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Pocillopora tuahiniensis: a new species of scleractinian coral (Scleractinia, Pocilloporidae) from French Polynesia

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Abstract

Pocillopora tuahiniensis **sp. nov.** is described based on mitochondrial and nuclear genomic data, algal symbiont genetic data, geographic isolation, and its distribution pattern within reefs that is distinct from other sympatric *Pocillopora* species (Johnston *et al.* 2022a, b). Mitochondrial and nuclear genomic data reveal that *P. tuahiniensis* **sp. nov.** is a unique species, sister to *P. verrucosa*, and in a clade different from that of *P. meandrina* (Johnston *et al.* 2022a). However, the gross in situ colony appearance of *P. tuahiniensis* **sp. nov.** cannot easily be differentiated from that of *P. verrucosa* or *P. meandrina* at Mo'orea. By sequencing the mtORF region, *P. tuahiniensis* **sp. nov.** can be easily distinguished from other *Pocillopora* species. *Pocillopora tuahiniensis* **sp. nov.** has so far been sampled in French Polynesia, Ducie Island, and Rapa Nui (Armstrong *et al.* 2023; Edmunds *et al.* 2016; Forsman *et al.* 2013; Gélin *et al.* 2017; Mayfield *et al.* 2015; Oury *et al.* 2021; Voolstra *et al.* 2023). On the fore reefs of Mo'orea, *P. tuahiniensis* **sp. nov.** is very abundant ≥ 10 m and is one of the most common *Pocillopora* species at these depths (Johnston *et al.* 2022b). It can also be found at a much lower abundance at shallow depths on the fore reef and back reef lagoon. The holotype is deposited at the Smithsonian Institution as USNM-SI 1522390 and the mtORF Genbank accession number is OP418359.

Key words: cryptic species, Pocillopora, coral, genomics, marine, Tropical South Pacific

Introduction

Species of *Pocillopora* Lamarck, 1816 are notoriously morphologically plastic, a feature of the genus that makes species identification using gross colony morphology difficult (Gélin *et al.* 2017; Johnston *et al.* 2018; Marti-Puig *et al.* 2014; Paz-García *et al.* 2015; Pinzón *et al.* 2013), although there is evidence that corallite morphology aligns with some genetically-identified species in some locations (Marti-Puig *et al.* 2014; Oury *et al.* 2023; Schmidt-Roach *et al.* 2014). In the last decade, the identification of *Pocillopora* species from genetic material has resulted in the resurrection of a species, *P. acuta* Lamarck, 1816 (Schmidt-Roach *et al.* 2013a, 2014), and the description of two new species, *P. aliciae* Schmidt-Roach, Miller, and Andreakis, 2013 (Schmidt-Roach *et al.* 2013b), and *P. bairdi* Schmidt-Roach 2014 (Schmidt-Roach *et al.* 2014). Using genomics to identify species has greatly improved our understanding of the distribution, ecology, reproduction, and evolution of *Pocillopora* (Burgess *et al.* 2021; Gélin *et al.* 2017; Johnston *et al.* 2022a; Oury *et al.* 2022; De Palmas *et al.* 2018; Paz-García *et al.* 2015; Pinzón *et al.* 2013; Torres *et al.* 2020; Turnham *et al.* 2021) but there is still much left to learn.

Here, *Pocillopora tuahiniensis* **sp. nov.** is described based on mitochondrial and nuclear genomic data, algal symbiont genetic data, its geographic isolation, and its distribution pattern within reefs that is distinct from other sympatric *Pocillopora* species (Johnston *et al.* 2022a, b). We deposited the holotype at the Smithsonian Institution as USNM-SI 1522390.

Order Scleractinia

Family Pocilloporidae Gray, 1842

Genus Pocillopora Lamarck, 1816

Pocillopora tuahiniensis sp. nov.

