geodiversitas
2026 • 48 • 6

Evolutionary history of reef-dwelling and associated lagoonal mollusc assemblages of the uplifted Niau Atoll (Tuamotu, French Polynesia) since the Pliocene

Bernard SALVAT,
Didier MERLE,
Jean LETOURNEUX,
Jean TRÖNDLÉ,
Lucien François MONTAGGIONI,
Edwige PONS-BRANCHU,
Jean-Pascal DUMOULIN &
Philippe BACCHET

art. 48 (6) — Published on 2 April 2026
www.geodiversitas.com

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

Directeur de la publication / *Publication director* : Gilles Bloch,
Président du Muséum national d'Histoire naturelle

Rédacteur en chef / *Editor-in-chief* : Sylvain Charbonnier

Rédacteur associé / *Associate editor*: Didier Merle

Éditeur technique (suivi éditorial) / *Desk editor (editorial process)* : Emmanuel Côtez (geodiv@mnhn.fr)

Éditeur technique (production) / *Desk editor (production)* : Emmanuel Côtez

Comité scientifique / *Scientific board* :
Christine Argot (Muséum national d'Histoire naturelle, Paris)
Beatrix Azanza (Museo Nacional de Ciencias Naturales, Madrid)
Raymond L. Bernor (Howard University, Washington DC)
Henning Blom (Uppsala University)
Gaël Clément (Muséum national d'Histoire naturelle, Paris)
Ted Daeschler (Academy of Natural Sciences, Philadelphie)
Cédric Del Rio (Muséum national d'Histoire naturelle)
Gregory D. Edgecombe (The Natural History Museum, Londres)
Ursula Göhlich (Natural History Museum Vienna)
Jin Meng (American Museum of Natural History, New York)
Brigitte Meyer-Berthaud (CIRAD, Montpellier)
Zhu Min (Chinese Academy of Sciences, Pékin)
Isabelle Rouget (Muséum national d'Histoire naturelle, Paris)
Sevket Sen (Muséum national d'Histoire naturelle, Paris, retraité)
Stanislav Štamberg (Museum of Eastern Bohemia, Hradec Králové)
Paul Taylor (The Natural History Museum, Londres, retraité)

Couverture / *Cover* :
Réalisée à partir des Figures de l'article/*Made from the Figures of the article*.

Geodiversitas est indexé dans / Geodiversitas *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Physical, Chemical, and Earth Sciences®
- Scopus®

Geodiversitas est distribué en version électronique par / Geodiversitas *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par / *Articles and nomenclatural novelties published in* Geodiversitas *are referenced by:*
- ZooBank® (http://zoobank.org)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:* ***Adansonia***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie* sous-sections *Algologie***, ***Bryologie***, ***Mycologie, Comptes Rendus Palevol***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

Les articles publiés dans *Geodiversitas* sont distribués sous licence CC-BY 4.0/*Articles published in* Geodiversitas *are distributed under a CC-BY 4.0 license*.
ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

Evolutionary history of reef-dwelling and associated lagoonal mollusc assemblages of the uplifted Niau Atoll (Tuamotu, French Polynesia) since the Pliocene

Bernard SALVAT
École pratique des Hautes Études, Paris Sciences et Lettres PSL Research University
Laboratoire UAR 3278, Centre national de la Recherche scientifique,
Université de Perpignan, Avenue de Villeneuve F-66860 Perpignan (France)
and Centre de Recherches insulaires et Observatoire de l'Environnement,
CRIOBE, Moorea (Polynésie française)
bsalvat@univ-perp.fr

Didier MERLE
Muséum national d'Histoire naturelle, Origines & Évolution,
Centre de Recherche en Paléontologie Paris (CR2P – MNHN, CNRS, Sorbonne Université),
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
didier.merle@mnhn.fr (corresponding author)

Jean LETOURNEUX
BP 112206 – 98709 Mahina, Tahiti (Polynésie française)
natualeyla@mail.pf

Jean TRÖNDLÉ
17 Rue Girounet, F-24130 La force (France)
j.trondle@orange.fr

Lucien François MONTAGGIONI
Aix-Marseille Université, CNRS-UMR 7330, IRD, INRAE, Centre d'Enseignement et de
Recherche de Géosciences de l'Environnement (CEREGE), F-13331 Marseille (France)
montaggioni@cerege.fr

Edwige PONS-BRANCHU
Jean-Pascal DUMOULIN
Laboratoire des Sciences du Climat et de l'Environnement, Institut Pierre-Simon Laplace,
Commissariat à l'Énergie atomique, Centre national de la Recherche scientifique, Université de
Versailles Saint-Quentin-en-Yveline (LSCE–IPSL, CEA, CNRS, UVSQ),
Université Paris-Saclay, F-91198 Gif-sur-Yvette (France)
edwige.pons-branchu@lsce.ipsl.fr/jean-pascal.dumoulin@lsce.ipsl.fr

Philippe BACCHET
BP 2720 – 98713 Papeete, Tahiti (Polynésie française)
bacchetphil@mail.pf

Submitted on 7 April 2025 | accepted on 12 May 2025 | published on 2 April 2026

urn:lsid:zoobank.org:pub:6AE2D214-E535-45E0-BF1B-41E3C2BC6C73

Salvat B., Merle D., Letourneux J., Tröndlé J., Montaggioni L. F., Pons-Branchu E., Dumoulin J.-P. & Bacchet P. 2026. — Evolutionary history of reef-dwelling and associated lagoonal mollusc assemblages of the uplifted Niau Atoll (Tuamotu, French Polynesia) since the Pliocene. *Geodiversitas* 48 (6): 87-125. https://doi.org/10.5252/geodiversitas2026v48a6. http://geodiversitas.com/48/6

ABSTRACT

The evolutionary history of the lagoonal molluscan thanatocenoses on the raised Niau Atoll (French Polynesia) is studied in relation to the geological evolution of the atoll and the episodic exchanges between the oceanic waters and those of the lagoon since the Late Pliocene. Three thanatocoenoses are described and compared with the extant fauna of the raised lagoon. The first one, located beneath a limestone pedogenetic crust, was recently dated to the Late Pliocene-Early Pleistocene and reveals a rich assemblage of 92 molluscan species. Seven new species are described, five of which are recognised after examining the shells under UV light: four gastropods *Cerithium niauense* Merle, n. sp. (UV), *Conus* (*Conus*) *letourneuxi* Merle, n. sp. (UV), *Conus* (*Tesselliconus*) *georgesrichardi* Merle, n. sp. (UV), *Bulla niauensis* Merle, n. sp. (UV), and three bivalves ?*Lunulicardia distorta* Merle, n. sp., *Indotellina fakaauensis* Merle, n. sp. and ?*Gafrarium troendlei* Merle, n. sp. (UV). The other two thanatocenoses are herein dated to the Mid and Late Holocene. With around ten species, their assemblages are much poorer than those of the Plio-Pleistocene and support numerous local extinctions. These extinctions are regarded as mainly resulting from the uplift of the atoll, which has led to the isolation and drying out of the lagoon to the present day, as well as reduced water exchanges with the open sea. Currently, only three species of molluscs are abundant in the lagoon, two of which were already present in the Plio-Pleistocene, the bivalve *Ctena bella* Conrad, 1837 and the gastropod *Cerithium punctatum* Bruguière, 1792, and another gastropod species *Clypeomorus brevis* (Quoy & Gaimard, 1834) was introduced in the atoll between 2008 and 2020.

KEY WORDS
French Polynesia,
Late Pliocene to Holocene,
atoll,
lagoon,
assemblages,
molluscs,
palaeoecology,
new species.

RÉSUMÉ

Histoire évolutive des assemblages de mollusques récifaux et lagunaires associés de l'atoll soulevé de Niau (Tuamotu, Polynésie française) depuis le Pliocène.

L'histoire des thanatocénoses lagunaires de mollusques sur l'atoll surélevé de Niau (Polynésie française) est étudiée en fonction de l'évolution géologique de l'atoll et des échanges épisodiques entre les eaux océaniques et celles du lagon. Trois thanatocénoses sont décrites et comparées avec la faune actuelle du lagon surélevé. La première située sous une croûte calcaire a été récemment datée du Pliocène supérieur-Pléistocène inférieur et révèle un riche assemblage de 92 espèces de mollusques. Sept espèces nouvelles sont décrites dont cinq ont été reconnues grâce à un examen des coquilles sous lumière UV : quatre de gastéropodes *Cerithium niauense* Merle, n. sp. (UV), *Conus* (*Conus*) *letourneuxi* Merle, n. sp. (UV), *Conus* (*Tesselliconus*) *georgesrichardi* Merle, n. sp. (UV), *Bulla niauensis* Merle, n. sp. (UV) et trois de bivalves ?*Lunulicardia distorta* Merle, n. sp., *Indotellina fakaauensis* Merle, n. sp. et ?*Gafrarium troendlei* Merle, n. sp. (UV). Les deux autres thanatocénoses sont datées dans ce travail respectivement de l'Holocène moyen et supérieur. Composées d'une dizaine d'espèces, elles présentent un peuplement très appauvri comparativement à celui du Plio-Pléistocène, ce qui indique de nombreuses extinctions à l'échelle locale. Ces extinctions résultent principalement du soulèvement de l'atoll qui a entraîné l'isolement et l'assèchement du lagon jusqu'à aujourd'hui, ainsi que d'une forte réduction des communications avec la mer. Actuellement, seules trois espèces de mollusques sont abondantes dans le lagon dont deux étaient déjà présentes au Plio-Pléistocène, le bivalve *Ctena bella* Conrad, 1837, le gastéropode *Cerithium punctatum* Bruguière, 1792 et une autre espèce de gastéropode introduite dans l'atoll entre 2008 et 2020 *Clypeomorus brevis* (Quoy & Gaimard, 1834).

MOTS CLÉS
Atoll,
lagon,
Polynésie française,
Pliocène supérieur à Holocène,
assemblages,
mollusques,
paléoécologie,
espèces nouvelles.

INTRODUCTION

The geological history of the Pliocene to Quaternary Indo-Pacific coral reefs is relatively well documented worldwide (Montaggioni & Braithwaite 2009; Montaggioni *et al.* 2023). Coral and molluscan assemblages have been particularly well studied in the various reef biozones from outer reef slopes to backreef zones. Changes in sea level in relation to the successive glacial and interglacial periods over the past 2.6 million years have resulted into significant changes in faunal assemblages (Harland *et al.* 1989; Paulay 1990; Lisiecki & Raymo 2005). Comparison of Pleistocene coral and malacological faunas with their Holocene and modern counterparts reveals that species extinctions have occurred in numerous Indo-Pacific reef sites on both global and regional to local scales. There is an abundant literature devoted to corals: Paulay & Spencer (1988) on Henderson Pitcairn islands group, Chevalier (1979) on French Polynesia, Stoddart (1973) and Potts (1984, 1985) worldwide, McManus (1985) on Southeast Asia, and to molluscs as well: Ostergaard (1928) on Oahu Hawaii, Ladd (1966, 1972, 1977, 1982) on West Pacific Islands, Hayasaka & Oki (1971) on Kagoshima Japan, Taylor (1978) on Aldabra (Indian Ocean), Crame (1986) on Kenya, and Paulay (1990) on tropical oceanic islands.

In 2008, Ludwig Blanc brought to one of the authors (JL) three specimens of an unidentified *Strombus* species collected from a marshy area just extracted by sub-surface dredging on the lagoon margin of Niau Atoll. In 2008 and 2010 a rich assemblage of fossil molluscs was collected at the same site (JL). This gave rise to the description of three new gastropod species (*Strombus blanci* Tröndlé & Salvat, 2010, *Terebra*

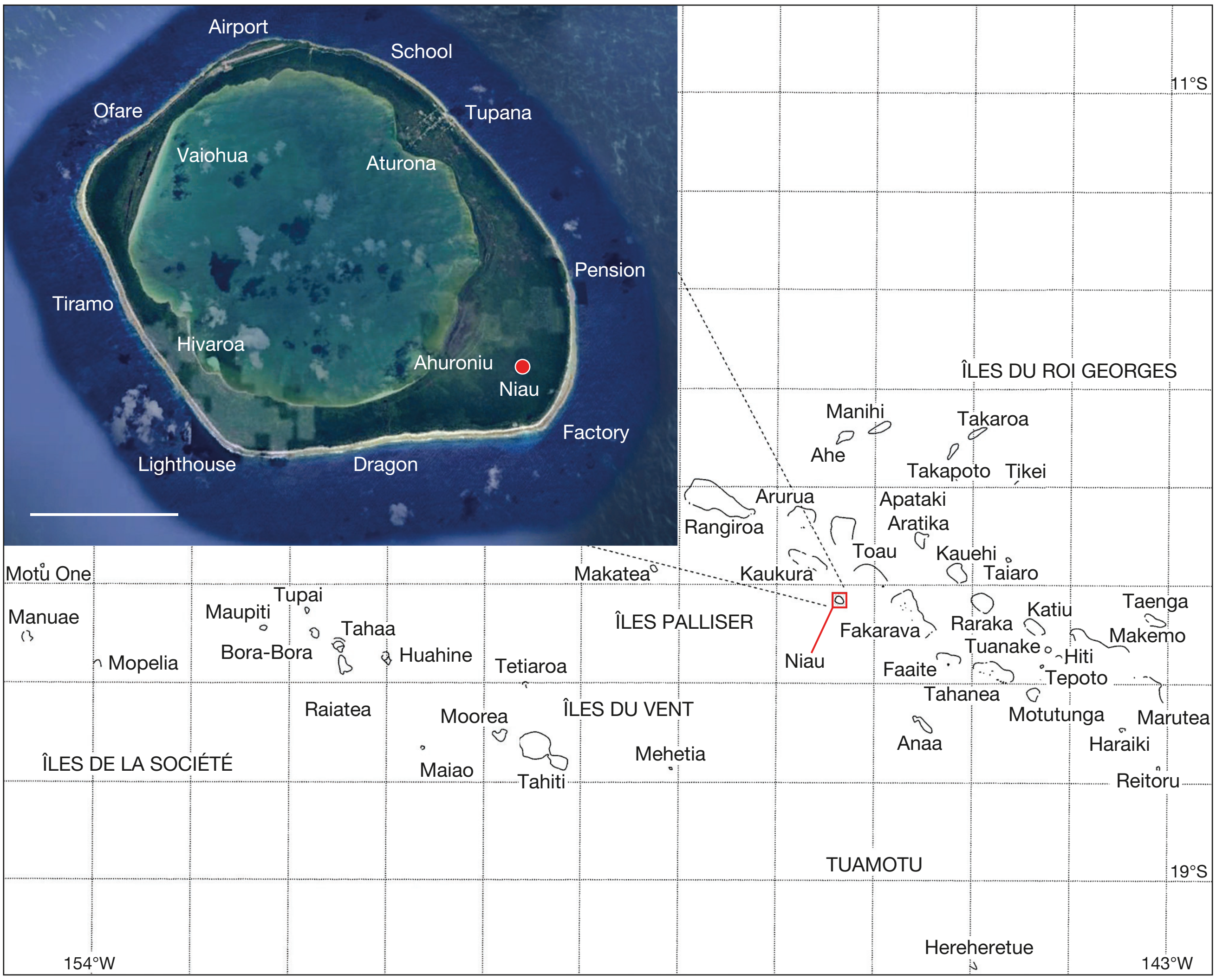


FIG. 1. — Geographic location of Niau Atoll (Tuamotu, French Polynesia) with local toponymy of sampling sectors.

niauensis Tröndlé & Letourneux, 2011 and *Turbo fakaauensis* Tröndlé & Letourneux, 2012) and to a comprehensive study of the 120 listed species (Salvat *et al.* 2018). This predominantly lagoonal assemblage was reported previously as dating from the last interglacial stage (128 000-116 000 years BP), with identifications of endemic species and species extinct since that time in French Polynesia, but it was later dated from the Plio-Pleistocene (Late Pliocene-Early Pleistocene) by Montaggioni *et al.* (2023). Moreover, in September-October 2022, we (BS) carried out on more recent lagoonal mollusc assemblages in order to obtain datations on Holocene material.

The objectives of the present paper are: 1. To identify and describe the molluscan new species and assemblages from both the reef rim and the lagoon in relation with the local stratigraphical history. 2. To reconstruct the evolutionary stages of molluscan development from the Late Pliocene (i.e. the last 4 million years) to the Holocene including speciation and extinction events.

ENVIRONMENTAL SETTINGS

GEOGRAPHY

Niau, also known as Fakaau, is a small, almost circular atoll in the Tuamotu archipelago in French Polynesia, located at 16°10' south latitude and 146°20' west longitude (Figs 1; 2A). Niau atoll is less than 50 km west of Fakarava, one of the largest atolls of the Tuamotu and located 350 km southwest of Tahiti. Niau is a closed atoll with a continuous emerged subcircular reef-rim, the width of which varies from 0.5 km in the northwest to 3.6 km in the southeast. The reef-rim completely isolates the lagoon waters from the open ocean. The total surface area of the atoll, bounded seawards by an outer reef-flat zone, is around 60 km^2. The emerged part, covered with vegetation, is 22.15 km^2 and its central lagoon 31.88 km^2. The atoll perimeter reaches 30 km (Andrefouet & Chauvin 2005; Butaud 2006).

Fig. 2. — Niau Atoll (Tuamotu, French Polynesia): **A**, aerial view of the northern part. In the foreground from left to right: village of Tupana, airplane runway and Ofare-Vaiohua sector; **B**, Coastline: fringing reef, conglomerate platform and beach, Ofare sector. Credit: A, P. Bacchet; B, B. Salvat.

OCEAN MARGIN

Niau Atoll is bordered by a fringing reef, 100 to 200 m wide (Fig. 2B) presenting the usual biozonation observed throughout the Tuamotu archipelago, from the ocean inwards: a reef front, usually, in the form of an algal crest where the ocean waves are breaking, a reef-flat zone a few decimeters deep at mean tide level, a conglomeratic platform ("old reef conglomerate") and a sandy beach. Along the north-western and

Fig. 3. — Niau Atoll (Tuamotu, French Polynesia): **A**, North-western rim side showing the Upper Pleistocene reef (last interglacial high sea stage) bordering the coast, South Ofare (Teruahina) sector; **B**, Southern reef-rim side, Mid Holocene algal crest, Phare sector. Credit: A, B. Salvat.

north-eastern edges, another fossil reef unit crops out between the modern reef flat and the coconut grove. In the northwest (Ofare) and northeast (Tupana) sectors (Figs 1; 3A) this unit occurs at the upper limit of the beach, with a micro-cliff 1 to 3 m high. This palaeo-reef had been spotted by Veeh (1966), but the collected and uranium/thorium (U/Th) dated coral specimens were not accurately field positioned. However, the dated reef outcrops are postulated to be those found at Ofare or south Ofare where they are very accessible. Veeh (1966) obtained ages ranging between 120 000 and 160 000 years BP. In the southern part of the atoll, the reef-flat zone facing the ocean is bounded seawards by an ancient *Porolithon* Foslie, 1909 dominated algal ridge, the height of which exceeds locally 1 m (Fig. 3B). Due to the breaking wave effects, this ridge is broken up into about 1 m-long, a few centimeters thick fragments.

UPLIFTED ATOLL AND "FEO" RELIEFS AS THE ELEVATED ATOLL REEF-RIMS

Niau is a slightly raised island, as interpreted to have been elevated by relatively recent tectonic movements (McNutt & Menard 1978; Lambeck 1981; Montaggioni 1989; Montaggioni *et al.* 2023). Except for the extreme north of the atoll, in the area of the airstrip, characterized by steep cliffs about 8 m high (Fig. 4A), the average altitude of the reef-rim is 3 to 4 m. These elevations make Niau a so-called "uplifted" atoll, when compared to most Tuamotu atolls, the maximum height of their framework-built surfaces (i.e. reef flats) rarely exceed 0.5 m above present mean sea level. These surfaces were overlain by sandy deposits, during the last millennia, thus resulting in maximum atoll elevations averaging about 5 m. Reliefs of "feo" type (Butaud 2006; Cibois *et al.* 2007; Salvat *et al.* 2018), regarded as markers of uplift (McNutt & Menard 1978; Lambeck 1981; Montaggioni *et al.* 2023) occurred in Niau atoll as well as in six other nearby uplifted atolls (Makatea, Mataiva, Tikehau, Rangiroa, Kaukura, Anaa). Feo are jagged fossil coral reliefs of approximately 3 to 4 m in height (Fig. 4B, feo inland and Fig. 5A feo on beach, Niau Atoll). A dense forest, difficult to penetrate, has developed over these reliefs, locally separated by excavations, about 2 to 3 m deep and covered with plant debris. Some excavations between the karstic reliefs lead to caves. The limestone rocks, constituting the core of the feo, are intensively calcitized and dolomitized.

THE COCONUT GROVE

These fossil reefs of feo type are bordered oceanwards and lagoonwards by a coconut grove, except in the airport sector to the north of the atoll, where the coast is made out of cliffs and devoid of fringing reef (Fig. 4A). These two coconut groves are nearly 8 km^2 in area (Butaud 2020), which are three times smaller than the feo-built, raised rim zone.

THE SWAMPS

The marshes near the lagoon exhibit low-growing or man-high halophytic vegetation. They cover a total of 1.22 km^2 (Butaud 2006). The swamp (Fig. 5B) is colonized by *Cladium mariscus* (L.) Pohl, 1810 (Cyperaceae Juss.) – "uuti" locally – and is found at the so-called "La Piscine" site (swimming pool), close to the ancient Ofare village that was used as an extraction area of materials for constructing the airplane runway in the early 2000. In the middle of this swamp, five dredging basins cover seven hectares. In the centre of swamps near Ofare and Aturona, there are archaeological sites which are currently under study: the Vaiohua platform (16°08'08.46"S, 146°23'09.48"W) and the marae from Aturona (16°08'26.53"S, 146°19'54.30"W). Another marshy area bordering the lagoon to the southwest also includes an archaeological site at Hivaroa marae (Fig. 1). At Ofare-Vaiohua (Fig. 1) in the *Cladium* P. Browne, 1756 marshy area, there are patchy, calcareous crusts among the low-growing or shrubby vegetation cover (Fig. 5B, C). These crusts are flat-topped and uniform, but almost entirely covered by a terrigenous, organic-rich deposit, about 0.30-0.70 m thick. Closed to the dredging basins, south of the Vaiohua platform, are found sandy mounds bearing large, 0.30-0.10 m thick, fragments of this calcareous crust at top. This crust is known by pedologists in hydromorphic marshy soils as "limestone crust" (Jamet & Trichet 1987) and reported by Butaud (2006) from Niau Atoll.

This pedogenetic crust type, also called "caliche" or "calcrete" (Lidz 2011), is a paleosol formed from limestone source rocks. In some arid to semi-arid regions, these paleosols can reach several metres in thickness, but in humid tropical climates, rarely exceeds a few centimetres. Caliches are products of chemical alteration resulting from microbial mediation during rainy and dry seasons. During rainy periods, limestone rocks are dissolved and percolating waters enriched in calcium and carbonate ions migrates downwards to the water table. During drier periods, infiltrated waters tend to rise upwards to the ground surface by capillarity. There, waters are evaporating, thus allowing Ca^{2+} and CO_3^{2-} ions to precipitate, thus generating a surficial crust.

