia, by the R/V “Alis” in the course of several campaigns. Several specimens of shells in private collections collected in Balut Is., Philippines at 100–150 m, showing the conchological features of *Profundiconus puillandrei* sp. nov., were also examined.

Description

Morphometric parameters: $S_L = 29\text{--}57$ mm; $RD = 0.53\text{--}0.62$; $RSH = 0.22\text{--}0.29$; $PMD = 0.81\text{--}0.90$.

Shell moderately small to medium sized (maximum length 57.0 mm). Shell profile ventricosely conical, with high spire. Spire profile sigmoid to slightly concave. Protoconch multispiral, with 3–3.5 whorls, white to yellow-brown. Last whorl of larval shell shows minute axial ridges. Early teleoconch whorls with nodules which are often indistinct after whorls 5 to 6, but may persist, forming nodulose ridge reaching shoulder on last whorl. Sutural ramp flat to slightly concave, with very fine striae and arcuate threads becoming obsolete in late whorls. Shoulder with distinct ridge, usually smooth, although nodulose or even strongly nodulose in some specimens. Last whorl with convex sides adapically, then almost straight and slightly concave abapically. Last whorl smooth or with very fine striae becoming more evident

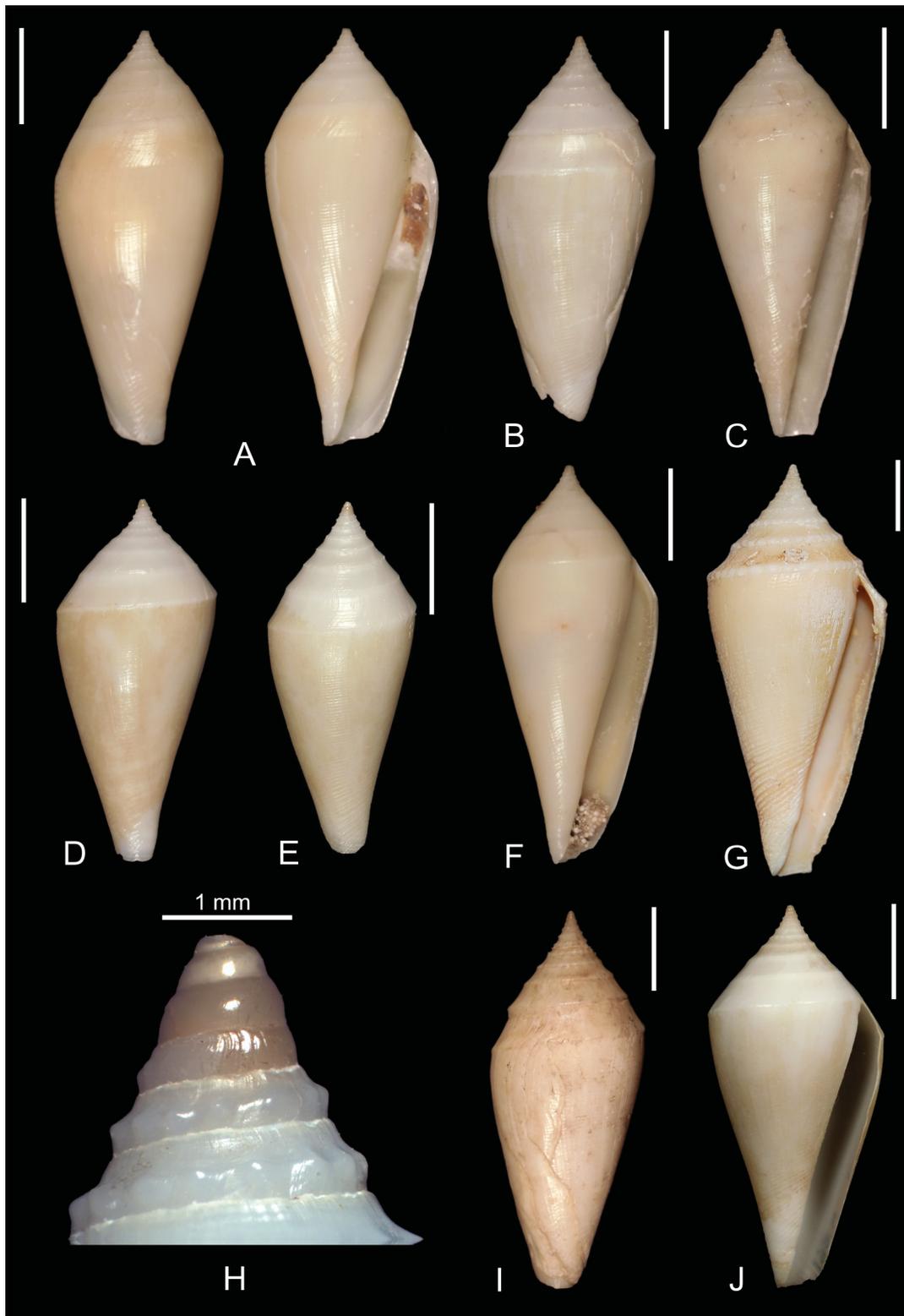


Fig. 12. *Profundiconus puillandrei* sp. nov. **A.** Holotype, 43.2 × 18.0 mm. **B.** Paratype 1, 39.6 × 17.3 mm. **C.** Paratype 2, 40.7 × 16.8 mm. **D.** Paratype 3, 35.0 × 15.5 mm. **E.** Paratype 4, 43.6 × 18.1 mm. **F.** Paratype 5, 43.6 × 18.1 mm. **G.** Paratype 6, 57.3 × 24.6 mm. **H.** Paratype 4, enlargement of the spire. **I.** Paratype 7, 45.2 × 18.5 mm. **J.** Paratype 8, 38.9 × 17.5 mm. Scale bars = 10 mm unless otherwise indicated.

towards base. Spire and last whorl patternless, white to pale straw-yellow in colour. Columella white. Aperture pale yellow or white. Periostracum yellow, thin and translucent. Operculum with serrations.

Radular tooth examined in holotype (Fig. 13A), in paratypes 3 (Fig. 13B–D), 6 and 9, and in an additional non-type specimen. 48 to 62 teeth in radular sac. Radular tooth small for size of shell: its total length relative to shell length $S_L/T_L = 75\text{--}105$. Anterior portion shorter than posterior section of tooth ($T_L/AP_L = 3.1\text{--}3.6$). With one barb and pointed blade which covers 50–62% of anterior portion of tooth. External cusp present, extending between 64 and 90% of length of anterior portion of tooth. External cusp laterally widened and serrated, with 4–5 small denticles. Large adapical opening occupying most of anterior portion of tooth ($100AO_L/AP_L = 64\text{--}75$). Fringe of closely spaced projections pointing towards apex immediately below waist. Shaft fold present. Large and prominent basal spur on top of slanted base of tooth.