Holotype: The holotype (USNM-SI 1522390) was collected from Mo'orea, French Polynesia (17.517 S 149.762 W) at 20 m on December 20, 2021, by S.C. Burgess. The genetic identity of the holotype was confirmed using the mitochondrial open reading frame marker (mtORF; accession number OP418359) (Flot & Tillier 2007) as mtORF haplotype 10 (Forsman *et al.* 2013). This mitochondrial marker as a species identifier of *P. tuahiniensis* sp. nov has been supported by multiple independent genomic studies (Johnston *et al.* 2022a; Oury *et al.* 2023; Voolstra *et al.* 2023). Preserved DNA of the holotype is stored at the Smithsonian Institution and Florida State University.

Skeletal characteristics of the holotype: The corallum measures 19 cm in length, 16 cm in width, and 15 cm in height (Figures 1a, 2a). The corallum is hemispherical and the branches are fairly evenly spaced, separated by approximately 1–2 cm. Branches are straight and robust, and most branches ramify. Verrucae are evenly distributed and are equal in size and shape, approximately 1 mm. Verrucae are not verrucose at their tips, but rather are jagged and crown shaped (Figures 1b, 1c). The inner corallite diameter ranges between 0.54–0.65 mm (Figures 1d–1f). Within the corallite, short, wide columellae are present, and septa, if present, are weakly developed and form 1–3 hexamerally arranged rows (Figures 1e, 1f). Short spinulae are evenly distributed across the coenosteum (Figures 1d–1f).



FIGURE 1. Photographs and SEM of the *P. tuahiniensis* holotype USNM-SI 1522390 showing **a**) a side view of holotype, **b**) spacing and shape of verrucae, **c**) close up of verrucae, **d**) verrucae and corallites, and **e**) and **f**) close ups of corallites showing the wide, flattened columellae.

Color and pigmentation of live colony: Colonies may be brown, pink, or pale yellow, and like many *Pocillopora* species, have pigment concentrated in the oral opening of the polyps, forming a dark ring. The holotype was pale yellow (Figure 2a, b).

Habitat and biology: On the fore reefs of Mo'orea, *P. tuahiniensis* **sp. nov.** is very abundant ≥ 10 m and is the most common *Pocillopora* species at these depths. It can also be found at a much lower abundance at 5 and 10 m on the fore reef (Johnston *et al.* 2022b) as well as in the back reef lagoon. Reproduction has not been observed in *P. tuahiniensis* sp. nov but reproduction is hypothesized to occur via broadcast spawning based on the broadcast spawning observed in sister lineages, *P. cf. verrucosa* in the Red Sea (Bouwmeester *et al.* 2011, 2021), and *P. me-andrina* Dana 1846 and *P. grandis* Dana 1846 on the Great Barrier Reef (Schmidt-Roach *et al.* 2012).

Distribution: From genetic surveys of *Pocillopora* that have used the mtORF marker to date, *P. tuahiniensis* **sp. nov.** was initially thought to be endemic to French Polynesia (Edmunds *et al.* 2016; Forsman *et al.* 2013; Gélin *et al.* 2017; Johnston *et al.* 2018; Mayfield *et al.* 2015; Oury *et al.* 2020, 2021; De Palmas *et al.* 2018; Pinzón *et al.* 2013; Robitzch *et al.* 2015; Sawall *et al.* 2015; Schmidt-Roach *et al.* 2014). However, recent geographic sampling in the tropical South Pacific has recovered this species at Ducie Island and Rapa Nui using genomic data (Armstrong *et al.* 2023; Voolstra *et al.* 2023).

Etymology: The species name derives from the Tahitian word for sister, tuahine. Genomic data indicate that *Pocillopora tuahiniensis* **sp. nov.** is sister species to *P. verrucosa* (mtORF haplotypes 3a, 3b, 3f, 3h) in French Polynesia (Johnston *et al.* 2022a). Haplotype identification following Pinzón *et al.* (2013). The species name attributed to mtORF haplotypes 3b, 3d, 3f, 3g on the Great Barrier Reef is *P. verrucosa* (Ellis and Solander 1786) (Schmidt-Roach *et al.* 2014); see comments in Remarks below. Because *Pocillopora tuahiniensis* **sp. nov.** had until recently only been found in French Polynesia, the etymology of its name, i.e., Tahitian, reflects this geographic location where it was first identified to be a unique species using genomics.