THE LAGOON

The lagoon at Niau occupies the central part of the island, completely bordered by coconut groves and locally by marshy areas. The lagoon is called "vaitamae" by the natives, meaning "fermented, rotten, withered" water (Torrente 2018). Its surface area is approximately 22 km^2; its depth averages 2 m. Small, deeper basins can reach 5 to 6 m depth. Due to lack of direct water exchange with the ocean, the lagoon is brackish and salinity does not exceed 32 g/l occasionally (Landret 1977; Lagouy pers. com. 2009). After heavy rains as in March 2010 (Galzin & Verducci pers. com.,) salinity was shown to vary between 23.1 and 23.6 g/l and temperature between 29.9°C and 31.8°C. Ocean water resurgences through the reef mass and karstic structures, locally called "marite", explain such a salinity in the lagoon. These "marite" occasionally presenting bubbling waters are a few metres deeper than the bottom of the neighboring lagoon. Strong swells during cyclonic periods bring ocean waters into the lagoon, through overwashing of the emerged atoll rim in its lowest places. This was learned by Agassiz (1903) during the Albatross Expedition in 1899-1900: the atoll rim at Niau would have been overwashed

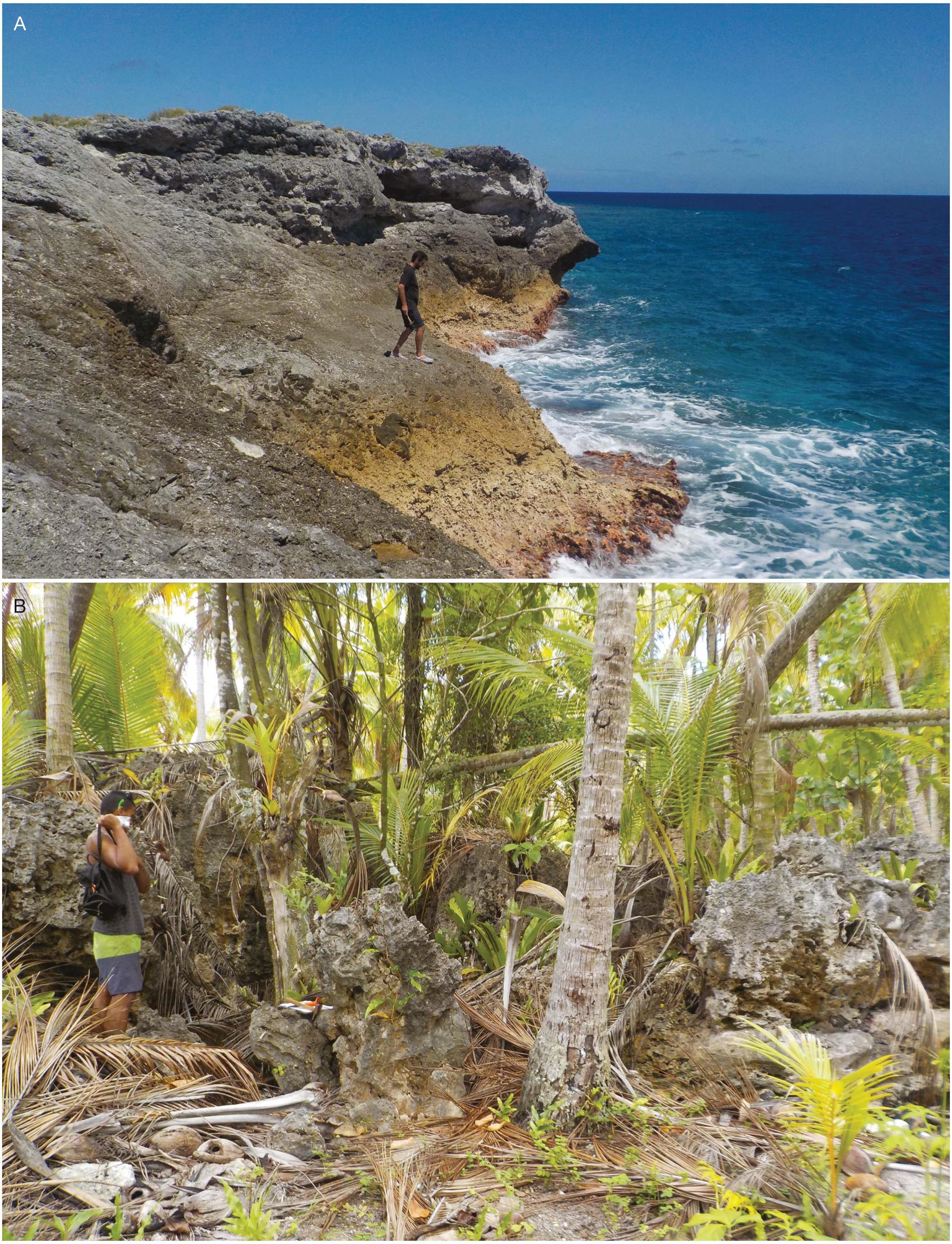


FIG. 4. — Niau Atoll (Tuamotu, French Polynesia): **A**, Cliff north of the atoll, airport area, showing the Mid-Upper Pleistocene reef unit; **B**, central part of the reef rim, Plio-Pleistocene feo zone, Vaiohua sector. Credit: B. Salvat.

during the 1878 cyclone. He noted that the lagoonal waters were very salty and at a temperature of 28°C. The "Pacific Island Pilot", a navigation manual from 1920 and 1926, reported that before the 1878 cyclone, the lagoon was a kind of freshwater lake becoming brackish since this hazard event. However, this observation should be taken with caution. During the cyclones in 1983 (Orama in February; Veena in April) which destroyed the majority of buildings in Niau, it was reported to us by Ms. Torohia (resident at Tupana) that waves broke in Ofare and Tupana areas and overwashed the reef-rim to reach the lagoon. Note also that during usual, calm periods, intense evaporation of lagoonal waters is operating, thus increasing salinity. Therefore, one must consider that the lagoonal water regime typified by infiltration from the ocean through the karstified rim structure, precipitation, evaporation and occasional massive flooding during cyclonic events determines salinity values that can vary greatly over several decades.

The Niau lagoon is partly filled with "kopara" (or "opara" locally), consisting of cyanobacterial mats, coloured from red to green (Rougerie *et al.* 1997; Trichet & Delage 1999), up to 2-3 m in maximum thickness and found at depths of 4 to 6 m on the bottom (Galzin & Verducci pers. com.). Apart from the molluscan fauna, the lagoon contains three fish species only: 1) *Chanos chanos* (Forsskål, 1775) or milkfish, from the family Chanidae Günther, 1868 (Galzin & Verducci pers. comm.); 2) *Oreochromis mossambicus* (Peters, 1852) or "tilapia" from the family Cichlidae Bonaparte, 1835, introduced in the 1950s (Tröndlé & Salvat 2010); and 3) a small goby *Bathygobius cocosensis* (Bleeke, 1854). The first species, locally called as "pati", is feeding on kopara and is an important local food resource (Torrente, 2018). We also note the presence of a shrimp, *Palaemon debilis* Dana, 1852 from the family Palaemonidae Rafinesque, 1815. The molluscan fauna, currently living in the lagoon, was identified taken into account some recent species introductions.

AGE AND DEPOSITIONAL HISTORY OF THE EMERGED ATOLL RIM

Based on isotope dating (Montaggioni *et al.* 2023), the raised carbonate reliefs that make up the atoll rim are proven to belong to three distinct reef generations.

Plio-Pleistocene Feo Unit

The oldest, deeply calcitized feo, dated by using the strontium isotope method in several sectors are Late Pliocene or Early Pleistocene in age: top of the Airport cliff (samples N49 and N51): 1.124 Ma (between 1.2 and 0.94 Ma) and 1.140 Ma (between 1.31 and 0.96 Ma); inner island airport sector (sample N100): 1.893 Ma (between 1.488 Ma and 2.105 Ma); Ecole (school, Fig. 1) sector in the north-north-east of the atoll (sample N98): 1.411 Ma (1.690 to 1.220 Ma); Pension sector to the east (sample N14): 1.328 Ma (between 1.200 to 1.485 Ma); Dragon sector to the south (sample N7, beach site; sample N87, inland site): 3.672 – 3.800 Ma – and 3.146 Ma; Tiramo sector to the southwest (sample N84): 1.092 Ma (see Montaggioni *et al.* 2023: supplementary material, table S5).

Two caliche samples (Fig. 5B, C) were dated using the strontium isotope method. Ages range from 2.245 Ma (sample N42) to 2.505 Ma (sample N44). This Early Pleistocene age relates to deposition of this reef unit as observed along the northern rim side. However, the Sr-derived ages could be biased, due to mixing between marine and fresh water Sr isotopes during caliche formation. This may result in apparent rejuvenation of caliche deposits.

In the Plio-Pleistocene feo zone some large valves of giant clam *Tridacna gigas* (Linnaeus, 1758) and *Tridacna squamosa* Lamarck, 1819 have been collected by natives. We noted also the presence of scattered specimen of large *Codakia punctata* (Linnaeus, 1758) with their two valved closed. Strontium isotope dating of a shell *Tridacna gigas* sample (Niau TG) returned an age of 2.337 Ma (Early Pleistocene), consistent with the age of the internal feo zone.

Plio-Pleistocene age of molluscan and coral thanatocenosis

Based both on the available data on Niau geological history about fifteen years ago and on the apparently "fresh" nature of the molluscan shells collected at 4 m deep within loose sediments, Tröndlé & Salvat (2010) inferred an age of 120 000 years (Late Pleistocene) for *Striatostrombus blanci* (Tröndlé & Salvat, 2010). This age was also attributed to the two other new species of molluscs extracted from the same lagoonal deposit (*Oxymeris niauensis* (Tröndlé & Letourneux, 2011) and *Turbo fakaauensis* Tröndlé & Letourneux, 2012). In 2013, the attempt to date three molluscan shells extracted from the thanatocenosis (*Striatostrombus* Dekkers & S. J. Maxwell, 2018, *Polinices* Montfort, 1810 and *Indotellina* Huber, Langleit & Kreipl, 2015 using the uranium/thorium method proved inconclusive, due to diagenesis. Corals (*Porites* sp. and *Leptoria phrygia* (Ellis & Solander, 1786)) collected close to the pool area where molluscs had been first collected, were subjected in 2014 to strontium isotope dating (University of Frankfurt, unpublished data). These returned ages between 2.78 and 4.74 million years. In order to confirm these results, some specimens of the molluscan assemblage were re-dated using the strontium isotope method. From the two selected *Striatostrombus blanci* shells, were subsampled one superficial and one internal fragment, which yielded ages between 2.017 and 3.064 million years (N *Strombus* 1 and 2, see Montaggioni *et al.* 2023: supplementary material, table S4). Dating of two other *Codakia punctata* (Linnaeus, 1758) valves and of a merulinid coral sample gave similar ages, between 2.912 and 3.814 million years (N17 coral et N18 bivalve, see Montaggioni *et al.* 2023: supplementary material, table S4). As a summary, the age of the molluscan and coral assemblage ranges between 2.0 and 3.8 million years, revealing it is Plio-Pleistocene.

Upper Pleistocene Unit (Late Pleistocene age)

Adjoining the Upper Pliocene feo unit, there are two reef systems along the north-western and eastern rim sides locally

Fig. 5. — Niau Atoll (Tuamotu, French Polynesia): **A**, Southern reef-rim side, Pliocene reef remnants, Dragon sector, Niau Atoll (Tuamotu, French Polynesia); **B**, *Cladium mariscum*-rich swamp with caliche patches, Vaiohua sector; **C**, caliche with an incorporated coral colony, Vaiohua sector. Credit: B. Salvat.

identified by Veeh (1966) as belonging to the last interglacial high sea stand about 120 000 yr BP. The newly dated U/Th coral specimens are affected by incipient diagenetic alteration. Accordingly, the newly obtained ages refer to "approximate ages", not "absolute" or "true" ages (Montaggioni *et al.* 2023: supplementary material, table S3): at South Ofare, 135 005 ± 2289 cal. years BP (sample N27), at Tupana 132 067 ± 1686 cal. years BP (sample N72). These re-calculated ages are close to those related to the last interglacial high sea maximum, beginning at 128 000 cal. year BP (Murray-Wallace & Woodroffe

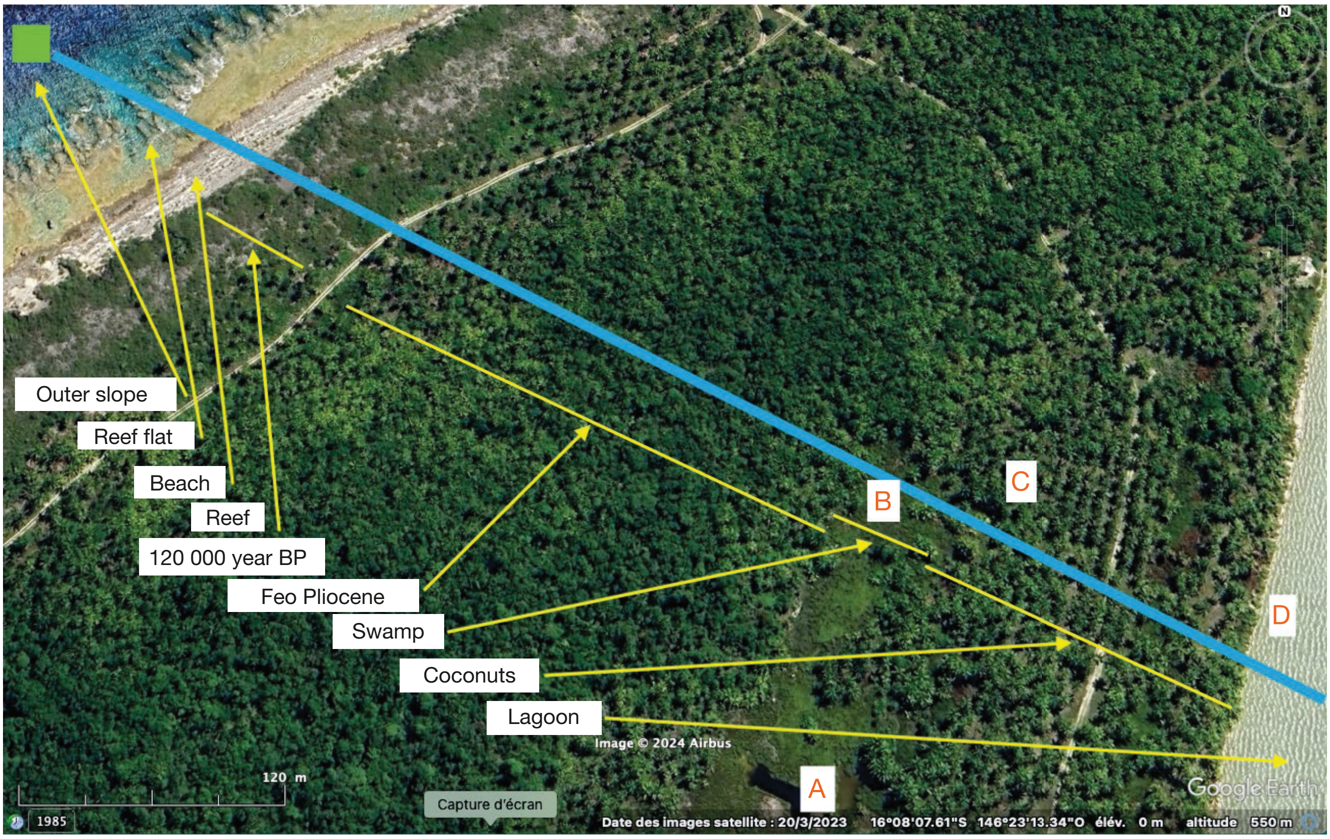


Fig. 6. — Google Earth view of the Ofare-Vaiohua sector, northwest of Niau Atoll (Tuamotu, French Polynesia). Delineation of the different geomorphological units from the ocean to the lagoon with the location of the main mollusc collecting points. **A**, "Piscine" sector, Plio-Pleistocene thanatocenosis dredged from swamps; **B**, Vaiohua archeological platform, Late Holocene thanatocenosis; **C**, coconut grove with Late Holocene thanatocenosis (taro pit); **D**, lagoon, modern assemblage.

2014). Consequently, these reef units are regarded as belonging to the last interglacial period that is the chemiostratigraphic MIS 5e, i.e. Late Pleistocene in age (Montaggioni *et al.* 2023). These cannot have developed from 135 000 years BP at the end of the low-sea stand (MIS 6: about 185 000 to 135 000 yr BP), that was during the Mid-Pleistocene (Murray-Wallace & Woodroffe 2014), at the time when sea level was probably lower than 100 m below its present position (Rohling *et al.* 1998; Masson-Delmotte *et al.* 2010).

Mid Holocene algal ridge on the reef flat ocean margin

An exposed algal crest, dated by the U/Th method, yielded an age of 4695 ± 0.052 years BP (sample N18, Montaggioni *et al.* 2023: supplementary material, table S3) corresponding to the Mid Holocene, emplaced at a time when the average ocean level was approximately 0.80 m higher than present. Similar algal features are found in most outer reef crests in the Tuamotu (Takapoto, Fakarava) and in the Society (Tetiaroa).

Overwiew of the depositional history of the atoll rim

The standard tectonic behaviour of mid-plate, mid-ocean volcanic islands is to sink after cessation of eruptive activity. This sinking (thermal subsidence) results mainly from the cooling and load increase of the underlying oceanic crust, which is no longer "heated" by the rise of magmatic asthenospheric (mantle) material. The uplift of seven islands in the north western part of the Tuamotu archipelago (Mataiva, Tikehau, Rangiroa, Kaukura, Niau, Anaa and Makatea) was recently demonstrated as resulting from the interplay between the northwestward migration of the Pacific lithospheric plate and the volcanic rejuvenation of the Society hotspot, resulting in a regional mantle bump ("asthenospheric bumping model" (Montaggioni *et al.* 2023, 2024). When the drifting plate that supports the seven atolls mentioned above, has entered the zone of influence of the Society hot spot (currently centered in the vicinity of Mehetia), the atolls have been uplifted incrementally over the last 2 million years, depending on their geographical position (Montaggioni *et al.* 2023, 2024). The exposed parts of the atoll rim at Niau are believed to have started to deposit about 4 Ma ago, during the Late Pliocene times, when sea level was about 20 to 30 m above its present position. Then, according to the standard thermal subsidence effect, Niau has been drowned since this time, resulting in the deposition of Early Pleistocene reef generations. Niau is likely to have been uplifted not prior to 0.5 to 0.3 Ma, presumably in relation to the intense Mehetia activity (Montaggioni *et al.* 2023). Accordingly, the Plio-Pleistocene reef unit have undergone long periods of emergence during which karst erosion deeply altered them, resulting in the present geomorphic features. The uplift of the atoll has resulted in an isolation and drying of the lagoon until now.

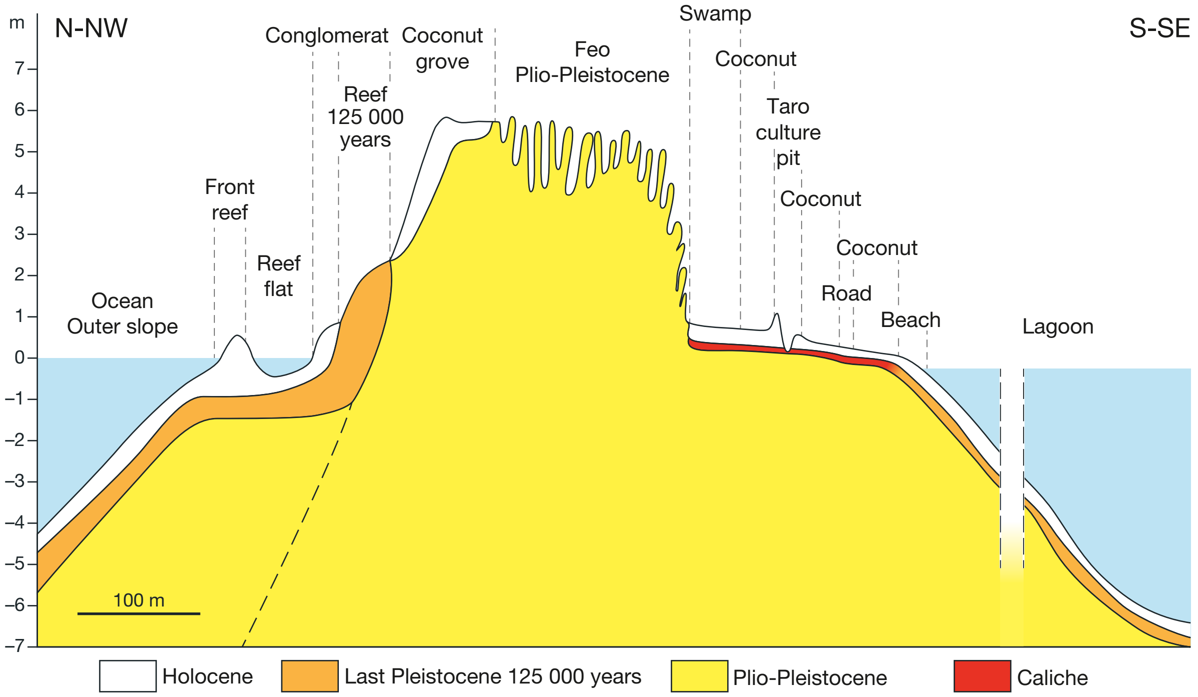


FIG. 7. — Topographical profile and morphological units of the Vaiohua sector from the ocean to the lagoon, Niau Atoll (Tuamotu, French Polynesia).

MATERIAL

MATERIAL FOR THE MOLLUSCAN STUDIES

One of the authors of the present paper (JL) collected in 2008 and 2009 a molluscan assemblage, composed of 120 species to be identified (identifications made by JT and JL) and listed by Salvat *et al.* (2018) and dated by Montaggioni *et al.* 2023 from the Plio-Pleistocene. This assemblage was dredged down to 4 meters deep from swamps near the Vaiohua sector which are presently locally called "la Piscine" (swimming pool; 16°08'22.32S, 146°23'14.09W; Fig. 1). The collection of this assemblage labelled "collection Letourneux, Niau" was housed at the Malacology Laboratory of the Muséum national d'Histoire naturelle in Paris. It gave rise to the description of three new gastropod species (*Strombus blanci* Tröndlé & Salvat, 2010, *Terebra niauensis* Tröndlé & Letourneux, 2011 and *Turbo fakaauensis* Tröndlé & Letourneux, 2012). New field researches on Holocene in 2020 (BS) have been carried in the localities of Aturona (samples N54 to N63), Vaiohua near the archeological platform (samples N103 to N106, N108, N90 to N94, TP1A and TP1B), Vaiohua on taro pit (sample N107) and in the modern material lagoon (Vaiohua near the shore, sample N95), see Figures 1 and 6 for the location. They allow us to collect other molluscan assemblages, which have been added to the collection, which is now housed in the collection of Palaeontology of the Muséum (sector fossil invertebrates).

MATERIAL FOR THE RADIOMETRIC STUDIES

For radiocarbon analysis on Holocene material, four samples were taken at three points: Aturona (sample N57, *Quidnipagum palatam* Iredale, 1929), Vaiohua near the archeological platform (samples N103 and N121, *Cerithium* sp.) and Vaiohua taro pit (sample 107, *Ctena bella* Conrad, 1837).

METHODS

OBSERVATION OF COLORED PATTERNS FROM FOSSIL MOLLUSCS UNDER UV LIGHT

The observation of colour patterns on fossil shells in natural light is difficult, as the degradation of the pigments happens quickly after the death of the animal and continues also during fossilization. A solution to the problem is the use of ultraviolet light (UV), as the colour pattern of the fossil shells becomes visible with the exposure of wavelengths below 365 nm. In fact, the colored areas have not completely lost their pigments and can take on a white, beige, yellow or red color. These still pigmented surfaces contrast with a more depigmented background which, under UV light, often takes on a dark tint. This contrast between the different shell areas forms the color pattern. In the last fifteen years, many works have pointed out that the colour pattern of gastropods and bivalves can be easily revealed for the Cenozoic era and are important for their identification at species level (see Caze *et al.* 2011; Psarras *et al.* 2021 for more references). This technique is used herein to study fossil molluscs from Niau that potentially display a colored pattern (e.g., Conidae J. Fleming, 1822). The shots were conducted using the same UV exposure (3600 Å). The photographs are presented as they were taken or sometimes in reverse image. We used Photoshop to create digital negative/inverse images of the photographs taken under UV light, thereby reconstructing what the shell would have looked like when the animal was alive.

RADIOMETRIC DATING

The carbon-14 method is applicable to samples younger than 50 000 years. Radiocarbon ages are expressed in years BP by reference to 1950. Gastropods and bivalves extracted from the swamps and aroid taro culture pits were radiocarbon dated at the LMC14/LSCE laboratory (Gif-sur-Yvette). The sample preparation was conducted according to the protocol developed by Dumoulin *et al.* (2017). The measurements were carried out using Artemis accelerator mass spectrometer (AMS) (Moreau *et al.* 2020; Beck *et al.* 2024). The ages obtained were calibrated with the IntCAL Marine 20 curve (Heaton *et al.* 2020) and the Oxcal4.4 software (Bronk Ramsey 2001). The reservoir age correction used was made with ΔR 140 ± 20 years based on data obtained for French Polynesia (Petchey *et al.* 2008).

ABBREVIATIONS

Repositories

NHMUK	Natural History Museum, London (BMNH);
MNHN	Muséum national d'Histoire naturelle, Paris;
MNHN.F	MNHN, Paleontology collection;
MNHN.IM	MNHN, Marine Invertebrates;
EPHE	École pratique des Hautes Études, Moorea and Perpignan.

Shell measurements

H	height;
APL	antero-posterior length;
DVL	dorso-ventral length;
P	primary cords (following the methodology on identification used by Merle (2001, 2005) for the muricids;
s	secondary cords.

RESULTS

Although surveys on Niau Atoll were carried out at different locations of the emerged reef rim and of the swamps and the lagoon, the results are presented site by site along a transect running from the fringing reef to the lagoon, located in the Ofare area, northwest of the atoll. On Figure 6, from an aerial Google Earth image, are delineated the different geomorphic features and units: outer reef slope, fringing reef-flat zone, conglomerate pavement, successive emerged, fossil reef units, coconut grove, feo zone (i.e. Plio-Pleistocene feo reef unit), swamp with the archaeological site of Vaiohua, coconut grove, beach, lagoon. Figure 7 gives a topographic profile across the same area, with location of the different geomorphic units. Figure 8 is a detailed morphological profile, restricted to the Vaiohua swamp site, the coconut grove and the lagoon margin. Due to the lack of precise topographical surveys, the ocean and the lagoon surfaces are considered to be at the same level.

LAGOON MOLLUSCAN ASSEMBLAGES SINCE THE LATE PLIOCENE

The Plio-Pleistocene molluscan assemblage beneath the limestone crust (assemblage n°1, see Fig. 8)

New insights into the composition of the Plio-Pleistocene molluscan assemblages.
Table 1 gives the new list of 92 species which is the up dated list of 120 species previously published by Salvat *et al.* (2018). It includes the species mentioned in the 2018 list after deletion of those which were only mentioned at the generic level with sp., after corrections of names following synonymies, and after an order of presentation considering the evolution of the classification of molluscs since 2018, and with the addition of the new species described in this article (section below, Systematic palaeontology). An abundance index was assigned to each of these 92 listed species (Table 1) in the collected assemblage. Only five species revealed an abundance greater than 100 individuals (code D in Table 1). These species are *Fragum fragum* (Linnaeus, 1758), *Finella pupoides* A. Adams, 1860, typical species of sandy lagoonal habitat, *Cerithium punctatum* Bruguière, 1792*, Cerithium niauense* Merle, n. sp. and *Clypeomorus bifasciata* (G. B. Sowerby II, 1855), species which generally inhabit hoa (channels between islets on atoll rim) and intertidal limestone flagstones. *Striatostrombus blanci* (Tröndlé & Salvat, 2010) and *Oxymeris niauensis* (Tröndlé & Letourneux, 2011) as other strombids and terebrids species are characteristics of lagoon shallow sandy bottoms. The molluscan assemblage also includes back-reef species such as *Turbo fakaauensis* Tröndlé & Letourneux, 2012 and supralittoral species such as *Nerita plicata* Linnaeus, 1758 and *Littorina coccinea* (Gmelin, 1791).

