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# New taxonomic and phylogeographic data on three nominal species of the genus *Septaria* Férussac, 1807 (Gastropoda: Cycloneritida: Neritidae)

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## Abstract

Due to superficial morphological similarities, there is often confusion in the identification of some species of the genus *Septaria*. A combined analysis of the genital anatomy, morphometric and DNA, based on a portion of the COI gene, applied to three nominal species of this genus, confirmed the validity of *Septaria tahitiana* Eichhorst, 2016, and suggested that *Septaria borbonica* (Bory de Saint Vincent, 1804) is a subspecies of *Septaria porcellana* (Linnaeus, 1758), both taxa with disjunct distribution areas: *Septaria borbonica* in the western Indian Ocean and *Septaria porcellan*a the western Pacific and eastern Indian Oceans. The possible presence of *Septaria tesselata* (Lamarck, 1816) in Mayotte (Comoros Archipelago) needs to be confirmed.

## Résumé

En raison de similitudes morphologiques superficielles, il y a souvent confusion dans l'identification de certaines espèces du genre *Septaria*. Une analyse combinée, de l'anatomie de l'appareil génital, morphométrique et ADN, basée sur une partie du gène COI, appliquée à trois espèces nominales de ce genre, a confirmé la validité de *Septaria tahitiana* Eichhorst, 2016, et a suggéré que *Septaria borbonica* (Bory de Saint Vincent, 1804) est une sous-espèce de *Septaria porcellana* (Linnaeus, 1758), deux taxons dont les aires de répartition sont disjointes: *Septaria borbonica* dans l'océan Indien occidental et *Septaria porcellana* dans l'océan Pacifique occidental et l'océan Indien oriental. La présence possible de *Septaria tesselata* (Lamarck, 1816) à Mayotte (archipel des Comores) doit être confirmée.

**Keywords:** Indo-Pacific, shell morphometrics, mitochondrial DNA, taxonomy, phylogeny, mollusc

## Introduction

Tropical island rivers are often subject to extreme climatic variations and seasonal hydrological variations (McDowall 2007; Crandall *et al*. 2010; Abdou *et al*. 2015). These freshwater ecosystems often represent isolated and fragmented habitats, colonized by a well adapted fauna of molluscs, fish and crustaceans with a diadromous life cycle (Abdou *et al*. 2015), involving a mandatory marine phase. In the Indo-Pacific zone, the molluscs that are part of this fauna include estuarine and freshwater nerites of several genera.

*Septaria* Férussac, 1807 is one of the 16 genera of gastropod molluscs in the family Neritidae (Eichhorst 2016a). It is distinguished from the other neritid genera essentially by its internal operculum, a character unique in this family, its reduced columellar surface called septum, and its patelliform shell shape. The genus *Septaria* is supposedly comprises 14 species, including 11 freshwater species and three brackish water species. The latter three are *Septaria clypeolum* (Récluz, 1843) from the Philippines, *Septaria livida* (Reeve, 1856) from Vanuatu and Fiji and *Septaria tesselata* (Lamarck, 1816) from the West Pacific and the Indian Oceans. In her major revision of the genus *Septaria*, Haynes (2001) recognised 13 species, with *S. clypeolum* becoming a synonym of *S. tesselata*. The species of the genus *Septaria* are mainly found in tropical rivers in the Indo-Pacific zone. They presumably colonized the freshwater environment by multiple invasions from the sea (Kano *et al*. 2002). On the basis of morpho-anatomical

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characters, Haynes (2001) proposed a phylogenetic analysis tending to show that the genus *Septaria* is polyphyletic. However, this analysis is highly questionable because her phylogenetic tree does not support the alleged polyphyly. Instead, the tree shows an unresolved trichotomy at its base, a topology that does not support the monophyly of the genus *Septaria*, but does not refute it either. To our knowledge, there has not yet been any molecular phylogeny of the genus that explored this issue.

Due to morphological similarities and given intraspecific variability, *Septaria* species have often been confused (Haynes 2001). Many authors have, for example, confused *S. porcellana* (Linnaeus, 1758) (Fig. 1A) and *S. borbonica* (Bory de Saint Vincent, 1804) (Fig. 1B), the type species of the genus. Indeed, these species are similar in appearance, but actually present both, morphological and anatomical differences (Haynes 2001; Eichhorst 2016b). In addition, their geographic distributions do not overlap, with *S. borbonica* occurring only in the Western Indian Ocean, where *S. porcellana* has never been found. *Septaria tahitiana* Eichhorst, 2016 (Fig. 1C) is a replacement name for *S. taitana* Mousson, 1869, this latter name being a nomen nudum as it appeared in an unpublished catalogue (Eichhorst 2016b: 837). *Septaria tahitiana* only occurs in French Polynesia and was long thought to be conspecific with *S. porcellana* (Pointier & Marquet 1990; Resh *et al*. 1990, 1992; Liu & Resh 1997; Bunje & Lindberg 2007) because of its similar morphology. Yet, *S. porcellana* is not present in French Polynesia and more generally in the Central Pacific (Haynes 2001; Eichhorst 2016b).

The present contribution aims to shed new light on the taxonomy and phylogeography of *S. porcellana, S. borbonica* and *S. tahitiana,* using DNA sequence, morphometric and anatomical data.

