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Stimpson, 1860**

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Taxonomic study of the freshwater shrimps genus *Atyoida* Randall, 1840 (Crustacea: Decapoda: Atyidae) in Polynesia with a revalidation of *A. tahitensis* Stimpson, 1860.

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ABSTRACT

Numerous specimens of *Atyoida* were collected in Polynesia during specific samplings led by the Muséum national d'Histoire naturelle (MNHN, Paris) from 1983 to 2017. In the context of an integrative taxonomy, all the Polynesian specimens were morphologically and genetically studied. The molecular study proved that the specimens were split in two different clades separated by 7% genetic distance (16S) and geographically structured that can be considered as two distinct species. In this article, *A. tahitensis* Stimpson, 1860 from Eastern Polynesia is revalidated as a distinct species from *A. pilipes* (Newport 1847) from Vanuatu to Marquesas archipelago. The morphological study, besides coloration patterns (Body blackish on its back, ornamented on its flanks with numerous bluish dots and longitudinal stripes for *A. tahitensis*; orange-yellow back as well as the antennular peduncle, telson and uropods with the flanks whitish ornamented with numerous blue-black patterns of various shapes for *A. pilipes*), did not allow us to find characters to distinguish easily the two species. Detailed re-descriptions and the geographical distribution of these two species are given and a neotype deposited in the MNHN (Paris) is designated for *A. tahitensis*.

INTRODUCTION

The freshwater shrimp genus *Atyoida* Randall, 1840 belongs, in the *Atya* group, to the *Atya*-like shrimps which Chace (1983) defined as the group with the “carpus of second pereopod deeply excavated and a little longer than broad”. The genus *Atyoida* has a wide but disjoint distribution in the Indo-Pacific region where it includes, until now, three valid species (*viz.* *Atyoida pilipes* (Newport 1847), *Atyoida serrata* (Spence Bate 1888) and *Atyoida bisulcata* (Randall 1840).

Until recently, the taxonomy of atyid shrimps was mainly based on morphological characters. In the genus *Caridina*, some of these characters have been proven highly variable within a species (e.g. rostrum shape and indentation or coloration) and so taxonomically non-informative, making it difficult to establish boundaries between them (von Rintelen and Cai 2009; de Mazancourt *et al.* 2017). Thus, there is a need for an integrative and standardized approach to improve the group's systematics, focusing on informative morphological features and using molecular characters (Page *et al.* 2005; Page and Hughes 2011; de Mazancourt *et al.* 2017). To illustrate this problem, we focus here on *Atyoida pilipes*, which is a common species in the higher course of the Polynesian rivers.

Polynesia forms a triangle delimited by Hawaii, New Zealand and Easter Island. We can distinguish Northern Polynesia (Hawaii), Western Polynesia (Tuvalu, Tokelau, Wallis and Futuna, Tonga, Niue, Samoa, Cook Islands) and Eastern Polynesia (French Polynesia, Pitcairn Island and Easter Island). Chace (1983) clarified the status of *A. pilipes*, briefly described from Samoa by Newport (1847). *A. pilipes* was reported many times under various names in Eastern Polynesia: (i) in Tahiti as *Atyoida tahitensis* by Stimpson (1860), *Atya brevirostris* by Seurat (1934), *Atya serrata* by Edmondson (1935) and *Vanderbilta rosamondae* by Boone (1935); (ii) in Marquesas islands as *Atya serrata* for specimens collected in 1922 by Père Delmas and by the Pacific Entomological Survey, 1929-30, by Edmondson (1935), *Atya serrata* and *Ortmannia alluaudi* by Adamson (1935); (iii) in Rapa island and Mangareva island as *Atya serrata* collected by the Mangarevan Expedition of Bernice Bishop Museum in 1934 (Edmondson 1935). This species (*sensu* Chace 1983), until now has also been reliably reported from the Philippines and eastern Lesser Sunda Islands at about 12° East longitude eastward through the Pacific high islands, as far north as Kume-Jima in the Ryukyus at about 26° North (Cai and Shokita 2006), as far south as Rapa in Austral archipelago (French Polynesia) at about 27°35' South, and as far east as Mangareva in Gambier islands at about 135° West. It seems to be absent from the Asian mainland.