The analysis of new specimens from this assemblage under UV light reveals five new species: *Cerithium niauense* Merle, n. sp., *Conus* (*Conus*) *letourneuxi* Merle, n. sp., *Conus* (*Tesselliconus*) *georgesrichardi* Merle, n. sp., *Bulla niauensis* Merle, n. sp. and ?*Gafrarium troendlei* Merle, n. sp. Two other species are described herein ?*Lunulicardia distorta* Merle, n. sp. and *Indotellina fakaauensis* Merle, n. sp. Moreover, the identification of two specimens to *Tellinella virgata* (Linnaeus, 1758) is still uncertain. All these new species seem endemic from Niau as *Turbo fakaauensis*, *Striatostrombus blanci* and *Oxymeris niauensis* for which the colour pattern was also researched under UV light. Their stratigraphic range is restricted to the Plio-Pleistocene, except *Cerithium niauense* Merle, n. sp. which is still present in Late Holocene deposits as mentioned later in the paragraph related to the assemblage above the limestone crust. The detailed systematic analysis is provided below in the section "Systematic palaeontology".

The Mid and Late Holocene molluscan assemblage above the limestone crust (assemblage n°2, see Fig. 8)

The *Sesuvium* swamp surface near the Aturona marae exhibits a humus layer, 15 cm thick, overlain by a sandy bed (sample N54) containing only Thiaridae, *Melanoides tuberculata* (O. F. Müller, 1774) specimens. A mound, about fifty square metres, occurs approximately 0.30 m above the *Sesuvium* swamp, containing shrubs of *Pemphis acidula* J.R. Forst. & G. Forst., 1775.

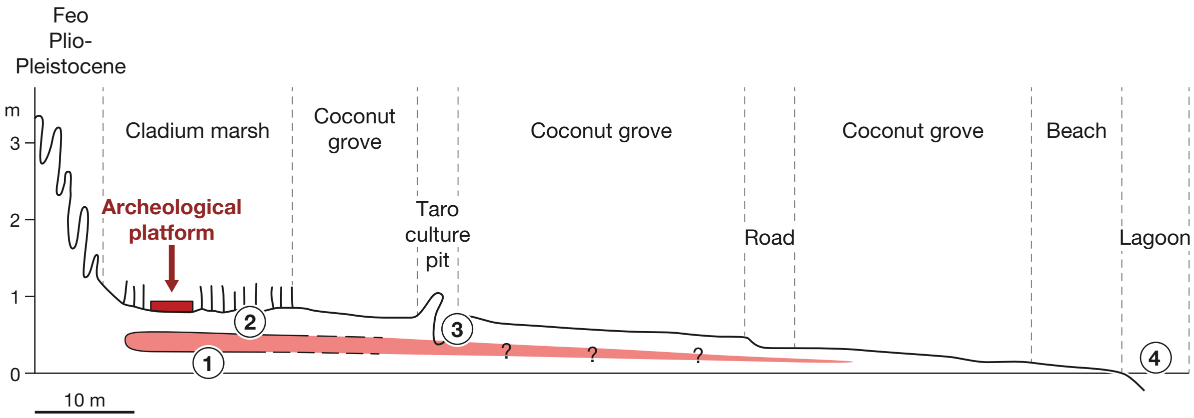


Fig. 8. — Topographic profile of the Ofare-Vaiohua sector, northwest sector of Niau Atoll (Tuamotu, French Polynesia) with mollusk assemblages: **1**, Plio-Pleistocene; **2**, Holocene beds overlying the caliche; **3**, Holocene deposits accessible from taro culture pits; **4**, Modern lagoon. Caliche in red. The assumption is made that the level of the lagoon is the same as that 0 m of the ocean.

From a 0.50 m deep hole dug at base of the shrubs (samples N57 to N63), were collected 30 specimens of *Ctena bella*, 26 of *Gafrarium pectinatum* (Linnaeus, 1758), seven of *Cerithium niauense* Merle, n. sp., one specimen of *Tellinella virgata* (Linnaeus, 1758) and one valve of *Quidnipagus palatam* Iredale, 1929 (sample N57). The latter returned an age of 5715 years BP or the interval 6238-5912 cal yr BP after calibration (Mid Holocene) and corrected for marine reservoir age (Table 3).

Close to the Vaiohua archaeological platform (16°08'08.46S and 146°23'09.48W) there was conducted a detailed examination of several holes in the swamp. This reveals a terrigenous layer, about 0.20 m thick, overlying a shell sand overlying the limestone crust. From this sandy bed, were collected twelve samples (N90-N91, N93-N94, N103-N106, N108, N121, TP1A and TP1B). This sand bed overlies limestone caliche surfaces at depths of 0.40-0.30 m. After sieving, these sediments delivered molluscs, together with some fragments *Acropora* Oken, 1815 less than 1 cm long. The molluscan species vary in abundance and the collected material contains: very numerous valves of *Ctena bella* Conrad, 1837, 39 unidentifiable depigmented specimens of *Cerithiums* sp., 37 specimens of *Cerithium rostratum* G.B. Sowerby II, 1855, 17 specimens of *Cerithium niauense* Merle, n. sp., 15 specimens of *Gafrarium pectinatum* (Linnaeus, 1758), ten specimens of *Dendrostrea sandvichensis* (G.B. Sowerby II, 1871) and some other species including one or two specimens of *Cerithium columna* G. B. Sowerby I, 1834 and *Fragum fragum* (Linnaeus, 1758). Table 2 lists all species collected and Figure 9 illustrates the main species identified in this assemblage. Cerithiidae specimens (*Cerithium* sp.) in the above-mentioned molluscan assemblages have been radiocarbon dated. The relevant ages are given in Table 3. The *Cerithium* sp. in samples N103 and N121 give calibrated ages of 3845-and 3290-years BP, corresponding to calibrated age intervals of 3982-3627 cal yr BP and 3310-2954 cal yr BP after correction for marine reservoir age. This indicates that this assemblage relates to thanatocenosis the species of which were alive between 3 and 4 millennia ago (Late Holocene). In conclusion, considering the dating of mollusks on the site of Aturona (Mid Holocene) and the site of Vaiohua near the archaeological platform (Late Holocene), we qualify the inventoried assemblage as Mid and Late Holocene assemblage.

The Late Holocene molluscan assemblage in the selected taro pit above the limestone crust (assemblage n°3, see Fig. 8)

In the coconut grove, between the marshy area where the Vaiohua archaeological platform is located and the lagoon margin, there are ancient horticultural pits, locally called "maite", present in the form of small embankments and trenches dug by the former inhabitants in order to culture taro (*Colocasia esculanta* (L.) Schott, 1832) as a food tuber), fresh water stagnation in pits allowing the cultivation (Chazine 1990; Niva 2020). The difference in height between the top of the slope and the bottom of the trench is about 3-4 m as those observed in many other atolls (Chazine 1990). The sediments currently deposited at the top of the embankments are those which were extracted by the inhabitants at approximately 1 to 2 m depth to form pits. In addition to some *Acropora* detritus, the extracted sediments contained a shell assemblage (sample N107) listed on Table 2 dominated by *Ctena bella* (Conrad, 1837) with rare *Cerithium columna* G. B. Sowerby I, 1834 and *Cerithium niauense* Merle, n. sp. individuals and even rarer *Fragum fragum* (Linnaeus 1758). *Ctena bella* shells returned an age of 2195 years BP or the interval 1904-1610 cal yr BP after calibration and correction for reservoir age (Table 3).

The modern molluscan assemblage of the lagoon (assemblage n°4, see Fig. 13)

In the lagoon, there are very few living species of molluscs listed on Table 2 and distributed according to two assemblages. The first includes species, abundant throughout the lagoon with shells accumulating along the lagoonal shores: *Ctena bella* (Conrad, 1837) is the dominant bivalve, associated with gastropods *Clypeomorus brevis* (Quoy & Gaimard, 1834) and *Cerithium punctatum* Bruguière, 1792 (Fig. 10, sample N95). Some fragments of *Pinctada maculata* (Gould, 1850) are associated with these deposits but only of small individuals. These species are living both in and on sediments and shell accumulate beneath the thick kopara bed, typical of the Niau lagoon. The salinity varies between 23 and 32 g/l, but can drop in response to heavy precipitations and the water temperature is close to 30°C. The second assemblage includes five species that live in and near oceanic water resurgences across the karstified atoll feo reliefs, at some points in the center of the lagoon, so-called "marite" by the natives and with cooler ocean waters and to salinity close to 36 g/l: *Cerithium columna* (G. B. Sowerby I, 1834), *Quidnipagus palatam* Iredale, 1929, *Gibberulus gibbosus* (Röding, 1798)*, Notocochlis gualteriana* (Récluz, 1844), *Fragum fragum* (Linnaeus, 1758) and *Longchaeus maculosus* (Lamarck, 1822) – See Table 2, column modern lagoon, noted marite.

SYSTEMATIC PALAEONTOLOGY

The taxa presented in this section follow the systematic classification given in Molluscabase website (https://www.molluscabase.org) for new species and those described previously.

Class GASTROPODA Cuvier, 1795
Subclass CAENOGASTROPODA L. R. Cox, 1960
Order CAENOGASTROPODA *incertae sedis*
Superfamily Cerithioidea J. Fleming, 1822
Family Cerithiidae J. Fleming, 1822
Subfamily Cerithiinae J. Fleming, 1822

Genus *Cerithium* Bruguière, 1789

Type species. — *Cerithium adansonii* Bruguière, 1792, by subsequent designation (ICZN opinion 1109, 1978).

Cerithium niauense Merle, n. sp.
(Figs 9D-F; 11)

urn:lsid:zoobank.org:act:8A430C74-7DDA-4FEE-922E-7C9F2FD0D3D8

Cerithium tenellum – Salvat *et al.* 2018: table 1 [non *Cerithium tenellum* G. B. Sowerby II, 1855].

Type material. — **Holotype**. **France** • French Polynesia, Niau Atoll, "La Piscine": 6°08'22.32"S, 146°23'14.09"W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98401 (Letourneux coll.); H 20.1 mm (Fig. 11A-C).
Paratypes. **France** • 1 spm; same data locality as the holotype; Plio-Pleistocene; MNHN.F.A98402 (Letourneux coll.); H 19.1 mm (Fig. 11D-F) • 1 spm; Vaihuoa, near archeological platform (sample N106); Late Holocene; MNHN.F.A98404 (Salvat coll.); H 15 mm (Fig. 11G, H) • idem; MNHN.F.A98405 (Salvat coll.); H 15.5 mm (Fig. 11I, J), • 1 spm; same locality and age (sample N108); MNHN.F.A98403 (Salvat coll.); H 20 mm (Fig. 11K, L) • 1 spm; idem (sample TP1A); MNHN.F.A98406 (Salvat coll.): H 20.8 mm (Fig. 11M, N) • 1 spm; idem (samples TP1A); MNHN.F.A98407 (Salvat coll.); H 16 mm (Fig. 11O, P) • 1 spm; idem (samples TP1B); MNHN.F.A98408 (Salvat coll.); H 23 mm (Fig. 11Q, R) • 1 spm; idem (samples TP1B); MNHN.F.A98409 (Salvat coll.); H 19.9 mm (Fig. 11S, T) • 1 spm; idem (samples TP1B); MNHN.F.A98410 (Salvat coll.); H 14.6 mm (Fig. 11U, V).

Additional material. — **France** • 148 spm; same as the holotype; Plio-Pleistocene; MNHN.F.A98414 (Letourneux coll.) • 1 spm; Aturona (sample N58); Mid Holocenee; MNHN.F.A98417 (Salvat coll.) • 2 spm; idem (sample N57); MNHN.F.A98418 (Salvat coll.) • 4 spm; idem (sample N63); MNHN.F.A98420 (Salvat coll.) • 1 spm; Vaihuoa, near archeological platform (sample N90); Late Holocene; MNHN.F.A98419 (Salvat coll.) • 4 spm; idem (sample N91); MNHN.F.A98425 (Salvat coll.) • 16 spm; idem (sample N106); MNHN.F.A98424 (Salvat coll.) • 8 spm; idem (sample TP1A); MNHN.F.A98427 (Salvat coll.) • 11 spm; idem (sample TP1B); MNHN.F.A98428 (Salvat coll.) • 1 spm; idem (sample N105); MNHN.F.A98411 (Salvat coll.); Fig. 9D • 1 spm; idem (sample 105); MNHN.F.A98412 (Salvat coll.); Fig. 9E • 1 spm; idem (sample 105); MNHN.F.A98413 (Salvat coll.); Fig. 9F • 11 spm; idem (sample N105); MNHN.F.A98423 (Salvat coll.) • 8 spm; idem (sample N93); MNHN.F.A98415 (Salvat coll.) • 1 spm; idem (sample N108); MNHN.F.A98421 (Salvat coll.) • 1 spm, idem (sample N104); MNHN.F.A98422 (Salvat coll.) • 3 spm; idem (sample N94); MNHN.F.A98416 (Salvat coll.) • 1 spm; idem (sample N103); MNHN.F.A98426 (Salvat coll.).

Etymology. — From the type locality, Niau Atoll.

Type horizon. — Plio-Pleistocene (molluscs assemblage), see Figs 7; 8.

Type locality. — French Polynesia, Niau Atoll, "La Piscine": 6°08'22.32"S, 146°23'14.09"W.

Distribution. — Only know from the type locality, from Early Pliocene to Late Holocene.

Description

Shell medium in size, subangulate, slightly cyrtoconoid. Protoconch unknown. Apical angle 34°. Height of last whorl: 43.5% of shell lenght. Sculpture on spire consisting of weak to moderately strong, slightly curved axial ribs that are swollen near the posterior suture. On last whorl, one varical node in opposite side of the outer lip. Early whorls with three primary beaded cords (P1-P3), P2 being more prominent. Secondary cords s1 and s3 occasionnal. Last whorl with three slightly beaded primary cords (P1-P3) more prominent than the anterior cords (P4-P7). Secondary cords s1, s2, s3 and s4 occasionnal. Under UV light, beaded cords fairer than the background. Height of aperture: 32.5% of shell lenght. Outer lip slightly thickened. Inner lip callused, weakly detached. Anal notch moderately deep. Parietal callus weak.

Comparisons

The sculpture of *Cerithium niauense* Merle, n. sp. is variable. In Plio-Pleistocene material, axial ribs can be more or less prominent and rows of cords on P1 to P3 can be more or less beaded. This variation allows to distinguish two extreme morphotypes, one characterized by well formed axial ribs (e.g., Fig. 11A-C) and one characterized by a beaded sculpture with low ribs (e.g., Fig. 11D-F). Transitional forms link these two morphotypes, showing that they belong to a same species. Holocene material displays a similar variation with two same extreme morphotypes (e.g., Fig. 11I, J; 11K, L) and no diagnostic characters allowing to distinguish a different species. All shells of *C. niauense* Merle, n. sp. are regularly slightly cyrtoconoid, their axial ribs are slightly curved and P2, the most prominent cord, is well distinct from P3. Plio-Pleistocene shells are creamy and

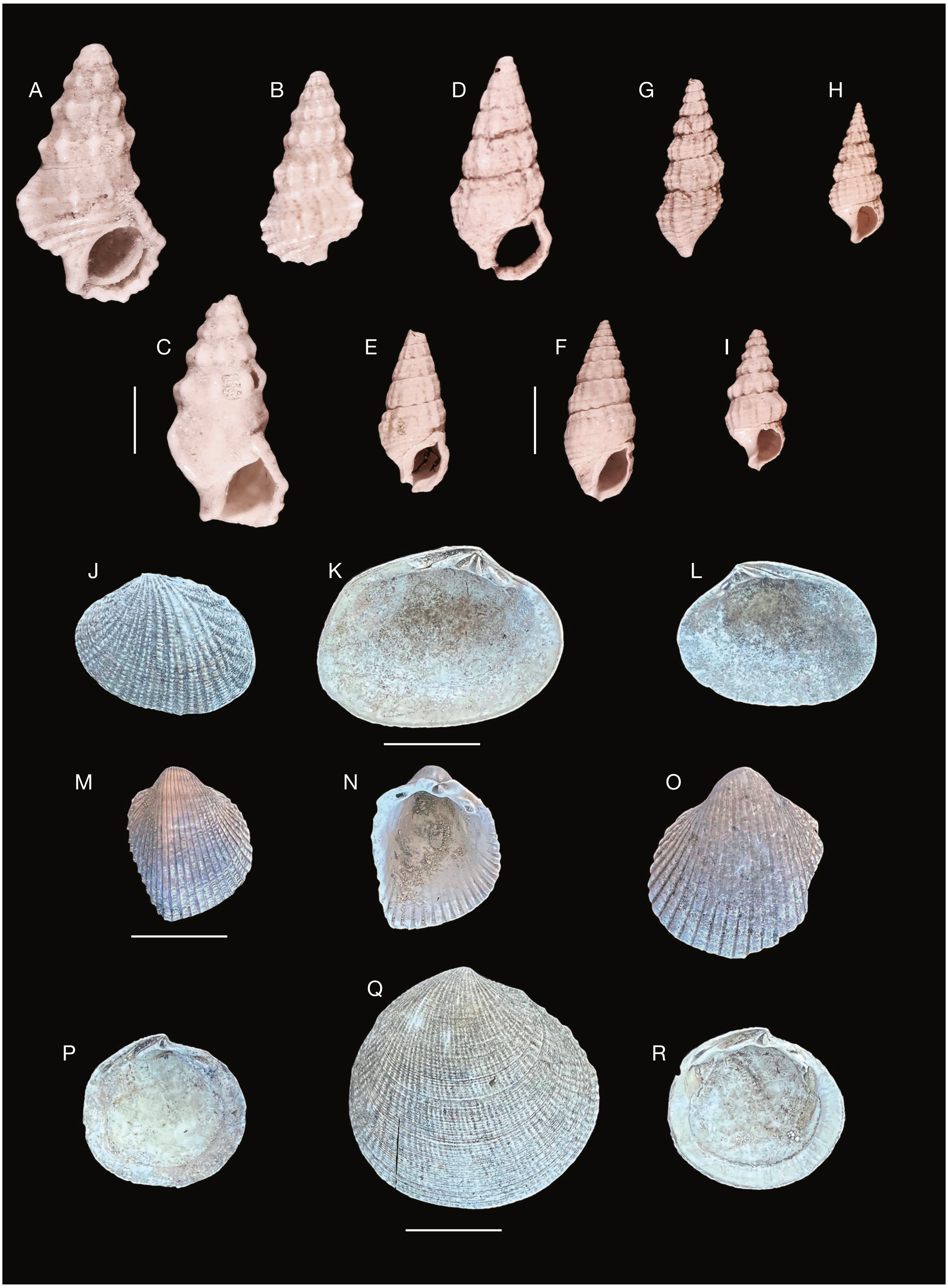
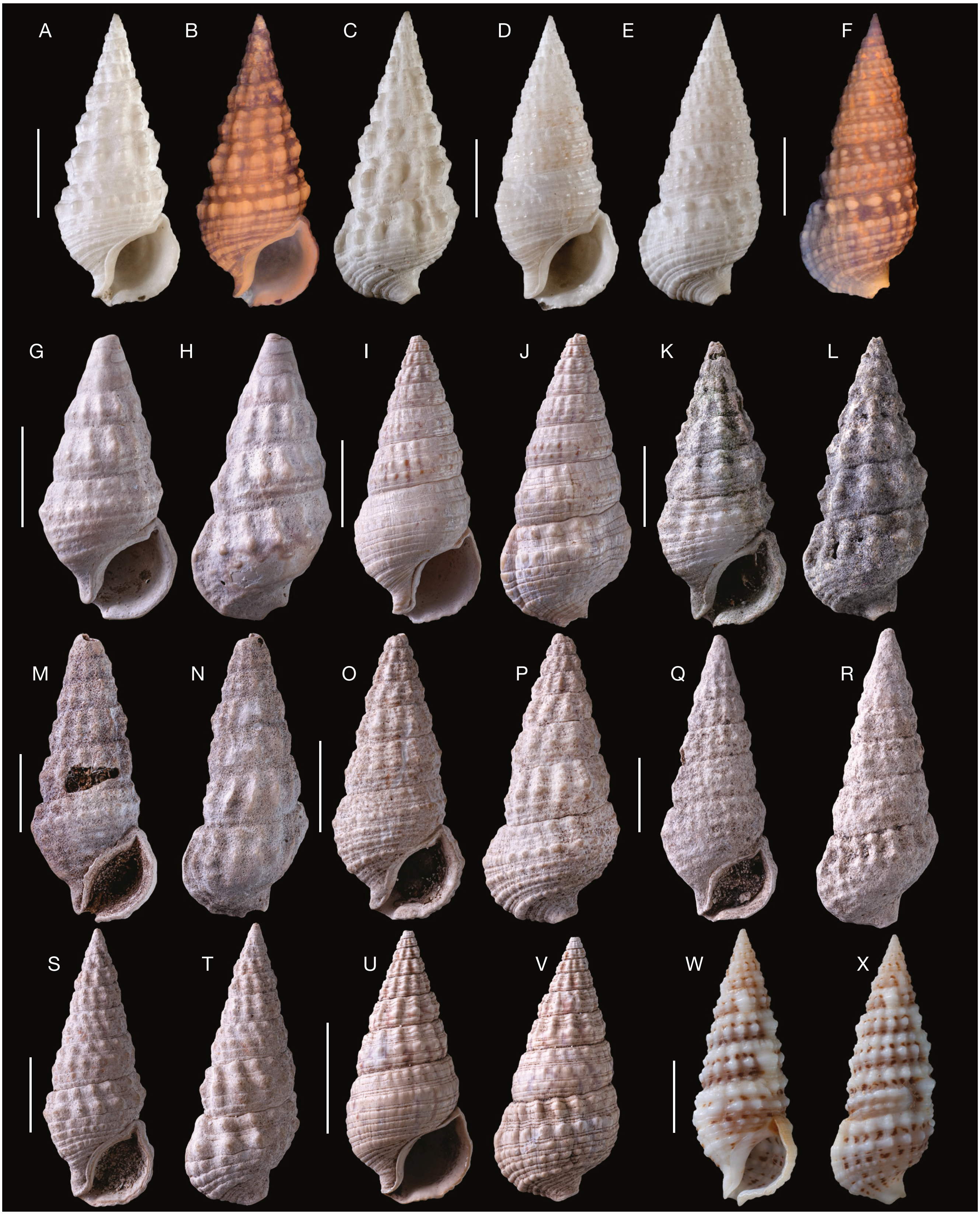


FIG. 9. — Species assemblage of Late Holocene sediments deposited above the caliche (sample N105, Vaihuoa, near Archeological platform), Niau Atoll (Tuamotu, French Polynesia): **A**-**C**, *Cerithium columna* G. B. Sowerby I, 1834; **A**, MNHN.F.A98459; **B**, MNHN.F.A98460; **C**, MNHN.F.A98461; **D**-**F**, *Cerithium niauense* Merle, n. sp.: **D**, MNHN.F.A98411; **E**, MNHN.F.A98412; **F**, MNHN.F.A98413; **G**-**I**, *Cerithium rostratum* G. B. Sowerby II, 1855: **G**, MNHN.F.A98462; **H**, MNHN.F.A98463; **I**, MNHN.F.A98464; **J**-**L**, *Gafrarium pectinatum* (Linnaeus, 1758): **J**, MNHN.F.C02086; **K**, MNHN.F.C02087; **L**, MNHN.F.C02088; **M**-**O**, *Fragum fragum* (Linnaeus, 1758): **M**, MNHN.F.C02089; **N**, MNHN.F.C02090; **O**, MNHN.F.C02091; **P**-**R**, *Ctena bella* (Conrad, 1837): **P**, MNHN.F.C02092; **Q**, MNHN.F.C02093; **R**, MNHN.F.C02094. Scale bars: 10 mm. Credit: J.-P. Pointier.

Fig. 10. — Assemblage of the four common species living in the lagoon (sample N95, Vaihuoa, lagoon shore), Niau Atoll (Tuamotu, French Polynesia): **A**-**C**, *Clypeomorus brevis* (Quoy & Gaimard, 1834): **A**, MNHN.F.C02095; **B**, MNHN.F.C02096; **C**, MNHN.F.C02097; **D**-**G**, *Cerithium punctatum* Bruguière, 1792: **D**, MNHN.F.C02098; **E**, MNHN.F.C02099; **F**, MNHN.F.C02100; **G**, MNHN.F.C02101; **H**-**J**, *Ctena bella* (Conrad, 1837): **H**, MNHN.F.C02102; **I**, MNHN.F.C02103; **J**, MNHN.F.C02104; **K**-**M**, *Pinctada maculata* (A. Gould, 1850): **K**, MNHN.F.C02105; **L**, MNHN.F.C02106; **M**, MNHN.F.C02107. *Ctena bella* is the dominant bivalve with *Clypeomorus brevis*. Scale bar: 10 mm. Credit: J.-P. Pointier.