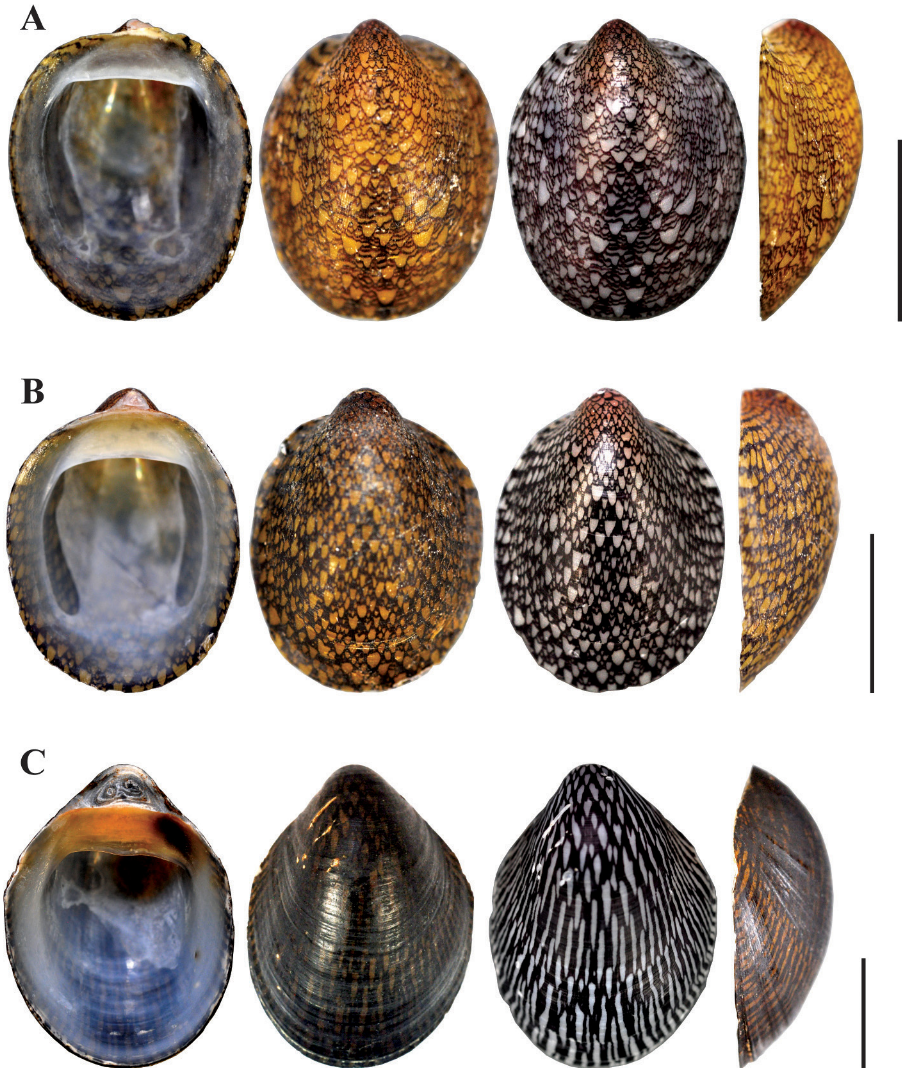

**FIGURE 1.** A *Septaria porcellana* (Linnaeus, 1758), MNHN-IM-2013-62871 (Okinawa, Japan) B *Septaria borbonica* (Bory de Saint-Vincent, 1804), MNHN-IM-2013-78206 (Mohéli, Comoros) C *Septaria tahitiana* Eichhorst, 2016, MNHN-IM-2013-62864 (Moorea, French Polynesia). From left to right: Ventral view, dorsal view, dorsal view without periostracum, side view. Scale bars: 10 mm.

## Material and methods

**Sampling.** The material was collected during various field missions to the Comoros in 2005, 2006 and 2013, and to Moorea and Tahiti (French Polynesia) in 2014. Additional samples were obtained from the Indo-Pacific region (Reunion Island, Mauritius, Japan (Okinawa) and French Polynesia) (Table 1).

**TABLE 1.** List of specimens used for morphometric and molecular analysis. The identification number is shown for the GenBank sequences and for material deposited at MNHN (MNHN ID). Individual marked (*) could not be included in the morphometric analysis

| Locality | No of individuals | Year | MNHN ID | GenBank ID |
|---|---|---|---|---|
| ***Septaria tahitiana*** Eichhorst, 2016 | | | | |
| Moorea (French Polynesia) | 4 | 2014 | IM-2013-62862 | MW307286 |
| | | | IM-2013-62863 | MW307287 |
| | | | IM-2013-62864 | MW307288 |
| | | | IM-2013-62866 | MW307284 |
| Tahiti (French Polynesia) | 1 | 2014 | IM-2013-62865 | MW307285 |
| ***Septaria porcellana*** (Linnaeus, 1758) | | | | |
| Okinawa (Japan) | 6 | 2014 | IM-2013-62867 | MW307278 |
| | | | IM-2013-62868 | MW307279 |
| | | | IM-2013-62869 | MW307280 |
| | | | IM-2013-62870 | MW307281 |
| | | | IM-2013-62871 | MW307282 |
| | | | IM-2013-62872 | MW307283 |
| Okinawa (Japan) | 1 | | | AB477514 |
| ***Septaria borbonica*** (Bory de Saint-Vincent, 1804) | | | | |
| Mauritius | 2 | 2013 | IM-2013-78197 | MW307275 |
| | | | IM-2013-78199 | MW307274 |
| Reunion Island | 2 | 2013 | IM-2013-78201* | MW307273 |
| | | | IM-2013-78202 | MW307272 |
| Moheli (Comoros) | 3 | 2013 | IM-2013-78204 | MW307277 |
| | | | IM-2013-78206 | MW307276 |
| | | | IM-2013-78209 | MW307271 |

In the field, the specimens were collected on sight. They are, in fact, nearly always visible to the naked eye, living on rocks and boulders along riverbeds. Specimens were fixed in 95% ethanol. Species were identified based on morphological characters, using the literature (Haynes 2001; Eichhorst 2016b) and by comparison with the collections held at the Muséum national d'Histoire naturelle de Paris (MNHN). Samples from the historical collections of MNHN were also used for morphometric analysis (Table 2).