Distribution and habitat

New Caledonia (Norfolk Ridge and Loyalty Ridge) and New Zealand (Kermadec Ridge), at depths from 380 to 1100 m (Fig. 14). Several empty shells matching *P. puillandrei* sp. nov. from Balut Is., Mindanao, Philippines, have been examined. The identity of these specimens from the Philippines

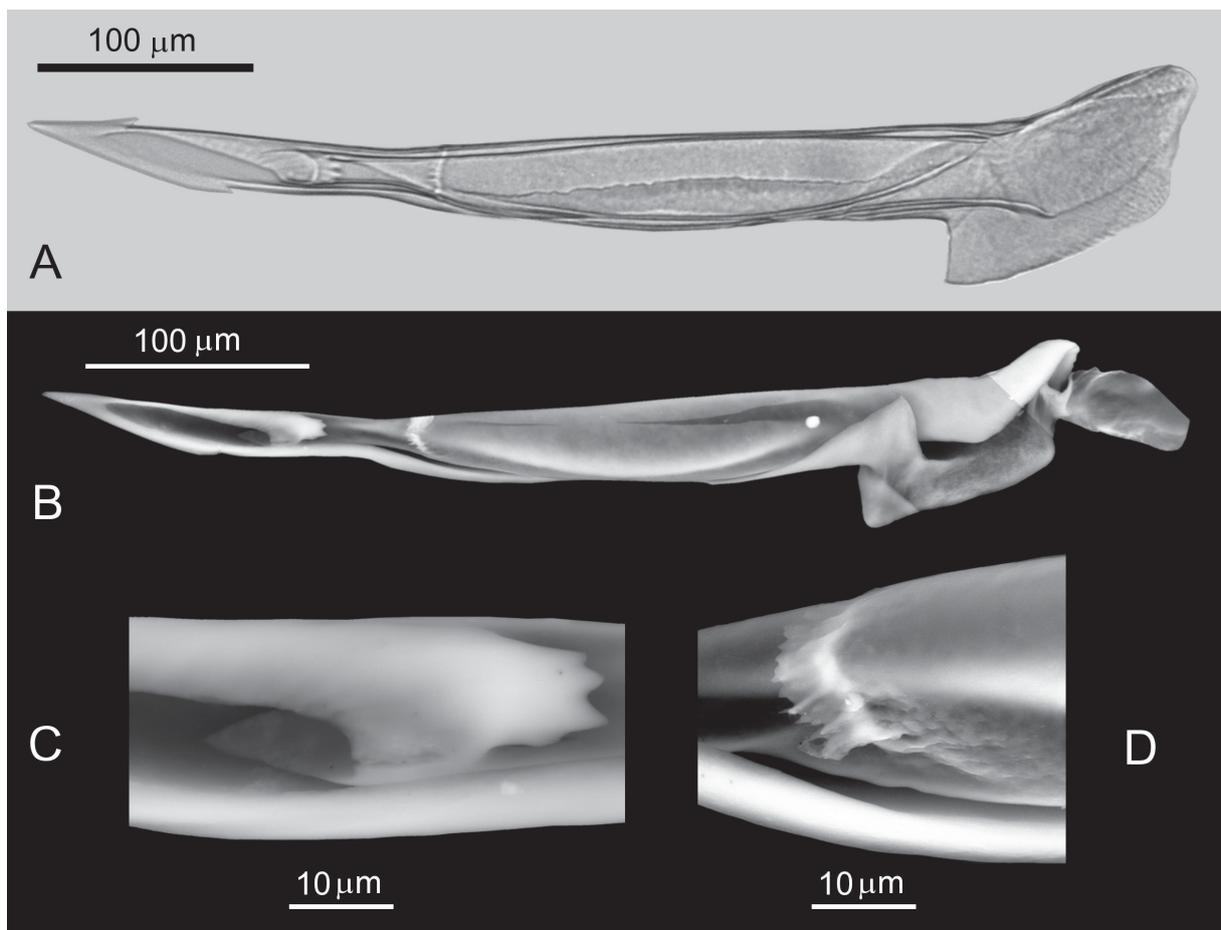


Fig. 13. Radular teeth extracted from *Profundiconus puillandrei* sp. nov. **A.** Optical photomicrograph (holotype, MNHN IM-2000-30771, S_L 43.2 mm). **B.** SEM photomicrograph (paratype 3, MNHN IM-2000-30774, S_L 35.0 mm). **C.** Enlargement of the external cusp. **D.** Enlargement of the middle section of B.

(allocated in several private collections) could not be confirmed by radular or molecular studies, but the conchological features seem consistent with the identification of these specimens (often labelled as *Conus* cf. *ikedai*, or *Conus darkini* “albinistic”) as *P. puillandrei* sp. nov. This is a feasible possibility given the multispiral protoconch of this species (suggesting a planktonic larval development), and might represent a significant range extension to the Philippines.

Remarks

Profundiconus puillandrei sp. nov. has been dredged alive from 1030–1180 m off Curtis Island, Kermadec Ridge, New Zealand (identified as *Conus smirna*; see Marshall 1981). This observation makes this species one of the deepest-living ones among the known cone snails. *P. puillandrei* sp. nov. was initially identified as “giant” *P. vaubani* (Fig. 1I). Apart from being smaller in size, *P. vaubani* has a paucispiral protoconch of 1.75 whorls and a ridge at the shoulder with axial costae, which are absent in the case of *P. puillandrei* sp. nov. The shell pattern of *P. vaubani* consists of light brown axial streaks from base to spire, whereas the shell of *P. puillandrei* sp. nov. is patternless. The radular teeth of *P. vaubani* (Fig. 2A–C) and *P. puillandrei* sp. nov. (Fig. 13) are superficially similar, but the tooth of *P. vaubani* has a much larger relative size, with $S_L/T_L = 27\text{--}31$ compared to $75\text{--}105$ for *P. puillandrei* sp. nov. The new species can also be compared with *P. profundorum* (Fig. 1A, L) and *P. smirnooides* (Fig. 1D). Like *P. puillandrei* sp. nov., these two species have multispiral protoconchs. There are no significant differences in shell shape among these species: ANCOVA for MD, HMD and SH, using species hypothesis as a factor and S_L as covariate, did not yield statistically significant results. However, they differ significantly in average shell length: *puillandrei* S_L 39.82 mm, *profundorum* S_L 96.93 mm ($t = 10.28$, $p = 2.13 \times 10^{-12}$; $U = 0$, $p = 5.15 \times 10^{-7}$), *smirnooides* S_L 76.09 mm ($t = -10.20$, $p = 5.25 \times 10^{-10}$; $U = 0$, $p = 2.5 \times 10^{-5}$).