Fig. 11. — *Cerithium niauense* Merle, n. sp. from the Plio-Pleistocene (**A**-**F**) and the Late Holocene at Vaihuoa near archeological platform (**G**-**V**) of Niau Atoll (Tuamotu, French Polynesia): **A**, holotype, MNHN.F.A98401, ventral face; **B**, idem in ventral face under UV light; **C**, idem, dorsal face; **D**, paratype MNHN.F.A98402, ventral face; **E**, idem, dorsal face, **F**, idem, dorsal face under UV light; **G**-**H**, paratype (sample N106), MNHN.F.A98404, ventral (**G**) and dorsal (**H**) faces; **I**, **J**, paratype



(sample N106), MNHN.F.A98405, ventral (**I**) and dorsal (**J**) faces; **K**, **L**, paratype (sample N108), MNHN.F.A98403, ventral (**K**) and dorsal (**L**) faces; **M**, **N**, paratype (sample TP1A), MNHN.F.A98406, ventral (**M**) dorsal (**N**) faces; **O**, **P**, paratype (sample TP1A), MNHN.F.A98407, ventral (**O**) and dorsal (**P**) faces; **Q**, **R**, paratype (sample TP1B), MNHN.F.A98408, ventral (**Q**) and dorsal (**R**) faces; **S**, **T**, paratype (samples TP1B), MNHN.F.A98409, ventral (**S**) and dorsal (**T**) faces; **U**, **V**, paratype (sample TP1B), MNHN.F.A98410, ventral (**U**) and dorsal (**V**) faces; **W**, **X**, *Cerithium tenellum* G. Sowerby II, 1855 (Limpelaer coll.), Pelotes Point, Philippines, present day, ventral (**X**) and dorsal (**Y**) faces for comparison with *C. niauense* Merle, n. sp. Scale bars: 5 mm. Credits: A-F, P. Loubry; G-Y, L. Cazes. B and F, photos taken under UV, other photos taken in natural light. A-F, M-V, material from Letourneux coll.; G-L, material from Salvat coll.

sediment sometimes included in these shells is whitish, whereas Holocene shells are withish pale grey and display a dark grey sediment within their shell when present. *Cerithium tenellum* G. B. Sowerby II, 1855, originally described from Philippines, is reminiscent to *C. niauense* Merle, n. sp., but differs by having a conical shape, straigh axial ribs and P3 almost fused with P2, and no varical nodes. *Cerithium filosum* G. B. Sowerby II, 1865, also originally described from Philippines, displays a prominent beaded secondary cord s1 and has varical nodes lacking on the spire of *C. niauense* Merle, n. sp.

Order LITTORINIMORPHA Golikov & Starobogatov, 1975
Superfamily STROMBOIDEA Rafinesque, 1815
Family STROMBIDAE Rafinesque, 1815

Genus *Gibberulus* Jousseaume, 1888

TYPE SPECIES. — *Strombus gibberulus* Linnaeus, 1758 by monotypy.

Gibberulus gibbosus (Röding, 1798)
(Fig. 12A, B)

Lambis gibbosa Röding, 1798: 62, n°786-788.

Gibberulus gibbosus – Wilson 1993: 158, pl. 21, fig. 12. — Salvat *et al.* 2018: table 1. — Maxwell *et al.* 2021: 100, figs 8-10.

Gibberulus gibberulus gibbosus – Boutet *et al.* 2020: 302.

TYPE MATERIAL. — **Syntype. Philippines** • Maxwell *et al.* (2021: 100) wrote that Röding (1798: 62, n°786-788) designated a holotype refering to the illustration of Martini (1777: pl. 27, fig. 794), but Röding (1798: 62) did not designate a holotype.

TYPE LOCALITY. — Cebu Island, Philippines (Abbott 1960:144, fig. 8).

FIGURED MATERIAL. — **France** • 1 spm; French Polynesia, Niau Atoll, La Piscine": 6°08'22.32S, 146°23'14.09W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98429 (Letourneux coll.); H 47.1 mm (Fig. 12A, B).

OTHER MATERIAL. — **France** • 21 spm; French Polynesia, Niau Atoll, La Piscine": 6°08'22.32S, 146°23'14.09W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98430 (Letourneux coll.) • 3 spm; same; MNHN.F.A98431 (Letourneux coll.).

DISTRIBUTION. — Plio-Pleistocene, French Polynesia (this work) to today, Philippines, eastern Indonesian Archipelago, northeastern Papua New Guinea and associated Island chains (Maxwell *et al.* 2021: 104, fig. 11).

DESCRIPTION

See Maxwell *et al.* (2021: 99).

COMMENTS

The figured material displays a uniform pinkish-yellow background interrupted by around seven small grey spiral bands. This residual pattern suggests that the coloured background was interrupted by unpigmented spiral bands. The colour pattern of *Gibberulus gibbosus* is very variable (see Maxwell *et al.* (2021: figs 8-10), but it is also interrupted by white spiral bands. These white bands correspond to the small grey bands observed under UV light and indicate that the residual colour pattern on the Plio-Pleistocene fossils is strongly reminiscent of the colour pattern of the extant *Gibberulus gibbosus*.

Genus *Striatostrombus* Dekkers & S. J. Maxwell, 2018

TYPE SPECIES. — *Striatostrombus blanci* (Tröndlé & Salvat, 2010) by original designation.

Striatostrombus blanci (Tröndlé & Salvat, 2010)
(Fig. 12C, D)

Strombus (*s.l.*) *blanci* Tröndlé & Salvat, 2010: 616, figs 2A-G, J; 3; 4C-E. — Salvat *et al.* 2018: table 1.

Striatostrombus blanci – Dekkers & Maxwell 2018: 224.

TYPE MATERIAL. — **Holotype. France** • French Polynesia, Niau Atoll, La Piscine": 6°08'22.32S, 146°23'14.09W; Plio-Pleistocene (molluscs assemblage); MNHN-IM-2000-23289; H 34.5 mm.

PARATYPE. — **France** • 1 spm; same as the holotype; EPHE coll.; H 36 mm • 1 spm; idem; Letourneux coll.; H 35 mm • 1 spm; idem; MNHN.F.A98433 (Tröndlé coll.); H 40 mm • 1 spm; idem; G. Kronenberg coll.; H 36 mm.

FIGURED MATERIAL. — 1 spm; idem; MNHN.F.A98432; H 31.3 mm (Fig. 12C, D).

TYPE HORIZON. — Plio-Pleistocene (molluscs assemblage) (see Figs 7-8).

TYPE LOCALITY. — French Polynesia, Niau Atoll, "La Piscine": 6°08'22.32"S, 146°23'14.09"W.

DISTRIBUTION. — Only know from the type locality.

DESCRIPTION

See Tröndlé & Salvat (2010: 616) and Dekkers & Maxwell (2018: 224).

COMMENTS

This species is close to *Striatostrombus micklei* (Ladd, 1972) from the Late Miocene of Marshall Archipelago (Dekkers & Maxwell 2018). When *S. blanci* was described, traces of a colour pattern were not researched. Under UV light, the studied material displays a uniform grey background (Fig. 12D) that suggests that the species was probably poorly pigmented and devoid of colour pattern.

Order NEOGASTROPODA Wenz, 1938
Superfamily MURICOIDEA Rafinesque, 1815
Family MURICIDAE Rafinesque, 1815
Subfamily ERGALATAXINAE Kuroda, T. Habe & Oyama, 1971

Genus *Drupella* Thiele, 1925

TYPE SPECIES. — *Drupa cornus* Röding, 1798 by original designation.

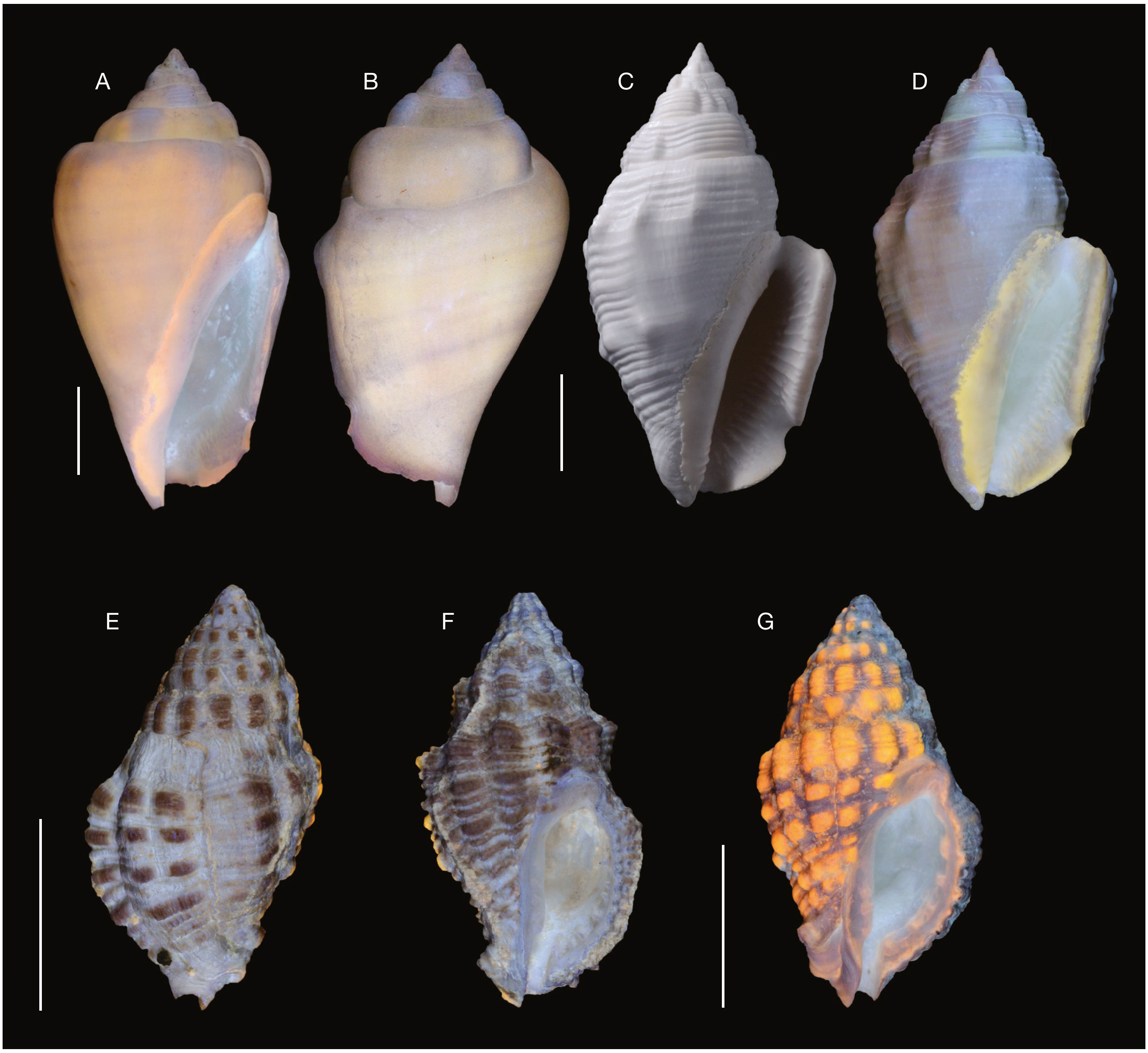


Fig. 12. — Strombidae (**A**-**D**) and Muricidae (**E**-**G**) from the Plio-Pleistocene assemblage of Niau Atoll (Tuamotu, French Polynesia): **A**, **B**, *Gibberulus gibbosus* (Röding, 1798), MNHN.F.A98429: **A**, ventral face under UV light; **B**, dorsal face under UV light; **C**, **D**, *Striatostrombus blanci* (Tröndlé & Salvat, 2010), MNHN.F.A98432: **C**, ventral face in natural light; **D**, ventral face under UV light; **E**-**G**, *Drupella margariticola* (Broderip, 1833): **E**, **F**, MNHN.F.A98434, ventral and dorsal faces under UV light; **G**, MNHN.F.A98435, ventral face under UV light. Scale bars: 10 mm. Credits P. Loubry (MNHN/CNRS). All material from Letourneux coll. housed at MNHN.

Drupella margariticola (Broderip, 1833)
(Fig. 12E-G)

Murex margariticola Broderip, 1833: 177.

Purpura lineolata Blainville, 1832: 206 [non Risso, 1826].

Purpura violacea Lesson, 1842: 186 [non Kiener, 1836].

Morula margarticola – Salvat & Rives 1975: 317, fig. 216.

Cronia (*Cronia*) *margariticola* – Tröndlé & Houart 1992: 85, figs 5-7, 37.

Ergalatax margariticola – Houart 2008: 105, figs 8, 14, 41-45.

Drupella margariticola – Claremont *et al.* 2011: 105, fig. 1a. — Salvat *et al.* 2018: table 1. — Boutet *et al.* 2020: 373.

Type material. — **Lectotype**. **Australia** • Designated by Emerson & d'Attilio (1981: 81); Lord Howe Island; BMNH1981146.

Figured material. — **France** • 1 spm; French Polynesia, Niau Atoll, “La Piscine”: 6°08'22.32”S, 146°23'14.09”W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98434 (Letourneux coll.); H 22.9 mm (Fig. 12E, F) • 1 spm; idem; MNHN.F.A98435 (Letourneux coll.); H 25.1 mm (Fig. 12G).

Other material. — **France** • 4 spm; same data as the Figured material; MNHN.F.A98465 (Letourneux coll.).

Type locality. — Australia, Tasman Sea, Lord Howe Island.

Distribution. — Plio-Pleistocene (molluscs assemblage), French Polynesia, Niau Atoll to today, Indo-West-Pacific.

Description

See Tröndlé & Houart (1992: 85).

Comments

Two specimens display a residual colour pattern, but with a different degree of diagenesis. One is almost pristine (Fig. 12E, F) and its colour pattern is similar to that found in extant specimens. The other specimen exhibits yellow spots where the nodules are, that indicates strongly pigmented nodules (Fig. 12G). Unpigmented areas correspond to spiral grooves and intervarical spaces. This pattern is reminiscent to living specimens having brown or black nodules interrupted by fairer or white spiral grooves.

Superfamily CONOIDEA J. Fleming, 1822
Family CONIDAE J. Fleming, 1822

Genus *Conus* Linnaeus, 1758

TYPE SPECIES. — *Conus marmoreus* Linnaeus, 1758, by subsequent designation (Children 1823).

Subgenus *Conus* Linnaeus, 1758

Conus (***Conus***) ***letourneuxi*** Merle, n. sp.
(Fig. 13A-D)

urn:lsid:zoobank.org:act:5DDF566A-05C5-43D7-B2D5-BB49C5189FC7

Conus marmoreus – Salvat *et al.* 2018: table 1 [non *Conus marmoreus* Linnaeus, 1758].

TYPE MATERIAL. — **Holotype**. **France** • French Polynesia, Niau Atoll, “La Piscine”; 6°08’22.32”S, 146°23’14.09”W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98436 (Letourneux coll.); H 70.5 mm.

ETYMOLOGY. — Dedicated to Jean Letourneux.

TYPE HORIZON. — Plio-Pleistocene (molluscs assemblage) (see Figs 7; 8).

TYPE LOCALITY. — French Polynesia, Niau Atoll, “La Piscine”: 6°08’22.32”S, 146°23’14.09”W.

DISTRIBUTION. — Only known from the type locality.

Description

Shell moderately large, with very low conical spire. Apical angle 118°. Teleoconch of 9 whorls, whorl tops smooth delimited by a shoulder very slightly lower than the suture. Suture moderately impressed. Subsutural sinus deep, strongly curved, strongly asymmetrical. Last whorl with concave subsutural platform, slighlty angled at shoulder placed below suture, regularly conical below, position of maximum diameter close below shoulder, not constricted at base. Siphonal fasciole weakly developed. Weak, close set spaced cords from the base to the center of last whorl and fasciole. Aperture relatively narrow with parallel sides, hardly widening abapically; siphonal canal short. Colour pattern poorly preserved consisting large dark triangular spots surrounded by light yellow fluorescent bands under UV light.

Comparisons

The residual colour pattern of *Conus* (*Conus*) *letourneuxi* n. sp. (Fig. 13C, D) is reminicent to that of *Conus* (*Conus*) *marmoreus* (Linneaus, 1758), *Conus* (*Conus*) *bandanus* Hwass in Bruguière, 1792 and *Conus* (*Eugeniconus*) *marchionatus* Hinds, 1843. The shells of *C.* (*C.*) *marmoreus* and *C.* (*C.*) *bandanus* have a crenulated spire, whereas that of *C.* (*C.*) *letourneuxi* n. sp. is smooth. *C.* (*E.*) *marchionatus* displays a smooth spire, but it is flatter than that of *C.* (*C.*) *letourneuxi* n. sp. and the shape of its triangular spots is more rounded.

Subgenus *Tesselliconus* da Motta, 1991

TYPE SPECIES. — *Conus tessulatus* Born, 1778 by original designation.

Conus (***Tesselliconus***) ***georgesrichardi*** Merle, n. sp.
(Figs 13E-Q; 14A-L; 15A-D)

urn:lsid:zoobank.org:act:00915CC5-39F5-478D-84BA-87551894B565

Conus eburneus – Salvat *et al.* 2018: table 1 [non *Conus eburneus* Hwass in Bruguière, 1792].

Conus litteratus – Salvat *et al.* 2018: table 1 [non *Conus litteratus* Linnaeus, 1758].

Conus pertusus – Salvat *et al.* 2018: table 1 [non *Conus pertusus* Hwass in Bruguière, 1792].

Conus tessulatus – Salvat *et al.* 2018: table 1 [non *Conus tessulatus* Born, 1778].

TYPE MATERIAL. — **Holotype**. **France** • French Polynesia, Niau Atoll, “La Piscine”: 6°08’22.32”S, 146°23’14.09”W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98437 (Letourneux coll.); H 43.4 mm (Figs 13E-H; 15A, B).
Paratypes. **France** • 1 spm; same data as the holotype; MNHN.F.A98438; H 39.4 mm (Fig. 13I, J) • 1 spm; idem; MNHN.F.A98439; H 89.6 mm (part of the last whorl, Fig. 13K) • 1 spm; idem; MNHN.F.A98440; H 35.9 mm (Fig. 13L-O) • 1 spm; idem; MNHN.F.A98441; H 34 mm (Fig. 13P, Q) • 1 spm; idem; MNHN.F.A98442; H 29.6 mm (Fig. 14A, B) • 1 spm; idem; MNHN.F.A98443; H 28.1 mm (Fig. 14C) • 1 spm; idem; MNHN.F.A98444; H 22 mm (Fig. 14D, E) • 1 spm; idem; MNHN.F.A98445; H 36.7 mm (Fig. 14F, G) • 1 spm; idem; MNHN.F.A98446; H 35.6 mm (Fig. 14H, I; 15C, D) • 1 spm; idem; MNHN.F.A98447; H 23 mm • 1 spm; idem; MNHN.F.A98448; H 23.6 mm (Fig. 14J-L). All paratypes from Letourneux coll.

ADDITIONAL MATERIAL. — **France** • 3 spm; same data as the holotype; MNHN.F.A98449 (Letourneux coll.).

ETYMOLOGY. — Dedicated to Georges Richard.

TYPE HORIZON. — Plio-Pleistocene (molluscs assemblage) (see Figs 7; 8).

TYPE LOCALITY. — French Polynesia, Niau Atoll, “La Piscine”: 6°08’22.32”S, 146°23’14.09”W.

DISTRIBUTION. — Only know from the type locality.

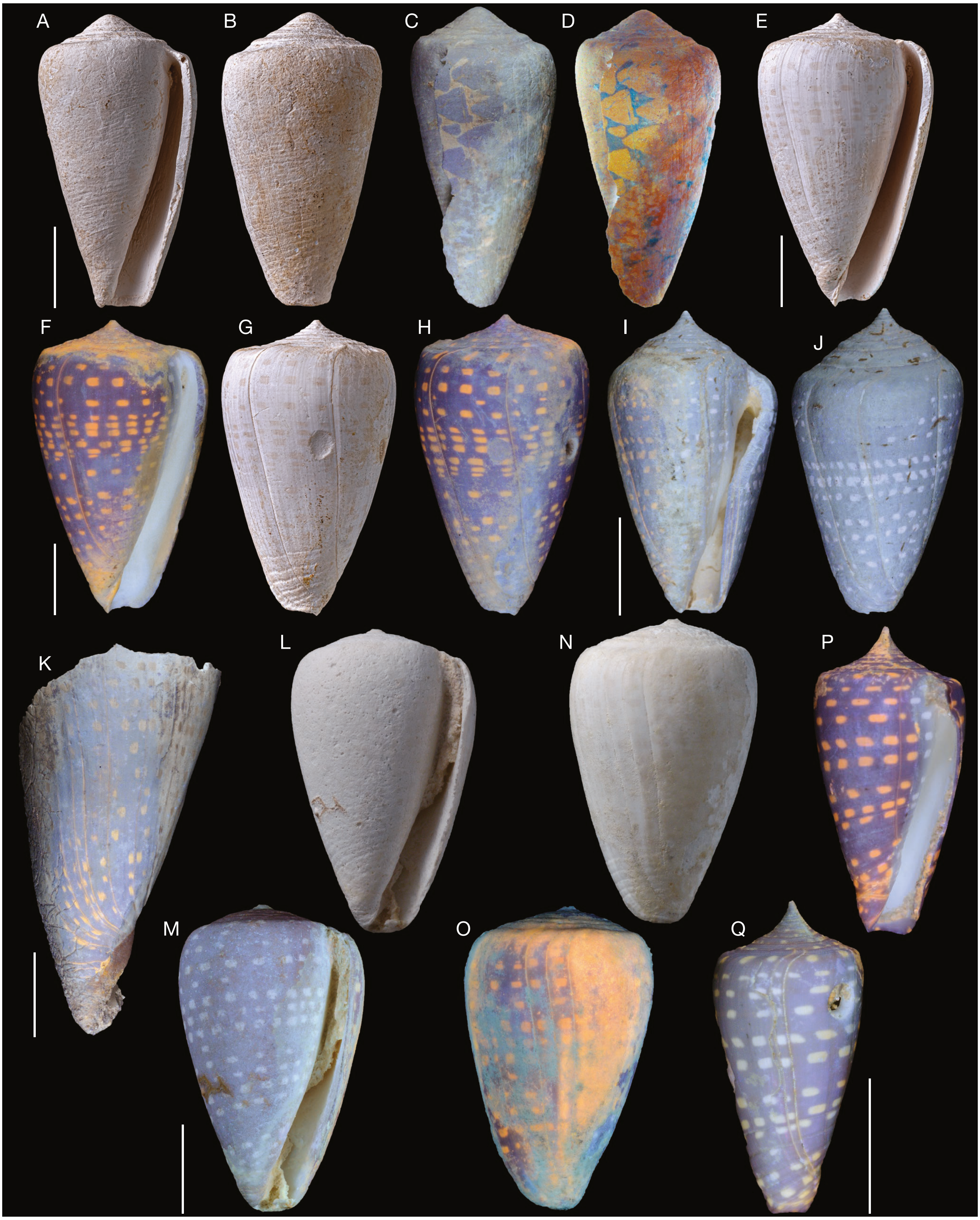


Fig. 13. — *Conus* (*Conus*) *letourneuxi* Merle, n. sp. (**A**-**D**) and *Conus* (*Tesselliconus*) *georgesrichardi* Merle, n. sp. (**E**-**Q**) from the Plio-Pleistocene assemblage of Niau Atoll (Tuamotu, French Polynesia): **A**-**D**, holotype, MNHN.F.A98436 (Letourneux coll.), ventral (**A**) and dorsal (**B**) faces in natural light, profil view under UV light (**C**) and in inverse UV light (**D**); **E**-**H**, holotype, MNHN.F.A98437, ventral face in natural light (**E**) and under UV light (**F**), dorsal face in natural light (**G**) and under UV light (**H**); **I**, **J**, paratype, MNHN.F.A98438, ventral (**I**) and dorsal (**J**) faces under UV light; **K**, paratype, MNHN.F.A98439, broken specimen in ventral face under UV light; **L**-**O**, paratype, MNHN.F.A98440, ventral face in natural light (**L**) and under UV light (**M**), dorsal face in natural light (**N**) and under UV light (**O**); **P**-**Q**, paratype, MNHN.F.A98441, ventral (**P**) and dorsal (**Q**) faces under UV light. Scale bars: A-D, K, 20 mm; E-J, L-Q, 10 mm. Credits: A, B, E, F, L-N, L. Cazes (MNHN/CNRS); C, D, F, H, I, J, K-M, O, P. Loubry (MNHN/CNRS). All material from Letourneux coll. housed at MNHN.

DESCRIPTION

Shell large (MNHN.F.A98439 (Fig. 13K) part of the last whorl = 89.6 mm), with low coeloconoid to conical spire. Apical angle 135°. Teleoconch of 7-8whorls, whorl tops smooth except for close-set, comma-shaped growth lines, concave, delimited by shoulder raised very slightly below suture. Suture weakly impressed. Subsutural sinus shallow, slightly curved, moderately asymmetrical. Last whorl with horizontal, flat subsutural platform, smoothy angled at shoulder placed almost at suture, regularly conical below, position of maximum diameter close below shoulder, not constricted at base. Siphonal fasciole weakly developed; a few weak, widely spaced cords over base and fasciole, strengthening slightly abapically. Aperture relatively narrow with parallel sides, widening abapically; siphonal canal short. Under UV light, residual colour pattern consisting of two components: (1) pale, yellow-white fluorescent spots, spirally aligned and (2) dark, non-fluorescent background. Small rectangular spots of unequal size, distributed on the last whorl in four zones from shoulder to base. Zone a (first posterior quarter of whorl): 3-4 rows of sparse dots; zone b (second posterior quarter of whorl): 3-6 rows of close-set dots; zone c (first anterior quarter of whorl: 2-3 spaced rows of sparse dots; zone c (second anterior quater of whorl): 4-8 rows of more or less spaced dots (Fig. 15A-D).

