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On the validity of Noah's giant clam *Tridacna noae* (Röding, 1798) and its synonymy with Ningaloo giant clam *Tridacna ningaloo* Penny & Willan, 2014

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Abstract. A new giant clam species, *Tridacna ningaloo* Penny & Willan, 2014 has been described from Ningaloo Reef, Western Australia. Meanwhile, it has been suggested that Noah's giant clam, *Tridacna noae* (Röding, 1798), previously resurrected from synonymy with *T. maxima* (Röding, 1798), is an invalid name. We assessed the validity of resurrecting *T. noae* and designating a neotype for it against the rules of zoological nomenclature and found no flaw in these acts. We then compared the genetic and morphological characters used in the respective diagnoses of *T. noae* and the newly-described *Tridacna ningaloo*. No difference was apparent between *T. ningaloo* and *T. noae* except, possibly, in mantle ornamentation patterns. In particular, the holotype of *T. ningaloo* possesses a mitochondrial DNA haplotype identical to *T. noae*. Thus, the hypothesis that *T. ningaloo* is a species distinct from *T. noae* was not supported by clear morphological evidence and it was contradicted by the available genetic evidence. *Tridacna ningaloo* should be regarded as a junior synonym of *T. noae*.

Keywords. Genetics; taxonomy; nomenclature; cryptic species; *Tridacna maxima*.

INTRODUCTION

Giant clams (genera *Hippopus* Lamarck, 1799 and *Tridacna* Bruguière, 1797; Bivalvia: Cardiidae) are among the most remarkable inhabitants of coral reefs: they are large, conspicuous and often colourful; they have raised the attention of early naturalists and they have fascinated adventurers. The conservation of giant clams also raises concern, given their multiple commercial and cultural uses, and their vulnerability to fishing (Rosewater, 1965; Newman & Gomez, 2000; bin Othman et al., 2010). Updated taxonomy and distributions of giant clams are required to assist in their conservation (Newman & Gomez, 2000; bin Othman et al., 2010; Borsa et al., 2015). Giant clam taxonomy has seen a surge in new species descriptions since Rosewater's (1965) revision of the group. Recently-described new species in the genus *Tridacna* include *T. rosewateri* Sirenko & Scarlato, 1991, *T. tevoroa* Lucas, Ledua & Braley, 1990, and *T. costata* Roa-Quiaoit, Kochzius, Jantzen, Al-Zibdah & Richter, 2008 in Richter et al. (2008). The latter two species were subsequently shown to be junior synonyms of species described decades before, respectively, *T. mbalavuana* Ladd, 1934 and *T. squamosina* Sturany, 1899 (Newman & Gomez, 2000; Huber & Eschner, 2011). Another species, Noah's giant clam *T. noae* (Röding, 1798), has been recently resurrected from synonymy with the small giant clam, *T. maxima* (Röding, 1798) after it was found to be reproductively isolated from the latter (Su et al., 2014). The name *T. noae* was chosen upon comparing the shell characteristics of specimens from Japan and Taiwan with the historic drawings (Chemnitz, 1784: plate 49, fig. 494) on which the initial description of *T. noae* was based (Su et al., 2014). An additional

giant clam species, *T. ningaloo* Penny & Willan, 2014 was published recently. In the same paper, Penny & Willan (2014: p. 202) suggested that *T. noae* might be an invalid species: “We are aware that some workers (Kubo and Iwai 2007; Su et al. 2014) recognise an additional species from the tropical northwestern Pacific Ocean, but the characters by which this species is defined morphologically, as well as its taxonomy and the nomenclature, are too controversial for us to accept it as valid at present”.

Tridacna noae under its present taxonomic definition (Su et al., 2014) has a large Indo-Pacific distribution (Fig. 1), which includes Ningaloo Reef, Western Australia as indicated by mitochondrial DNA sequences (Huelsenken et al., 2013; Borsa et al., 2015). Ningaloo Reef is also the type locality of *T. ningaloo*, which its authors (Penny & Willan, 2014) initially identified as a cryptic species distinct from *T. maxima* based on the very same set of sequences as Huelsenken et al.’s (2013). Huelsenken et al.’s (2013) *Tridacna* sp. specimens were identified as *T. noae* by Borsa et al. (2015). There is no mitochondrial DNA evidence in Huelsenken et al.’s (2013) samples from Ningaloo Reef (15 individuals labelled “*Tridacna* sp.”) of material other than *T. noae*.