**Morphometric analysis and reproductive anatomy.** A total of 234 specimens, representing the three species (154 *S. borbonica*, 36 *S. porcellana* and 44 *S. tahitiana*), were analysed using morphometric analysis (Tables 1 and 2). The length (L), width (W) and height (H) of each shell were measured using a 0.03 mm precision calliper (Fig. 2). The ratios L/W and L/H were calculated and used as quantitative variables to avoid any bias that could be introduced by an allometric effect, as well as their average, minima and maxima for each species. The Kruskal-Wallis (KW) test, a non-parametric statistical test, alternative to the ANOVA, was performed, using XLSTAT (Addinsoft 2020) to explore differences among the three nominal species and complement the morphometric analysis with, as null hypothesis H0: there is no significant difference between the nominal taxa studied, and as alternative hypothesis Ha: at least one nominal taxon is significantly different from the others. The KW test was used for both the L/H ratio and the L/W ratio. In order to identify which taxon is significantly different from the others, Dunn's multiple pairwise comparisons procedure was used.

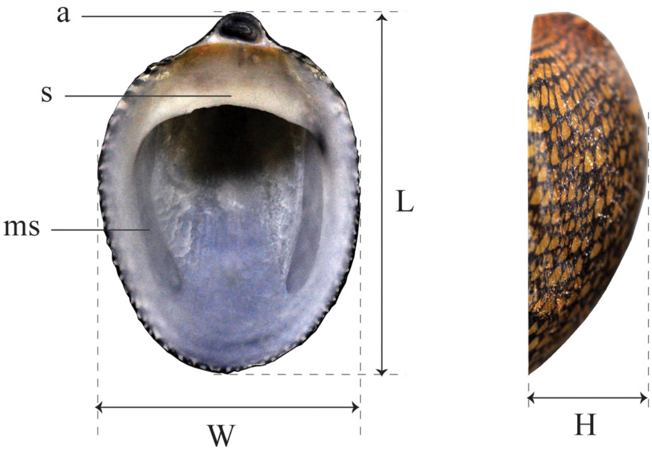

**FIGURE 2**. Shell measurement protocol. H height L length W width. a apex, ms muscle scar, s septum.

Haynes (2001) was followed here for the analysis of the reproductive system.

**COI analysis.** A fragment of the mitochondrial gene coding for the first subunit of *Cytochrome oxydase I* (*COI*) was sequenced for 18 individuals (7 *S. borbonica*, 6 *S. porcellana* and 5 *S. tahitiana*) (Table 1). DNA extraction, PCR and quality control were performed according to the protocol used by Abdou *et al*. (2017). Sequences were aligned using Muscle (Edgar 2004). Phylogenetic analysis was performed with the Bayesian inference (BI) method, under *MrBayes* 3.2 (Ronquist *et al.* 2012) partitioning by codon position with 5 million generations and sampling every 100 generations, and 10% of trees were eliminated as burnin after checking for convergence. The HKY+I substitution model was selected by jModelTest 2.1.1 (Darriba et al. 2012). Intra- and interspecific p-distances were estimated in the software MEGA 7 (Kumar et al. 2016). Three sequences were taken from GenBank, one of *S. porcellana* (AB477514), one of *Neritilia rubida* (AB102712) and one of *Neritina pulligera* (AB477502). The last two served as outgroup. All sequences have been deposited in Genbank (accession numbers MW307271-MW307288).

For *S. porcellana* and *S. borbonica*, shared haplotypes were searched using DnaSP v5.1 software (Librado & Rozas 2009). To visualize the genealogical relationships between haplotypes and their geographic distribution, a haplotype network was constructed with the Median-Joining method implemented in Network v10.0.0.0 (Bandelt *et al*. 1999), using default settings.

**TABLE 2:** Dry and wet (in ethanol) specimens used solely for the morphometric analysis

| Locality | **Author/Year** | **No of specimens** | **MNHN ID** |
|---|---|---|---|
| ***Septaria tahitiana*** Eichhorst, 2016 | | | |
| Moorea (French Polynesia) | Abdou leg., 2014 | 3 | IM-2013-78194 |
| Moorea (French Polynesia) | Pointier leg., 1985 | 9 | IM-2016-7846 |
| Tahiti (French Polynesia) | Fontaine leg., 2004 | 5 | IM-2016-7847 |
| Tahiti (French Polynesia) | Gargominy & Fontaine leg., 2004 | 1 | IM-2016-7848 |
| Tahiti (French Polynesia) | Gargominy & Fontaine leg., 2005 | 6 | IM-2016-7849 |
| Tahiti (French Polynesia) | Gargominy & Fontaine leg., 2002 | 15 | IM-2016-7850 |
| ***Septaria porcellana*** (Linnaeus, 1758) | | | |

