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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 porcellana* the western Pacific and eastern Indian Oceans. The possible presence of *Septaria tessellata* (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 tessellata* (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 tessellata* (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. tessellata*. 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 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.

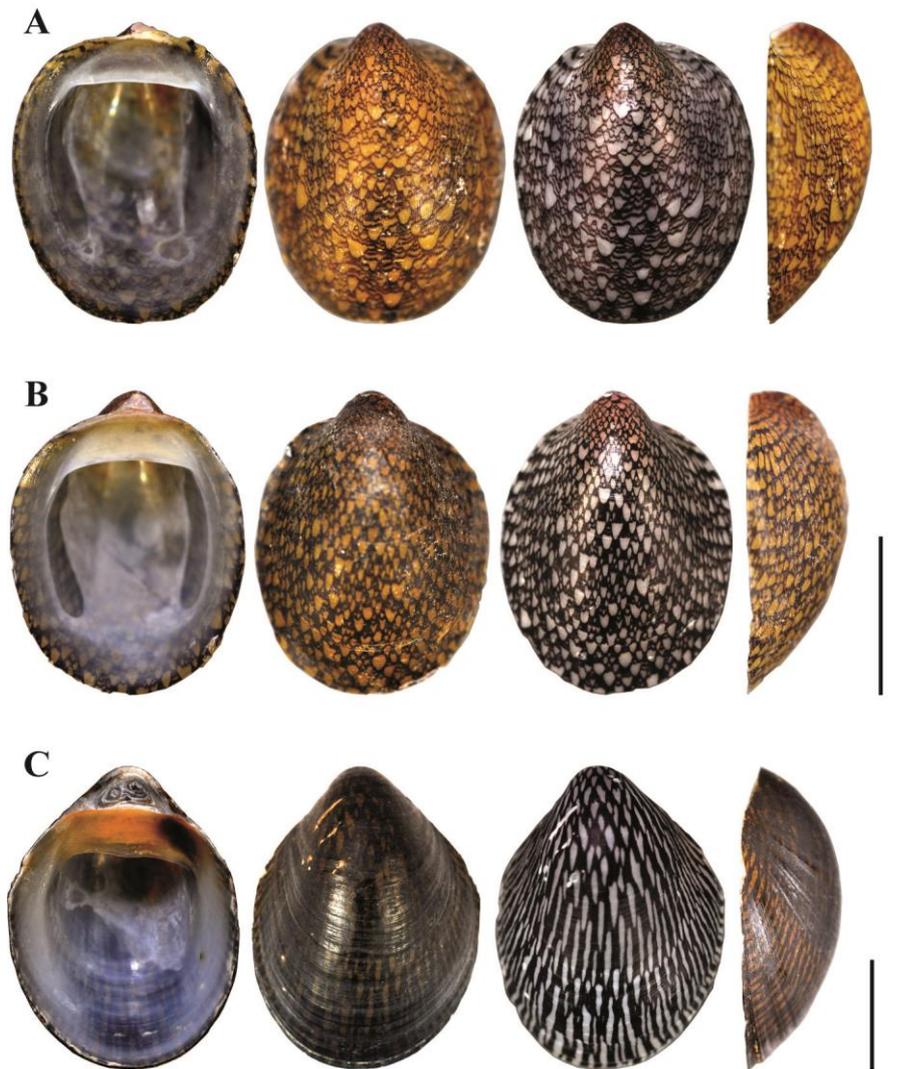


Figure 1. **A** *Septaria porcellana* (Linnaeus, 1758), MNHN-IM-2013-62871 (Okinawa, Japan) **B** *Septaria borbonica* (Bory de Saint-Vincent, 1804), MNHN-IM-2013-78206 (Mohéli, Comoros) **C** *Septaria tahitiana* Eichhorst, 2016, MNHN-IM-2013-62864 (Moorea, French Polynesia). From left to right: Ventral 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
<i>Septaria tahitiana</i> 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
<i>Septaria porcellana</i> (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
<i>Septaria borbonica</i> (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).

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

Locality	Author/Year	No of specimens	MNHN ID
<i>Septaria tahitiana</i> 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
<i>Septaria porcellana</i> (Linnaeus, 1758)			
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	Staad Coll., 1969	2	IM-2016-7853
New Guinea	Staad 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
<i>Septaria borbonica</i> (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	Staad 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
Mayotte (Comoros)	Abdou leg., 2006	1	IM-2013-78212
Mayotte (Comoros)	Abdou leg., 2006	1	IM-2013-78213
Mayotte (Comoros)	Jousseau 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

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.