COMPARISONS

Among French Polynesian Conidae bearing spiral rows of dots, *C.* (*Tesselliconus*) *georgesrichardi* n. sp. may be compared with *Conus* (*Elisaconus*) *litteratus* (Linnaeus, 1758), *C.* (*Tesselliconus*) *tessulatus* Born, 1778 and *C.* (*T.*) *eburneus* (Hwass in Bruguière, 1792). *C.* (*E.*) *litteratus* differs in having a planispiral spire, a narrow, concave subsutural platform and a shoulder placed above the suture. *Conus* (*E.*) *litteratus* displays around 20-25 row of dots, instead 15-18 in *C.* (*T.*) *georgesrichardi* n. sp. In addition, the rows are regularly aligned from the shoulder to the base on last whorl, whereas those of *C.* (*T.*) *georgesrichardi* n. sp. are organised in four zones (a to d). The shell shape of *Conus* (*T.*) *tessulatus* is reminiscent to that *C.* (*T.*) *georgesrichardi* n. sp. and as in the Plio-Pleistocene species, the rows of dots are organised in four zones (Fig. 15E, F). However, *Conus* (*T.*) *tessulatus* species differs clearly by having in elongated larger dark dots. The colour pattern of *C.* (*T.*) *erburneus* consists in four similar zones of spiral rows of dots as in *C.* (*T.*) *georgesrichardi* n. sp. (Fig. 15G, H) However, the dots of *C.* (*T.*) *georgesrichardi* n. sp. are smaller and more close set in the zone b. Moreover, the spire of *C.* (*T.*) *georgesrichardi* n. sp. can be more conical, the shell shape is wider and some gerontic individuals can reach a larger size (H more than 89 mm).

Family TEREBRIDAE Mörch, 1852
Subfamily TEREBRINAE Mörch, 1852

Genus *Oxymeris* Dall, 1903

TYPE SPECIES. — *Buccinum maculatum* Linnaeus, 1767 by original designation.

Oxymeris niauensis (Tröndlé & Letourneux, 2011)
(Fig. 14M-P)

Terebra niauensis Tröndlé & Letourneux, 2011: 87, figs 1-5, 8, 9.

Terebra niauensis — Salvat *et al.* 2018: table 1.

TYPE MATERIAL. — **Holotype**. **France** • French Polynesia, Niau Atoll, “La Piscine”; 6°08’22.32”S, 146°23’14.09”W; Plio-Pleistocene (molluscs assemblage); MNHN-IM-2000-23684; H 96.5 mm.
Paratypes. **France** • 1 spm; same data as the holotype; EPHE coll.; H 89.55 mm • 9 spm; idem; MNHN-IM-2000-23686; H 78 mm, 81.6 mm, 74 mm, 62.7 mm, 62 mm, 60.4 mm, 55 mm, 50.7 mm, 48.9 mm • 1 spm; idem; Jean Tröndlé coll.; H: 61.2 mm • 1 spm; idem; Letourneux coll.; H 86.1 mm (Fig. 19N-P) • 1 spm; idem; G. Paulay coll.; H 84 mm • 1 spm; idem; A. Waren coll.; H 79.1 mm • 1 spm; idem; Mairie de Niau coll.; H 87.5 mm • 1 spm; idem; M. Boutet coll.; H 87.8 mm • 1 spm; idem; G. Kronenberg coll.; H 60.6 mm.

TYPE HORIZON. — Plio-Pleistocene (molluscs assemblage) (see Figs 7-8).

TYPE LOCALITY. — French Polynesia, Niau Atoll, “La Piscine”: 6°08’22.32”S, 146°23’14.09”W.

FIGURED MATERIAL. — One paratype (Letourneux coll.), Fig. 19M-P.

DISTRIBUTION. — Only known from the type locality.

DESCRIPTION

See Tröndlé & Letourneux (2011: 88).

COMMENTS

Tröndlé & Letourneux (2011) noted that UV light revealed only a few spots under the suture of the holotype. On the examined paratype, a dark band is also present under the suture of the penultimate and the last whorl of the specimen examined. These authors found strong shell similarities with *Oxymeris gouldi* (Deshayes, 1857), today Hawaii. *O. niauensis* looks also allied to *Oxymeris caledonica* (G. B. Sowerby III, 1909), today New Caledonia. Therefore, *O. niauensis* seems better placed in the genus *Oxymeris* Dall, 1903.

Subclass HETEROBRANCHIA Burmeister, 1837
Order CEPHALASPIDEA P. Fischer, 1883
Superfamily BULLOIDEA Gray, 1827
Family BULLIDAE Gray, 1827

Genus *Bulla* Linnaeus, 1758

TYPE SPECIES. — *Bulla ampulla* Linnaeus, 1758 by subsequent designation (Gray 1847).

Bulla niauensis Merle, n. sp.
(Fig. 16)

urn:lsid:zoobank.org:act:8C774DB3-F7BE-4DD8-838C-01E30AA984D9

Bulla vernicosa – Salvat *et al.* 2018: table 1 [non *Bulla vernicosa* Gould, 1859].

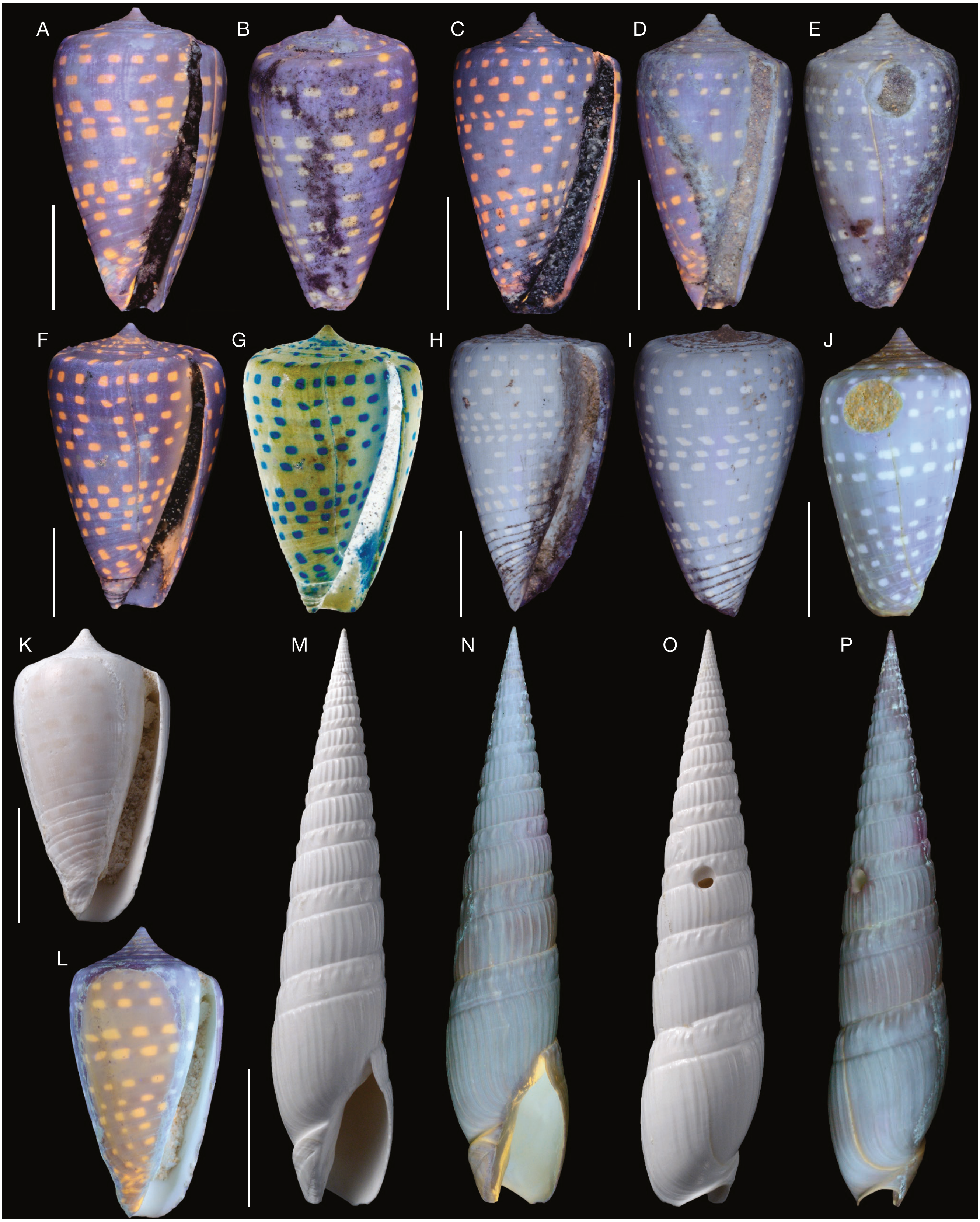


FIG. 14. — *Conus* (*Tesselliconus*) *georgesrichardi* Merle, n. sp. (**A**-**L**) and *Oxymeris niauensis* (Tröndlé & Letourneux, 2011) (**M**-**P**) from the Plio-Pleistocene assemblage of Niau Atoll (Tuamotu, French Polynesia): **A**, **B**, paratype, MNHN.F.A98442, ventral (**A**) and dorsal (**B**) faces under UV light; **C**, paratype, MNHN.F.A98443, ventral face under UV light; **D**, **E**, paratype, MNHN.F.A98444, ventral (**D**) and dorsal (**E**) faces under UV light; **F**, **G**, paratype, MNHN.F.A98445, ventral face under UV light (**F**) and in inverse UV light (**G**); **H**, **I**, paratype, MNHN.F.A98446, ventral (**H**) and dorsal (**I**) faces under UV light; **J**-**L**, paratype, MNHN.F.A98448 dorsal face under UV light (**J**) and ventral face in natural light (**K**) and under UV light (**L**); **M**-**P**, paratype, Letourneux coll., ventral face in natural light (**M**) and under UV light (**N**) and dorsal face in natural light (**O**) and under UV light (**P**). Scale bars: A-M, 10 mm; N-P, 20 mm. Credits: P. Loubry (MNHN/CNRS). A-L, material from Letourneux coll. housed at MNHN; M-O, material from Letourneux coll., at Tahiti.

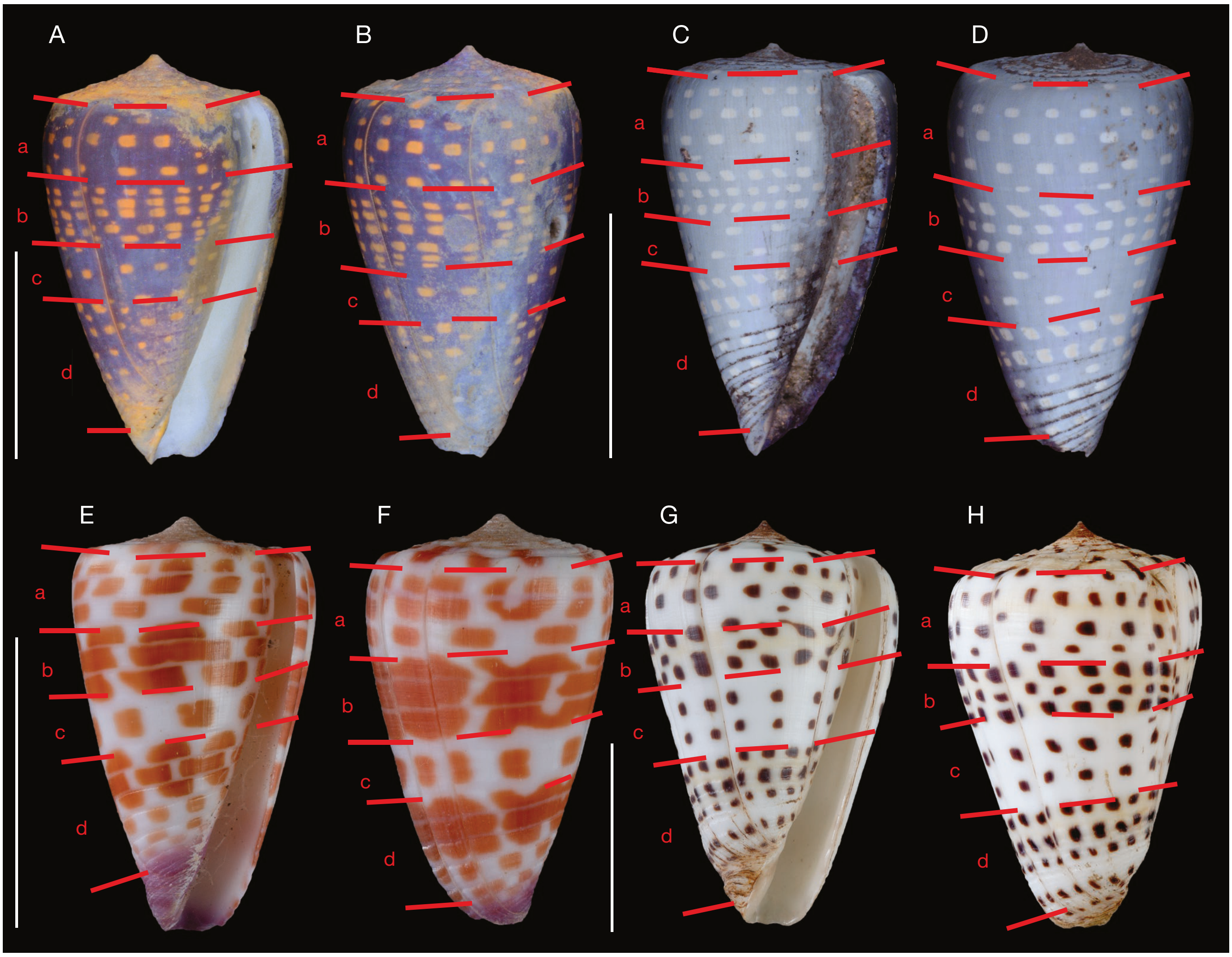


FIG. 15. — The fourth areas (**a**, **b**, **c**, **d**) of pigmentation in *Conus* (*Tesselliconus*) *georgesrichardi* Merle, n. sp. (**A**-**D**), *Conus* (*Tesselliconus*) *tessulatus* Born, 1778 (**E**, **F**) and *Conus* (*Tesselliconus*) *eburneus* Hwas, 1792 (**G**, **H**): **A**, **B**, holotype, MNHN.F.A98437 (Letourneux coll.), ventral face (**A**) and dorsal (**B**) faces under UV light, Plio-Pleistocene, Niau Atoll (Tuamotu, French Polynesia); **C**, **D**, paratype, MNHN.F.A98446 (Letourneux coll.), ventral (**C**) and dorsal (**C**) faces under UV light, Plio-Pleistocene, same locality; **E**, **F**, MNHN.IM (Tröndlé coll.), ventral (**E**) and dorsal faces (**F**), present day, Papeete (Faaone), Tahiti island (Tuamotu, French Polynesia); **G**, **H**, MNHN.IM (Pierrot coll.), ventral (**G**) and dorsal faces (**H**), present day, Tahiti island. Scale bars: 20 mm. Credits: P. Loubry (MNHN/CNRS).

TYPE MATERIAL. — **Holotype. France** • French Polynesia, Niau Atoll, “La Piscine”; 6°08’22.32”S, 146°23’14.09”W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98450 (Letourneux coll.); H 25.4 mm (Fig. 16A-E).
Paratypes. France • 1 spm; same data as the holotype; MNHN.F.A98452 (Letourneux coll.); H 25.7 mm • 1 spm; idem; MNHN.F.A98451 (Letourneux coll.), H 24.5 mm (Fig. 16F, G).

ADDITIONAL MATERIAL. — **France** • 3 spm; same data as the holotype; MNHN.F.A98453 (Letourneux coll.).

ETYMOLOGY. — From the type locality Niau (French Polynesia).

TYPE HORIZON. — Plio-Pleistocene (molluscs assemblage) (see Figs 7; 8).

TYPE LOCALITY. — French Polynesia, Niau Atoll, “La Piscine”, 6°08’22.32”S, 146°23’14.09”W.

DISTRIBUTION. — Only know from the type locality.

DESCRIPTION

Shell thick, shape subquadrangular, wider anteriorly. Parietal callus thin; collumella thick. Spire aperture wide. Outer lip straight posteriorly, rounded anteriorly. Under UV light, residual pattern composed of two levels of residual pigmentation: a lighter background and dark stripes from wavy to zigzagging.

COMPARISONS

Bulla ampulla (Linnaeus, 1758) resembles *Bulla niauensis* Merle, n. sp., but differs by having a subquadrangular shape. The colour pattern displays mainly a fair background and darker dots and tending to collapse in small dots of irregular shape. *Bulla vernicosa* A. Gould, 1859 is more quadrangular than *Bulla niauensis* n. sp. and its outer lip is straighter anteriorly. The colour pattern of *Bulla vernicosa* is fair brown, with darker small dots. In reverse UV light, the pattern of *Bulla niauensis* n. sp. is also fair brown,

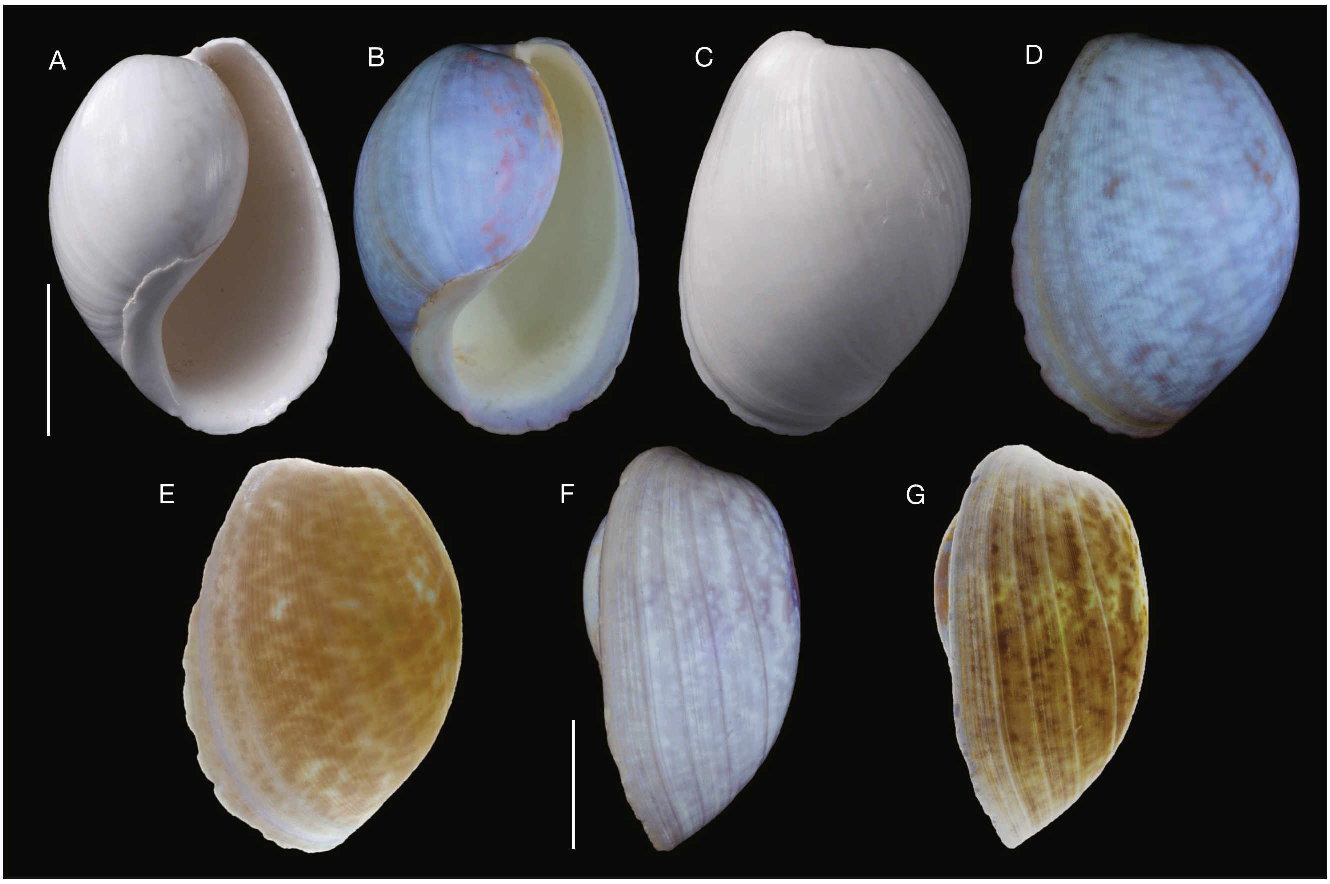


Fig. 16. — *Bulla niauensis* Merle, n. sp. from the Plio-Pleistocene assemblage of Niau Atoll (Tuamotu, French Polynesia): **A**-**E**, holotype, MNHN.F.A98450 (Letourneux coll.), ventral face in natural light (**A**) and under UV light (**B**), dorsal face in natural light (**C**), under UV light (**D**) and in inverse UV light (**E**); paratype, MNHN.F.A98451 (Letourneux coll.), profil view under UV light (**F**) and in inverse UV light (**G**). Scale bars: 10 mm. Credits: P. Loubry (MNHN/CNRS).

but it bears dark stripes from wavy to zigzagging, lacking in *Bulla vernicosa* (see Malaquias & Reid 2008: fig. 27L-Q).

Class BIVALVIA Linnaeus, 1758
Order CARDIIDA A. Férussac, 1822
Superfamily Cardioidea Lamarck, 1809
Family Cardiidae Lamarck, 1809
Subfamily Fraginae R. B. Stewart, 1930

Genus *Lunulicardia* J. E. Gray, 1853

Type species. — *Cardium retusum* Linnaeus, 1767 by monotypy.

?*Lunulicardia distorta* Merle, n. sp.
(Fig. 17A-H)

urn:lsid:zoobank.org:act:24555983-F607-4A6A-A048-4767EA62CCEE

Lunulicardia sp. — Salvat *et al.* 2018: table 1.

Type material. — **Holotype**. **France** • 1 spm (right valve); French Polynesia, Niau Atoll, “La Piscine”; 6°08’22.32”S, 146°23’14.09”W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A99068 (Letourneux coll.); DVL 18 mm (Fig. 17A, B, G).
Paratypes. **France** • 1 spm (right valve); same data as the holotype; MNHN.F.A99821 (Letourneux coll.); DVL 21.8 mm (Fig. 17E, F) • 1 spm (left valve); MNHN.F.A99822 (Letourneux coll.); DVL 29.9 mm (Fig. 17C, H) • 1 spm (left valve); MNHN.F.A99823 Letourneux coll.); DVL 28.7 mm (Fig. 17D) • 6 spm (2 right valves, 4 left valves); MNHN.F.A99055 (Letourneux coll.); DVL 21.8 mm.

Etymology. — From the Latin adjective *distortus* (meaning distorted), because of the strongly curved the posterior area of the shell.

Type horizon. — Plio-Pleistocene (molluscs assemblage) (see Figs 7; 8).

Type locality. — French Polynesia, Niau Atoll, “La Piscine”, 6°08’22.32”S, 146°23’14.09”W.

Distribution. — Only known from the type locality.