This paper addresses two issues of interest to giant clam taxonomists, conservation biologists, and reef ecologists. The first one concerns the validity of the name *T. noae*, i.e. whether this name should be kept to designate the cryptic species morphologically close to *T. maxima* that has initially been discovered in Japan and Taiwan (Kubo & Iwai, 2007; Su et al., 2014). The second issue is whether *T. ningaloo* is taxonomically distinct from *T. noae*.

METHODS

For examining the availability of the name *T. noae* and the validity of resurrecting it, we referred to the relevant articles of the International Code of Zoological Nomenclature, 4th edition (International Commission on Zoological Nomenclature, 1999), hereafter abbreviated as the Code. Relevant parts of the Code are Chapter 4 on criteria of availability, including Article 12 on names published before 1931, Chapter 6 on the validity of names and nomenclatural acts, including Article 23 on the principle of priority; and Chapter 16 on types in the species group, including Article 75 on neotypes and Article 76 on type locality.

We compared *T. ningaloo* with *T. noae* on the basis of their diagnoses in, respectively, Penny & Willan (2014) and Su et al. (2014). Diagnostic or partly-diagnostic characters include DNA sequences, shell morphology, and mantle ornamentation. Nucleotide sequences at the 16S ribosomal RNA (*16S*) and the

cytochrome oxidase subunit 1 gene (*COI*) loci used for the comparison of *T. noae* with other species in the genus *Tridacna* are listed in table 1 of Borsa et al. (2015). At the time of writing, *T. ningaloo* sequences, including those of the holotype, are not yet accessible from GenBank (<http://www.ncbi.nlm.nih.gov/>) or from related public sequence databases. However, we note from figure 5 of Penny & Willan (2014) that the concatenated (*16S* + *COI*) nucleotide sequence of *T. ningaloo*'s holotype is identical to the concatenated (*16S* + *COI*) nucleotide sequence of individual no. ET918 (Huelsen et al. 2013). This individual, itself from Ningaloo Reef, is represented by GenBank sequences JX974878 and JX974908 at loci *16S* and *COI*, respectively. The complete mitochondrial DNA sequence of *Acanthocardia tuberculata* (Linnaeus, 1758) (Bivalvia: Cardiidae) (GenBank DQ632743), which is phylogenetically close to *Tridacna* spp. (Plazzi & Passamonti, 2010) was chosen as reference for numbering nucleotides at the *COI* locus. The sequences were aligned visually under BIOEDIT (Hall, 1999). The variable nucleotide sites were then highlighted using MEGA 6 (Tamura et al., 2013).

RESULTS

Röding's (1798) mention of *T. noae* (under "*Tridachnes* ... *T. Noae*. Die Vater Noahmuschel") and his explicit reference to figure no. 494 of Chemnitz (1784) satisfy the requirement of availability expressed in Article 12.1 of the Code. To further assess the validity of the name *T. noae*, we consulted all the articles and books cited in the References section of the present paper and searched for potential senior synonyms to *T. noae*. We are not aware of such species descriptions earlier than Röding's (1798). If it were the case, the name associated with such a description would now be considered *nomen oblitum* and *T. noae* be maintained, because it has been used widely since it has been formally fixed by P.F. Röding (Röding, 1798; McLean, 1947; Kubo & Iwai, 2007; Su et al., 2014; Borsa et al., 2015, and references therein). The requirement of Article 23.1 of the Code is thus fulfilled. Röding (1798) did not explicitly designate a holotype for *T. noae* and neither is there mention of the existence of one in Rosewater's (1965) revision. The designation of a neotype was justified because the original description of *T. noae* is insufficient to distinguish it with certainty from *T. maxima* (Rosewater, 1965; Su et al., 2014). Su et al. (2014) explicitly stated: "Since no type material is extant and no types have been designated to date, a neotype of *Tridacna noae* is hereby designated" thus satisfying Condition 75.3.1 of the Code. They provided a list of characters allowing the partial (their table 4 and figure 6) or complete (their figures 2-5 and 7) distinction of *T. noae* from *T. maxima* and from all other extant *Tridacna* species (their table 3 and figures 2-5), as well as reference to previous work allowing the recognition of *T. noae* as an entity genetically and morphologically distinct, and reproductively isolated from *T. maxima*; this satisfies Condition 75.3.2 of the Code. Condition 75.3.3 of the Code was met by the provision of the precise length and height of the

