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The forgotten giants of the Western Indian Ocean reefs

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Abstract - We addressed the evolutionary history of *Tridacna* giant clams by combining molecular phylogenies with the geographic distribution of lineages across the Indo-West Pacific, with a focus on the Western Indian Ocean (WIO). A giant clam initially identified as *T. maxima* was genetically distinct and identified as *T. elongatissima*, a long-forgotten species from Mozambique. Two nominal species endemic to the Mascarene basin, *T. lorenzi* and *T. rosewateri* were found to be a single and same, distinct species. *Tridacna elongatissima* turned out to be the sister species of *T. squamosina*, another recently resurrected species endemic to the Red Sea. The *T. elongatissima-T. squamosina* pair was itself sister to *T. rosewateri*, highlighting this part of the world as a hotspot of endemism for giant clams. With two unrelated lineages in the WIO, one of which was sister to a third lineage endemic to the Red Sea, lineage diversification patterns within the widespread *T. maxima* mirrored those of *T. elongatissima*, *T. rosewateri* and *T. squamosina*. The same geographic barriers and speciation processes may thus have acted repeatedly at different periods in the Pleistocene.

Keywords – *Tridacna*; giant clam; Indo-West Pacific; phylogeography; endemism

Giant clams have long fascinated adventurers and naturalists. These large shallow-water molluscs certainly are among the most colourful, conspicuous and emblematic species of the Indo-Pacific coral reefs. They have been exploited for thousands of years for their flesh and shell. Giant clam conservation is also an increasingly urging issue because of the vulnerability of giant clams to overharvesting. Surprisingly, up to recent years, giant clams have remained incompletely known and described, and their evolutionary history was poorly understood.

As *Tridacna* giant clams exclusively occur in coral reefs of the Indo-West Pacific (IWP), we believed that studying the mode and tempo of their speciation would provide us with clues on the evolutionary history of modern coral reef communities in the IWP. We addressed this objective by combining molecular phylogenies with the geographic distribution of *Tridacna* lineages across the IWP. With well-dated, albeit rare fossil records, we had a model of choice to link phylogenetic patterns to past geological events.

When we started our phylogeographic research on giant clams in the late 2000s, a robust phylogeography of Coral-Triangle and Pacific *Tridacna* lineages was already partly available but little was known from the Indian Ocean. A distinctive *T. maxima* lineage and a newly rediscovered species (*T. squamosina*) had been reported from the Red Sea, but no phylogeographic information was then available from the western Indian Ocean (WIO). Hence our focus on *Tridacna* giant clams from that part of the tropical IWP. During field work, several participants in this study – then working as separate teams – independently noticed giant clams initially identified as *T. maxima* but presenting somewhat distinctive features. We noticed the sharply pointed triangular interstices between folds, and the remarkable emerald-green colour of the mantle edge. Nucleotide sequences at the COI locus confirmed this giant clam was distinct from *T. maxima*, and from all other known *Tridacna* spp. then documented in public sequence databases. With an endemic species in the Red Sea (*T. squamosina*), two unverified rare species endemic to the Mascarene Basin (*T. rosewateri* and *T. lorenzi*), and now a new cryptic lineage in the WIO, we felt that we had an increasingly interesting subject to investigate. Our different teams merged efforts and datasets and pursued the phylogeographic work all together.

We managed to extract DNA from dried muscle tissue and ligament from the type material of *T. rosewateri* and from other specimens from the WIO region preserved in museum collections. Morphological and molecular analyses enabled us to identify the distinct *Tridacna* lineage present in the WIO as *T. elongatissima*, a long- forgotten species from Mozambique then synonymised with *T. maxima*, thereby adding a taxonomic hue to our primarily phylogeographic study. Meanwhile, *T. lorenzi* and *T. rosewateri* were found to be a single and same, distinct species. This newly resurrected WIO-endemic *Tridacna elongatissima* turned out to be the

sister species of *T. squamosina*! These two species had evolved independently in, respectively, the WIO and the Red Sea (or perhaps an adjacent northwestern Indian Ocean refuge), revealing a geographic barrier between the two regions. The *T. elongatissima*–*T. squamosina* pair was itself sister to *T. rosewateri*, highlighting this part of the world as an hotspot of endemism for giant clams. With two unrelated lineages in the WIO, one of which was sister to a third lineage endemic to the Red Sea, lineage diversification patterns within the widespread *T. maxima* mirrored those of *T. elongatissima*, *T. rosewateri* and *T. squamosina*. Thus, the same geographic barriers and speciation processes may have acted repeatedly at different periods in the Pleistocene.

We are aware, though, that no uniform explanation holds for the evolutionary history of species in the tropical IWP. At least we were able to refine our understanding of lineage diversification and endemism of *Tridacna* giant clams in the WIO and Red Sea region. Future investigations may add to the story. Beyond the specific case of giant clams, our results emphasize the interest of sampling understudied regions of the tropical IWP, such as the WIO, to refine the evolutionary puzzle of this vast and complex geographic ensemble.