Description

Shell moderately thin, strongly inflated in older specimens; strongly oblique, with a strong posterior sulcus. Shell up to 29.9 in DVL and 23.5 mm in APL. Anterior margin obliquely rounded; ventral margin oblique, descending toward carina; posterior margin strongly sinuate concave in its center. Carina sharply expressed, rounded and smooth. Shell equivalve and inequilateral with angulate,

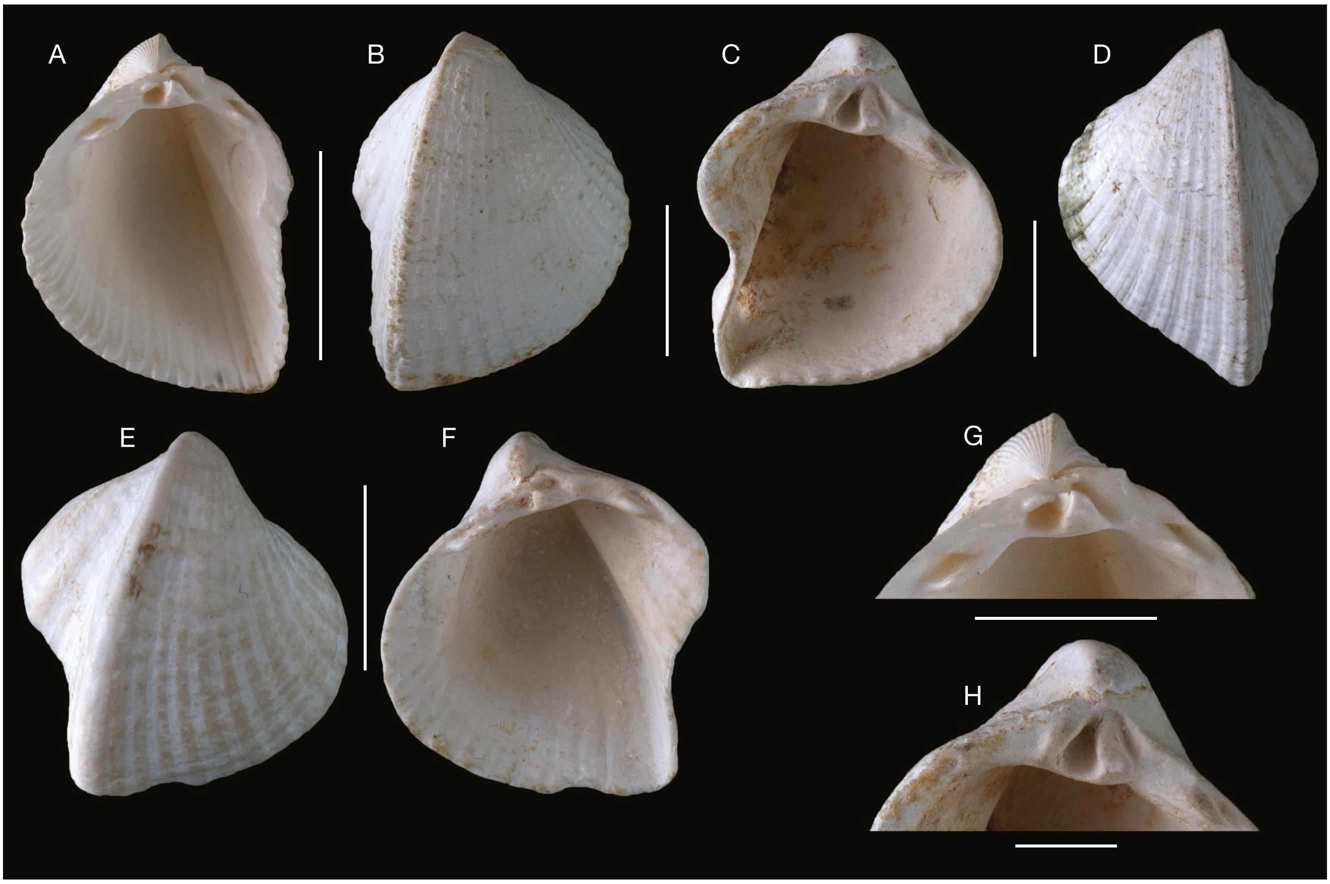


FIG. 17. — ?*Lunulicardia deformata* Merle, n. sp. from the Plio-Pleistocene assemblage of Niau Atoll (Tuamotu, French Polynesia): **A**, **B**, holotype, MNHN.F.A99068, right valve, internal (**A**) and external viewes (**B**); **C**, paratype, MNHN.F.A99822, left valve, internal view; **D**, paratype, MNHN.FA99823, left valve, external view; **E**, **F**, paratype, MNHN.A.99821, external (**E**) and internal (**F**) views; **G**, enlarged view of the hinge ot the holotype; **H**, enlarged view of the hinge of the paratype MNHN.F.A99822. Scale bars: A-F, 10 mm, G, H, 5 mm. Credits: P. Loubry. Material from Letourneux coll. housed at MNHN.

weakly prosogyrous umbones placed in anterior half and extending above dorsal line. Shell surface densely radially sculptured, with 13-18 anterior ribs and 10-12 porterior ribs. Anterior ribs low, rather flat, slightly split by a central groove and separated by narrow interspaces less than 3/4 rib in breadth. Posterior ribs low becoming larger near the ventral margin. Pallial line entire, positioned moderately close to the ventral margin and connecting two medium-sized subovate scars. Shell margin finely crenulate ventrally, but with coarser crenulations on posterior margin. Posterior part well delineated from anterior by carinal groove. Hinge line strong and rather thick, with two cardinal teeth and two prominent lateral teeth. Posterior lateral tooth in right valve and anterior lateral in left valve strong.

COMPARISONS

The Plio-Pleistocene assemblage from Niau contains two species of Fraginae, *Fragum fragum* (Linnaeus, 1758) and ?*Lunulicardia distorta* Merle, n. sp. *Fragum fragum* is less carinate, its posterior margin is slightly convex and the surface of its ribs is squamous (see Fig. 9M-O). In the living fauna from French Polynesia, Boutet *et al.* (2020) report three other species of *Fragum* Röding, 1798: *F. mundum* (Reeve, 1845), *F. sueziense* (Issel, 1869) and *F. whitleyi* Iredale, 1919. They differ easily from ?*Lunulicardia distorta* Merle, n. sp. by their weak carina and their convex posterior margin. Members of *Lunulicardia* J. E. Gray, 1853 (type species: *Cardium retusum* Linnaeus, 1767 by monotypy, present day: Indo-West Pacific from Japan to Australia to South Africa) are reminiscent of *?Lunicardia distorta* Merle, n. sp. in their angulate carina, but have a concave posterior margin. *Americardia* Stewart, 1930 (type species: *Cardium medium* Linnaeus, 1758 by original designation, present day, Western Atlantic) has a weakly angulate carina, more ribs (22-25 anterior ribs), but is slightly reminiscent of ?*Lunulicardia distorta* Merle, n. sp. in its weakly concave posterior margin. *Americardia lightbourni* Lee & Huber, 2012 from Bermuda Island displays a very concave posterior margin as it is in ?*L. distorta* n. sp., but differs by many other characters (weakly angulate carina, numerous ribs with a squamous surface). Finally, ?*L. distorta* n. sp. is a very peculiar species for the Tuamotu archipelago. Its attribution to *Lunulicardia* is also uncertain as its posterior margin is strongly concave, whereas it is convex in species usually attributed to this genus.

Superfamily TELLINOIDEA Blainville, 1814
Family TELLINIDAE Blainville, 1814
Subfamily TELLININAE Blainville, 1814

Genus *Tellinella* Mörch, 1853

TYPE SPECIES. — *Tellina virgata* Linnaeus, 1758, by subsequent designation (Schmidt F. C. 1818).

***Tellinella* cf. *virgata* (Linnaeus, 1758)**
(Fig. 18A-C)

Tellina virgata – Salvat *et al.* 2018: table 1.

FIGURED MATERIAL. — **France** • 1 left valve; French Polynesia, Niau Atoll, "La Piscine"; 6°08'22.32"S, 146°23'14.09"W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98454 (Letourneux coll.); APL 69.7 mm (Fig. 18A-C).

OTHER MATERIAL EXAMINED. — **France** • 2 spm; same data as Figured material; MNHN.F.A98455 (Letourneux coll.)

DESCRIPTION
Shell rather large for family. Shape ovate-slightly elongate and subequilateral. Sculpture of commarginal striae becoming slightly oblique near posterior end; posterior slope with well distinct commarginal striae; anterior lateral tooth elongate, rather thick, moderately close to cardinals; posterior lateral tooth rather thick, distant from cardinals; pallial sinus poorly visible. Residual colour pattern uniform showing poorly defined concentric bands crossed by several very weak transverse lines more visible on the anterior part of valve.

COMMENTS
This shell (Fig. 18A-C) resembles living *Tellinella virgata* (see Fig. 18D-E) but its shape is more ovate with a higher dorsoventral lenght. In addition, its residual colour pattern don't display well large transverse dark bands, as observed in the syntype (P-Z 0010893) of the Linnean collection [https://www.linnean.org/research-collections/linnaean-collections] and as in other specimens (Fig. 18D, E). Thus, the attribution of this specimen to *Tellinella virgata* is provisional and is proposed with some doubts.

Genus *Indotellina* M. Huber, Langleit & Kreipl, 2015

TYPE SPECIES. — *Tellina chariessa* A. E. Salisbury, 1934 by original designation.

Indotellina fakaauensis Merle, n. sp.
(Fig. 18F-L)

urn:lsid:zoobank.org:act:AF800AD8-3ACD-488C-8306-9EF6C41342BE

Soletellina sp. – Salvat *et al.* 2018: table 1.

Soletellina sp. – Salvat *et al.* 2020: 27, pl. 2, fig. 4.

TYPE MATERIAL. — **Holotype**. **France** • 1 complete spm (right and left valves); French Polynesia, Niau Atoll, "La Piscine"; 6°08'22.32"S, 146°23'14.09"W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A99067 (Letourneux coll.); APL 93.2 mm (Fig. 18F-I).
Paratypes. **France** • 1 complete spm; same data as the holotype; MNHN.F.A99069 (Letourneux coll.); APL 99.8 mm (Fig. 18J, K) • 1 complete spm; MNHN.F.A99824 (Letourneux coll.); APL 104 mm (Fig. 18L) • 1 complete spm with a broken right vave; MNHN.F.A99978 (Letourneux coll.) • 5 spm; MNHN.F.A99151 (Letourneux coll.).

ETYMOLOGY. — From the type locality, Fakaau: Paumotu name for Niau.

TYPE HORIZON. — Plio-Pleistocene (molluscs assemblage) (see Figs 7-8).

TYPE LOCALITY. — French Polynesia, Niau Atoll, "La Piscine": 6°08'22.32"S, 146°23'14.09"W.

DISTRIBUTION. — Only know from the type locality.

DESCRIPTION
Larger shell extending to 104 mm in APL and to 55 mm in DVL, elongate, moderately inequilateral, equivalved, subsolid, rather compressed and with weak flexure posteriorly. Umbo slightly behind middle, rather inconspicuous and blunt. Anterior margin broadly rounded; ventral margin elongate, slightly convex, rising arcuately posteriorly; anterior dorsal margin straight to gently convex, fairly elongate, and gently descending; posterior dorsal margin elongate, slightly descending and weakly convex; posterior margin weakly biangulate, concave ventrally. Surface of shell smooth with only concentric growing striae. Ligament area thin and shallow on anterior dorsal margin and deeper and slightly wider on posterior dorsal margin; weakly developed escutcheon; lunule poorly developed. Commissure line of the ventral margin slightly twisted in its posterior part. Hinge line well developed. In left valve, cardinal complex consisting of an anterior, strong bifid tooth with subequal lobes, and of a posterior, elongate and thin laminate tooth; anterior lateral tooth obsolete; posterior lateral tooth obsolete, distal to cardinal complex; cardinal hinge plate extensive, particularly anteriorly. In right valve, cardinal complex consisting of a posterior, slightly skewed, well-developed, bifid cardinal tooth with subequal lobes, and of anterior slightly thickened, laminate, cardinal tooth; anterior lateral tooth small; posterior lateral tooth obsolete and distal to cardinal complex; anterior lateral tooth closer to cardinal complex. Muscle scars moderately well impressed; anterior and posterior adductor muscles scar irregularly semilunate. Pallial sinus subequal in opposite valves; pallial line poorly distinct.

COMPARISONS
This species was first identified as a Psammobiidae J. Fleming, 1828 of the genus *Soletellina* Blainville, 1824, a junior synonym of *Hyatula* Modeer, 1793 (type species *Hiatula dyphos* (Linnaeus, 1771) by subsequent designation. *Hyatula diphos* (= *Soletellina radiata* Blainville, 1824) is a present-day Indo-West Pacific species and is reminiscent of *Indotellina* in its smooth surface and in its elongate and inequilateral shape with a posterior margin longer than the anterior margin. *Hiatula diphos* differs from *Indotellina* by lacking lateral tooth and by having a moderately long nymph. Moreover, its posterior margin is less angular and more convex than that of *Indotellina*. Until now, *Indotellina*

Fig. 18. — Tellinidae (**A**-**L**) from the Plio-Pleistocene assemblage of Niau Atoll (Tuamotu, French Polynesia): **A**-**C**, *Tellinella* cf. *virgata* (Linnaeus, 1758), MNHN.F.A98454, left valve, internal view in natural light (**A**), external view in natural light (**B**) and under UV light (**C**); **D**, **E**, *Tellinella virgata* (Linnaeus, 1758) for comparison, MNHN.F.C02108 (Salvat coll.), present day, Rurutu island (Tuamotu, French Polynesia), left valve (**D**) and right valve (**E**); **F**-**L**, *Indotellina fakaauensis* Merle, n. sp.; **F**-**I**, holotype MNHN.F.A99067, external view of the right valve (**F**), external view of the left valve (**G**), view of the posterior margin (**H**), view of the ventral margin (**I**); **J**, **K**, paratype MNHN.F.A99069, internal view of the right valve (**J**), internal view of the left valve (**K**); **L**, paratype MNHN.F.A99824, external view of the right valve. Scale bars: 10 mm. Credits: A-C, F-L, P. Loubry (MNHN/CNRS); D-E, L. Cazes (MNHN/CNRS). A-C, F-L, material from Letourneux coll. housed at MNHN.

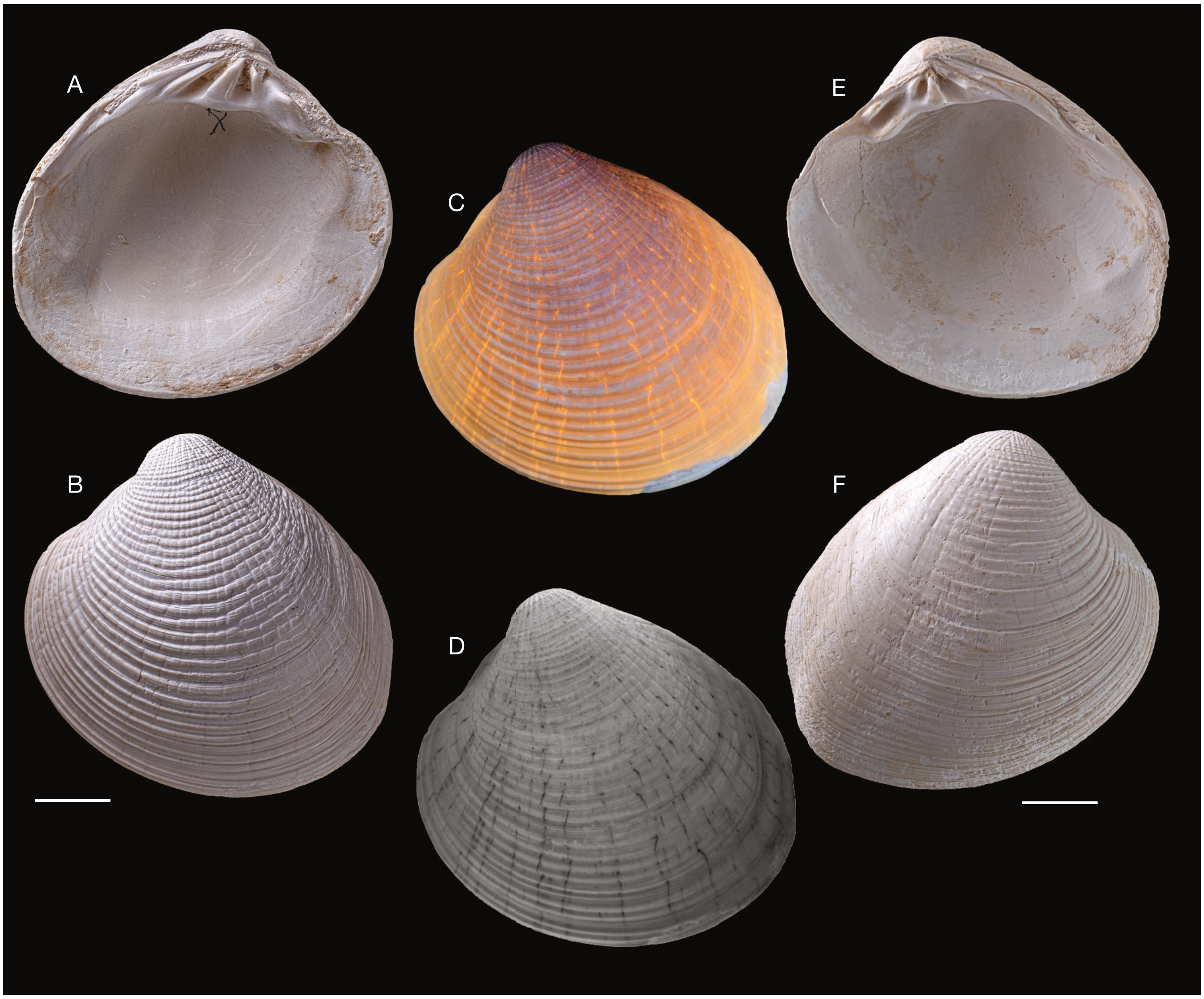


Fig. 19. — ?*Gafrarium troendlei* Merle, n. sp. from the Plio-Pleistocene assemblage of Niau Atoll (Tuamotu, French Polynesia): **A**-**D**, holotype, MNHN.F.A98456, left valve, internal view in natural light (**A**), external view in natural light (**B**), under UV light (**C**) and in inverse UV light (**D**); **E**, **F**, paratype, MNHN.F.A98457, right valve, internal view (**E**) and external view (**F**) in natural light. Scale bars: 10 mm. Credits: A-C, P. Loubry (MNHN/CNRS); E, F, L. Cazes (MNHN/CNRS). Material from Letourneux coll. housed at MNHN.

was only known by its type species, *Indotellina chariessa* A. E. Salisbury, 1934 [junior synonym of *Tellina elegans* W. Wood, 1828, not Deshayes (1824)]. It is a present-day Indo-West Pacific species but there is an unpublished record in the Pliocene from Niué atoll in Western Polynesia (see https://www.gbif.org/occurrence/1064827107 and Paulay & Spencer 1992 for the geological context). According to Boutet *et al.* (2020), this species is missing in the present-day Polynesian fauna. *Indotellina chariessa* is very similar to *Indotellina fakaauensis* Merle, n. sp. and both species share an angulate posterior margin and a hinge with lateral tooth. However, *Indotellina fakaauensis* can be distinguished by its more rectilinear ventral margin, its less angulate posterior margin and its more convex dorso-posterior margin. *Indotellina fakaauensis* is located just outside the geographical range of *I. chariassae* and it is possible that its presence in the Tuamotu Archipelago results from a Pliocene speciation phase separating both species and followed by its extinction.

Order VENERIDA Gray, 1854
Superfamily Veneroidea Rafinesque, 1815
Family Veneridae Rafinesque, 1815
Subfamily Gouldiinae R. B. Stewart, 1930

Genus *Gafrarium* Röding, 1798

Type species. — *Venus pectinata* Linnaeus, 1758 by subsequent designation (Dall 1902).

?***Gafrarium troendlei*** Merle, n. sp.
(Fig. 19)

urn:lsid:zoobank.org:act:2AB9871C-6D0C-4858-A136-0CD4E1AF64E4

Gafrarium sp. – Salvat *et al.* 2018: table 1.

TYPE MATERIAL. — **Holotype. France** • 1 left valve; French Polynesia, Niau Atoll, "La Piscine"; 6°08'22.32"S, 146°23'14.09"W; Plio-Pleistocene (molluscs assemblage); MNHN.F.A98456 (Letourneux coll.); APL 53 mm (Fig. 19A-D).
Paratypes. France • 10 left valves, 6 right valves, one complete specimen (two valves); same data as the holotype; MNHN.F.A98458 (Letourneux coll.) • 1 spm, MNHN.F.A98457 (Letourneux coll.); APL 52 mm (Fig. 19E, F).

ETYMOLOGY. — Dedicated to Jean Tröndlé.

TYPE HORIZON. — Plio-Pleistocene (molluscs assemblage) (see Figs 7; 8).

TYPE LOCALITY. — French Polynesia, Niau Atoll, La Piscine": 6°08'22.32S, 146°23'14.09W.

DISTRIBUTION. — Only known from the type locality.

DESCRIPTION

Shell weakly suborbicular, solid, thick; umbones flat, prosogyrate; lunule elongate heart-shaped, poorly raised, weakly delineated by incised line; escutcheon poorly defined, narrow; anterodorsal margin short, rounded terminally; ventral margin convex slightly angulate near posterior margin; posterodorsal margin moderately convex, angulate at its posterior termination. Sculpture radially, divaricately ribbed at early stages of growth and of dense concentric ribs at later stage of growth. Hinge of left valve with anterior lateral tooth solid, thick, peg-like; anterior cardinal very thin, separated from median cardinal by narrow V-shaped socket; median cardinal thick, oblique, raised; posterior cardinal free, thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of right valve with broad anterior pit, anterior lateral short, anterior cardinal short, slightly oblique, median cardinal, thick, peg-like, slightly oblique; posterior cardinal oblique, peg-like; posterior lateral, parallel to nymph. Anterior muscle adductor scars trapezoidally shaped, posterior adductor scars ovate. Pallial line wide; pallial sinus diminutive. Residual colour pattern formed of radial, narrow and more or less wavy yellow fluorescent lines (Fig. 18C).

COMPARISONS

This enigmatic species was previoulsy identified as *Circe plicatina* (Lamarck, 1818) in collection and as *Gafrarium* sp. (Salvat *et al.* 2018). Valves of *Circe plicatina* are more trigone in shape, their sculpture is less divaricate near the umbo, their cardinal teeth are less solid, less thick and their anterior pits are less broad. Early stages of growth of shells of *Circe scripta* (Linnaeus, 1758), type species of *Circe* Schumacher, 1817 resemble those of *Circe plicatina* and differ from those of ?*Gafrarium troendlei* n. sp. in having only concentric ribs. In addition, both species of *Circe* differs by having more compressed shells. The early stages of growth of ?*Gafrarium troendlei* Merle, n. sp. are reminscent to *G. harteae* and other species of *Gafrarium* Röding, 1798 in having a dominant radial sculpture of ribs tending sometimes to be divaricated. However, ?*G. troendlei* Merle, n. sp. can be easily distinguished from *G. harteae* Huber, 2010 and the type species of the *Gafrarium* Röding, 1798, *Gafrarium pectinatum* (Linnaeus, 1758), by its a dominant concentric sculpture and by its smooth, not crenulated ventral margin (see Fig. 9J-L). *Gafrarium tumidum* Röding, 1798, currently present on part of the south-west coast of Tahiti from Port Phaëton to Vairao, differs by its stronger radial sculpture and by the shape of its cardinal plate and muscle impressions. Among other species of *Gafrarium*, a dominant concentric sculpture is found in *G. eaquivocum* (Holten, 1802). Therefore, we prefer attribute ?*Gafrarium troendlei* Merle, n. sp. to *Gafrarium* than *Circe*, but this attribution is provisional, because the characters of this species are not fully typical of *Gafrarium*.

DISCUSSION

The absolute radiometric dates obtained make it possible to pinpoint the timing of events in the Niau lagoon since the Late Pliocene. In addition, the updating of the faunal content from the Plio-Pleistocene and the identification of Holocene assemblages make it possible to reconstruct the evolution of malacological assemblages up to the contemporary period. Thus, the following discussion is therefore divided into the following sections 1°) Paleoenvironment changes of the Niau atoll from Plio-Pleistocene to the Holocene and its consequences on the molluscan assemblages; 2°) Characteristics of the mollusc assemblage from the Plio-Pleistocene; 3°) Characteristics of the mollusc assemblage of the Holocene above the limestone crust; 4°) Characteristics of the mollusc assemblage of the modern lagoon.

PALEOENVIRONMENT CHANGES OF THE NIAU ATOLL FROM THE PLIO-PLEISTOCENE TO THE HOLOCENE AND ITS CONSEQUENCES ON THE MOLLUSCAN ASSEMBLAGES

The compositional attributes of the coral-molluscan thanatocenoses of Plio-Pleistocene are clearly those of a lagoonal environment, suggesting continuous water exchanges between the lagoon and the open ocean. These exchanges may have occurred through passes and channels (hoa), probably favoured by the fact that, during the Late Pliocene, higher sea stands were about + 20 m above present sea level (Grant *et al.* 2019) and a rich fauna of molluscs developed there as evidenced by the 92 species identified (Table 1). The coral-molluscan beds were later occluded by deposition of sandy sediments beneath the limestone crust (caliche), 2.505-2.245 Ma (Early Pleistocene). From about 0.5 Ma, the atoll started to be uplifted. Exchanges between ocean and lagoon waters may have occurred periodically over the Pliocene feo edifices of the atoll, as sea level was higher than present, especially, during MIS 11 to 9 stages (respectively about 400 000 and 320 000 yr BP). This uplift of the coral edifices allows the development of a malacological fauna with very few species, which experienced compositional changes during the Holocene (see Table 2) in conjunction with the reduction of the surface of the lagoon and the revegetation of its border. There is, however, a gap in deposition and associated mollusc assemblages between the Pleistocene and the Mid Holocene. This may be due to a lack of deposition or subsequent erosion at the site. The persistence of several species from both assemblages, such as *Ctena bella* and *Cerithium niauense* Merle, n. sp., nevertheless proves that during this intermediate period, these species continued to live in lagoon localities others than those surveyed at Vaiohua. The next and final stage refers to the current lagoon with particular hydrological characteristics. This lagoon was inhabited by surviving species and species introduced by man. In addition to the molluscan species inhabiting the entire lagoonal zone, some species limited to the "marite" spots in response to cooler ocean waters and to salinity close to 36 g/l (*Quidnipagus palatam* Iredale, 1929*, Gibberulus gibbosus* (Röding, 1798), *Notocochlis gualteriana* (Récluz, 1844) and *Longchaeus maculosus* (Lamarck, 1822) are probably more recent according to present sea level in the ocean and the lagoon and the porosity of the karstic edifice of Niau.

Characteristics of the Plio-Pleistocene molluscan assemblage

The species of the feo zone

In this Plio-Pleistocene feo zone, we noted the presence of randomly distributed specimens of three species: *Tridacna gigas* Linnaeus, 1758, *Tridacna squamosa* Lamarck, 1819 and *Codakia punctata* (Linnaeus, 1758). The first one no longer exists in French Polynesia but has still a wide distribution in the Indo-Pacific. By contrast, *Tridacna squamosa* is still present in Polynesia, but relatively rare, living along outer reef slopes surrounding the high volcanic islands and atolls. *Tridacna maxima*, a clam smaller in size than the two previously cited *Tridacna* species, was not reported in the feo zone but is very abundant in Polynesian lagoons, with high densities, especially in closed atolls lagoons of the Tuamotu. *Codakia punctata* occurs in French Polynesia coarse sand reef habitats but usually specimens are smaller that those observed in in the feo zone of Niau.