Streams of Austral, Gambier, Society and Marquesas Islands (French Polynesia) were surveyed by the Muséum national d'Histoire naturelle (MNHN, Paris) from 1983 to 2001 (see: Marquet 1988; Marquet 1991; Fossati and Marquet 1998; Keith and Vigneux 2002; Keith *et al.* 2002) and more recently in September and October 2017. Rivers of Futuna (Territory of Wallis and Futuna Islands) were sampled in October 2004 (see Keith and Marquet 2011), rivers of Rarotonga (Cook Islands) in July 2010 (see Keith *et al.* 2013) and rivers of Upolu (Samoa) in July 2008 (see: Keith *et al.* 2013) and in August 2014. One of the aims of the MNHN is to carry out faunistic inventories of rivers in tropical islands in order to establish a better protection of

these fragile ecosystems and, in this context, to clarify the taxonomy of poorly known organisms. As more and more specimens were collected from different islands in Polynesia, we started to have doubts about the taxonomy of *A. pilipes* in this area. The purpose of this study was to analyse the specimens of *Atyoida* in Polynesia by using an integrative taxonomic approach and to assess the validity of the species and its geographical distribution.

MATERIAL AND METHODS

Collection of specimens

Specimens from Polynesia were collected by electrofishing (portable Dekka 3,000 electric device, Germany or SAMUS 1,000, Poland: <http://www.electro-fisher.net/>). All material preserved in 75%-95% alcohol has been deposited in the collections of the Muséum national d'Histoire naturelle in Paris (MNHN).

Abbreviations for morphological analyses

The following abbreviations are used in the present text: cl, carapace length (mm): measured from the post-orbital margin to the posterior margin of the carapace. P1: first pereopod. P2: second pereopod. P3: third pereopod. P5: fifth pereopod. P11: first male pleopod. P12: second male pleopod.

Morphological comparison

A total of 55 recent specimens identified as *A. pilipes* from various Polynesian islands, 2 from Fiji and 4 from Vanuatu were morphologically studied. The rostrum, the general cephalon, the pereopods 1, 2, 3 and 5 and the abdomen were observed using a stereoscopic microscope. The proportions of the various joints of the appendages were measured using microphotographs and AnalySIS Works software (Olympus). Drawings were made using the 'Digital Inking' method (Coleman 2003, 2006) by tracing vectorial paths on stacks of high-resolution photographs using Adobe Illustrator.

DNA extraction, amplification and sequencing

Molecular analyses were realised on mitochondrial DNA, on the 16S ribosomal RNA fragment, to differentiate more finely each specimen by species and location by genomic difference. A total of 50 specimens of *Atyoida* were genetically studied.

Total DNA was extracted from abdominal muscle samples using the NucleoSpin 96 Tissue Core (Macherey-Nagel) protocol. For each sample, PCR reactions contained: 15.44µl of H₂O, 2 µl of Taq buffer (15mM + MgCl₂), 1µl of DMSO (1ng/ml), 1µl of BSA, 0,8µl of dNTP (6.6mM), 0.32µl of Forward primer (16Sar-Lmod : TACTTCTGCCTGTTTATCAAAAA) and 0.32µl of Reverse primer (16Sbmod : GGTCTGAACTCAAATCATGTAAA), both at 10pM, 0.12µl of Taq polymerase (Qiagen), and 3µl of purified DNA from extraction. PCR program was: 4min at 94°C, then 35 cycles in 3 step with 30sec at 94°C, 40sec at 42°C and 1min at 72°C. The program finished with 7min at 72°C. DNA samples were sent to ©Eurofins for sequencing using Sanger method in both directions to minimize mistakes. All sequences are deposited in GenBank (Numbers **XXXXXXXXXX to XXXXXXXXXXXX**, see Table 1).

Molecular analysis

Analyses were performed using Geneious 7.1.8. A multiple alignment was realised between all sequences with MUSCLE algorithm (Edgar, 2004). Using Bayesian information criterion in jModelTest (Darriba *et al.* 2012; Guindon and Gascuel 2003) we retained the GTR + G + I model. From this alignment, a phylogenetic tree is produced by MrBayes 3.2.6, available on CIPRES Science Gateway V3.3 server (Miller *et al.* 2010; <https://www.phylo.org>), running for 10,000,000 generations, a sampling frequency of 1,000 and a burn in of 10%. Support for nodes was determined using posterior probabilities calculated by MrBayes. With MEGA X (Kumar *et al.* 2018), another phylogenetic tree was made by maximum likelihood using the same substitution model. Robustness of the nodes was assessed using non-parametric bootstrapping (Felsenstein, 1985) with 1,000 bootstrap replicates.