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

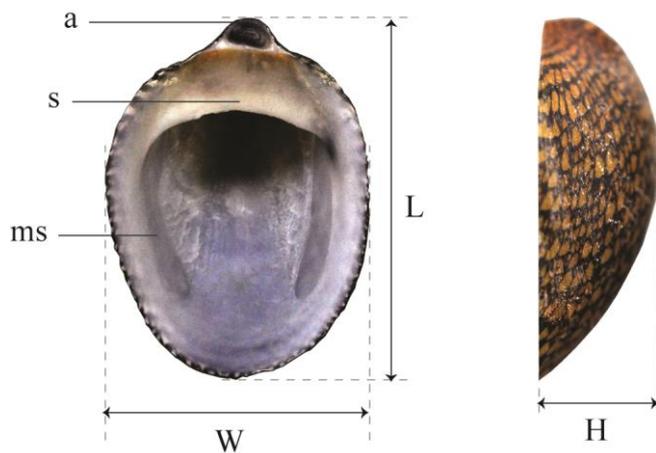


Figure 2. Shell measurement protocol. H height L length W width. a apex, ms muscle scar, s septum.

COI analysis. A fragment of the mitochondrial gene coding for the first subunit of *Cytochrome oxidase 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.

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.

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

	<i>S. borbonica</i>	<i>S. porcellana</i>	<i>S. tahitiana</i>
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)

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.

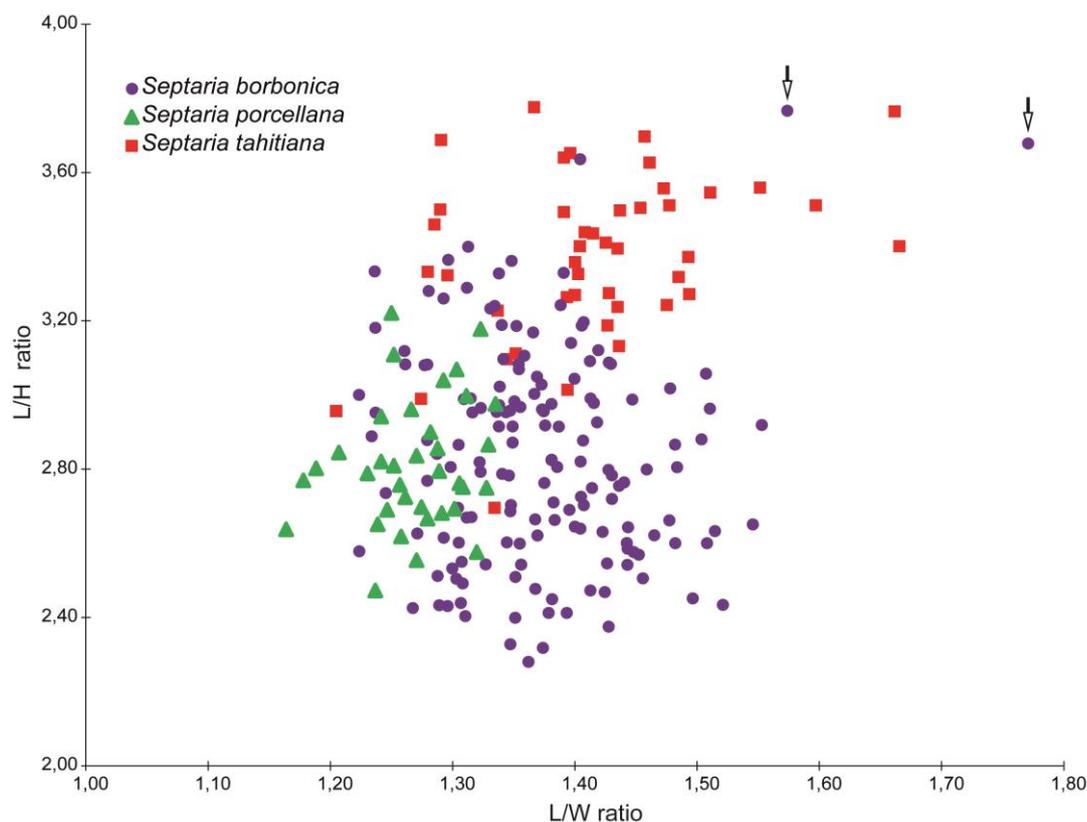


Figure 3: Cloud of points representing the L/W and L/H ratios of *Septaria borbonica*, *S. porcellana* and *S. tahitiana*.