Taxonomic history and previous records: *Pocillopora solida* Quelch 1886, *P. setchelli* Hoffmeister 1925, and *P. squarrosa* Dana 1846 have been described from French Polynesia. *Pocillopora setchelli* was considered a junior synonym of *P. damicornis* (Linnaeus, 1758) by Veron and Pichon (1976) but Hoeksema and Cairns (2023) currently consider it to be a synonym of *P. brevicornis* Lamarck 1816. *Pocillopora solida* and *P. squarrosa* are considered taxa inquirendum (Hoeksema & Cairns 2023).

The holotype of *P. solida* is deposited in the National History Museum in London, England (BMNH1886.12.9.22). The specimen is 14 cm in height and 12 cm in width and is neither compact nor spherical. The holotype of *P. solida* is described as a large specimen, distinct from all other known forms, which grew horizontal having branches that are elongated and much divided with verrucae that are very unequal, irregularly placed, rarely crowded, and generally separated by spaces more than their own diameter (Quelch 1886). Unlike *P. tuahiniensis* **sp. nov.**, the verrucae of *P. solida* become obsolete towards the center of the colony (Figure 3a). In contrast, the corallum of *P. tuahiniensis* **sp. nov.** colonies are round and compact with branches that are evenly spaced, and verrucae that are equal in size, regularly spaced, and continue along branches towards the center of the colony (Figures 1 and 2).

The holotype of *P. squarrosa* is deposited in the Smithsonian Museum in Washington, D.C., USA (USNM443). The corallum is described as rudely hemispherical with branches that are closely crowded, stout, nearly straight, unequally compressed, and uneven, with rounded summits (Dana 1846). Unlike *P. tuahiniensis* **sp. nov.**, the USNM443 specimen clearly presents styloid columellae within its corallites, similar to that observed in *P. grandis* Dana, 1846.

The first documentation of *P. tuahiniensis* **sp. nov.** in the literature identified it using genetics from a morphologically undescribed sample. Forsman *et al.* (2013) first identified *P. tuahiniensis* **sp. nov.** as haplotype 10, a novel genetic lineage from Mo'orea using PCR amplification of the mtORF marker (Flot & Tillier 2007). mtORF haplotype 10 has also been identified as Primary Species Hypothesis (PSH) 14 by Gélin *et al.* (2017) using both the mtORF marker and 13 microsatellites. mtORF haplotype 10 was identified as the *P. verrucosa* morphotype in that study. Johnston *et al.* (2022a) first identified mtORF haplotype 10 as a unique lineage of *Pocillopora* at Mo'orea using genomic and algal symbiont data. More recently, both Oury *et al.* (2023) and Voolstra *et al.* (2023) have recovered mtORF haplotype 10 as a distinct lineage from a greater geographic sampling effort using independent nuclear genomic approaches, identifying haplotype 10 as GSH 14 and SVD 5, respectively.

Until recently, genetic sampling had only recovered *P. tuahiniensis* **sp. nov.** from French Polynesia (Edmunds *et al.* 2016; Forsman *et al.* 2013; Gélin *et al.* 2017; Johnston *et al.* 2018; Mayfield *et al.* 2015; Oury *et al.* 2020, 2021; De Palmas *et al.* 2018; Pinzón *et al.* 2013; Robitzch *et al.* 2015; Sawall *et al.* 2015; Schmidt-Roach *et al.* 2014). Within French Polynesia, *P. tuahiniensis* **sp. nov.** had been sampled from Nororotu, Maiao, Tetiaroa, and Mo'orea (Edmunds *et al.* 2016; Gélin *et al.* 2017; Mayfield *et al.* 2015). However, greater geographic sampling in the tropical south Pacific has recently identified this species at Ducie Island and Rapa Nui as well (Armstrong *et al.* 2023; Voolstra *et al.* 2023).