The mollusc assemblage beneath the limestone crust

Examination of the list of 92 mollusc species identified in the Plio-Pleistocene assemblage (Table 1) reveals three groups of species with different geographical distributions:

1) The first group, including ten species (three previously described and seven newly described in the present article) is almost 10% of the assemblage, which represents a significant speciation rate. All these species should be considered as endemic to Niau and to the paleontological field, as long as they are not found in modern or old reef edifices elsewhere in the world. The lack of work on the fossil malacological fauna in French Polynesia makes it impossible to know whether these species from the Niau lagoon are not found in Plio-Pleistocene fossil assemblages from other atolls in the region. All these species are extinct.

2) The second group includes 11 species that are now extinct in French Polynesia (see Table 1), but currently exist in other Indo-Pacific reef edifices. This represents a local and regional extinction rate of around 10%, as important as the speciation rate corresponding to endemic species.

and 3) The third group is the largest, with 71 species that are common to French Polynesian coral edifices, recently inventoried by Boutet *et al.* (2020).

In addition, these 92 species are also divided into two subgroups depending on whether they live on sandy or rocky habitat but sand dwelling species are the most abundant in the assemblage as revealed by the abondance index in Table 1. Rocky dwelling species were interpreted as transported into the lagoon, possibly through hoa, at the time when the lagoon communicated with the ocean, or over the emerged atoll reef-rim during cyclonic periods as reported by the inhabitants during the 1983 cyclone. Finally, this assemblage is representative of a sandy lagoon with a dominance of endogenous species and with addition of numerous reef-dwelling species when the lagoon was connected with the open ocean.

Characteristics of the Holocene molluscan assemblage above the Limestone Crust

In the Holocene assemblage (taro pits excluded, see Table 2), *Cerithium* Bruguière, 1789, the most abundant genus with three species (*Cerithium columna* G. B. Sowerby I, 1834, *C. rostratum* G. B. Sowerby II, 1855 and *C. niauense* Merle, n. sp.) corresponds to gastropods, which are living in the intertidal zone and feed off the microflora covering calcareous substrates as the mentioned caliche or coarse sediments. Indeed, their favorite habitat is that of supra-littoral calcareous flagstones, inward of reef flat zones or, more particularly, on the edges of water exchange channels (hoa) between motu which are topographically quite similar to the limestone crust. Other species, mainly bivalves (*Ctena* Mörch, 1861*, Gafrarium* Röding, 1798 and *Fragum* Röding, 1798) are indicative of fine to coarse sediments in which these were inhabiting. This molluscan assemblage is typical of lagoonal habitat, with limestone substrates for gastropods and coarse and fine sand for bivalves.

Compared to the thanatocenosis of molluscs collected beneath the limestone crust, this assemblage above the said crust is ten times less rich, nine species against 92 species. In addition to this quantitative impoverichment, comparison of the two assemblages allows some additional comments. Although these two assemblages inhabited the lagoon after an interval of around two million years (Early Pleistocene deposits beneath the crust and Holocene deposits above the crust), we note that among the most abundant species present beneath the crust (see Table 1, column abundances, code D = more more than 100), *Cerithium punctatum* Bruguière, 1792, *Clypeomorus bifasciata* (G. B. Sowerby II, 1855) and *Finella pupoides* A. Adams, 1860 no more are present above the crust. The disappearance of *Cerithium punctatum* from Holocene sediments is temporary, however, since the species has reappeared in the present-day lagoon. Contrary *Ctena bella* (Conrad, 1837) and *Cerithium niauense* Merle, n. sp. are still present as well as *Fragum fragum* (Linnaeus, 1758), see Table 2. Such a faunal impoverishment is likely to have been

TABLE 1. — Assemblage of the 92 molluscan species identified at specific rank from the Plio-Pleistocene of Niau Atoll (Tuamotu, French Polynesia). Abundances: **A**, from 1 to 5 shells or valves; **B**, between 6 and 20; **C**, between 21 and 100; **D**, more than 100. Substrates: **S**, sandy; **H**, hard. Distribution: **IP**, Indo-Pacific; **WP**, West Pacific; **P**, Pacific. ▲, Endemic and extinct species (**bold**); ✶, species only extinct in French Polynesia.

Families	**Species**	**Abundances**	**Substrates**	**Distributions**
Scissurellidae	*Scissurella mirifica* (A. Adams, 1862)	A	H	WP
Skeneidae	*Lodderena emeryi* (Ladd, 1966)	A	H	WP
Turbinidae	*Astralium confragosum* (Gould, 1851)	A	H	P
	***Turbo fakaauensis* Tröndlé & Letourneux, 2012** ▲	A	H	Endemic
Tornidae	*Lophocochlias parvissimus* (Hedley, 1899)	A	H	IP
Neritidae	*Nerita chamaeleon* Linnaeus 1758 ✶	C	H	IP
	Nerita plicata Linnaeus 1758	B	H	IP
	Nerita histrio Linnaeus, 1758	B	H	IP
Cerithiidae	*Cerithium columna* Sowerby I, 1834	B	S	IP
	Cerithium echinatum Lamarck, 1822	B	S	IP
	Cerithium nodulosum Bruguière, 1792 ✶	A	S	IP
	Cerithium punctatum Bruguière, 1792	D	S	IP
	Cerithium rostratum G.B. Sowerby II, 1855	C	S	IP
	***Cerithium niauense* Merle, n. sp.** ▲	D	S	Endemic
	Cerithium zebrum Kiener, 1841	C	H	IP
	Clypeomorus bifasciata (G.B. Sowerby II, 1855) ✶	D	H	IP
	Rhinoclavis aspera (Linnaeus, 1758)	A	S	IP
Modulidae	*Indomodulus tectum* (Gmelin, 1791)	A	H	IP
Planaxidae	*Hinea fasciata* (Pease, 1868)	A	H	IP
Scaliolidae	*Finella pupoides* A. Adams, 1860	D	S	IP
Littorinidae	*Littoraria coccinea* (Gmelin, 1791)	A	H	IP
	Peasiella conoidalis (Pease, 1868)	A	H	IP
Naticidae	*Notocochlis gualteriana* (Récluz, 1844)	C	S	IP
	Polinices mammilla (Linnaeus, 1758)	C	S	IP
Barleeidae	*Protobarleeia myersi* (Ladd, 1966) ✶	B	H	WP
Rissoinidae	*Apataxia cerithiiformis* (Tryon, 1887)	A	H	IP
Zebinidae	*Zebinella tenuistriata* (Pease, 1868)	A	H	IP
	Rissoina oryza Garrett, 1873 ✶	A	H	WP
Truncatellidae	*Taheitia scalariformis* (Reeve, 1842)	C	S	WP
Cypraeidae	*Lyncina propinqua* (Garrett, 1879)	A	H	IP
	Mauritia maculifera Schilder, 1932	A	H	IP
	Mauritia scurra (Gmelin, 1791)	A	H	IP
	Monetaria moneta (Linnaeus, 1758)	C	H	IP
	Naria erosa (Linnaeus, 1758)	C	H	IP
Strombidae	*Canarium mutabile* (Swainson, 1821)	A	S	IP
	Gibberulus gibbosus (Röding, 1798)	C	S	IP
	***Striatotrombus blanci* (Tröndlé & Salvat, 2010)** ▲	C	S	Endemic
Cymatiidae	*Gutturnium muricinum* (Röding, 1798)	B	H	IP
Tonnidae	*Malea pomum* (Linnaeus, 1758)	A	H	IP
Columbellidae	*Euplica borealis* (Pilsbry, 1904) ✶	B	H	WP
Nassariidae	*Nassarius bellulus* (A. Adams, 1852) ✶	A	S	IP
	Nassarius papillosus (Linnaeus, 1758)	A	S	IP
Muricidae	*Drupella margariticola* (Broderip, 1833)	B	H	IP
Mitridae	*Strigatella litterata* (Lamarck, 1811)	A	H	IP
	Carinomitra saltata (Pease, 1865)	A	H	WP
Conidae	*Conus catus* Hwass in Bruguière, 1792	A	H	IP
	***Conus letourneuxi* Merle, n. sp.** ▲	A	H	Endemic
	***Conus georgesrichardi* Merle, n. sp.** ▲	C	H	Endemic
Terebridae	***Oxymeris niauensis* (Tröndlé & Letourneux, 2011)** ▲	B	S	Endemic
Acteonidae	*Pupa sulcata* (Gmelin, 1791)	C	S	IP
Pyramidellidae	*Parthenina cossmanni* (Hornung & Mermod, 1924)	A	S	IP
	Herviera gliriella (Melvill & Standen, 1896)	A	S	IP
	Miralda scopulorum (Watson, 1886)	A	S	WP
	Odostomia sperabilis Hedley, 1909	B	S	WP
	Otopleura mitralis (A. Adams, 1854)	A	S	IP
	Otopleura nitida (A. Adams, 1854)	A	S	IP

Table 1. — Continuation.

Families	Species	Abundances	Substrates	Distributions
Pyramidellidae (continuation)	*Longchaeus maculosus* (Lamarck, 1822)	A	S	IP
	Pyrgulina pupaeformis (Souverbie, 1865)	A	S	IP
	Turbonilla mumia (A. Adams, 1861)	A	S	IP
Bullidae	***Bulla niauensis* Merle, n. sp.** ▲	B	S	Endemic
Tornatinidae	*Acteocina sandwicensis* Pease, 1860	C	S	WP
Ellobiidae	*Allochroa layardi* (H. & A. Adams, 1855)	A	H	IP
	Melampus castaneus (Muehlfeldt, 1818)	A	H	IP
	Microtralia alba (Gassies, 1865) ✱	A	H	WP
	Microtralia lucida (Pease, 1869)	A	H	WP
Mytilidae	*Modiolus auriculatus* (Krauss, 1848)	B	H	IP
	Musculus viridulus (H. Adams, 1871)	A	H	IP
Arcidae	*Acar congenita* (E.A. Smith, 1885)	A	S	IP
	Anadara oceanica (Lesson, 1831)	A	S	IP
	Barbatia foliata (Forsskal in Niebuhr, 1775)	A	H	IP
Philobryidae	*Cratis kanekoi* Hayami & Kase, 1993	A	S	WP
Vulsellidae	*Electroma alacorvi* (Dillwyn, 1817) ✱	A	H	IP
Ostreidae	*Dendostrea sandvichensis* (G.B. Sowerby II, 1871)	A	H	IP
Gryphaeidae	*Hyotissa numisma* (Lamarck, 1819)	A	H	IP
Margaritidae	*Pinctada maculata* (Gould, 1850)	B	H	IP
Cardiidae	*Fragum fragum* (Linnaeus, 1758)	D	S	IP
	?***Lunulicardia deformata* Merle, n. sp.** ▲	B	S	Endemic
	Tridacna maxima (Röding, 1798)	A	H	IP
Tellinidae	*Jactellina clathrata* (Deshayes, 1835)	B	S	IP
	Pinguitellina robusta (Hanley, 1844)	A	S	IP
	Cadella crebrimaculata (G.B. Sowerby II, 1868)	A	S	WP
	Scissulina dispar (Conrad, 1837)	C	S	IP
	Scutarcopagia scobinata (Linnaeus, 1758)	A	S	IP
	Quidnipagus palatam Iredale, 1929	B	S	IP
	Tellinella cf. *virgata* (Linnaeus, 1758)	A	S	?IP
	***Indotellina fakaauensis* Merle, n. sp.** ▲	B	S	Endemic
	Tonganaella perna (Spengler, 1798)	A	S	IP
Chamidae	*Chama limbula* Lamarck, 1819	A	H	IP
Lucinidae	*Codakia punctata* (Linnaeus, 1758)	B	S	IP
	Ctena bella (Conrad, 1837)	B	S	IP
Veneridae	*Gafrarium pectinatum* (Linnaeus, 1758)	C	S	IP
	?***Gafrarium troendlei* Merle, n. sp.** ▲	B	S	Endemic

caused by uplift of the atoll, thus resulting in the connection failure between the lagoon and the open sea.

The few species collected on the taro pit of Late Holocene age (Tables 2; 3) are just suffered an impoverichment when compared to those collected above the limestone crust, noting the maintenance of *Ctena bella* and *Cerithium niauense* Merle, n. sp. This is in accordance with shell age deposition in the two assemblages, as differing from only 1000 years (see Table 3).

CHARACTERISTICS OF THE MOLLUSCAN ASSEMBLAGE OF THE MODERN LAGOON

The modern malacological fauna of the lagoon as observed in 2022 (Table 2) is divided in two groups. The first group includes six species inhabiting "marite", local name for oceanic water resurgences in the lagoon across the karstified atoll feo reliefs, only in a few points in the centre of the lagoon. We do not consider that this group of species is representative of the molluscan fauna in the whole lagoon. It includes four species already present in the Plio-Pleistocene units of Niau: *Notocochlis gualteriana* (Récluz, 1844), *Gibberulus gibbosus* (Röding, 1798), *Longchaeus maculosus* (Lamarck, 1822), *Fragum fragum* (Linnaeus, 1758) and *Quidnipagus palatam* Iredale, 1929. The material collected in 2008 and 2022 also includes a very few *Melanoides tuberculata* (O. F. Müller, 1774). We consider that they came from swamps which are their habitat and not the lagoon. Small fragments of *Pinctada maculata* individuals (Gould, 1850) are observed in shore deposits, but it was possible to find alive some specimens in the lagoon.

The second group relates to three very abundant species inhabiting within the lagoon: *Ctena bella* (Conrad, 1837), *Cerithium punctatum* Bruguière, 1792 and *Clypeomorus brevis* (Quoy & Gaimard, 1834) as observed in 2022. But the assemblage observed in 2008 was different (Salvat *et al.* 2018) with only *Ctena bella* and *Cerithium punctatum*. *Clypeomorus brevis* has been introduced to Niau during the last decade, and in 2022 the expansion of this gastropod in the lagoon proved to have been rapid that skeletal deposits on the edge of

Table 2. — Assemblages of molluscan species from the Mid Holocene (Aturona), Late Holocene (Vaiohua, archeological platform), Late Holocene (Vaiohua, taro pit) and modern lagoon of Niau Atoll (Tuamotu, French Polynesia). As a reminder, species already present in the Plio-Pleistocene are provided in the first column. **m** for species only present in "marite".

Families	**Species**	**Plio-Pleistocene**	**Mid Holocene (Aturona)**	**Late Holocene (Vaiohua archaeological platform)**	**Late Holocene (Vaiohua, taro pit)**	**Modern Lagoon**
Cerithiidae	*Cerithium columna* G.B. Sowerby I, 1834	×	–	×	×	m
	Cerithium punctatum Bruguière, 1792	×	–	–	–	×
	Cerithium rostratum G.B. Sowerby II, 1855	×	–	×	–	–
	Cerithium niauense Merle, n. sp.	×	×	×	×	–
	Clypeomorus brevis (Quoy & Gaimard, 1834)	–	–	–	–	×
Thiaridae	*Melanoides tuberculata* (O. F. Müller, 1774)	×	×	–	–	–
Naticidae	*Notocochlis gualteriana* (Récluz, 1844)	×	–	–	–	m
Strombidae	*Gibberulus gibbosus* (Röding, 1798)	×	–	–	–	m
Pyramidellidae	*Longchaeus maculosus* (Lamarck, 1822)	×	–	–	–	m
Ostreidae	*Dendostrea sandvichensis* (G. B. Sowerby II, 1871)	×	–	×	–	–
Margaritidae	*Pinctada maculata* (Gould, 1850)	×	–	–	–	×
Cardiidae	*Fragum fragum* (Linnaeus, 1758)	×	–	×	×	m
Tellinidae	*Quidnipagus palatam* Iredale, 1929	×	×	–	–	m
	Tellinella virgata (Linnaeus, 1758)	×	×	–	–	–
Lucinidae	*Ctena bella* (Conrad, 1837)	×	×	×	×	×
Veneridae	*Gafrarium pectinatum* (Linnaeus, 1758)	×	×	×	–	–

Table 3. — Radiocarbon data: fraction of modern carbon (**pMC**), conventional ages and calibrated ages (Niau Atoll, French Polynesia). The ages obtained were calibrated with the IntCAL Marine 20 curve (Heaton *et al.* 2020) and the Oxcal4.4 software (Bronk Ramsey 2001). The reservoir age correction used was made with ΔR 140 ± 20 years based on data obtained for French Polynesia (Petchey *et al.* 2008).

Sample numbers	**Labcodes**	**Nature**	**Locations**	**mg C**	**Delta C13**	**pMC**	**Err pMC**	**Ages in years**	**Err age BP**	**Calibrated age (years cal BP)**	**Epoch**
N 57	71233	*Quidnipagum palatam*	Aturona	1.22	3.80	49.09739	0.16352	5715	30	6238-5912	Mid Holocene
N 103	SAC -70407	*Cerithium* sp.	Vaiohua	1.14	0.50	61.95487	0.17497	3845	30	3982-3627	Late Holocene
N 107	71234	*Ctena bella*	Vaiohua (Taro pit)	1.25	5.30	76.11125	0.21268	2195	30	1940-1610	Late Holocene
N 121	SAC -70408	*Cerithium* sp.	Vaiohua	0.83	–1.40	66.39803	0.17884	3290	30	3310-2954	Late Holocene

the lagoon are mainly composed of their dead shells. Further evidence of this introduction of *Clypeomorus brevis* is provided by the shell necklaces and other decorative ornements that the inhabitants make to decorate their houses or to crown passing visitors when they leave. The necklaces worn by Niau inhabitants formerly included almost exclusively *Ctena bella* valves, without any *Clypeomorus brevis* or *Cerithium punctatum* the last one being too small to be threaded. By contrast, the necklaces offered to visitors in 2022 consisted mainly of *Clypeomorus* shells.

The current characteristic fauna of the Niau lagoon therefore is limited to three species. This assemblage is typically less rich than that of the Mid-Late Holocene one and older ones. *Ctena bella* is present in the Niau lagoon since the Late Pliocene in the molluscan assemblage collected beneath the caliche crust in amazing abundance. This bivalve is also quantitatively dominant in all other assemblages until the modern times, including the sedimentary deposits overlying the caliche (dated at 3000-4000 years BP), the ancient cultivation taro pits (dated at around 2000 years BP) and the modern lagoon. *Ctena bella* has probably been a permanent species living in the lagoon and its surrounding zones for more than three million years during higher sea stands, and may have survived in specific refuge zones during lower sea stands. Contrary to *Ctena bella*, *Cerithium niauense* Merle, n. sp. inhabiting the Niau lagoon from the Late Pliocene to the Late Holocene has disappeared. *Cerithium punctatum*, already present in the Late Pliocene assemblage but not very abundant, is absent in the Mid-Late Holocene deposits but present and abundant in the modern lagoon. *Clypeomorus brevis* was introduced in the last decade. It is noteworthy that the three species widely colonizing the Niau lagoon tolerate significant variations in salinity and temperature. The inflow of ocean water during cyclones considerably changes the physico-chemical characteristics of the lagoon waters, especially if occurring after a long period of heavy rainfall or of strong evaporation. It is undoubtedly that *Ctena bella* and *Cerithium punctatum* owe their prosperity to their euryhaline and eurythermal capacities in the lagoon since more than 3 million years. The recent extinction of *Cerithium niauense* Merle, n. sp., which appears to have had the same geological history and the same ecological requirements at Niau as *Ctena bella* and *Cerithium punctatum*, seems difficult to explain. However, *Ctena bella* and *Cerithium punctatum* have a wider geographical distribution, which suggests a greater likelihood of adaptation to local environmental changes. *Cerithium niauense* Merle, n. sp., on the other hand, was endemic and therefore appeared to be at greater risk of extinction.

CONCLUSION

The uplifted atoll of Niau is a rather unique example in the central South Pacific, as it allows us to trace the response of malacological assemblages to environmental changes from the Late Pliocene to the present day, in a well constrained temporal context. This work documents, in particular, the faunal extinctions observed during the Holocene, which are largely the result of the restriction of exchange with the open sea and the closure of the lagoon, in response to the uplift of the atoll. Thus, the Plio-Pleistocene assemblage, rich in more than 90 species, was replaced in the Mid and Late Holocene by very impoverished assemblages with a species richness of no more than ten. Species endemic to the Plio-Pleistocene of the Niau Atoll account for 10% of the total malacological assemblage. They have been particularly hard hit by extinctions, with only species, *Cerithium niauense* Merle, n. sp., surviving from the Holocene. Future studies should be focused on comparison of the faunal composition between Niau and other Pacific atolls. Moreover, the deep origin of Pliocene faunas in Polynesia is also poorly known. The Makatea atoll, of Early Miocene age (Montaggioni *et al.* 1985), contains the oldest known malacofauna from French Polynesia, but it has been little studied and is known only from a list of a few taxa.

Acknowledgements
Warm thanks are given to Anton Eisenhauer, University of Frankfurt for providing dating results in 2013; to René Galzin and Magali Verducci for releasing ecological information about the Niau lagoon in 2010; to Michel Pichon for identifying the coral the species *Leptoria phrygia* (Ellis & Solander, 1786); to the “Department Environment, Culture et Patrimoine” of the French Polynesian Government for giving authorization to prospect on Niau Atoll in September-October 2022 as part of an archaeological mission organized and financially supported by the “Centre International de Recherche Archéologique de Polynésie” – incentive action led by Eric Conte, “Maison des Sciences de l’Homme”, “Université de la Polynésie française”; to Guillaume Molle and Vahine Rurua, archaeologists, for much appreciated collaboration in the field as well as Rodolphe Tehaamaru known as “Steven” and Heimaura Tiho known as “Tiho”; to the local authorities and the population of Niau for their kind welcome; to colleagues Nicolas Puillandre (MNHN) for loan of conids, Loïc Limpelaer for the the loan of *Cerithium tenellum*, Jean-Pierre Pointier (EPHE) for some figures, Eric Brunaud for his help in drawing graphics, Lilian Cazes and Philippe Loubry (MNHN/CNRS) for the photos of shells under natural light and under UV light, Blanchard Bouchard (MNHN) from reconstructing some brocken bivalves and Alexandre Lethiers for the infography. This paper benefited from the reviews of Jean-Jacques Cornée (Géosciences, Montpellier) and Jean-Paul Saint Martin (MNHN).

REFERENCES

Abbott R. T. 1960. — The genus *Strombus* in the Indo-Pacific. *Indo-Pacific Mollusca* 1: 35-146. https://www.biodiversitylibrary.org/part/201049

Agassiz A. 1903. — The Coral Reefs of the Tropical Pacific. *Memoirs of the Museum of Comparative Zoology at Harward* 28 (5): 1-410. https://doi.org/10.5962/bhl.title.41332

Andrefouet S. & Chauvin C. 2005. — *Atlas des récifs coralliens de Polynésie française*. Institut de recherche pour le développement (IRD), Nouméa, 131 p. https://www.documentation.ird.fr/hor/fdi:010045822

Beck L., Caffy I, Delqué-Koli E., Dumoulin J.-P., Goulas C., Hain S., Moreau C., Perron M., Setti V., Sieudat M. & Thellier B. 2024. — 20 years of AMS 14C dating using the ARTEMIS facility at the LMC14 national laboratory: review of service and research activities. *Radiocarbon* 66 : 2024: 1041-1053. https://doi:10.1017/RDC.2023.23

Blainville H. M. D. (de) 1824. — Mollusques, Mollusca (Malacoz.), *in* Cuvier F. (ed.), *Dictionnaire des sciences naturelles*. Vol. 32. Levrault, Strasbourg et Paris & Le Normant, Paris. http://www.biodiversitylibrary.org/page/25299230

Blainville H. M. D. (de) 1832. — Disposition méthodique des espèces récentes et fossiles des genres Pourpre, Ricinule, Licorne et Concholépas de M. de Lamarck, et description des espèces nouvelles ou peu connues, faisant partie de la collection du Muséum d’Histoire naturelle de Paris. *Nouvelles Annales du Muséum d’Histoire naturelle* 1: 189-263. https://www.biodiversitylibrary.org/page/33122454

Born I. (von) 1778. — *Index rerum naturalium Musei Cæsarei Vindobonensis. Verzeichniß der natürlichen Seltenheiten des kaiserliches und königliches Naturalien Cabinets zu Wien.* Pars I. Testacea. Kraus, Vienna, 458 p. https://www.biodiversitylibrary.org/bibliography/11581

Boutet M., Gourguet R. & Letourneux J. 2020. — *Mollusques marins de Polynésie française*. Au Vent des Îles & Université de la Polynésie française, Papeete, 768 p.

Broderip W. J. 1833. — Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming. *Proceedings of the Committee of Science and Correspondence of the Zoological Society of London* 2: 173-179. https://www.biodiversitylibrary.org/part/382429

Bronk Ramsey C. 2001. — Development of the radiocarbon calibration program OxCal. *Radiocarbon* 43 (2A): 355-363. https://doi.org/10.1017/S0033822200038212

Butaud J. F. 2006. — *Étude de la flore vasculaire de l'atoll soulevé de Niau, cartographie de sa végétation, caractérisation de l'habitat du Martin-Chasseur de Niau et priorités de conservation*. Société ornithologique de Polynésie, Papeete, 38 p.

Butaud J. F. 2020. — Patrimoine végétal de l'atoll soulevé de Niau. *Bulletin de la Société des Études océaniennes* 350-351: 32-46.

Caze B., Merle D., Saint Martin J.-P. & Pacaud J.-M. 2011. — Contribution of residual colour patterns to the species characterization of Caenozoic molluscs (Gastropoda, Bivalvia). *Comptes Rendus Palevol* 10 : 171-179. https://doi.org/10.1016/j.crpv.2010.10.005

Chazine J. M. 1990. — Évolution des établissements humains en milieu insulaire des Tuamotu (Polynesie française). *Notes et Documents de Sciences Humaines* 13: 1-60.