neotype, along with a series of pictures (Su et al., 2014; their figures 6G-6L) representing the two valves of its shell under different angles; we here add that the neotype of *T. noae* is numbered “13” in table 2 and figures 2, 3 of Su et al. (2014) and marked “13” with waterproof ink on the interior of its two valves (Su et al., 2014; their figures 6H and 6K). Condition 75.3.4 of the Code was addressed through searching the relevant taxonomic literature (Chemnitz, 1784; Röding, 1798; McLean, 1947; Rosewater, 1965). The authors further wrote that “the shells of the [cryptic] species were consistent with the figure referred to by Röding for the species he named ‘noae’”, thus satisfying Condition 75.3.5 of the Code. There is no mention of a type locality by Röding (1798) or any indication from Chemnitz (1784) on the geographical origin of the specimen he examined, making Condition 75.3.6 inapplicable in the present case. Last, Su et al. (2014) wrote that “the neotype specimen ... is deposited in the National Museum of Natural Science, Taiwan, with catalogue number NMNS-6928-001”, thus fulfilling Condition 75.3.7 of the Code. The type-locality of *T. noae* is the locality where the neotype was collected, which is Naliao, Taiwan (Su et al., 2014).

Table 1 presents the nucleotide sites of the partial *COI* gene sequence that distinguish *T. noae* from all other *Tridacna* species currently considered as valid with the exception of *T. mbalavuana*, *T. rosewateri* and *T. squamosina*, for which no *COI* gene sequences were available. Fifteen such sites were identified across a fragment 399 base-pairs (bp) long. Sequence GenBank JX974908 (*T. ningaloo*), which is 390 bp long and spans 14 of the 15 diagnostic nucleotides sites, unambiguously identifies it as *T. noae* (Table 1). At locus *16S*, *T. noae* also possesses nucleotide G at site 268 (numbered starting from the first nucleotide of GenBank KC456036, which is that of *T. noae*'s neotype) whereas all other *Tridacna* spp. except, perhaps, *T. rosewateri* for which no sequence is yet available, have A at this site. *T. ningaloo 16S* sequence GenBank JX974878 does not span this site. In summary, at locus *COI* we found no nucleotide that would distinguish *T. ningaloo* from *T. noae*, as represented by the three sequences listed in Table 1; neither did we find diagnostic differences at locus *16S*, where *T. ningaloo* is represented by sequence GenBank JX974878 and *T. noae* by homologous sequences GenBank KC456036, KC456040, KC456041 and DQ119339. Actually, the partial *16S* sequence of *T. ningaloo* was identical to that of *T. noae*'s neotype. Table 2 compares the morphological characters highlighted in the diagnostic features of *T. noae* relative to *T. maxima* (Su et al., 2014; their table 4) with the homologous characters used in the diagnosis of *T. ningaloo* (see Penny & Willan, 2014). No morphological character distinguished *T. ningaloo* from *T. noae* as redescribed by Su et al. (2014), except uncertainty concerning mantle colour patterns. The pictures of live *T. ningaloo* presented along the original description of the species (Penny & Willan, 2014) have poor resolution. The authors of *T. ningaloo*, S.S. Penny and R.C. Willan, kindly allowed us to examine higher-resolution pictures of *T. ningaloo*'s holotype and paratype. Neither specimen seemed to