Species delimitation analyses were realised with ABGD v. 07/12/18 method (Puillandre *et al.* 2011) to estimate intra and interspecific divergence in our data using JC69 distances. Priors were left as default (Pmin: 0.001; Pmax 0.1; 10 steps; relative gap width: 1.5; 20 bins).

Results

Phylogenetic analysis

A total of 68 sequences of 16S were used in the analysis, including 50 sequences of *Atyoida* newly produced and 7 retrieved from GenBank. As outgroup, 8 sequences of *Atyopsis* and 2 of *Australatya* were retrieved from GenBank and a sequence of *Macrobrachium australe* was newly produced. (Table 1).

Phylogenetic trees obtained by Maximum Likelihood and Bayesian method being congruent, only the Bayesian tree is shown here with support values of the two methods, above the branch

for Bayesian posterior probabilities and below the branch for bootstrap numbers (Fig. 1). These values confirm the robustness of the tree.

(Table 1 here)

(Figure 1 here)

The ABGD method found 8 different species in our sample. We observe 2 clades in the tree, structured according to geography. Clade 2 is present in Cook Islands, in Austral and in Society archipelagos. Specimens in Clade 1 are present in Vanuatu, Fiji, Samoa and Marquesas.

It is commonly accepted that from 3% of genetic distance in 16S, we have distinct species (Page *et al.* 2007a; Lefébure *et al.* 2006). Here, we have a genetic distance higher than 7%, we can then consider that these species are different (Fig. 2). Terminal taxa shown in the tree are named according to the species delimitation results.

(Figure 2 here)

Morphological analyses

Measurements (Table 2) and observations made on the specimens allowed us to confirm the molecular results in recognising 2 species: *A. pilipes* (Newport 1847) and *A. tahitensis* Stimpson, 1860. The re-description of these species present in Polynesia, as well as an identification key follow.

(Table 2 here)

Taxonomy

Family Atyidae De Haan, 1849

Genus *Atyoida* Randall, 1840

Body pigmented, eyes well developed; short rostrum, dorsal carina typically unarmed, 0-4 ventral teeth; anterior margin of carapace armed with antennal spine, pterygostomian margin sharply or bluntly acute; supraorbital spines absent; telson with setigerous posterior margin overreaching posterolateral angles; 3rd maxilliped with uncinat terminal spine; pereopods without exopods; 1st and 2nd pereopods with chelae heteromorphic (with or without palm),

fingers tipped with brushes of setae, carpus of both appendages excavate distally, 3rd pereopod without meral spur in large males; 1st pleopod of male with endopod tapering sinuously but rather regularly to slender apex; 2nd pleopod of male with appendix masculina subcylindrical, spinose over more than distal half.

Atyoida pilipes (Newport 1847)

(Figure 3)

Atya pilipes Newport, 1847: 160 [type locality: "Apia, Upolu, New Zealand" (corrected to "Apia, Upolu, Navigator or Samoan group" by Dana, 1852: 533)].

Atyoida pilipes - Chace, 1983: fig. 3 page 13.

Atyoida pilipes - Keith *et al.* 2002: 38-39 (partim).

Atyoida pilipes - Keith and Marquet, 2011: 34-35.

Atyoida pilipes - Mary *et al.* 2006: 33.

Atyoida pilipes - Keith *et al.* 2010: 32-33 (partim).

Atyoida pilipes - Keith *et al.* 2013: 72-73 (partim).

Not *Atya serrata* - not *Ortmania alluaudi*. Adamson, 1939: 36.

Not *Atya serrata* - Edmondson, 1935: 14, fig.i.