Remarks: Using the mtORF marker, Johnston *et al.* (2022b) found that *P. tuahiniensis* **sp. nov.** is most abundant at depths around 10 m and greater on the fore reefs of Mo'orea, whereas co-occurring species have distinctly different relative abundance patterns across depth. Among these co-occurring species are *P. meandrina* Dana 1846 and *P. verrucosa* (Ellis and Solander 1786). Johnston *et al.* (2022a) recognized *P. verrucosa* as a single lineage at Mo'orea (and includes mtORF haplotypes 3a, 3b, 3e, 3f, and 3h; haplotype identification following Pinzón *et al.* (2013)). Along with *P. tuahiniensis* **sp. nov.**, these species are the most abundant species on the fore reefs of Mo'orea.



FIGURE 2. *In situ* appearance of *Pocillopora* species photographed at Mo'orea, French Polynesia. **a)** Close up of *P. tuahinien-sis* holotype USNM-SI 1522390 at 20 m depth; **b)** surroundings of holotype, with holotype USNM-SI 1522390 in the center; **c)** *P. tuahiniensis* **sp. nov.** at 10 m depth; **d)** *P. tuahiniensis* **sp. nov.**, left, and *P. verrucosa*, right, at 10 m depth; **e)** *P. meandrina* at 10 m depth. All colonies were identified using the mtORF and PocHistone markers following the protocol described in Johnston *et al.* (2018). The identity of colonies in **c, d,** and **e** are included in the datasets of (Burgess *et al.* 2021; Johnston *et al.* 2022a).

The Great Barrier Reef is the type locality for P. verrucosa (Ellis and Solander 1786) and Schmidt-Roach et al. (2014) associated mtORF haplotypes 3b, 3d, 3f, and 3g to this species. Oury et al. (2023), however, resolved three different lineages associated with mtORF haplotype 3, with GSH 13a containing haplotypes 3c, 3e, 3g, 3j, GSH 13b containing haplotype 3a, and GSH 13c containing haplotypes 3b, 3d, 3f, 3h, 3i. They conclude that GSH 13a is restricted to the Red Sea, Arabian Gulf, and Western Indian Ocean (WIO) but that GSH 13b and GSH 13c are widespread based on the geographic distribution of the corresponding mtORF haplotypes reported in prior literature, despite in their study only sampling GSH 13b from the WIO and GSH 13c mostly from the Tropical South Pacific. While there may be some geographic segregation between mtORF 3 haplotypes found by Oury et al. (2023), the mtORF haplotypes recovered at Mo'orea were found to be a single genomic lineage (Johnston et al. 2022a) and include those mtORF haplotypes used to identify *P. verrucosa* from its type locality, therefore we identify all mtORF 3 haplotypes at Mo'orea as P. verrucosa. Likewise, Oury et al. (2023) found two distinct lineages (GSH 9a and GSH 9b) associated with the mtORF haplotype 1a + PocHistone lineage (genetic identification following Johnston et al. (2018)) used to identify P. meandrina. GSH 9a is found in both the Pacific and Indian Oceans, and encompasses the type locality, Hawai'i, for P. meandrina Dana 1846. GSH 9b is restricted to the Western Indian Ocean. We thus conclude that GSH 9a, and what we call haplotype 1a P. meandrina is P. meandrina Dana 1846, while GSH 9b may be a regional endemic that needs further identification.