exhibit finely whitish-delineated ocellate spots on the mantle's margin, an important feature in *T. noae*'s re-description (Su et al., 2014). Nevertheless, such individuals with finely whitish-delineated ocellate spots are present in Coral Bay, which is part of the Ningaloo Reef complex (Fig. 2). Other characters mentioned in the diagnosis of *T. ningaloo* include the following: "posterior end of valves bluntly subtruncate; termination of interdigitating processes sharply triangular; angle of intersection of hinge plate and posterior ridge less than 120°; up to 8 vertical plications on interior of posterior margin of valve; hinge less than half length of shell with ligament terminating before end of valve; cardinal tooth rounded; anterior lateral teeth short; byssal notch deep; posterior pedal retractor muscle almost equal in size to adductor muscle" (Penny & Willan, 2014). Not one of these characters was used in the redescription of *T. noae* (Su et al. 2014). However, the foregoing features are all present in either the drawing of Chemnitz's (1784: fig. 494) specimen subsequently referred to as *T. noae* (Röding, 1798) or in the pictures of *T. noae*'s neotype (Su et al., 2014).

DISCUSSION

Since it has been formally described by Röding (1798), *T. noae* has been used as a valid species name by a number of authors, until recently. The morphology of the shell being not fully diagnostic between *T. maxima* and *T. noae* (Su et al., 2014), *T. noae* could have been considered a *nomen dubium* (International Commission on Zoological Nomenclature, 1999: p. xxvii). This is no longer the case, because these doubts have been lifted by the fixation of a neotype. We here examined the circumstances under which Su et al. (2014) resurrected *T. noae* and we found no flaw in this nomenclatural act.

Defining species as separately evolving metapopulation lineages (de Queiroz, 2007), one expects to observe either reproductive isolation, or consistent genetic differences, or substantial morphological differences between sister species, at a degree depending on whether separation is complete or only incipient (de Queiroz, 2007). There is no necessity to solely rely on morphological characters in the description or in the diagnosis of a species (Cook et al., 2010). *Tridacna noae* as redescribed recently (Su et al., 2014) includes a genetic diagnosis. Large genetic differences between *T. maxima* and *T. noae* (17-26% nucleotide divergence at the *COI* locus; Su et al., 2014) point to millions of years of separate evolution since their last common ancestor. Unviable hybrid embryos indicate that the two species are reproductively isolated (Su et al., 2014). Notwithstanding genetic evidence, Penny & Willan (2014) have invoked controversy in the morphological definition of *T. noae*. We agree that shell morphological characters may not be sufficient for an unambiguous diagnosis of *T. noae* relative to *T. maxima*, but mantle ornamentation patterns so seem to be, at least in Japan and Taiwan (Kubo & Iwai, 2007; Su et al.,

2014). Above all, mitochondrial sequences provide a profusion of nucleotide substitutions allowing unambiguous diagnosis of *T. noae* relative to all other extant *Tridacna* species (Su et al., 2014). Conversely, we found no difference among the genetic and morphological characters on which the diagnoses of *T. noae* and *T. ningaloo* are based, except, possibly, in mantle ornamentation patterns. In the diagnosis of *T. ningaloo*, no mention is made of the “oval patches with different colours bounded by white margins” (Su et al., 2014) that are thought to be characteristic of *T. noae* (Kubo & Iwai, 2007; Su et al., 2014; Borsa et al., 2015). However, giant clams with typical *T. noae* mantle patterns do occur at Ningaloo Reef.