...*Continued on the next page*

**TABLE 2:** (Continued)

| Locality | **Author/Year** | **No of specimens** | **MNHN ID** |
|---|---|---|---|
| Okinawa (Japan) | Maeda & Iida leg., 2014 | 4 | IM-2013-78195 |
| Okinawa (Japan) | Maeda & Iida leg., 2014 | 3 | IM-2013-78196 |
| Philippines | Letellier Coll., 1949 | 2 | IM-2016-7851 |
| Philippines | Marche Coll., 1882 | 1 | IM-2016-7852 |
| Palau | Staadt Coll., 1969 | 2 | IM-2016-7853 |
| New Guinea | Staadt Coll., 1969 | 4 | IM-2016-7854 |
| New Hebrides (now Vanuatu) | Soyer Coll., 1969 | 13 | IM-2016-7855 |
| Upolu (Samoa) | Denis Coll., 1945 | 1 | IM-2016-7856 |
| ***Septaria borbonica*** (Bory de Saint-Vincent, 1804) | | | |
| Mauritius | Griffith & Albrecht leg.,2013 | 2 | IM-2013-78198 |
| Mauritius | Griffith & Albrecht leg.,2013 | 4 | IM-2013-78200 |
| Mauritius | Griffith & Albrecht leg.,2013 | 1 | IM-2016-7857 |
| Mauritius | Mission P. Carié, 1918 | 4 | IM-2016-7858 |
| Mauritius | Boivin Coll., 1853; ex Robillard | 2 | IM-2016-7859 |
| Mauritius | Letellier Coll., 1949 | 1 | IM-2016-7860 |
| Mauritius | Unknown | 1 | IM-2016-7861 |
| Mauritius | Staadt Coll., 1969 | 2 | IM-2016-7862 |
| Reunion Island | Valade leg., 2013 | 1 | IM-2013-78203 |
| Reunion Island | Don de Mr Alluand, 1946 | 3 | IM-2016-7863 |
| Reunion Island | Unknown | 4 | IM-2016-7864 |
| Reunion Island | Unknown | 2 | IM-2016-7865 |
| Reunion Island | Rang Coll., 1826 | 3 | IM-2016-7866 |
| Reunion Island | Mission G. Petit, 1926 | 5 | IM-2016-7867 |
| Reunion Island | Mission G. Petit, 1926 | 7 | IM-2016-7868 |
| Reunion Island | Mission G. Petit, 1926 | 7 | IM-2016-7869 |
| Reunion Island | Unknown | 7 | IM-2016-7870 |
| Reunion Island | Férussac Coll., 1837 | 2 | IM-2016-7871 |
| Seychelles | Dufo Coll., 1839 | 2 | IM-2016-7872 |
| Seychelles | Dufo Coll., 1839 | 4 | IM-2016-7873 |
| Seychelles | Dufo Coll., 1839 | 3 | IM-2016-7874 |
| Moheli (Comoros) | Abdou leg., 2013 | 2 | IM-2013-78205 |
| Moheli (Comoros) | Abdou leg., 2013 | 3 | IM-2013-78207 |
| Moheli (Comoros) | Abdou leg., 2013 | 3 | IM-2013-78208 |
| Moheli (Comoros) | Abdou leg., 2005 | 5 | IM-2016-7875 |
| Moheli (Comoros) | Abdou leg., 2005 | 4 | IM-2016-7876 |
| Moheli (Comoros) | Abdou leg., 2005 | 12 | IM-2016-7877 |
| Moheli (Comoros) | Millot Coll., 1954 | 1 | IM-2016-7878 |
| Mayotte (Comoros) | Abdou leg., 2006 | 1 | IM-2013-78210 |
| Mayotte (Comoros) | Abdou leg., 2006 | 1 | IM-2013-78211 |

*...Continued on the next page*

**TABLE 2:** (Continued)

| Locality | **Author/Year** | **No of specimens** | **MNHN ID** |
|---|---|---|---|
| Mayotte (Comoros) | Abdou leg., 2006 | 1 | IM-2013-78212 |
| Mayotte (Comoros) | Abdou leg., 2006 | 1 | IM-2013-78213 |
| Mayotte (Comoros) | Jousseaume Coll., 1921 | 2 | IM-2016-7879 |
| Mayotte (Comoros) | Abdou leg., 2006 | 1 | IM-2016-7880 |
| Mayotte (Comoros) | Abdou leg., 2006 | 5 | IM-2016-7881 |
| Mayotte (Comoros) | Abdou leg., 2006 | 1 | IM-2016-7882 |
| Mayotte (Comoros) | Abdou leg., 2006 | 1 | IM-2016-7883 |
| Mayotte (Comoros) | Abdou leg., 2006 | 4 | IM-2016-7884 |
| Anjouan (Comoros) | Mouron Coll., 1540 | 8 | IM-2016-7885 |
| Anjouan (Comoros) | Decary Coll., 1921 | 4 | IM-2016-7886 |
| Anjouan (Comoros) | Abdou leg., 2005 | 1 | IM-2016-7887 |
| Anjouan (Comoros) | Abdou leg., 2005 | 5 | IM-2016-7888 |
| Anjouan (Comoros) | Abdou leg., 2005 | 2 | IM-2016-7889 |
| Anjouan (Comoros) | Abdou leg., 2005 | 8 | IM-2016-7890 |
| Grande Comore (Comoros) | Humblot Coll., 1887 | 2 | IM-2016-7891 |
| Grande Comore (Comoros) | Humblot Coll., 1887 | 3 | IM-2016-7892 |