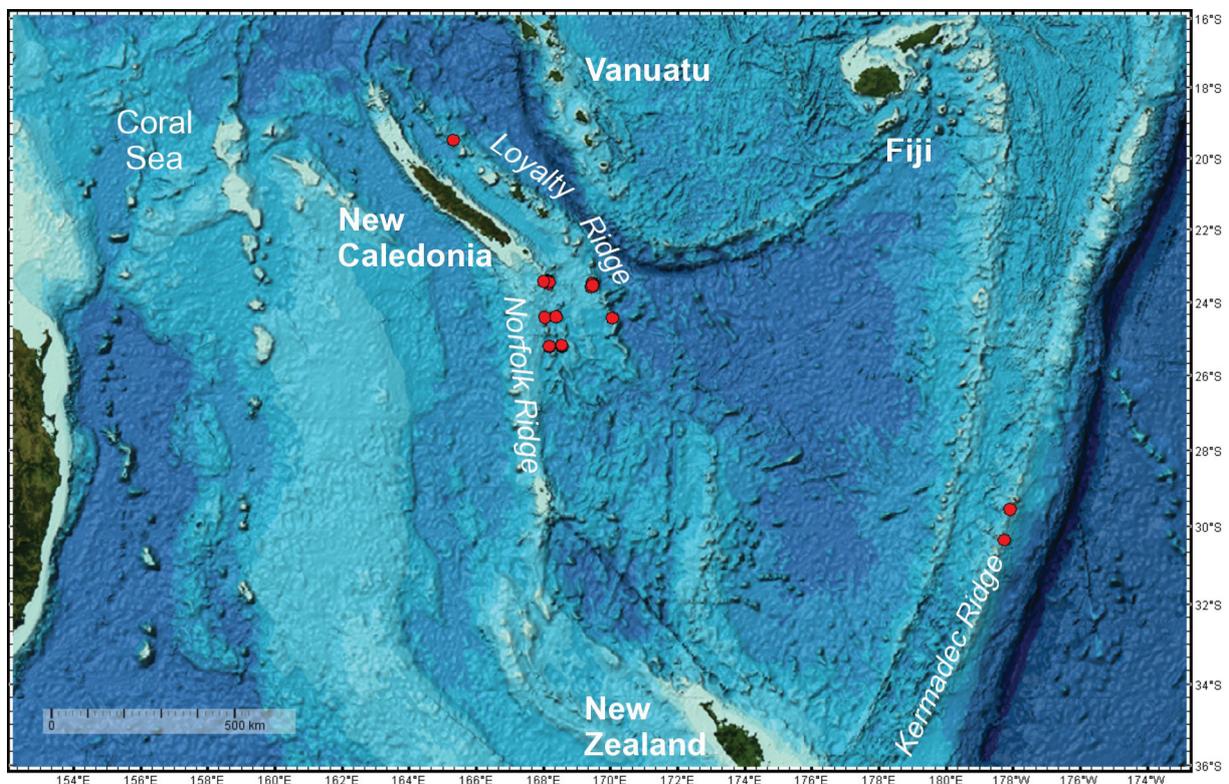


Fig. 14. Distribution map for *Profundiconus puillandrei* sp. nov. Red circles indicate the points where the species has been collected.

The shell of *P. puillandrei* sp. nov. has a distinct shoulder ridge, usually smooth but some times nodulose, which is absent in *P. profundorum* and less developed and always smooth in *P. smirnoides*. The shell of *P. puillandrei* sp. nov. is patternless, whereas both *P. profundorum* and *P. smirnoides* exhibit a characteristic pattern of broad, pale brown spiral bands on each side of centre, often interrupted by creamy white axial streaks in the case of *P. smirnoides*. The morphology of the radular tooth of *P. puillandrei* sp. nov. (Fig. 13) and of *P. smirnoides* (Fig. 9H) is very different. The radular tooth of *P. profundorum* is unknown, preventing its comparison with the tooth of *P. puillandrei* sp. nov.

Most of the shells of *P. puillandrei* sp. nov. examined were not nodulose at the shoulder ridge (Fig. 12). About 10% of the specimens studied had a nodulose spire and shoulder ridge (i.e., paratype 6, Fig. 12G), coming mainly from Loyalty Ridge. These include two of the sequenced individuals, which, however, were genetically similar to the ones with a smooth ridge. Moreover, nodulose and non-nodulose specimens exhibit analogous radular and protoconch morphology. The presence of nodules at the spire and shoulder causes an apparent difference in shape, which is possibly the main source of intraspecific phenotypic variability within this species. Nodulose specimens may resemble a small *P. teramachii* (e.g., paratype 6, Fig. 12G), a distinct but related species as inferred from the tree in Fig. 5. The shell of *P. teramachii* is also patternless and has a ground colour and protoconch morphology similar to that of *P. puillandrei* sp. nov. The radular tooth of *P. teramachii* (Fig. 2D–F) is also similar to that of *P. puillandrei* sp. nov. (Fig. 13). However, *P. teramachii* attains a larger size ($S_L = 55\text{--}111$ mm), has a lower spire (RSH 0.11–0.22 versus 0.22–0.29 in *P. puillandrei* sp. nov.) and usually exhibits a broadly carinate shoulder. *P. puillandrei* sp. nov. is phylogenetically related to *P. neotorquatus* stat. nov., *P. neocaledonicus* sp. nov., *P. teramachii* and *P. smirnoides*.

***Profundiconus neocaledonicus* sp. nov.**

[urn:lsid:zoobank.org:act:6581A3CA-DA2E-44A2-8E6E-2600CCA3B1D3](https://doi.org/10.21203/rs.3.rs-1000000/v1)

Figs 15A–J, 16A–C, 17

Conus profundorum – Rolan & Raybaudi-Massilia 1994: 33, pl. 11, fig. 82 (non *Chelyconus* (*Profundiconus*) *profundorum* Kuroda, 1956). — Röckel *et al.* 1995a: 381, pl. 27, fig. 16. — Röckel *et al.* 1995b: 563, fig. 22.

Profundiconus cf. *profundorum* – Puillandre *et al.* 2014: Supplementary Material 1 (unfigured).

Etymology

The epithet of this species makes reference to its distribution in deep water around New Caledonia.

Type material examined

Holotype

NEW CALEDONIA: 45.9 × 21.7 mm, R/V *Alis*, TERRASSES Expedition, st. DW 3076, Banc Crypthélie, Norfolk Ridge, 23°14'12" S, 168°13'18" E, 390–570 m (MNHN IM-2009-18227; Fig. 15A; GenBank accession number (*cox1* sequence): KJ550428).