Two alternative hypotheses are proposed and discussed in the following. The first hypothesis is that *T. ningaloo* is a species distinct from *T. noae*. It is not yet clear whether the apparent lack of thinly whitish-contoured, ocellated spots on the mantle’s edge is a feature solely of the specimens chosen as type material, or of all individuals of *T. ningaloo*. It cannot be excluded that the apparent lack of such spots in the type material of *T. ningaloo* be the extreme of a continuum. Not only was there no genetic difference between *T. noae* and *T. ningaloo* based on the mitochondrial DNA marker, but the fact that the mitochondrial haplotype of some *T. ningaloo* specimens was identical to those sampled from *T. noae* would indicate very recent or current genetic exchange between the two species through introgressive hybridization. This in turn would imply that the two species cross-breed, in fact challenging the hypothesis of distinct biological species. They would have cross-bred to the point of erasing any genuine *T. ningaloo* mitochondrial haplotypes, as no mitochondrial sequence other than those characteristic of known *Tridacna* species including *T. noae* has been reported from Ningaloo Reef so far (Huelsen et al., 2013; Penny & Willan, 2014). Thus, morphological evidence does not clearly separate *T. ningaloo* from *T. noae*, while the available genetic evidence contradicts the hypothesis of *T. ningaloo* being a species distinct from *T. noae*. In summary, based on the available evidence, this first hypothesis should be rejected. The second, alternative hypothesis is that the giant clam described as *T. ningaloo* is a local population of *T. noae*, implying that the two names are synonymous. The principles of priority and nomenclatural stability expressed in the Code then command that *T. noae* be the only name maintained.

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(<http://www.biodiversitylibrary.org/>), and Google Books (<http://books.google.com/>). The background map of Figure 1 was edited from images downloaded from Digital Vector Maps, San Diego (<http://digital-vector-maps.com/>). TTC's initial observations on Coral Bay giant clams are accessible from <http://chaitt.blogspot.com/2008/08/coral-bay-experience-3-giant-clams.html/>. SA, PB, CF and LLL conceived the paper and contributed to the data reviewed in it. TTC and HK further contributed data and ideas. PB wrote the paper. All authors reviewed and approved the final manuscript.

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Table 1. Nucleotide substitutions at the cytochrome oxidase enzyme subunit 1 (*COI*) locus that distinguish *Tridacna noae* (Röding, 1798) from other species in the genus *Tridacna* Bruguière, 1797. *n.a.* not acknowledged.

| Species | Sample locality | GenBank accession no. | Nucleotide site no. ^c | | | | | | | | | | | | | | |
|--------------------|--------------------|-----------------------|----------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 4 | 4 | 4 | 5 |
| <i>T. crocea</i> | Indo-Malay region | EU341379 | T | A | T | A | T | T | A | T | A | T | A | C | A | T | A |
| <i>T. derasa</i> | n.a. | GQ166591 | . | T | . | . | A | . | G | . | T | . | . | T | G | . | . |
| <i>T. gigas</i> | Samar, Philippines | KJ202113 | . | T | . | . | A | . | . | G | . | C | . | . | G | G | . |
| <i>T. maxima</i> | Taiwan | DQ155301 | . | T | . | . | C | . | . | . | T | . | . | . | . | . | . |
| <i>T. ningaloo</i> | Ningaloo Reef | JX974908 ^a | – | G | C | G | G | C | C | C | G | A | G | G | C | C | C |
| <i>T. noae</i> | Taiwan | KC456023 ^b | C | G | C | G | G | C | C | C | G | A | G | G | C | C | C |
| <i>T. noae</i> | Taiwan | DQ168140 | C | G | C | G | G | C | C | C | G | A | G | G | C | C | C |
| <i>T. noae</i> | Molucca Sea | KF446463 | C | G | C | G | G | C | C | C | G | A | G | G | C | C | C |
| <i>T. squamosa</i> | Indo-Malay region | EU346364 | . | T | . | . | A | . | . | . | . | . | . | . | . | . | . |

^a sequence of *Tridacna* sp. individual ET918 of Huelsken et al. (2013) identical to that of *T. ningaloo*'s holotype (Penny & Willan, 2014; their figure 5)

^b neotype (Su et al., 2014)

^c numbering of nucleotide sites starts at the first nucleotide of the *COI* gene in the Cardiidae *Acanthocardia tuberculata* (GenBank DQ632743) (Dreyer & Steiner, 2006); the fragment considered in the comparison was comprised between nucleotide sites nos. 187 and 585 of the gene; *dot* nucleotide identical to homologous nucleotide in GenBank EU341379 (*T. crocea*); *dash* no data