(Figure 3 here)

Material examined

Polynesian material:

SAMOA. UPOLU: Tuafaleloa river, 1♂, cl 5mm (MNHN-IU-2018-3023; DNA: CA1950), 1♂, cl 4.8mm (MNHN-IU-2019-242; DNA: CA1949), 1♀ovig., 7.9mm (MNHN-IU-2019-497; DNA: CA2363) and 1♀ovig., cl 8.8mm (MNHN-IU-2019-155), 13°53.774'S, 171°40.026'W, July 08, 2014, 250m a.s.l., coll. P. Gerbeaux. – Falefa river, 1juv., cl 3.2mm, (MNHN-IU-2019-162; DNA: CA2362), 1♂, cl 4.6mm (MNHN-IU-2018-3213; DNA: CA2367), 1♂, cl 5.2mm (MNHN-IU-2018-2979; DNA: CA2364), 1♂, cl 5.2mm (MNHN-IU-2018-2976; DNA: CA2366), 1♀ovig., cl 8.8mm (MNHN-IU-2019-499; DNA: CA2361), 13°54.728'S, 171°36.137'W, July 10, 2014. 53m a.s.l., coll. P. Gerbeaux. SAVAI: Faleata river, 1juv., cl 4.6mm (MNHN-IU-2018-2952; DNA: CA2370), 1♂, cl 5.5mm (MNHN-IU-2018-2948; DNA: CA2369), 1♀ovig., cl 7.8mm (MNHN-IU-2019-239; DNA: CA2368), and 1♀ovig., cl 7.9mm (MNHN-IU-2019-495; DNA: CA2365), 13°43.761'S, 172°19.548'W, July 12, 2014, 195m

a.s.l., coll. P. Gerbeaux. – Seugagogo river, 1♂, cl 4.9mm (MNHN-IU-2019-489; DNA: CA2371), 13°40.313'S, 172°19.548'W, August 09, 2013, 773m a.s.l., coll.? WALLIS AND FUTUNA TERRITORY. FUTUNA: Vainifao river, 1juv., cl 4.3mm (MNHN-Na-15750; DNA: CA2135), 1juv., cl 4.7mm (MNHN-Na-15750; DNA: CA2136), and 1♂, cl 4.5mm (MNHN-IU-2018-2983; DNA: CA2377), 14°17.738'S, 178°08.423'W, October 12, 2004, 150m a.s.l., coll. P. Keith, G. Marquet, N. Mary. FRENCH POLYNESIA. HIVA OUA: Taooa river, 1♂, cl 4.6mm (MNHN-IU-2018-2988; DNA: CA2069), and 1♀ ovig., cl 5.5mm (MNHN-IU-2018-2989; DNA: CA2068), 09°49.750'S, 139°04.419'W, October 09, 2017, 220m a.s.l., coll. E. Feunteun, P. Keith, G. Marquet. NUKU HIVA: Taipivai river, 1♂, cl 4.9mm (MNHN-IU-2018-2975; DNA: CA2385), 1♂, cl 5mm (MNHN-IU-2018-3003; DNA: CA2386), 1♂, cl 5.6mm (MNHN-IU-2018-2987; DNA: CA2374), and 1♀, cl 8.3mm (MNHN-IU-2018-2984; DNA: CA2375), 08°51.126'S, 140°06.066'S, 140°06.066'W, October 18, 2017, 130m a.s.l., coll. E. Feunteun, P. Keith, G. Marquet. UAOU: Unnamed rivulet, 1 juv., cl 4.0mm (MNHN-IU-2018-2982; DNA: CACA2388), 1 juv., cl 4.9mm (MNHN-IU-2018-2993; DNA: CA2389), 1 juv., cl 4.7mm (MNHN-IU-2019-156; DNA: CA2391), 1 juv., cl 4.9mm (MNHN-IU-2018-2949; DNA: CA2395), 1 juv., cl 4.8mm (MNHN-IU-2019-159; DNA: CA2072), 1♂, cl 4.2mm (MNHN-IU-2018-2953; DNA: CA2393), 1♂, cl 5.1mm (MNHN-IU-2018-3017; DNA: CA2392), 1♂, cl 5.5mm (MNHN-IU-2019-477; DNA: CA2390), 1♂, cl 4.9 mm (MNHN-IU-2019-166), 1♀, cl 5.7mm (MNHN-IU-2018-2985; DNA: CA2394), 1♀, cl 6.2 mm (MNHN-IU-2018-3274; DNA: CA2396), 1♀, cl 6.8mm (MNHN-IU-2018-3275; DNA: CA2397), 1♀, cl 9.1mm (MNHN-IU-2018-3276; DNA: CA2398), 09°25.452'S, 140°03.409'W, October 14, 2017, 149m a.s.l., Coll. E. Feunteun, P. Keith, G. Marquet.