Paratypes

NEW CALEDONIA: 61.3 × 28.1 mm, R/V *Alis*, EXBODI Expedition, st. DW 3889, Mont Vauban Partie SE, 22°25' S, 171°41' E, 350 m (MNHN 2009-31323; paratype 1; Fig. 15B); 52.6 × 24.7 mm, R/V *Alis*, SMIB 8 Expedition, st. DW 167, Norfolk Ridge, 23°38' S, 167°43' E, 430–452 m (MNHN IM-2000-30780; paratype 2; Fig. 15C); 46.7 × 20.4 mm, R/V *Alis*, TERRASSES Expedition, st. DW 3060, Banc Stylaster, Norfolk Ridge, 23°39' S, 167°44' E, 440–450 m (MNHN IM-2009-18225; paratype 3; Fig. 15G; GenBank accession number (*cox1* sequence): KJ550427); 71.8 × 37.0 mm, R/V *Coriolis*, CHALCAL 2 Expedition, st. DW 82, S New Caledonia, 23°14' S, 168°04' E, 304 m (MNHN IM-2000-30782; paratype 4; Fig. 15D); 92.0 × 42.0 mm, R/V *Alis*, NORFOLK 1 Expedition,

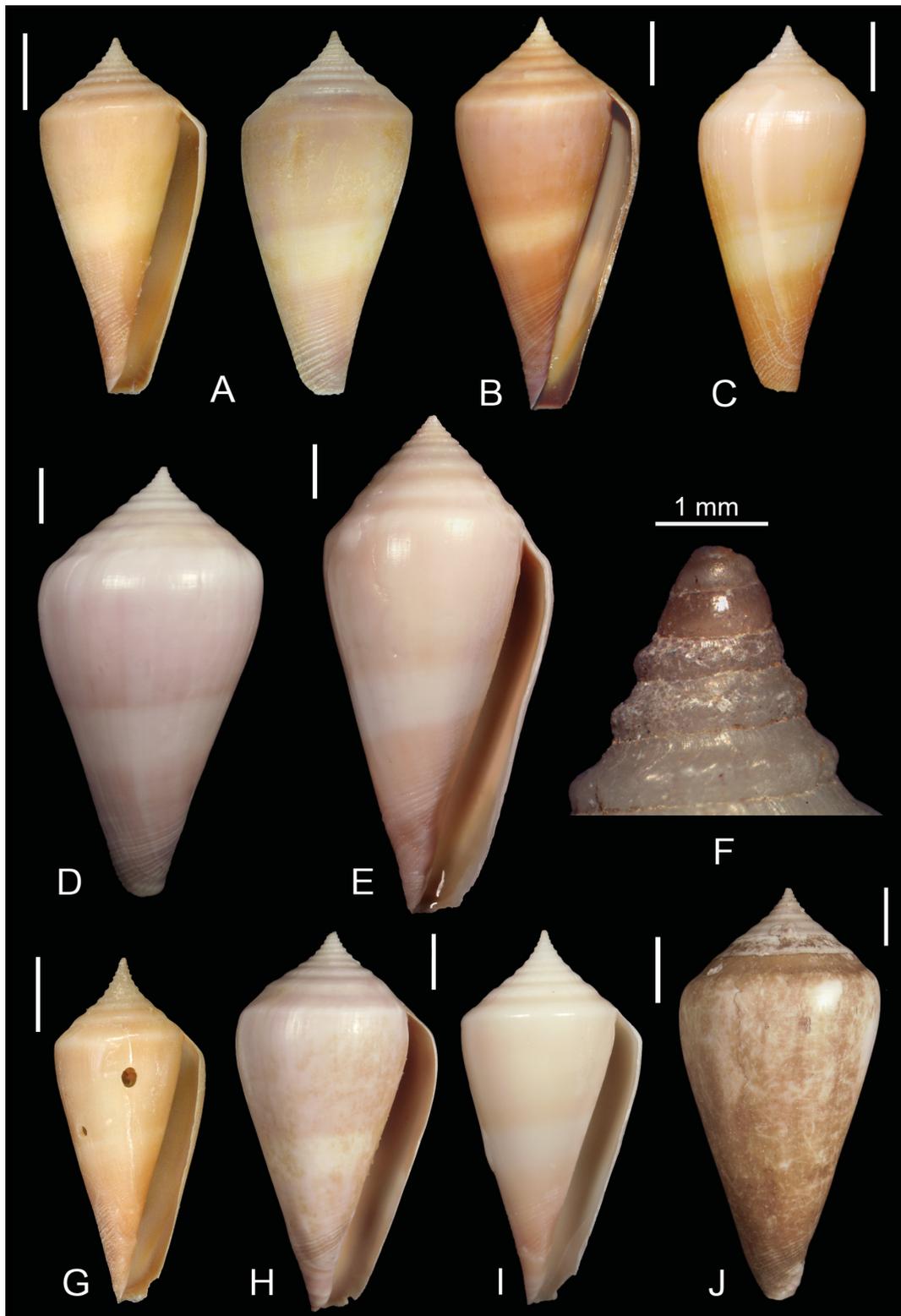


Fig. 15. *Profundiconus neocaledonicus* sp. nov. **A.** Holotype, 45.9 × 21.7 mm. **B.** Paratype 1, 61.3 × 28.1 mm. **C.** Paratype 2, 52.6 × 24.7 mm. **D.** Paratype 4, 71.8 × 37.0 mm. **E.** Paratype 5, 92.0 × 42.0 mm. **F.** Paratype 1, enlargement of the spire. **G.** Paratype 3, 46.7 × 20.4 mm. **H.** Paratype 6, 40.0 × 16.8 mm. **I.** Paratype 7, 54.5 × 25.4 mm. **J.** Paratype 8, 67.3 × 33.0 mm. Scale bars = 1 mm unless otherwise indicated.

st. DW 1732, Banc P, Norfolk Ridge, 23°20' S, 168°16' E, 347–1063 m (MNHN IM-2000-30783; paratype 5; Fig. 15E); 65.1 × 32.5 mm, R/V *Alis*, MUSORSTOM 6 Expedition, st. DW 406, Loyalty Ridge, 20°41' S, 167°07' E, 373 m (MNHN IM-2000-30784; paratype 6; Fig. 15H); 54.5 × 25.4 mm, R/V *Coriolis*, CHALCAL 2 Expedition, st. CC1, S New Caledonia, 24°55' S, 168°22' E, 500 m (MNHN IM-2000-30785; paratype 7; Fig. 15I); 67.3 × 33.0 mm, R/V *Alis*, NORFOLK 1 Expedition, st. DW 1657, Banc N, Norfolk Ridge, 23°28' S, 167°52' E, 305–332 m (MNHN IM-2000-30786; paratype 8; Fig. 15J); 61.5 × 28.7 mm, R/V *Alis*, NORFOLK 1 Expedition, st. DW 1658, Banc N, Norfolk Ridge, 23°26' S, 167°50' E, 320–336 m (MNHN IM-2000-30787; paratype 9); 65.5 × 35.7 mm, R/V *Alis*, NORFOLK 1 Expedition, st. DW 1652, Banc N, Norfolk Ridge, 23°26' S, 167°50' E, 290–378 m (MNHN IM-2000-30788; paratype 10); 53.4 × 22.8 mm, R/V *Alis*, BATHUS 3 Expedition, st. CP 811, Norfolk Ridge, 23°41' S, 168°15' E, 383–408 m (MNCN 15.05/60172; paratype 11).

Type locality

NEW CALEDONIA: Banc Crypthélia, Norfolk Ridge, 23°14' S, 168°13' E, 390–570 m (TERRASSES Expedition st. DW3076).