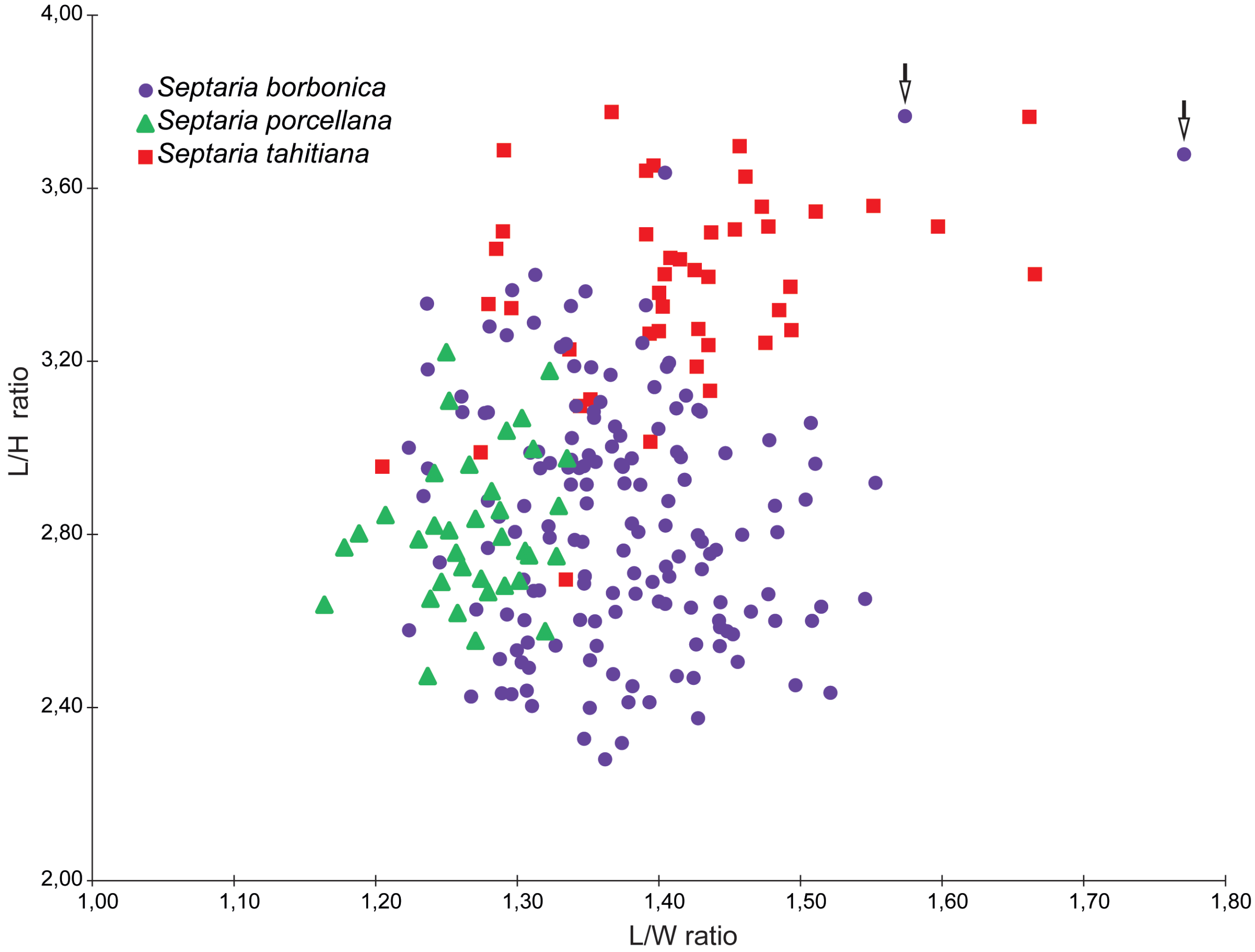

**FIGURE 3:** Cloud of points representing the L/W and L/H ratios of *Septaria borbonica*, *S. porcellana* and *S. tahitiana*.

## Results

**Morphometric analysis and reproductive anatomy.** The averages, minima and maxima of the measurements are shown in Table 3. The cloud of points in Figure 3 graphically represents the L/W and L/H ratios. It shows that the *S. tahitiana* individuals are at the top of the graph with a high L/W ratio (average 1.42). Individuals belonging to *S. porcellana* are leftmost in a low L/H ratio (average 2.81), but they are largely mixed with specimens of *S. borbonica*. The representatives of the latter occupy a central position in relation to the two axes and cover practically the entire space of the cloud. Two samples from Mayotte, supposed to belong to *S. borbonica* (Fig. 4A, B), are distinguished from all others of the same taxon. They are indicated by arrows in Figure 3.

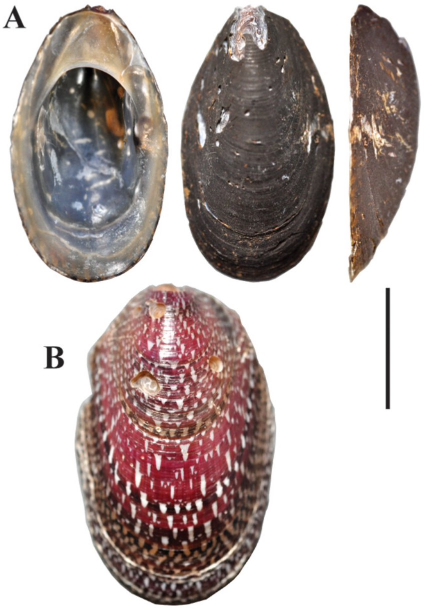

**FIGURE 4. A, B**. Samples supposed to belong to *Septaria borbonica* but for which the identification is doubtful. A MNHN-IM-2013-78211 (Mayotte, Comoros) B MNHN-IM-2013-78212 (Mayotte, Comoros), dorsal view without periostracum. Scale bar: 10 mm.

For the KW test applied to L/H and to L/W, the calculated p-value is lower than the significance level alpha in both cases ($p<0.0001$; $\alpha=0.05$). The Dunn‘s multiple pairwise comparisons procedure, concerning the L/H variable, distinguishes two significantly different groups, one represented by *Septaria tahitiana*, and the other by *S. borbonica* and *S. porcellana*. With regard to the variable L/W, three groups are distinguished, represented by the three nominal taxa.