Other material:

FIJI. TAVEUNI: Lavena river, 1♂, cl 5.2mm (MNHN-IU-2018-3277; DNA: CA1962), and 1♀, cl 5.2mm (MNHN-IU-2018-3278; DNA: CA1961), 16°52.164'S, 179°54.333'W, February 25, 2013, altitude 91m a.s.l., coll. P. Gerbeaux, P. Keith, G. Marquet. VANUATU. TANNA: Lembau river, 1♂, cl 5.6mm (MNHN-IU-2018-3279; DNA: CA1952), and 1♀, cl 6.3mm (MNHN-IU-2018-3280; DNA: CA1951), 19°23.005'S, 169°18.852'E, June 29, 2015, 260m a.s.l., coll. D. Kalfatak, C. Lord, G. Segura. ANEITYUM: Inugé river, 1♂, cl 4.8mm (MNHN-IU-2018-3281; DNA: CA1956), 1♂, cl 4.8mm (MNHN-IU-2018-3282; DNA: CA1955), 20°12.458'S, 169°46.993'E, June 25, 2015, 219m a.s.l., coll. D. Kalfatak, C. Lord, G. Segura.

Comparative material:

Atyoida bisulcata Randall, 1840

HAWAII: 1 ♀ ovig., cl 9mm (MNHN-Na-987), "HMS Challenger", loaned from British Museum, 1919. – MAUI. "freshwater stream in canyon 5 miles east of Lahaina, April 12, 1902 1 ♀, cl 12mm (MNHN-Na-10672), April 12, 1902, coll. M.J. Rathbun, loaned from US. Nat. Museum, 1912.

Atyoida serrata (Bate 1888)

REUNION ISLAND: MNHN-Na 967. 2 juv., cl 2.9 and 3.7 mm, first experience of Bordage, small pond in the garden of the Saint Denis Museum (see Bordage, 1908).

MNHN-Na 970, 1 ♂, cl 4.3mm, second experience of Bordage (see Bordage, 1908).

MNHN-Na 971, 1 juv., cl 3.0 mm, first experience of Bordage (see Bordage, 1908).

Description

Cephalothorax. Rostrum short (Fig. 3n), 0.2-0.4 of cl, reaching near to or slightly beyond end of basal segment of antennular peduncle, with dorsal margin convex, apex slightly ventrally, ventral margin unarmed; Antennal spine fused with inferior orbit angle, acute; pterygostomian margin acute.

Eyes well developed. Antennular peduncle stout, 0.43 (♀) - 0.63 (♂) times as long as carapace; basal segment shorter than half length of antennular peduncle, second segment longer than third segment. Stylocerite reaching 0.86-0.93 length of the basal segment of antennular peduncle.

Pereiopods. Epipods on first 4 pereiopods. P1 and P2 similar in size and shape. Chelae dimorphic, caridinoid in shape in males and atyoid in females. ♂P1 (Fig. 3b) chela about 1.7-4.7 times as long as wide, movable finger 3.5-6.1 times as long as wide 1.8-12.0 times length of palm; ♀P1 (Fig. 3a) chela 1.9-4.2 times as long as wide, dactylus 3.5-5.3 times as long as wide, with tufts of long setae distally, carpus excavated strongly anteriorly, 0.9-1.4 times as long as wide. ♂P2 chela 2.1-4.0 times as long as wide: movable finger 3.6-5.3 times as long as wide, 1.6-11.5 times length of palm; ♀P2 (Fig. 3c) chela 2.1-4.3 times as long as wide, dactylus 3.6-5.2 times as long as wide, with tufts of long setae distally, P2 carpus excavated strongly anteriorly, 1.0-1.6 times as long as wide. P3 (Fig. 3d) with row of setae on outer surface of each joint, very short dactylus (Fig. 3f) ending in a strong claw, 1.7-3.7 times as long as wide (terminal spine included) with 3-5 spines on flexor margin in addition to the terminal spine; propodus 3.9-7.5 times as long as wide, 2.2-3.7 times as long as dactylus. P5 (Fig. 3e) with setae only present on merus; dactylus (Fig. 3g) short 2.1-5.1 as long as wide with 4-14 spines on flexor margin; propodus 6.0-10.4 times as long as wide, 2.9-4.8 times as long as dactylus.