Other material examined

NEW CALEDONIA: 39.9 × 18.8 mm, R/V *Alis*, NORFOLK 2 Expedition, st. DW 2156, Ile des Pins, 22°54' S, 167°15' E, 468–500 m (MNHN IM-2007-34866; GenBank accession number (*cox1* sequence):

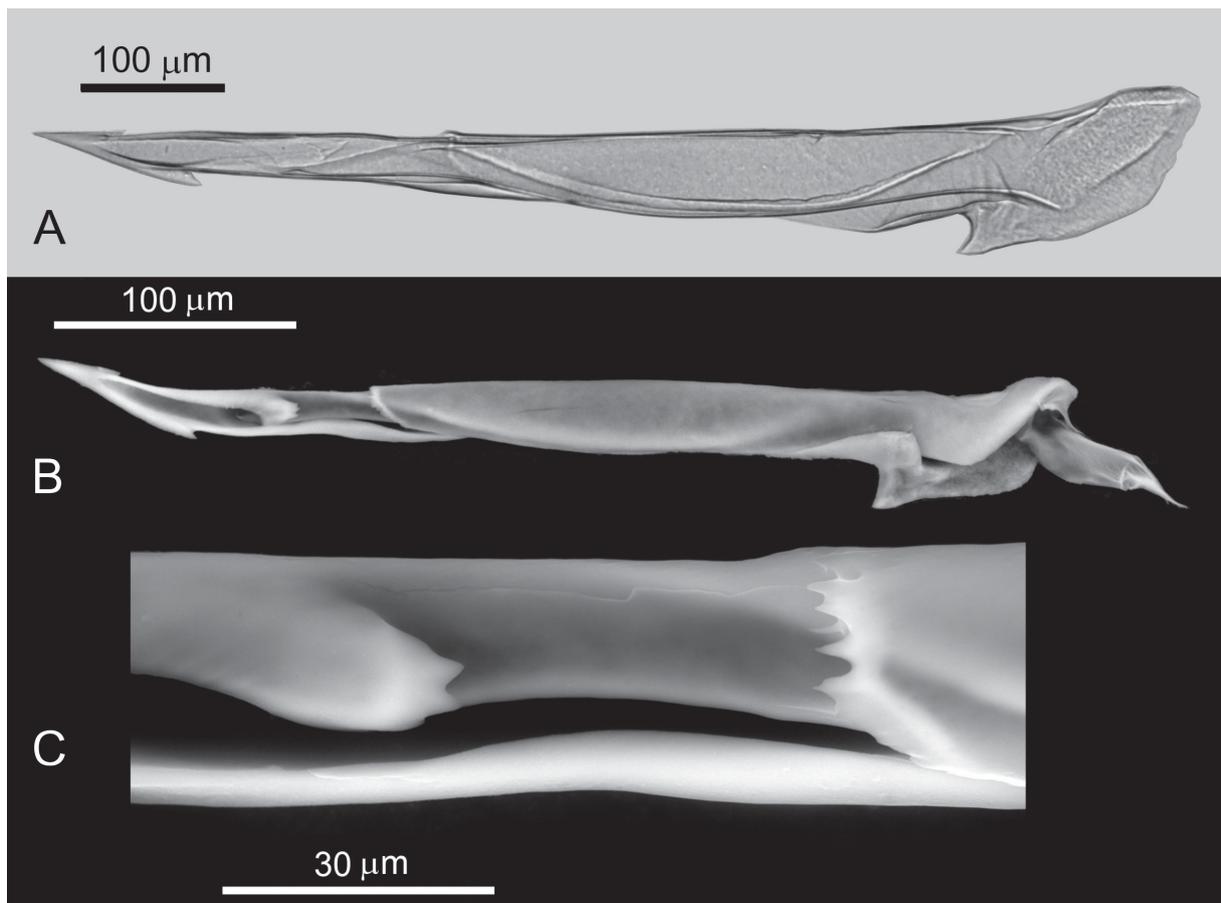


Fig. 16. Radular teeth extracted from *Profundiconus neocaledonicus* sp. nov. **A.** Optical photomicrograph (paratype 1, MNHN IM-2009-31323, S_L 61.3 mm). **B.** SEM photomicrograph (paratype 7, MNHN IM-2000-30785, S_L 54.5 mm). **C.** Enlargement of the middle section of B.

KJ550426). This specimen was databased (<http://colddb.mnhn.fr/catalognumber/mnhn/im/2007-34866>) and sequenced, but the shell was destroyed in the process and is no longer available.

Additionally, we examined 32 more specimens from 18 uncataloged MNHN lots collected at several stations in Norfolk Ridge and Loyalty Ridge, New Caledonia, in the course of several campaigns.

Description

Morphometric parameters: $S_L = 45\text{--}80$ mm; $RD = 0.54\text{--}0.66$; $RSH = 0.16\text{--}0.22$; $PMD = 0.81\text{--}0.92$.

Medium-sized to moderately large (maximum length 92.0 mm). Shell profile ventricosely conical to conical, with rounded shoulder and spire low to moderately high. Spire profile sigmoid, occasionally slightly concave. Protoconch multispiral of 3 or more whorls, white to pale violet-brown (Fig. 15F). First 4–7 postnuclear whorls nodulose. Teleoconch sutural ramp flat, slightly concave or sigmoid in later whorls, smooth, with cords absent. Last whorl smooth, with fine spiral ribs at base. Ground colour creamy-white to cream. Last whorl with two broad violet-brown, light brown or tan spiral bands above and below midbody, which exhibits broad ground-coloured spiral band. Colour is darker towards base, usually purplish. Narrow ground-colour spiral band often present at height of shoulder. Spire patternless, of ground colour, occasionally showing diffuse pale violet-brown or light brown on top of teleoconch whorls. Aperture light to pinkish brown. Periostracum olive, thin, translucent, smooth. Operculum with lateral serrations.