According to Haynes (2001), males of the three taxa do not produce spermatophores but, while the female of *S. tahitiana* has a dorsal spermatophore sac, those of *S. porcellana* and *S. borbonica* have a remnant ventral spermatophore sac.

**COI analysis.** Partial sequences of 615 base pairs of the *COI* gene were analysed for 19 individuals. Seven sequences belong to *S. borbonica* (Comoros, N= 3; Mauritius, N= 2 and Reunion Island, N= 2), five to *S. tahitiana* (Moorea, N= 4 and Tahiti, N= 1) and seven to *S. porcellana* (Okinawa, Japan), including one sequence recovered from GenBank (AB477514, Table 1). The Bayesian inference discriminates *S. tahitiana* compared to the other two taxa with a posterior probability (PP) of 1, but *S. porcellana* and *S. borbonica* are in the same clade (Fig. 5). The mean pairwise inerspecific p-distances for COI for the three taxa varied from 4.71% to 5.05%, whereas the mean intraspecific p-distances varied from 0.33% to 1.40% (Table 4).

The haplotype network (Fig. 6) shows two separate haplotype groups, corresponding to samples of *S. borbonica* from the western Indian Ocean and to *S. porcellana* from the Pacific Ocean. No haplotypes are shared by the two haplogroups. The seven samples from the Indian Ocean involve 5 haplotypes, one of which is shared by samples from Mauritius, Reunion Island and Comoros. The seven samples from the Pacific Ocean involve 3 haplotypes, one of which is shared by 5 individuals from Japan.

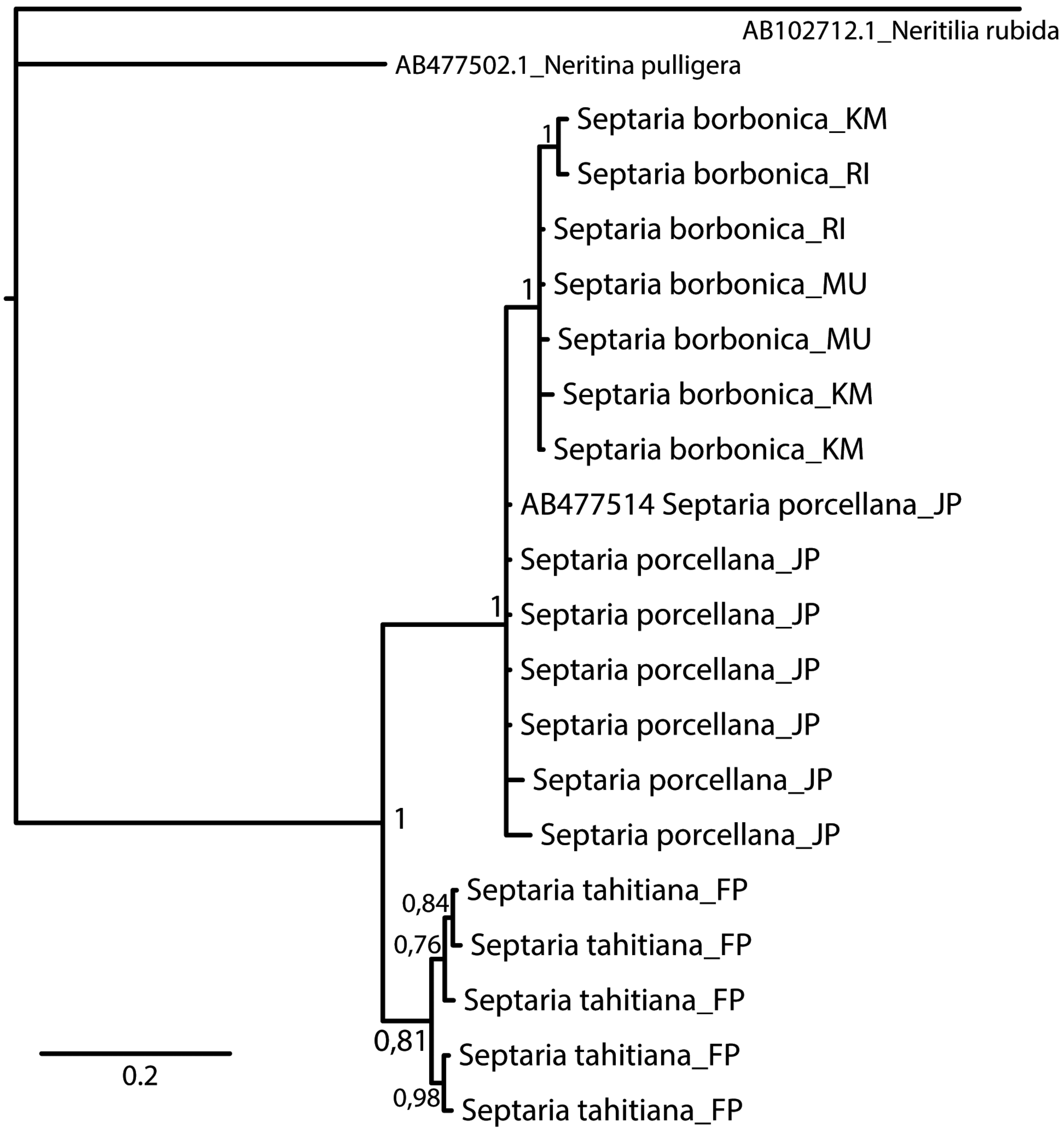

**FIGURE 5.** Bayesian analysis of the gene of the sub-unit 1 of the *Cytochrome oxydase* (COI). FP French Polynesia, JP Japan, KM Comoros, MU Mauritius, RI Reunion Island.