Abdomen. Sixth abdominal somite 0.37 times of carapace, 1.1 time as long as fifth somite, 0.84 as long as telson.

Telson (Fig. 3j) 2.3-3.1 times as long as wide, with one to five pairs of dorsal spinules, often not in pairs, one pair of dorsolateral spinules near dorsal end; posterior margin rounded with 4 to 9 plumose intermediate setae distinctly longer than lateral ones.

P11 (Fig. 3k): Endopod of male subtriangular, 2.7 times as long as wide, reaching 0.57 times of endopod, with a distinct appendix interna near distal end of endopod.

P12 (Fig. 3l): Appendix masculina of male reaching 0.57 times length of endopod, inner and distal surface densely lined with long spines; appendix interna at basal 0.36 times length of appendix masculina, extending to distal 0.34 length of appendix interna.

Preanal carina triangular (Fig. 3h) without spine.

Uropodal diaeresis (Fig. 3i) with 15-22 spinules.

Eggs (Fig. 3m): developed (visible eyes): 0.35-0.42 × 0.56-0.68mm; undeveloped: 0.32-0.36 × 0.49-0.58mm.

Habitat

In Nuku-Hiva (Marquesas islands), large males and females of *A. pilipes* are present, although in small numbers, at all altitudes; females, small males and ovigerous females are more abundant below 100m. *A. pilipes*, particularly females, occur mainly in water with high velocities and on coarse substrata (less sands, gravels and pebbles, more rocks). On contrary, males were indifferent with water velocity and their abundance did not depend on rocks. Large males appeared more frequent where the riverbeds have less vegetation, while small males were more frequent in shallow habitats (see Fossati & Keith, 2002). This habitat difference between males and females is to put in relation with their chelae. Indeed, females with their atyoid chelae are adapted for filter-feeding and males with their caridinoid chelae, to sweeping. Thereby females are localised in the currents and on the rocks and males in vegetation.

Colour pattern

The back (Fig. 5) is orange-yellow as well as the antennular peduncle, telson and uropods. The flanks are whitish ornamented with numerous blue-black patterns of various shapes.

Distribution

This species (Fig. 7) occurs in Vanuatu (Tanna, Aneityum), Fiji, Samoa, Futuna and Marquesas archipelago.

Remarks

As the type locality of *A. pilipes*, described by Newport, is Apia, Upolu Island, capital city of Samoa, we affirm that all specimens genetically and morphologically similar to those of Upolu belong to this species. The description of one specimen of *A. pilipes* by Newport is very succinct and therefore not informative: "Body smooth, rostrum simple, triangular, very short with a slight median ridge, fourth and five pairs of legs nearly equal, femoral joint with an oblique sulcus on the external surface, fringed with a margin of dense fine hairs".

Atyoida tahitensis (Stimpson 1860)

(Figure 4)

Atyoida tahitensis Stimpson, 1860: 28 [type locality: Tahiti, French Polynesia].

Not *Atya serrata* – Edmondson, 1935: 14, fig. i.

Not *Atyoida pilipes* - Keith *et al.* 2013: 72-73 (partim).

Not *Atyoida pilipes* - Keith *et al.* 2002: 38-39.

(Figure 4)

Material examined:

Neotype (here designated): FRENCH POLYNESIA. TAHITI. Mahina, 1♂ cl 5.6mm (MNHN-IU-2018-3290; DNA: CA2376), 17°32.241'S, 149°29.269'W, April, 1995, 114m a.s.l., coll. J. Poupin, E. Tavooso.