Radular tooth examined in paratypes 1 (Fig. 16A), 2 and 7 (Fig. 16B, C). 34–45 teeth in radular sac. Radular tooth of rather small relative size: its total length relative to shell length $S_L/T_L = 61\text{--}87$. Anterior portion shorter than posterior section of tooth ($T_L/AP_L = 3.1\text{--}3.4$). With one barb and pointed, prominent

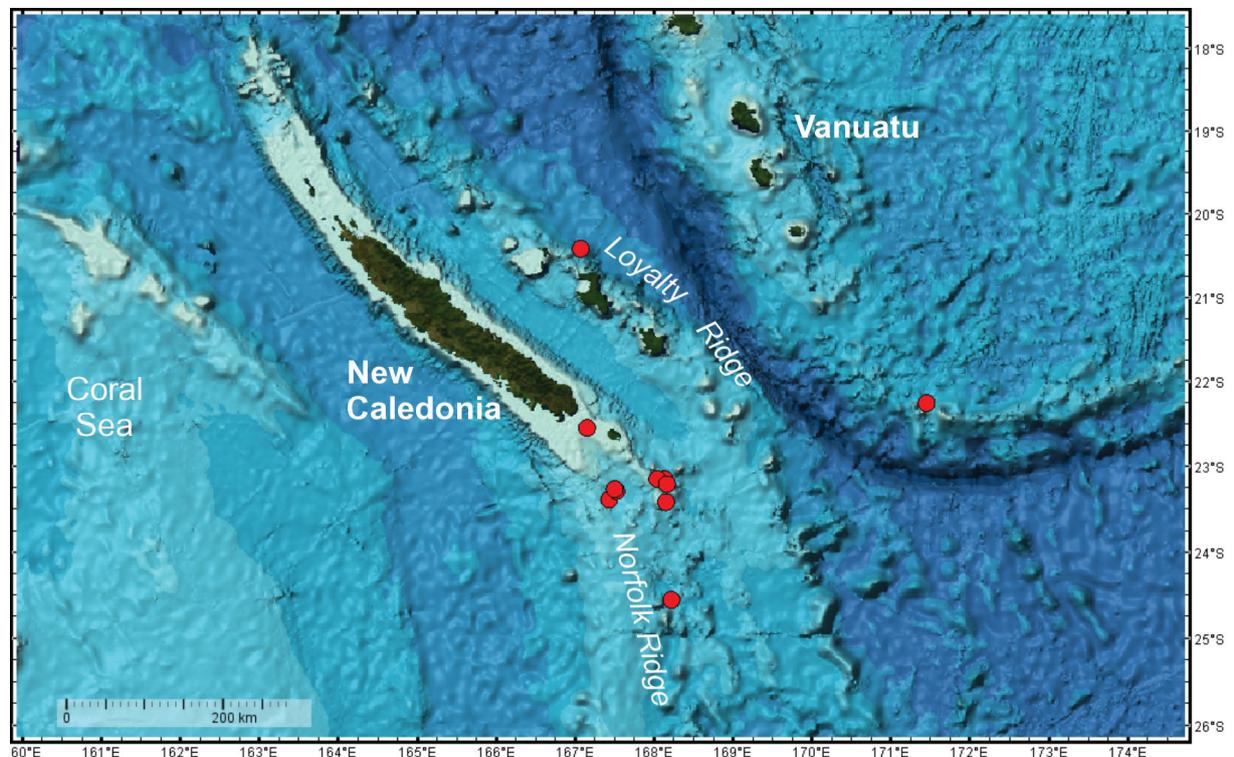


Fig. 17. Distribution map for *Profundiconus neocaledonicus* sp. nov. Red circles indicate the points where the species has been collected.

Table 3. Comparison between morphometric parameters for *P. neocaledonicus* sp. nov. (N = 28) and *P. profundorum* (Kuroda, 1956) (N = 26): Least-squares means and ANCOVA results.

Trait	LS mean values (mm)		F	p
	<i>P. neocaledonicus</i> (New Caledonia)	<i>P. profundorum</i> (Japan/China)		
MD	36.4	33.2	12.59	0.0008
HMD	51.7	49.8	5.77	0.02
SH	15.3	17.4	7.74	0.0075
S _L ¹	57.0	96.9	–	–

¹ For the pairwise comparison of mean S_L: t = -8.82, p = 6.63 × 10⁻¹²; U = 692, p = 1.43 × 10⁻⁸.

blade which covers 43–54% of apical portion of tooth. External cusp present, extending between 65 and 88% of length of anterior portion of tooth. External cusp not much widened laterally and serrations can be indistinct, with only 0–3 small blunt denticles. Large adapical opening occupying most of anterior portion of tooth (100AO_L/AP_L = 62–75). With characteristic fringe of closely spaced projections pointing towards the apex located immediately below waist (Fig. 16C). Shaft fold present. Large and prominent basal spur on top of slanted base of tooth.

Distribution and habitat

Norfolk Ridge and Loyalty Ridge, New Caledonia, at depths from 290 to 1100 m (Fig. 17). A couple of empty shells resembling *P. neocaledonicus* sp. nov. from Aliguay Island, Philippines, have been examined. The identity of these specimens from the Philippines (coming from the John K. Tucker collection, now with the INHS, Illinois, USA) could not be confirmed by radular or molecular studies. This observation might suggest an extension of the distribution range to the Philippines, but would require additional substantiation.

Remarks

Profundiconus neocaledonicus sp. nov. has long been considered a local form of *P. profundorum* from New Caledonia (Röckel *et al.* 1995a). *P. profundorum* was originally described based upon material from Japan (type locality: “Off Tosa, Japan; 100+ fathoms”) (Fig. 1A). In recent times, specimens of *P. profundorum* have become available from China (Fig. 1L). These specimens are characterised by their significantly larger mean shell length compared to the Japanese specimens (mean S_L *profundorum* from Japan: 74.3 mm; mean S_L *profundorum* from China: 111.05 mm; t = 13.12, p = 0; U = 0, p = 0.000028). Apart from differences in shell length, ANCOVA indicated no statistically significant differences between the morphometric parameters of *P. profundorum* from Japan and those from China (ANCOVA on MD: F = 1.94, p = 0.18; on HMD: F = 3.44, p = 0.08; on SH: F = 0.05, p = 0.82). Hence, we consider the Chinese and Japanese populations conspecific. Compared to *P. profundorum*, the shells of *P. neocaledonicus* sp. nov. from New Caledonia have a different shape, are consistently smaller in average shell length, and are also paler in colour. Table 3 shows the results of the ANCOVA with the morphometric shell parameters MD, HMD and SH as variables, and using species hypothesis as factor and S_L as covariate. Least-squares means are listed, along with average shell lengths for each of the species.

These results confirm that the shell of *P. neocaledonicus* sp. nov. is significantly broader, more conical (higher HMD) and lower-spined than the shell of *P. profundorum*, which also has a larger mean S_L. A discriminant function analysis (DFA) using MD, HMD, SH and S_L as variables and species hypothesis as factor correctly classified 94.4% of the specimens (all correct except two specimens of *profundorum*

misclassified as *neocaledonicus* and one specimen of *neocaledonicus* misclassified as *profundorum*). A DFA excluding S_L from the set of variables correctly classified 92.6% of the specimens (three *profundorum* were misclassified as *neocaledonicus* and one specimen of *neocaledonicus* misclassified as *profundorum*). These results indicate that *P. neocaledonicus* sp. nov. can be separated with a high degree of certainty from *P. profundorum* based on significant differences in size and shell shape. It was not possible to compare the radula of *P. neocaledonicus* sp. nov. with that of *P. profundorum*. The radular tooth morphology of *P. profundorum* is unknown, since all the published information (Rolán & Raybaudi-Massilia 1994) actually corresponds to specimens from New Caledonia, here introduced as *P. neocaledonicus* sp. nov. No preserved specimens of *P. profundorum* from Chinese or Japanese localities were available for radular or molecular analyses.