## Discussion

The L/W ratio of *S. tahitiana* (Table 3) indicates a narrower width than length, and therefore a more tapered shape than the other two taxa. In Figure 3, *S. tahitiana* is distinguished from the other two taxa even though there is a slight overlap. Overall, morphologically speaking, the shell of *S. borbonica* is slightly flatter and less rounded than that of *S. porcellana* (Table 3), as previously reported by Haynes (2001), but this is not really obvious. The morphological similarity between these two taxa is such that Eichhorst (2016b: 816) claimed that it is impossible to distinguish them "using just shell sharpe, colour and pattern. Even the opercula are similar. For these two species, locality is key to proper identification". Indeed, the shells of the two taxa have similar classical patterns on the outside, roughly triangular (Fig. 1A, B). This morphotype is the only one found in all observed *S. borbonica* shells from several islands in the Indian Ocean (Fig. 7C-H). In contrast, *S. porcellana,* which until now has never been reported in the western Indian Ocean, shows at least two additional very unusual patterns in (Fig. 7A, B), consisting of more or less thick lines radiating from the apex. Furthermore, the KW test supports the Ha hypothesis that at least one taxon is significantly different from the other two. Indeed, insofar as the calculated p-value $p<0.0001<\alpha=0.05$, it is advisable to reject the null hypothesis H0, and to retain the alternative hypothesis Ha. The multiple pairwise comparisons using Dunn's procedure, for the L/H variable, clearly separates *S. tahitiana* from *S. porcellana* and *S. borbonica* gathered in the same group.

Concerning genital anatomy, Haynes (2001) indicated that *S. tahitiana* and *S. porcellana* are sexually dimorphic, with males being significantly smaller than females. However, while females of *S. tahitiana* have a dorsal spermatophore sac, which is a plesiomorphic character, females of *S. porcellana* and *S. borbonica* have the same synapomorphy, viz a ventral (vestigial) spermatophore sac, the evolution being towards a simplification of the anatomy of the reproductive system (Haynes 2001).

The mean p-distances calculated for COI (Table 4) show a clear separation of *S. tahitiana* from *S. borbonica* (5.05%) on the one hand, and from *S. porcellana* (4.71%) on the other hand. The distance of 1.40% between *S. porcellana* and *S. borbonica* is very small raising doubts whether these taxa represent different species. For the family Neritidae, mean intraspecific genetic p-distance for COI would be less than 2.96% (Frey & Vermeij 2008) whereas Abdou *et al* (2017) suggested that mean sequence divergences >3% indicate interspecific differences. The distance of 1.40% is rather consistent with an intraspecific variation. Moreover, the cladogram in figure 5 shows clearly, on the one hand, that *S. tahitiana* forms a clade clearly separated from the other two taxa and, on the other hand, that *S. porcellana* does not constitute a clade dissociated from *S. borbonica*. There is therefore a convergence between the COI and morpho-anatomical data for these two taxa. Thus *S. porcellana* would rather be a polytypical species and *S. borbonica* one of its populations, probably in the process of speciation, due to its geographical isolation, as shown by the network of haplotypes (Fig. 6).

**TABLE 3:** Averages, minima and maxima calculated for L / W and L / H ratios

| | *S. borbonica* | *S. porcellana* | *S. tahitiana* |
|---|---|---|---|
| Number of samples | 154 | 36 | 44 |
| L/W: Av(Min; Max) | **1.37**(1.23; 1.77) | **1.27**(1.17; 1.34) | **1.42**(1.21; 1.66) |
| L/H: Av(Min; Max) | **2.84**(2.29; 3.76) | **2.81**(2.47; 3.22) | **3.37**(3.71; 3.77) |

**TABLE 4:** COI p-distances between *Septaria borbonica*, *S. porcellana* and *S. tahitiana*

| | ***S. borbonica*** | ***S. porcellana*** | ***S. tahitiana*** |
|---|---|---|---|
| ***S. borbonica*** | 0.47% | | |
| ***S. porcellana*** | **1.40%** | 0.33% | |
| ***S. tahitiana*** | **5.05%** | **4.71%** | 0.59% |

I have adopted an integrative congruence approach (DeSalle *et al*. 2005; Padial *et al*. 2010) according to which if two groups are distinguishable by at least two independent datasets, they belong to two different species. Three datasets were used in the present work, viz shell morphometry (Fig. 3), reproductive anatomy based on Haynes (2001) and COI sequences (Fig. 5). Table 5 summarizes these three datasets and facilitates comparisons. Based on these three datasets *S. tahitiana* could be consistenly differentiated from the other two taxa. In contrast, neither shell morphometrics, nor reproductive anatomy or COI sequences were able to distinguish between *S. porcellana* and *S. borbonica*. Therefore, it would be more logical to consider *S. borbonica* as a subspecies of *S. porcellana*. Its nomenclatural transcription thus becomes *Septaria porcellana borbonica* (Bory de Saint-Vincent, 1804).

As the Indo-Australian archipelago, the largest known and documented Indo-Pacific Barrier (Abdou *et al*. 2019), cannot be invoked in this case to explain the geographical isolation of *Septaria p.porcellana borbonica*, there must be another barrier within the Indian Ocean itself. Indeed, according to Haynes (2001) and Eichhorst (2016b), *Septaria p. porcellana* occurs in the western Pacific and eastern Indian Ocean (southern India, Andaman Islands, Indonesia), so it has not been impacted by fluctuations in the Great Indo-Pacific Barrier. The largest multi-species phylogeographic study in the Indo-Pacific, based on 56 species from 4 phyla and 27 families, to test biogeographic hypotheses, was conducted by Crandall *et al*. (2019). Among the five putative filtering barriers tested, there is one between the Western Indian Ocean Province (including Madagascar, the Mascarenes, Seychelles and Comoros, as defined by Briggs & Bowen (2012)), and the entire region formed by the East Indian Ocean and the West Pacific Ocean.