Additional information:
http://umr-entropie.ird.nc/index.php/home
https://cecilefauvelotird.wordpress.com/

From the cover: read the article on which this post is based …
Fauvelot, C, Zuccon, D, Borsa, P, et al. 2020. Phylogeographical patterns and a cryptic species provide new insights into Western Indian Ocean giant clams phylogenetic relationships and colonization history. *J. Biogeogr.* 47, 1086– 1105.
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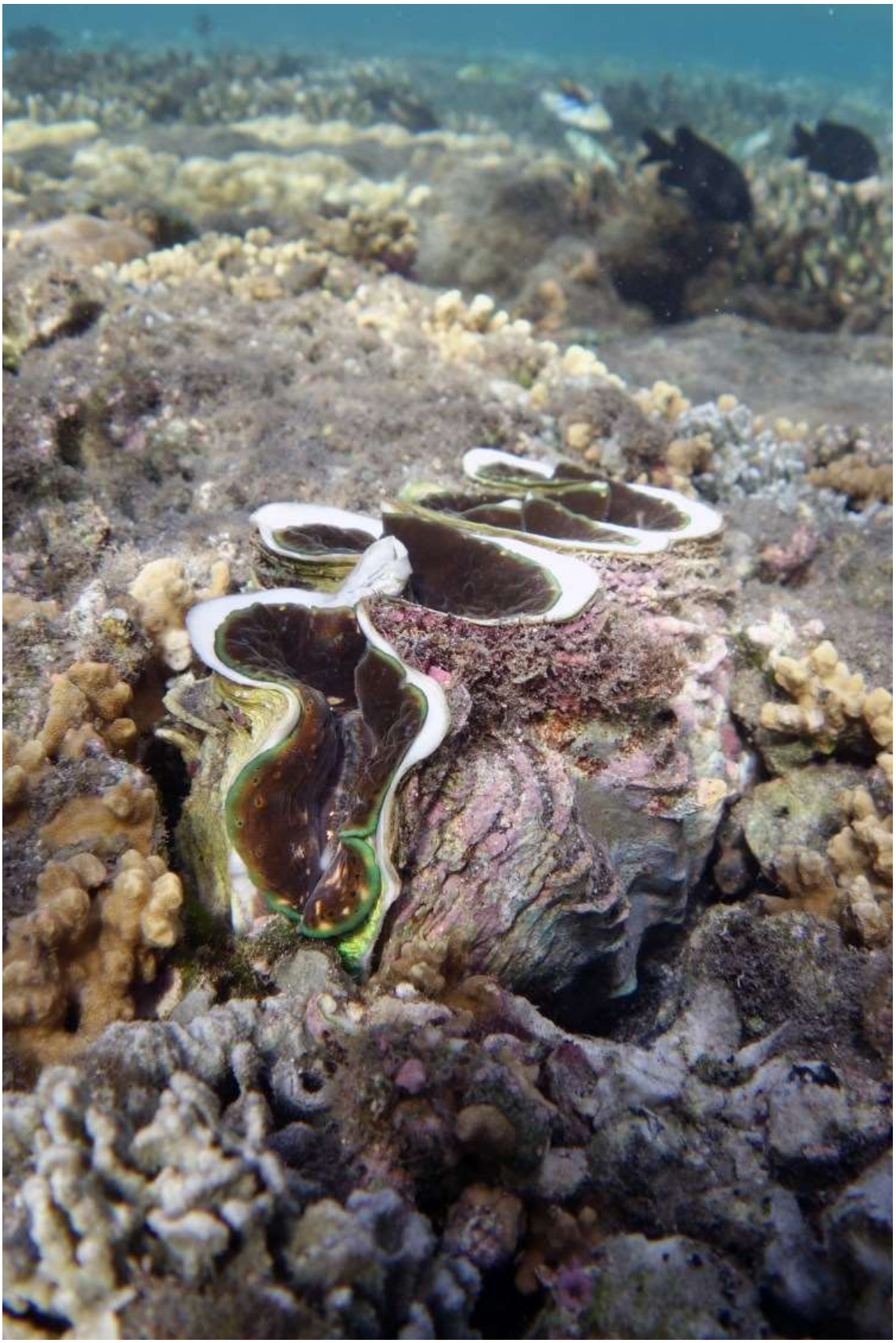
Image: C. Fauvelot (IRD) is doing a biopsy on a giant clam at Juan de Nova. Photo credit: T.B. Hoareau / TAAF-Iles Eparses research consortium.



Tridacna elongatissima from Etang Salé at Reunion Island. Photo credit: L. Bigot / Université de La Réunion.