Although the genetic differentiation of *P. neocaledonicus* sp. nov. from *P. smirnoides* and *P. teramachii* was not supported at the nodes on the tree in Fig. 5, *P. neocaledonicus* sp. nov. is easily separated from the sympatric species *P. smirnoides* based on shell and radular morphology. The shell of *P. smirnoides* (Fig. 1D) is significantly narrower, less conical and much more highly spired than that of *P. neocaledonicus* sp. nov. (ANCOVA with S_L as covariate: on MD:F = 103.91, $p = 0$; on HMD:F = 62.54, $p = 0$; on SH:F = 28.37, $p = 0$). It also has a significantly larger mean shell length (76.09 mm for *smirnoides* versus 57.03 mm for *neocaledonicus*, $t = -4.299$, $p = 0.00011$; $U = 285.5$, $p = 0.00055$). *P. smirnoides* has a pattern of brown spiral bands on each side of centre interrupted by creamy white axial streaks, whereas in *P. neocaledonicus* sp. nov. is much simpler, consisting of pale purplish-brown broad bands on each side of centre on a creamy-white ground colour. Comparison of the large and elongated radular tooth of *P. smirnoides* (Fig. 9H) with that of *P. neocaledonicus* sp. nov. (Fig. 16) also allows the straightforward separation of the two species. *P. teramachii* (Fig. 1B) has a very different shell, larger in size, and is patternless, with a characteristic stepped spire and with a broadly carinated shoulder, sometimes with densely set rounded tubercles, particularly in smaller adults.

The species *P. puillandrei* sp. nov., which lives sympatrically with *P. neocaledonicus* sp. nov., has a significantly smaller shell length ($t = 4.296$, $p = 0.0001$; $U = 53$, $p = 0.000066$), with differences in morphometric parameters that suggest that *P. puillandrei* sp. nov. has a narrower shell with a higher spire (ANCOVA with S_L as covariate on MD:F = 6.23, $p = 0.0168$; on HMD:F = 40.19, $p = 0$; on SH:F = 35.46, $p = 0$). This species shows a characteristic ridge at the shoulder, sometimes nodulose, whereas in *P. neocaledonicus* sp. nov. the shoulder is always rounded. The shell of *P. puillandrei* sp. nov. is patternless and does not exhibit the banding pattern visible in the shell of *P. neocaledonicus* sp. nov.

Röckel *et al.* (1995a: pl. 73, figs 17–18) illustrated one specimen identified as “*Conus* species no. 32”. This specimen measures 50 × 23 mm and comes from Nazca Ridge. Other specimens like the one illustrated in Röckel *et al.* (1995a) have been collected in deep-water on several seamounts across Sala y Gómez and Nazca Ridges in the course of several campaigns carried out by Russian research vessels in the 70’s and 80’s. The biota of the Nazca and Sala y Gómez submarine ridges was reviewed in Parin *et al.* (1997). The fauna of benthic and benthopelagic invertebrates of this area is much more closely related to the Indo-West Pacific than to the Eastern Pacific fauna and is characterized by a very high degree of endemism at the species level (51% among identified bottom invertebrates). We have been unable to examine the specimens from the Nazca Ridge area, but the available photos (Röckel *et al.* 1995a) show a striking resemblance to the shells of *P. neocaledonicus* sp. nov. collected on Norfolk Ridge, New Caledonia, at a distance of *c.* 10 500 km to the east. Further research might eventually prove their conspecificity, which would imply a considerable range extension for this species, or alternatively disclose a new species of *Profundiconus* most likely endemic to the Sala y Gómez and Nazca Ridge areas.

Discussion

The BA and ML phylogenetic trees based on a subsample of the mitochondrial *cox1* dataset produced by Puillandre *et al.* (2014) plus new *cox1* sequences (supplied by N. Puillandre) confirmed with high statistical support that species in the genus *Profundiconus* form a monophyletic group. *Profundiconus* had already been elevated to the rank of genus by da Motta (1991) and Raybaudi-Massilia (1992). Tucker & Tenorio (2009) placed this genus in the new family Conilithidae Tucker & Tenorio, 2009 (type genus: *Conilithes* Swainson, 1840; type species: *C. antidiluvianus* (Bruguière, 1792), a Pliocene fossil species, Fig. 1E; see Janssen *et al.* 2014a, 2014b), along with other Holocene conid genera including *Conasprella*, *Boucheticonus* and *Bathyconus* (but not *Cylinder* Montfort, 1810 or *Conus*). Therefore, according to the tree in Fig. 5, the so-defined family Conilithidae would be polyphyletic. In order to reconcile taxonomy and phylogeny, the family Conilithidae would need to be restricted to the fossil genus *Conilithes* (Rolán & Raybaudi-Massilia 1994) and *Profundiconus* if their morphological similarity is due to true synapomorphies, or alternatively *Profundiconus* would deserve its own family. The other living genera placed in Conilithidae by Tucker & Tenorio (2009) and Tucker & Tenorio (2013) would require placement in another suprageneric taxon, either family or subfamily, which would be sister group to the Conidae *sensu* Tucker & Tenorio (2013) (the so-called “Large Major Clade” of Duda & Kohn 2005, or the genus *Conus sensu* Puillandre *et al.* 2015). However, these taxonomic changes would require confirmation and support by more detailed molecular studies using additional gene markers, which allow for higher resolution of the reconstructed trees. Such studies and its taxonomic implications are beyond the scope of the present work, which is focused mainly on the characterization of genus *Profundiconus* as a whole.

The phylogenetic analyses of 55 specimens of *Profundiconus* showed individuals grouped in clades which do not correspond to any of the known species of *Profundiconus*. Such clades had already been recovered in the analysis by Puillandre *et al.* (2014) and were then labelled with letters, but the corresponding new taxa remained undescribed until now. Another two new species of *Profundiconus*, present in the tree in Fig. 5, were recently identified and described, namely *P. zardoyai* and *P. smirnoides* (Tenorio 2015a, 2015b). With all these recent additions and the new taxa included in the present work, the number of known living species of *Profundiconus* has been increased from 16 (Tucker & Tenorio 2013) to 26. This represents an increase of 62.5% in the total number of taxa existing in the genus and illustrates the potential for discovering new species of cone snails from the deep sea. We can anticipate that future surveys in deep waters across the Indo-West Pacific Ocean will yield *Profundiconus* species, many of which are expected to be new to science. Upon examination of the lots of material brought to the surface by research vessels, we can conclude that *Profundiconus* are one of the main components of the gastropod fauna at depths below 200 m, and that species of this genus may attain very small adult sizes, so they can possibly remain overlooked or confused with juveniles of other species. Study of the conotoxins produced by individuals of *Profundiconus* is another field yet to be explored, with findings that are unpredictable, but hitherto exciting at the present moment. Unfortunately, the phylogenetic relationships among species within *Profundiconus* are poorly resolved. This could be due to either the lack of enough phylogenetic signal in the molecular marker at this taxonomic level, a rapid radiation event at the origin of the genus, or the extinction of different lineages during the evolutionary history of the group. This fact enhances the need for an integrative approach for species delimitation combining genetic, morphological and ecological data (Edwards & Knowles 2014; Carstens *et al.* 2013), rather than relying on single locus genetic data only.