**TABLE 5:** Comparison of the three taxa against the data sets

| | ***S. borbonica*** | ***S. porcellana*** | ***S. tahitiana*** |
|---|---|---|---|
| **Morphology** | - Overall similar shell shape<br>- Grouped by KW test relative to the variable L/H, but separated with respect to L/W | | - More tapered shell shape<br>- Separated from the other two taxa by KW test |
| **Genital anatomy** | - Ventral spermatophore sac: a synapomorphy | | - Dorsal spermatophore sac: a plesiomorphy |
| **COI** | - Very small p-distance between the two taxa (=1.40%) | | - Large p-distance from other taxa (>3%) |
| **Distribution range** | - Known only in the Western Indian Ocean | - Known in the Western Pacific and Eastern Indian Oceans | - Only occurs in French Polynesia |

In addition, two specimens (Fig. 4A, B) supposed to belong to *S. borbonica* (indicated by arrows in Figure 3) are well off-centre with respect to the cloud of points representing the taxon. These are two samples from Mayotte, laterally compressed, and whose shell patterns correspond neither to those of *S. borbonica*, nor to those of *S. porcellana,* but for which molecular sequences are not available. Eichhorst (2016b: 815) has reported an unconventional morphe of this taxon "purplish-red shell with an elongate pattern collected [...] on Mayotte". It is possible that these samples belong to *S. tesselata* (Lamarck, 1816), a taxon with a similar morphological profile. This taxon and *S. borbonica* are the only two *Septaria* taxa reported from the Western Indian Ocean, among the 14 documented species of the genus.

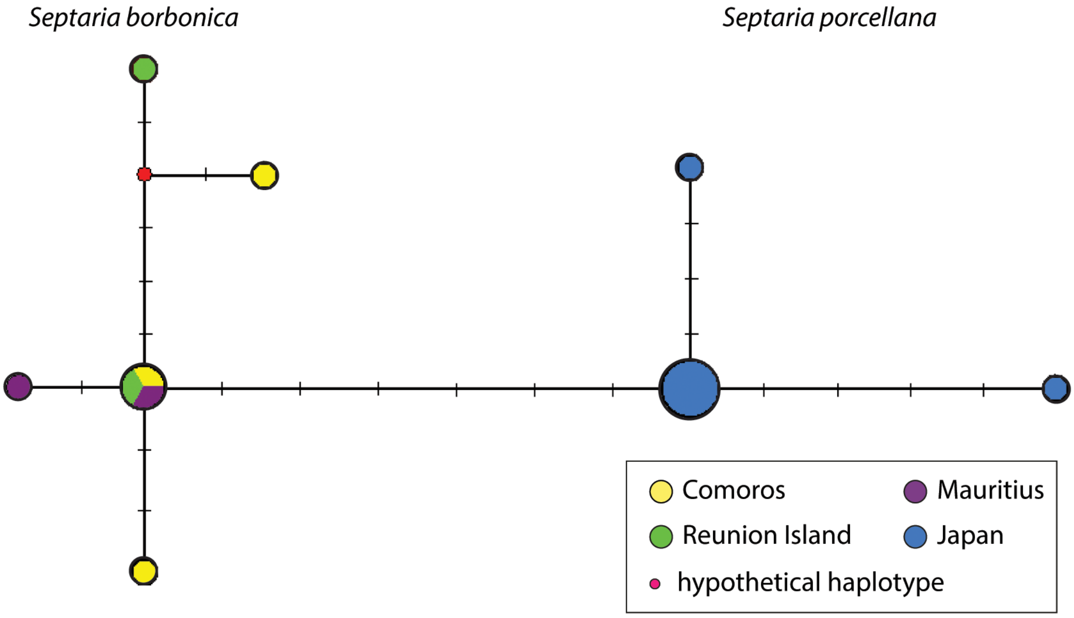

**FIGURE 6.** Haplotype network of the nominal species *Septaria borbonica* and *S. porcellana* according to the median-joining method. The circles are proportional to the frequency of occurrence, the number of mutations is indicated on the branches by dashes.

**FIGURE 7. A, B.** Two other different external patterns of the shell, found in *Septaria porcellana*. A. MNHN-IM-2013-62872 (Okinawa, Japan) B. MNHN-IM-2013-62867 (Okinawa, Japan). C–H. Samples of *S. borbonica* from different islands in the Indian Ocean have a common external pattern. C. MNHN-IM-2016-7863 (Reunion Island) D. MNHN-IM-2016-7857 (Mauritius) E. MNHN-IM-2016-7874 (Seychelles) F. MNHN-IM-2016-7880 (Mayotte, Comoros) G. MNHN-IM-2016-7887 (Anjouan, Comoros) H. MNHN-IM-2016-7892 (Grande-Comore, Comoros). Dorsal view without periostracum, below. Scale bars: 10 mm.

## Conclusion

This study confirms the status of *S. tahitiana* as a valid species and interprets *S. borbonica* as subspecies of *S. porcellana*. To better understand the phylogeography of this species, it would be interesting to date the separation of the two populations, and to determine the barrier, intermittent or not, preventing or limiting genetic exchanges between them. In addition, targeted sampling in Mayotte would be necessary to confirm or refute the suspected presence of *S. tesselata*.

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