Table 2. Diagnostic morphological characters listed for *Tridacna noae* (Röding, 1798) (Su et al., 2014) and comparison with homologous characters listed for *T. ningaloo* Penny & Willan, 2014 (from Penny & Willan, 2014).

| Character | Species | |
|--|--|--|
| | <i>T. noae</i> | <i>T. ningaloo</i> |
| Byssal orifice/opening | “Moderately wide” | “Markedly convex” |
| Guard tentacles of/around incurrent/inhalant siphon | “Presence” | “Possessing“ |
| Hyaline organs | “Sparse” | “Occurring irregularly across mantle to produce a mottled pattern, and regularly in a single marginal row” |
| Pattern of mantle edge/mantle | “One to several layers of oval patches with different colours bounded by white margins” | “Background colour solid blue, purple, green or fawn, and overlaid with darker mottled or dashed pattern, with submarginal row of dark spots” |
| Number of primary/radial ribs | “5-7” | “5” |
| Ribs scales | “Relatively spaced” | “Evenly spaced, partly crowded scutes” |
| Valve symmetry | “Inequilateral” | “Asymmetric” |

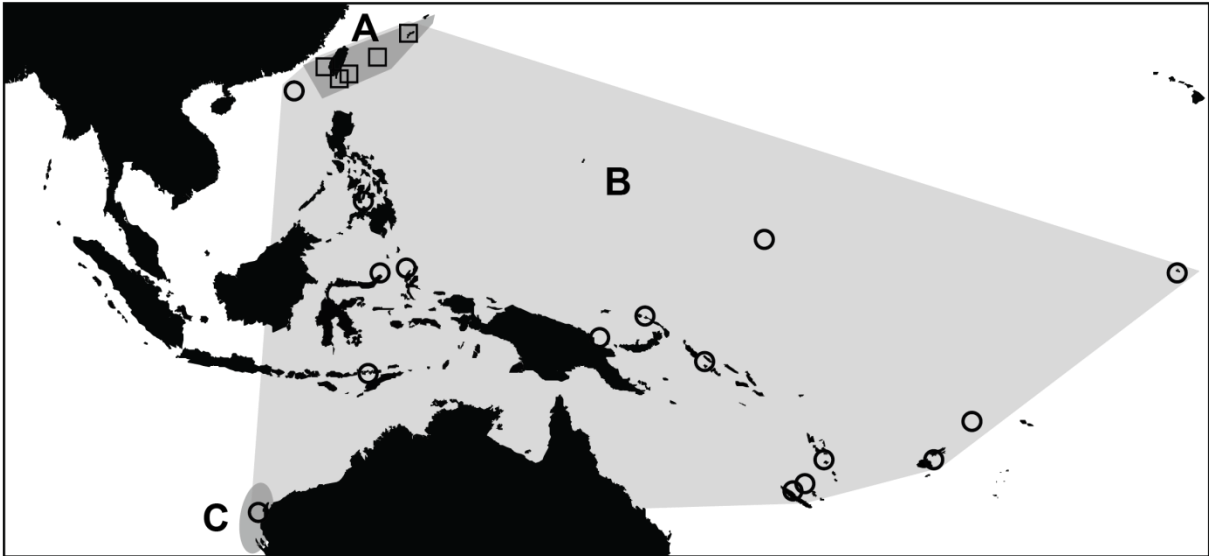


Fig. 1. Geographic distributions of *Tridacna noae* (Röding, 1798): (A) after Su et al. (2014); (B) updated by Borsa et al. (2015); and *T. ningaloo* Penny & Willan, 2014: (C) after Penny & Willan (2014). *Squares*: localities of *T. noae* specimens sampled by Su et al. (2014); *circles*: *T. noae* records compiled by Borsa et al. (2015).



Fig. 2. *Tridacna noae* (Röding, 1798) on the reef in Coral Bay, Western Australia, 23°09'S 113°47'E, 14 August 2008 (photographed by: Tsun-Thai Chai).