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

Taxon	S_L (mm)	AH (mm)	MD (mm)	HMD (mm)	SH (mm)
<i>profundorum</i>	67.0	49.1	29.4	41.7	17.9
<i>profundorum</i>	73.1	58.2	31.7	47.6	14.9
<i>profundorum</i>	103.9	81.5	47.4	69.0	22.4
<i>profundorum</i>	105.2	79.8	44.1	71.9	25.4
<i>profundorum</i>	108.3	83.7	46.7	71.8	24.6
<i>profundorum</i>	112.0	90.2	47.8	78.8	21.8
<i>profundorum</i>	115.5	91.0	47.2	76.0	24.5
<i>profundorum</i>	129.0	103.1	55.2	82.5	25.9
<i>profundorum</i>	104.0	83.3	47.4	70.7	20.7
<i>profundorum</i>	105.0	83.7	45.5	69.6	21.3
<i>profundorum</i>	111.1	87.3	52.6	75.8	23.8
<i>profundorum</i>	109.4	81.3	49.3	66.4	28.1
<i>profundorum</i>	81.0	60.0	35.9	50.4	21.0
<i>profundorum</i>	110.0	84.7	47.8	73.5	25.3
<i>profundorum</i>	87.0	68.2	36.0	56.5	18.8
<i>profundorum</i>	116.0	89.9	49.0	77.4	26.1
<i>profundorum</i>	77.6	58.0	34.4	49.0	19.6
<i>profundorum</i>	67.0	49.2	33.0	42.0	17.8
<i>profundorum</i>	66.0	51.5	28.9	41.6	14.5
<i>profundorum</i>	66.0	53.6	29.9	44.6	12.4
<i>profundorum</i>	83.0	66.0	36.6	54.6	17.0
<i>profundorum</i>	115.0	87.7	52.5	74.6	27.3
<i>profundorum</i>	106.0	81.6	51.5	70.3	24.4
<i>profundorum</i>	116.0	91.2	56.7	74.8	24.8
<i>profundorum</i>	75.6	57.0	32.9	46.7	18.6
<i>profundorum</i>	110.5	88.5	47.7	73.1	22.0
<i>neocaledonicus</i>	63.5	50.6	30.3	44.8	12.9
<i>neocaledonicus</i>	52.8	42.2	23.4	37.5	10.6
<i>neocaledonicus</i>	34.4	26.9	15.1	24.7	7.6
<i>neocaledonicus</i>	40.8	31.8	18.9	29.3	8.9
<i>neocaledonicus</i>	43.7	35.2	19.1	30.4	8.5
<i>neocaledonicus</i>	55.0	43.9	26.8	38.1	11.1
<i>neocaledonicus</i>	77.6	63.4	39.2	52.0	14.2
<i>neocaledonicus</i>	40.3	33.2	19.3	28.8	7.0
<i>neocaledonicus</i>	46.1	38.6	22.7	33.7	7.6
<i>neocaledonicus</i>	43.7	34.8	19.8	29.4	8.8
<i>neocaledonicus</i>	53.7	42.4	24.5	35.9	11.3
<i>neocaledonicus</i>	54.0	43.7	25.0	37.9	10.3
<i>neocaledonicus</i>	47.3	38.4	21.8	32.5	8.8
<i>neocaledonicus</i>	52.0	43.5	25.5	37.5	8.4

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

Taxon	S_L (mm)	AH (mm)	MD (mm)	HMD (mm)	SH (mm)
<i>neocaledonicus</i>	43.0	34.0	19.4	29.7	9.0
<i>neocaledonicus</i>	81.7	65.5	43.4	54.4	16.2
<i>neocaledonicus</i>	57.9	46.3	27.5	41.1	11.6
<i>neocaledonicus</i>	70.4	57.6	36.2	46.9	12.7
<i>neocaledonicus</i>	55.5	44.4	26.4	37.1	11.1
<i>neocaledonicus</i>	71.8	57.2	37.0	47.4	14.6
<i>neocaledonicus</i>	54.5	43.0	25.4	38.2	11.5
<i>neocaledonicus</i>	92.0	68.2	42.0	58.0	23.8
<i>neocaledonicus</i>	52.6	42.1	24.7	34.7	10.5
<i>neocaledonicus</i>	65.1	51.6	32.5	42.9	13.5
<i>neocaledonicus</i>	67.3	53.7	33.0	45.1	13.6
<i>neocaledonicus</i>	61.5	48.5	28.7	40.7	13.0
<i>neocaledonicus</i>	53.4	42.0	22.8	35.7	11.4
<i>neocaledonicus</i>	65.5	54.0	35.7	45.7	11.5
<i>puillandrei</i>	47.4	35.8	19.5	29.3	11.6
<i>puillandrei</i>	37.2	26.2	15.1	22.9	10.9
<i>puillandrei</i>	34.5	25.4	15.0	21.5	9.1
<i>puillandrei</i>	50.0	36.8	22.6	32.4	13.1
<i>puillandrei</i>	41.8	31.0	17.5	26.9	10.8
<i>puillandrei</i>	38.1	29.4	16.9	25.9	8.7
<i>puillandrei</i>	44.2	32.4	19.2	28.1	11.8
<i>puillandrei</i>	32.0	24.8	13.2	21.3	7.3
<i>puillandrei</i>	29.5	22.6	13.1	18.4	6.9
<i>puillandrei</i>	41.0	31.9	18.2	27.5	9.0
<i>puillandrei</i>	45.0	34.5	18.8	29.9	10.5
<i>puillandrei</i>	36.0	28.5	16.6	24.4	7.5
<i>puillandrei</i>	41.1	30.1	17.4	26.3	11.0
<i>smirnoides</i>	81.5	59.2	31.0	47.9	22.3
<i>smirnoides</i>	97.9	62.7	35.0	50.5	35.2
<i>smirnoides</i>	63.4	46.7	24.7	38.2	16.7
<i>smirnoides</i>	81.4	59.6	31.9	49.4	21.8
<i>smirnoides</i>	75.3	55.4	29.9	46.2	19.9
<i>smirnoides</i>	75.4	55.1	29.8	45.7	20.3
<i>smirnoides</i>	71.8	52.0	26.3	42.2	19.8
<i>smirnoides</i>	52.0	38.2	19.8	30.7	13.8
<i>smirnoides</i>	73.7	55.6	27.0	42.6	18.1
<i>smirnoides</i>	79.7	59.9	27.4	47.1	19.8
<i>smirnoides</i>	76.7	55.8	29.6	45.1	20.9
<i>smirnoides</i>	84.3	62.8	34.8	50.3	21.5