Chevalier J. P. 1979. — La faune corallienne (Scléractinaires et Hydrocoralliaires) de la Polynésie Française. *Cahiers de l'Indo-Pacifique* 1: 129-151.

Children J. G. 1823. — Lamarck's genera of shells. *Quarterly Journal of Science, Literature and the Arts* 14 (28): 298-322; 15(29): 23-52; 15(30): 216-258; 16 (31): 49-79; 16 (32): 241-264. http://biodiversitylibrary.org/page/14496865

Cibois A., Thibault J.-C. & Pasquet E. 2007. — *Les rousserolles de l'archipel des Tuamotu (Polynésie francaise) : aspect historique et stratégie de conservation*. Société ornithologique de Polynésie, Papeete, 76 p.

Claremont M., Reid D. G. & Williams S. T. 2011. — Evolution of corallivory in the gastropod genus *Drupella*. *Coral Reefs* 30: 977-990. https://doi.org/10.1007/s00338-011-0788-5

Crame J. A. 1986. — Late Pleistocene molluscan assemblages from the coral reefs of the Kenya coast. *Coral Reefs* 4: 183-1906. https://doi.org/10.1007/BF00427940

Da Motta A. J. 1991. — *A Systematic Classification of the Gastropod Family Conidae at the Generic Level*. La Conchiglia, Roma, 48 p.

Dall W. H. 1902. — Synopsis of the family Veneridae and of the North American Recent species. *Proceedings of the U.S. national Museum* 26: 335-412. https://doi.org/10.5479/si.00963801.26-1312.335.

Dall W. H. 1903. — Synopsis of the family Astartidae with a review od the American species. *Proceedings of the United States National Museum* 26: 933-951. http://hdl.handle.net/10088/13704

Dekkers A. M. & Maxwell S. J. 2018. — Presenting a new genus within Strombidae Rafinesque, 1815 (Mollusca: Gastropoda: Littorinimorpha) with notes on the taxonomic position of *Strombus* (*Lentigo*) *micklei* Ladd, 1972 and the validity of *Strombus* (*s.l.*) *blanci* Tröndlé & Salvat, 2010. *Proceedings of the Biological Society of Washington* 131: 220-226. https://doi.org/10.2988/18-00009

Deshayes G. P. 1824. — Description des coquilles fossiles des environs de Paris. Vol. 1 (Bivalvia). Deshayes, Paris, 392 p. https://www.biodiversitylibrary.org/page/36349276

Deshayes G. P. 1857. — Description d'espèces nouvelles du genre *Terebra*. *Journal de Conchyliologie* 6 (1): 65-102. https://biodiversitylibrary.org/page/15862590

Dumoulin J. P., Comby-Zerbino C., Delque-Kolic E., Moreau C., Caffy I., Hain S., Perron M., Thellier B., Setti V., Berthier B. & Beck L. 2017. — Status report on sample preparation protocols developed at the LMC14 Laboratory, Saclay, France: from sample collection to 14C AMS measurement. *Radiocarbon* 59 (3): 713-726. https://doi.org/10.1017/RDC.2016.116

Emerson W. K. & Attilio A. d' 1981. — Remarks on *Muricodrupa* Iredale, 1918 (Muricidae: Thaidinae), with the description of a new species. *The Nautilus* 95 (2): 77-82. https://www.biodiversitylibrary.org/part/40406

Gould A. A. 1859. — Descriptions of new species of shells brought home by the North Pacific Exploring Expedition. *Proceedings of the Boston Society of Natural History* 7: 138-142. https://biodiversitylibrary.org/page/9249698

Grant G. R., Naish T. R., Dunbar G. B., Stocchi P., Kominz M. A., Kamp P. J. J., Tapia C. A., Mckay R. M., Levy R. H., Patterson M. O. 2019. — The amplitude and origins of sea-level variability during the Pliocene epoch. *Nature* 574: 237-241. https://doi.org/10.1038/s41586-019-1619-z

Gray J. E. 1847. — A list of genera of recent species of Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London* 1847: 129-219. https://www.biodiversitylibrary.org/page/12862913

Gray J. E. 1853. — A revision of the genera of some of the families of Conchifera or bivalve shells. *Annals and Magazine of Natural History* (2) 11: 33-44, 398-402. https://biodiversitylibrary.org/page/13785724

Harland W. B., Armstrong R. L., Cox A. V., Craig L. E., Smith A. G. & Smith D. G. 1989. — *A Geologic Time Scale 1989*. Cambridge University Press, Cambridge, 263 p.

Hayasaka S. & Oki K. 1971. — Note on the marine molluscan fauna from the Pleistocene Kogashira formation in the Kagoshima city, south Kyushu, Japan. *Report of the Faculty of Sciences of Kagoshima University, Earth Science Biology* 4: 1-13.

Heaton T., Kohler P., Butzin M., Bard E., Reimer R., Austin W., Bronk-Ramsey C., Grootes P., Hughen K., Kromer B., Reimer P., Adkins J., Burke A., Cook M., Olsen J. & Skinner L. 2020. — Marine20 – the marine radiocarbon age calibration curve (0-55,000 cal BP). *Radiocarbon* 62 (4): 779-820. https://doi.org/10.1017/RDC.2020.68

Hinds R. B. 1843. — Descriptions of new shells from the collection of Captain Sir Edward Belcher, R.N., C.B. *Annals and Magazine of Natural History* 11: 255-257. https://www.biodiversitylibrary.org/page/42906950

Holten H. S. 1802. — *Enumeratio systematica conchyliorum beat J. H. Chemnitzii quondam ecclesiae Zebaothi Havniae pastoris, plurim societum sodialis p.p. quae publica auctione venduntur die 7me Decembris ano pres*. K. H. Scidelini, Copenhagen, 88 p. https://www.biodiversitylibrary.org/page/46195957

Houart R. 2008. — Rehabilitation of *Ergalatax martensi* (Schepman, 1892) (Gastropoda: Muricidae), senior synonym of *Ergalatax obscura* Houart, 1996, and description of *Ergalatax junionae*, new name for *Morula martensi* Dall, 1923. *The Nautilus* 122 (2): 99-106. https://www.biodiversitylibrary.org/part/174734

Huber M. 2010. — Formal description and designation of holotypes for 23 bivalve species and type species for 2 bivalve genera (Mollusca: Bivalvia). *Conchylia* 41 (1): 1-32. https://www.zora.uzh.ch/handle/20.500.14742/59700

Huber M., Langleit A. & Kreipl K. 2015. — Tellinidae, *in* Huber M. (ed.), *Compendium of Bivalves 2*. ConchBooks, Harxheim: 167-297.

Hwass C. H. 1792. — Cone. *Conus*, *in* Bruguière J. G. (ed.), *Encyclopédie méthodique ou par ordre de matières. Histoire naturelle des vers*. Vol. 1. Pancoucke, Paris: 586-757. https://www.biodiversitylibrary.org/page/33703247

International Commission of Zoological Nomenclature (ICZN) 1978. — Opinion 1109 (Case 2032), *Cerithium* Bruguière, 1789 (Gastropoda): designation of type-species under the Plenary Powers. *Bulletin of Zoological Nomenclature* 35: 97-98. http://biodiversitylibrary.org/page/12226686

International Commission of Zoological Nomenclature 2025. — The code online. Available at: https://www.iczn.org/the-code/the-code-online (Last access on 04/2025).

Global Biodiversity Information Facility 2025. — *Indotellina* M. Huber, Langleit & Kreipl, 2015. https://www.gbif.org/species/7866814 (last access on 04/2025).

Issel A. 1869. — *Malacologia del Mar Rosso. Ricerche zoologiche e paleontologiche*. Biblioteca Malacologica, Pisa, 387 p. http://www.biodiversitylibrary.org/item/43995

Iredale T. 1929. — Queensland molluscan notes, N° 1. *Memoirs of the Queensland Museum* 9 (3) 261-297. https://www.biodiversitylibrary.org/page/52430219

Jamet R. & Trichet J. 1987. — Étude du milieu terrestre des atolls de la Polynésie française. Caractéristiques et potentialités agricoles. *Cahiers ORSTOM (série Pédologie)* 23 (4): 275-293.

Jousseaume F. 1888. — Description des mollusques recueillis par M. le Dr. Faurot dans la Mer Rouge et le Golfe d'Aden. *Mémoires de la Société zoologique de France* 1: 165-223. http://biodiversitylibrary.org/page/10047746

Kiener L. C. 1836. — *Genre Poupre. Species general et iconographie des coquilles vivantes, famille des Purpurifères*. Vol. 8. Rousseau & J.B. Baillière, Paris, 151 p. https://doi.org/10.5962/bhl.title.969

Ladd H. S. 1966. — Chitons and Gastropods (Haliotidae through Ade- orbidae) from the Western Pacific islands. *U.S. Geological Survey Professional Paper* 531: 1-98. https://doi.org/10.3133/pp531

Ladd H. S. 1972. — Cenozoic fossil mollusks from Western Pacific Islands; gastropods (Turritellidae through Strombidae). *U.S. Geological Survey Professional Paper* 532: 1-79. https://doi.org/10.3133/pp532

Ladd H. S. 1977. — Cenozoic fossil mollusks from Western Pacific Islands; gastropods (Eratoidae through Harpidae). *U.S. Geological Survey Professional Paper* 533: 1-84. https://doi.org/10.3133/pp533

Ladd H. S. 1982. — Cenozoic fossil mollusks from Western Pacific Islands; gastropods (Eulimidae and Volutidae through Terebridae). *U.S. Geological Survey Professional Paper* 1171: 1-100. https://doi.org/10.3133/pp1171

Lamarck J. B. 1818. — *Histoire naturelle des Animaux sans Vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédés d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la Zoologie*. Vol. 5. Deterville, Paris, 612 p. https://www.biodiversitylibrary.org/bibliography/63986

Lambeck K. 1981. — Flexure of the ocean lithosphere from island uplift, bathymetry and geoid height observations: the Society Islands. *Geophysical Journal of the Royal Astronomical Society* 67: 91–114. https://doi.org/10.1111/j.1365-246X.1981.tb02734.x

Landret J. 1977. — *Le lagon de l'atoll de Niau*. Rapport interne CP-CNEXO, Papeete, 10 p.

Lesson R. P. 1842. — Mollusques recueillis dans la mer du Sud et l'Océan Atlantique. *Revue zoologique par la Société cuviérienne* 5: 184-187. https://www.biodiversitylibrary.org/page/14714713

Lidz B. H. 2011. — Calcrete/Caliche, *in* Hopley D. (ed.), *Encyclopedia of Modern Coral Reefs, Structure, Form and Process*. Springer, Dordrecht: 180-181. https://doi.org/10.1007/978-90-481-2639-2_195

Linnaeus C. 1758. — *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Laurentii Salvii. Stockholm, 824 p. https://www.biodiversitylibrary.org/bibliography/559

Linnean Society of London 2024. — Linnaean Collections. Available at: https://www.linnean.org/research-collections/linnaean-collections (last access on December 2024).

Lisiecki L. E. & Raymo M. E. 2005. — A Pliocene-Pleistocene stack of 57 globally distributed benthic D180 records. *Paleoceanography* 20: 1-17. https://doi.org/10.1029/2004PA001071

Malaquias M. A. E. & Reid D. G. 2008. — Systematic revision of the living species of Bullidae (Mollusca: Gastropoda: Cephalaspidea), with a molecular phylogenetic analysis. *Zoological Journal of the Linnean Society* 153: 453-543. https://doi.org/10.1111/j.1096-3642.2008.00369.x

Martini F. H. W. 1777. — *Neues systematisches Conchylien-Cabinet. Nach der Natur gezeichnet und mit lebendigen Farben erleuchtet*. Raspe, Nürnberg, 434 p. https://www.biodiversitylibrary.org/bibliography/123898

Masson-Delmotte V., Stenni B., Pol K., Braconnot P., Cattani O., Falourd S., Kageyama M., Jouzel J., Landais A., Minster B., Barnala J. M., Chappellaz J., Krinner G., Johnsen S., Röthlisberger R., Hansen J., Mikolajewicz U. & Otto-Bliesner B. 2010. — EPICA Dome C record of glacial and interglacial intensities. *Quaternary Science Reviews* 29: 113-128. https://doi:10.1016/j.quascirev.2009.09.030

Maxwell S. J., Hernandez Duran L. C., Rowell M. K. & Rymer T. L. 2021. — An iconography of extant *Gibberulus* Jousseaume, 1888 (Mollusca, Gastropoda, Strombidae), and the introduction of a new species from the southwestern Pacific. *Proceedings of the biological Society of Washington* 134: 89-115. https://doi.org/10.2988/0006-324X-134.1.89

McManus J. W. 1985. — Marine speciation, tectonics and sea-level changes in Southeast Asia. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 4: 133-138.

McNutt M. K. & Menard H. W. 1978. — Lithospheric flexure and uplifted atolls. *Journal of Geophysical. Research* 83: 1206-1212. https://doi.org/10.1029/JB083iB03p01206

Merle D. 2001. — The spiral cords and the internal denticles of the outer lip of the Muricidae: terminology and methodological comments. *Novapex* 2 (3): 69-91. https://www.biodiversitylibrary.org/page/42258207

Merle D. 2005. — The spiral cords of the Muricidae (Gastropoda, Neogastropoda): importance of ontogenetic and topological correspondences for delineating structural homologies. *Lethaia* 38: 367-379. https://doi.org/10.1080/00241160500355129

MolluscaBase Eds. 2025. — *MolluscaBase*. Available at: https://www.molluscabase.org/ (Last access on 03/2025).

Montaggioni L. F. 1985. — Île de Makatea, archipel des Tuamotu. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 1: 105-157.

Montaggioni L. F. 1989. — Le soulèvement polyphasé d'origine volcano-isostasique : clef de l'évolution post-oligocène des atolls du Nord-Ouest des Tuamotus (Pacifique central). *Comptes rendus de l'Académie des sciences, série 2, mécanique, physique, chimie, sciences de l'univers, sciences de la terre* 309: 1591-1598. https://gallica.bnf.fr/ark:/12148/bpt6k63270791/f669.image

Montaggioni L. F. & Braithwaite C. J. R. 2009. — Quaternary coral reef systems, Development Processes and Controlling Factors. *Developments in Marine Geology* 5: 1-532. https://doi.org/10.1016/S1572-5480(09)05017-9

Montaggioni L. F., Fournier F., Martin-Garin B., Marie L., Pons-Branchu E., Dapoigny A., Bacchet P. & Salvat B. 2024. — Le « bombement asthénosphérique » : mécanisme de l'évolution géologique des atolls dit « soulevés » dans le nord-ouest des Tuamotu. *Bulletin de la Société des Études océaniennes* 362: 71-115.

Montaggioni L. F., Pons-Branchu E., Fournier F., Martin-Garin B., Marie L. & Salvat B. 2023. — Revisiting the geodynamical history of the so-called "uplifted" atolls, north-west Tuamotu, French Polynesia, central South Pacific. *Earth Science Review* 244 (104532): 1-26. https://doi.org/10.1016/j.earscirev.2023.104532

Montaggioni L., Lauriat-Rage A., Von Cosel R., Dolin L., Le Calvez Y., Merle D., Roman J. & Vénec Peyré M.-T., 1985. — Depositional environments and paleoecology of an early Miocene atoll like reef platform (Makatea Islands, Central Pacific). *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 6: 575-580.

Montfort P. de 1808. — *Conchyliologie systématique et classification méthodique des coquilles*. Vol. 2. Schoell, Paris, 692 p. https://doi.org/10.5962/bhl.title.10571

Moreau C., Messager B., Berthier S., Hain B., Thellier J.-P. Dumoulin I., Caffy M., Sieudat E., Delqué-Koli S., Mussard M., Perron V., Setti L., & Beck. 2020. — "ARTEMIS, the 14c AMS facility of the LMC14 national laboratory: a status report on quality control and microsample procedures. *Radiocarbon* 62 (6): 1755-1770. https://doi.org/10.1017/RDC.2020.73

Mörch O. A. L. 1853. — *Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra & Gadea Comes de Yoldi, Regis Daniae Cubiculariorum Princeps, Ordinis Dannebrogici in Prima Classe & Ordinis Caroli Tertii Eques*. Fasc. 2. *Acephala, Annulata, Cirripedia, Echinodermata*. Klein L, Copenhagen, 74 p. https://doi.org/10.5962/bhl.title.12921

Modeer A. 1793. — Inledning til kunskapen om maskkraken i allmänhet; 5. Classen. Musslor, Cochleata. *Kongliga Vetenskaps Academiens Nya Handlinger* 14: 163-183.

Murray-Wallace C. V. & Woodroffe C. D. 2014. — Quaternary sea-level changes. Cambridge University Press, Cambridge, 484 p. https://doi.org/10.1017/CBO9781139024440

Niva P. 2020. — Enquête archéologique sur l'atoll de Niau. *Bulletin de la Société des Études océaniennes* 350-351: 142-164.

Ostergaard J. M. 1928. — Fossil marine mollusks of Oahu. *Bernice P. Bishop Museum Bulletin* 51: 5-32. https://doi.org/10.5962/bhl.title.58566

Paulay G. & Spencer T. 1988. — Geomorphology, paleoenvironments and faunal turnover, Henderson island, S.E. Polynesia. *Proceedings of the 6th International Coral Reef Symposium, Townsville* 3: 461-466.

Paulay G. 1990. — Effects of late Cenozoic sea-level fluctuations on the bivalve fauna of tropical oceanic islands. *Paleobiology* 16: 415-434. https://doi.org/10.1017/S0094837300010162

Paulay G. & Spencer T. 1992. — Niue island: geological and faunatic history of a Pliocene atoll. *Pacific Science Association Information Bulletin* 44 (3-4): 21-23.

Petchey F., Anderson A., Hogg A. G. & Zondervan A. 2008. — The marine reservoir effect in the Southern Ocean: an evaluation of extant and new Delta-R values and their application to archaeological chronologies. *Journal of the Royal Society of New Zealand* 38 (4): 243-262. https://doi.org/10.1080/03014220809510559

Pin C. & Bassin C. 1992. — Evaluation of a strontium-specific extraction chromatographic method for isotopic analysis in geological materials. *Analytica Chimica Acta* 269 (2): 249-255. https://doi.org/10.1016/0003-2670(92)85409-Y

Pons-Branchu E., Barbarand J., Caffy I. Dapoigny A., Drugat L., Dumoulin J. P., Medina Alcaide M. A., Nouet J., Sanchidrián Torti J. L., Tisnerat-Laborde N., Jiménez de Cisneros & Valladas H. 2022. — U-series and radiocarbon cross dating of speleothems from Nerja Cave (Spain): evidence of open system behavior. Implication for the Spanish rock Art chronology. *Quaternary Sciences Review* 290: 107634. https://doi.org/10.1016/j.quascirev.2022.107634

Potts D. C. 1984. — Generation times and Quaternary evolution of reef-building corals. *Paleobiology* 10: 48-58. https://doi.org/10.1017/S0094837300008010

Potts D. C. 1985. — Sea-level fluctuations and speciation in Scleractinia. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 4: 127-132.

Psarras K., Koskeridou P. & Merle D. 2021. — Late Miocene Conidae (Mollusca: Gastropoda) of Crete (Greece). Part 1: genera *Conilithes* and *Conus* (*Kalloconus*). *Geodiversitas* 43 (24): 1309-1339. https://doi.org/10.5252/geodiversitas2021v43a24. http://geodiversitas.com/43/24

Reeve L. A. 1845. — Monograph of the genus *Cardium, in* Reeve L. A. (ed.), *Conchologia Iconica, or, Illustrations of the Shells of Molluscous Animals*. Vol. 2 and unpaginated text. L. A. Reeve & Co., London: pl. 13-16 (january 1845), pl. 17-22 (March 1845). http://biodiversitylibrary.org/page/8937393

Risso A. 1826. — *Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes*. Levrault, Paris, 400 p. https://www.biodiversitylibrary.org/bibliography/58984

Röding P. F. 1798. — *Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturæ quæ olim collegerat Joa. Fried Bolten, M. D. p. d. per XL. annos proto physicus Hamburgensis.* Pars secunda continens Conchylia sive Testacea univalvia, bivalvia & multivalvia. Trapp, Hamburg, 199 p. https://doi.org/10.5962/bhl.title.16250

Rohling E. J., Fenton M., Jorissen F. J., Bertrand P., Ganssen G. & Caulet J.-P. 1998. — Magnitudes of sea-level lowstands of the past 500,000 years. *Nature* 394: 162-165. https://doi.org/10.1038/28134

Rougerie F., Jehl C. & Trichet J. 1997. — Phosphorus pathways in atolls: interstitial nutrient pool, cyanobacterial accumulation and Carbonate-Fluoro-Apatite (CFA) precipitation. *Marine Geology* 139 (1-4): 201-217. https://doi.org/10.1016/S0025-3227(96)00111-9

Salisbury A. E. 1934. — On the nomenclature of Tellinidae, with descriptions of new species and some remarks on distribution. *Proceedings of the Malacological Society of London* 21 (2): 74-91.

Salvat B. & Rives C. 1975. — *Coquillages de Polynésie*. Éditions du Pacifique, Papeete, 391 p.

Salvat B., Letourneux J., Tröndlé J. & Montaggioni L. 2020. — Niau, histoire géologique de l'île et du lagon. *Bulletin de la Société des Études océaniennes* 350-351: 19-31.

Salvat B., Tröndlé J. & Letourneux J. 2018. — Pleistocene mollusc assemblage in the slightly raised atoll lagoon of Niau (Tuamotu, French Polynesia). *Paläontologische Zeitschrift* 92: 411-424. https://doi.org/10.1007/s12542-018-0401-0

Schmidt F. C. 1818. — *Versuch über die beste Einrichtung zur Aufstellung: Behandlung und Aufbewahrung der verschiedenen Naturkörper und gegenstände der Kunst, vorzüglich der Conchylien-Sammlungen, nebst kurzer Beurtheilung der conchyliologischen Systeme und Schriften und einer tabellarischen Zusammenstellung und Vergleichung der sechs besten und neuesten conchyliologischen Systeme*. J. Perth, Gotha, 252 p. https://www.biodiversitylibrary.org/page/46054299

Sowerby G. B. II. 1855. — Monograph of the genus *Cerithium*, *in* G. B. Sowerby II (ed.), *Thesaurus Conchyliorum, or Monographs of Genera of Shells*. Vol. 2 (16). Sowerby G. B. II, London: 847-899. http://biodiversitylibrary.org/page/11076091

Sowerby G. B. II. 1865. — Monograph of the genus *Cerithium*, *in Conchologia Iconica: or, Illustrations of the Shells of Molluscous Animals*. Vol. 15. Reeve & Co., London, pls 1-20 and unpaginated text. https://www.biodiversitylibrary.org/page/10972735

Sowerby G. B. III. 1909. — Descriptions of new species of *Terebra*, *Pleurotoma*, *Trochus*, *Tellina*, *Dosina*, and *Modiola*. *Proceedings of the Malacological Society of London* 8 (4): 198-201. https://www.biodiversitylibrary.org/page/32058399

Stoddart D. R. 1973. — Coral reefs: the last two million years. *Geography* 58: 313-323.

Taylor J. D. 1978. — Faunal response to the instability of reef habitats: Pleistocene molluscan assemblages of Aldabra atoll. *Palaeontology* 21:1-30.

Thiele J. 1925. — Gastropoden der Deutschen Tiefsee-Expedition. II Teil. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899* 17 (2): 35-382.

Torrente F. 2018. — *Atoll de Niau. Mise en valeur du patrimoine culturel et historique*. Direction de l'Environnement de la Polynésie française, Papeete, 88 p.

Trichet J. & Delage C. 1999. — Sedimentary organic matter derived from cyanobacteria: composition, structure and properties of kopara deposits. *Bulletin de l'Institut océanographique de Monaco, Numéro spécial* 19: 203-208.

Tröndlé J. & Houart R. 1992. — Les Muricidae de Polynésie Française. *Apex* 7 (3-4): 67-149. https://www.biodiversitylibrary.org/page/41530412

Tröndlé J. & Letourneux J. 2011. — Description de *Terebra niauensis* n. sp. (Mollusca: Gastropoda: Terebridae) du Pléistocène de Niau. *Novapex* 12 (3-4): 87-90. https://www.biodiversitylibrary.org/page/54952940

Tröndlé J. & Letourneux J. 2012. — Description de *Turbo fakaauensis* n. sp. (Mollusca: Gastropoda: Turbinidae) du Pléistocène de Niau, Tuamotu (Polynésie française). *Novapex* 13 (2): 87-90. https://www.biodiversitylibrary.org/page/54946497

TRÖNDLÉ J. & SALVAT B. 2010. — La thanatocénose du lagon de l'atoll Niau (Polynésie française) avec la description d'une nouvelle espèce de *Strombus* (Mollusca, Gastropoda, Strombidae). *Zoosystema* 32 (4): 613-623. https://doi.org/10.5252/z2010n4a5

VEEH H. H. 1966. — Th230/U238 and U234/U238 ages of Pleistocene high sea level stand. *Journal of Geophysical Research* 71: 3379-3386. https://doi.org/10.1029/JZ071i014p03379

WILSON B. 1993. — *Australian Marine Shells*. Vol. 1. Odyssey Publishing, Kallaroo, 408 p.

WOOD W. 1828. — Supplement to the Index Testaceologicus; or A catalogue of shells, British and foreign. Richard Taylor, London, 59 p. http://biodiversitylibrary.org/page/22991199

Submitted on 7 April 2025;
accepted on 12 May 2025;
published on 2 April 2026.