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.

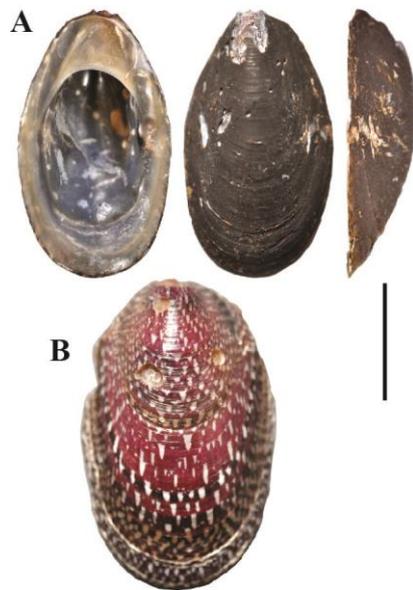


Figure 4. A, B. Samples supposed to belong to *Septaria borbonica* but for which the identification is doubtful. A MNHN-IM-2013-78211 (Mayotte, Comoros) B MNHN-IM-2013-78212 (Mayotte, Comoros), dorsal view without periostracum. Scale bar: 10 mm.

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 interspecific 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.

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

	<i>S. borbonica</i>	<i>S. porcellana</i>	<i>S. tahitiana</i>
<i>S. borbonica</i>	0.47%		
<i>S. porcellana</i>	1.40%	0.33%	
<i>S. tahitiana</i>	5.05%	4.71%	0.59%