FIGURE 3. Types of *Pocillopora* species closely related to *P. tuahiniensis* **sp. nov.** for morphological comparison. **a)** Holotype of *P. solida* Quelch 1886 (BMNH1886.12.9.22) collected from Tahiti, French Polynesia. This taxon is considered inquirendum. Images captured by The Trustees of the Natural History Museum, London. **b)** Colony photograph and corallite SEM of *P. verrucosa* (Ellis and Solander 1786) neotype (MTQG65923) collected from Lizard Island Lagoon, Australia. **c)** *Pocillopora danae* Verrill 1864 holotype (USNM696) collected from Fiji. *Pocillopora danae* is considered a junior subjective synonym of *P. verrucosa*. **d)** *Pocillopora grandis* Dana 1846 syntype (USNM700) collected from Fiji. **e)** *Pocillopora meandrina* Dana 1846 syntype (YPMIZ001970.CN) collected from Hawai'i. **f)** *Pocillopora nobilis* Verrill 1864 syntype (USNM658) collected from Hawai'i. Pocillopora nobilis Verrill 1864 syntype (USNM658) collected from Hawai'i.

The gross *in situ* colony appearance of *P. tuahiniensis* **sp. nov.** cannot easily be differentiated from that of *P. meandrina* or *P. verrucosa* at Mo'orea (Figure 2). The coralla of both *P. tuahiniensis* **sp. nov.** and *P. meandrina* are generally small, compact, and hemispherical, with branches that are flattened and meander towards the tips (Figure 1–3). *Pocillopora grandis* Dana 1846 also has branches that are flattened and meandering, but these branches can be paddle-like and are typically more robust than those of *P. meandrina*, *P. tuahiniensis* **sp. nov.**, and *P. verrucosa*

(Ellis and Solander 1786) (Figure 3d). The branches of *P. verrucosa* typically do not meander and may be both flattened and cylindrical with swollen appearing branch tips (Figures 2d, 3b–3c).

Both *P. tuahiniensis* **sp. nov.**, *P. meandrina*, and *P. grandis* have neatly arranged verrucae that are equal in size (Figures 1–3), but the verrucae of *P. tuahiniensis* **sp. nov.** tend to have a more jagged, crown-like appearance (Figure 1d–1e) in contrast to the rounded verrucae of *P. meandrina*, *P. verrucosa*, and *P. grandis* (Figure 3b–f). The verrucae of *P. verrucosa* are verrucose and equally distributed, but in contrast to *P. meandrina*, *P. grandis*, and *P. grandis*, and *P. tuahiniensis* **sp. nov.**, they are irregular in size, shape, and height (Schmidt-Roach *et al.* 2014) (Figure 3b–3c).

The spinulae of *P. tuahiniensis* **sp. nov.** are much reduced, if present, and columellae are short and wide (Figures 1e, 1f, and 3a). Columellae of *P. meandrina* are oval-convex to styloid and rarely obsolete (Schmidt-Roach *et al.* 2014). *Pocillopora grandis* can be differentiated from *P. meandrina* by its styliform columellae that may contain 1–3 stylae. The corallites of *P. verrucosa* are characterized as having many long, slender spinulae and absent to styloid columellae (Schmidt-Roach *et al.* 2014) (Figure 3b).

Mitochondrial and nuclear genomic data reveal that *P. tuahiniensis* **sp. nov.** is a unique species, sister to *P. verrucosa*, and in a clade different from that of *P. meandrina* (Johnston *et al.* 2022a). By sequencing the mtORF region, *P. tuahiniensis* **sp. nov.** can be easily distinguished from other *Pocillopora* species.

In French Polynesia, both *P. tuahiniensis* **sp. nov.** and *P. verrucosa* host the algal symbiont, *Cladocopium pacificum* Turnham, Sampayo, and LaJeunesse 2021, but *P. tuahiniensis* **sp. nov.** tends to host a population of *C. pacificum* that is genetically different from that hosted by *P. verrucosa* (Johnston *et al.* 2022a).

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We recognize that documentation is not always discovery. As guests, we recognize and give thanks for the land and water resources of Polynesia, in particular Mo'orea, and to the traditional owners of the land, both past and present. Māuruuru roa.

Nous reconnaissons que la documentation n'est pas toujours une découverte. En tant qu'invités, nous sommes reconnaissants et remercions les ressources en terre et en eau de la Polynésie, en particulier de Mo'orea, ainsi que les propriétaires traditionnels de la terre, passés et présents. Māuruuru roa.

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