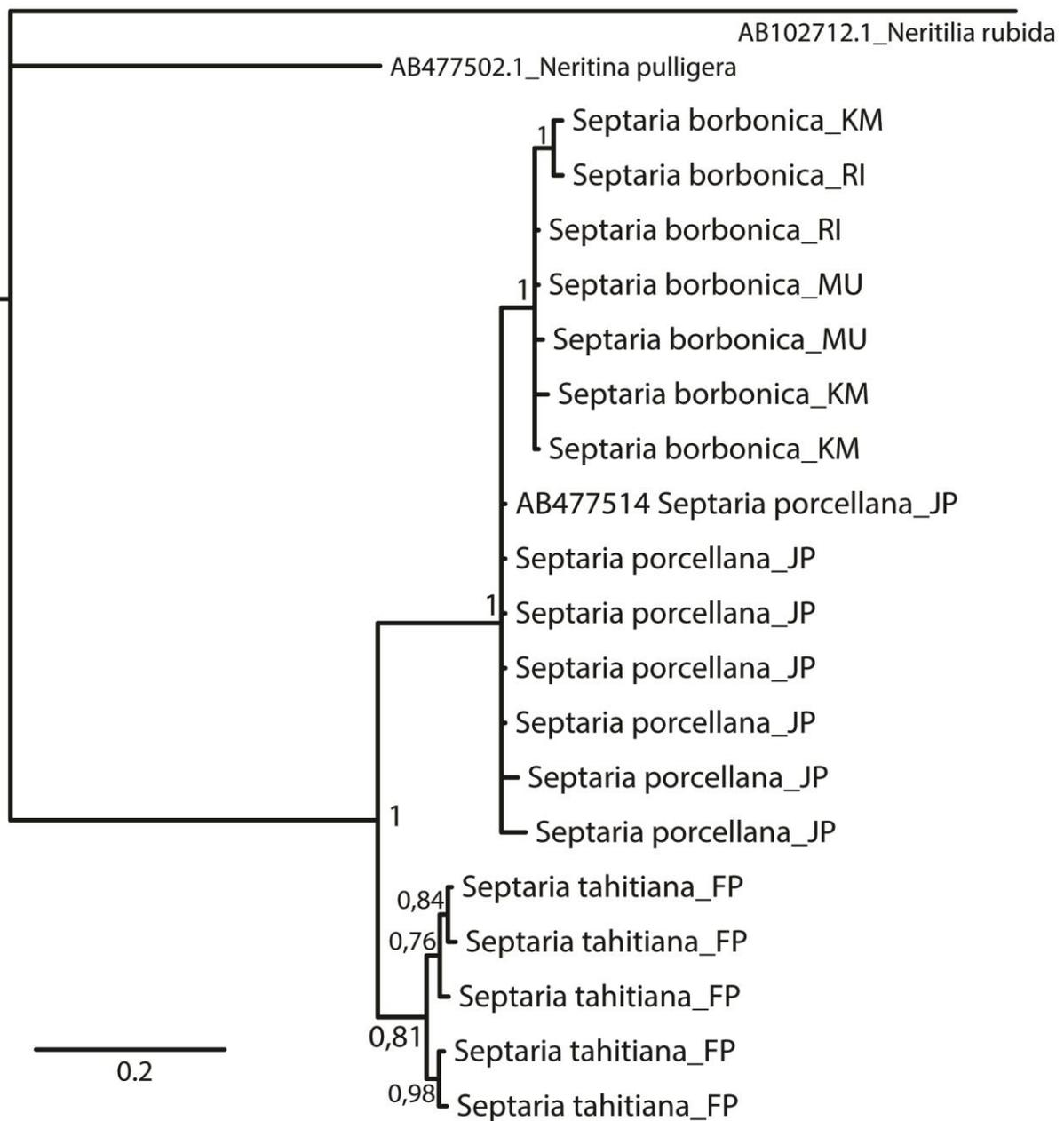


Figure 5. Bayesian analysis of the gene of the sub-unit 1 of the *Cytochrome oxidase* (COI). FP French Polynesia, JP Japan, KM Comoros, MU Mauritius, RI Reunion Island.

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 shape, 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 H_a 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 H_0 , and to retain the alternative hypothesis H_a . 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.



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.

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).

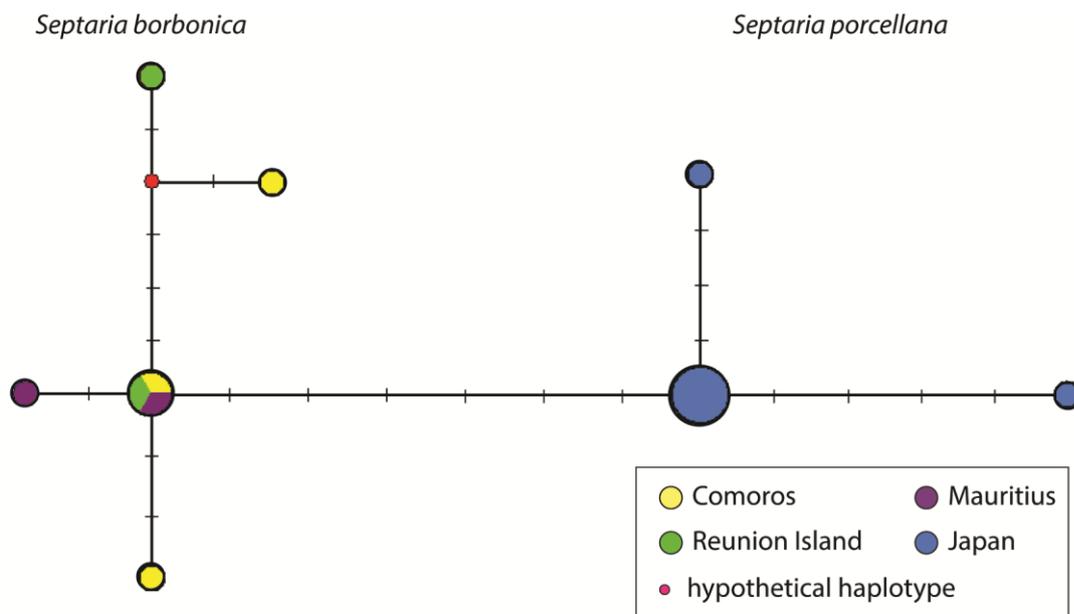


Figure 6. Haplotype network of the nominal species *Septaria borbonica* and *S. porcellana* according to the median-joining method. The circles are proportional to the frequency of occurrence, the number of mutations is indicated on the branches by dashes.

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 consistently 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).

Table 5: comparison of the three taxa against the data sets

	<i>S. borbonica</i>	<i>S. porcellana</i>	<i>S. tahitiana</i>
Morphology	- Overall similar shell shape - Grouped by KW test relative to the variable L/H, but separated with respect to L/W		- More tapered shell shape - 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

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.

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 is and *S. borbonica* are the only two *Septaria* taxa reported from the Western Indian Ocean, among the 14 documented species of the genus.

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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