FRENCH POLYNESIA. TAHITI. Papehere river, 1♂ immature, cl 3.1mm (MNHN-IU-2018-3283), 1♀ovig., cl 5,8mm (MNHN-IU-2018-3284; DNA: CA2060), 1♀ovig., cl 7.7mm (MNHN-IU-2018-3285; DNA: CA2381), 1♀ovig., cl 6.8 mm (MNHN-IU-2018-3286; DNA: CA2382), 1♀, cl 7,8mm (MNHN-IU-2018-3287; DNA: CA2384), 1♀, cl 7,1mm (MNHN-IU-2018-3288), and 1♀, cl 6.8mm (MNHN-IU-2018-3289; DNA: CA2387), 17°49.719'S, 149°17.067'W, October 02, 2017, 16m a.s.l., coll. G. Marquet, P. Tiberghien.- Mahina river, 1♀ ovig., cl 6.4mm (MNHN-IU-2018-3291; DNA: CA2378), and 1♀, cl 6.4mm, 17°32.241'S, 149°29.269'W, April, 1995, 114m a.s.l., coll. J. Poupin, E. Tavooso. MOOREA. Afeareatu river, 1juv., cl 4.5mm (MNHN-IU-2018-3292; DNA: CA2380), 1♂, cl 4.4mm (MNHN-IU-2018-3293; DNA: CA2065) and 1♂, 4.6mm (MNHN-IU-2018-3294; DNA: CA2064), 17°32.629'S, 149°48.555'W, November 05, 2017, 139m a.s.l., coll. G. Marquet, P. Tiberghien . RURUTU. Puputa river, 1♀, cl 5.7mm (MNHN-IU-2018-3295; DNA: CA2057) and 1♀, 6,7mm (MNHN-IU-2018-3296), 22°27.009'S, 151°21.061'W, September 26, 2017, 99m a.s.l., coll. G. Marquet,

P. Tiberghien. COOK ISLANDS. RAROTONGA. Avana river, 1♂, cl 5.4mm (MNHN-IU-2018-3297; DNA: CA2372), 1♀, cl 6.7mm (MNHN-IU-2018-3298; DNA: CA1978) and 1♀, cl 7.4 (MNHN-IU-2018-3299; DNA: CA1977), 21°14.462'S, 159°43.546'W, November 07, 2010, 12m a.s.l., coll. P. Gerbeaux, P. Keith; G. Marquet. MANGAREVA. Gatawake river, August 1986, 1♀ ovig., cl 6.1mm, 1♀, cl 6.0mm and 1♂, cl 3.6mm (USNM 231705).

Description

Cephalothorax. Rostrum short (Fig. 4n), 0.2-0.3 of cl, reaching near to end of basal segment of antennular peduncle, with dorsal margin convex, apex slightly ventrally, ventral margin unarmed; Antennal spine fused with inferior orbit angle, acute; pterygostomian margin acute. Eyes well developed. Antennular peduncle stout, 0.40 (♀) - 0.70 (♂) times as long as carapace; basal segment shorter than half length of antennular peduncle, second segment longer than third segment. Stylocerite reaching 0.81-0.94 length of the basal segment of antennular peduncle.

Pereiopods. Epipods on first 4 pereiopods. P1 and P2 similar in size and shape. Chelae dimorphic, caridinoid in shape in males and atyoid in females. ♂P1 (Fig. 4b) chela about 1.8-3.7 times as long as wide, movable finger 3.2-5.0 times as long as wide 1.1-7.4 times length of palm; ♀P1 (Fig. 4a) chela 2.0-3.9 times as long as wide, dactylus 3.9-6.0 times as long as wide, with tufts of long setae distally, carpus excavated strongly anteriorly, 0.8-1.2 times as long as wide. ♂P2 chela 1.8-4.0 times as long as wide: movable finger 3.9-5.3 times as long as wide, 1.4-7.4 times length of palm; ♀P2 (Fig. 4c) chela 1.9-3.9 times as long as wide, dactylus 3.9-5.3 times as long as wide, with tufts of long setae distally, P2 carpus excavated strongly anteriorly, 1.0-1.9 times as long as wide. P3 (Fig. 4d) with row of setae on outer surface of each joint, very short dactylus (Fig. 4f) ending in a strong claw, 2.2-3.7 times as long as wide (terminal spine included) with 3-6 spines on flexor margin in addition to the terminal spine; propodus 3.9-7.1 times as long as wide, 1.8-3.5 times as long as dactylus. P5 (Fig. 4e) with setae only present on merus; dactylus (Fig. 4g) short 1.7-4.4 as long as wide with 5-13 spines on flexor margin; propodus 6.0-10.4 times as long as wide, 2.7-8.8 times as long as dactylus.

Abdomen. Sixth abdominal somite 0.56 times of carapace, 1.4 time as long as fifth somite, 0.80 as long as telson.

Telson (Fig. 4j) 2.5-3.2 times as long as wide, with 2 to 3 pairs of dorsal spinules, often in pairs, one pair of dorsolateral spinules near dorsal end; posterior margin rounded with 6 à 13 plumose intermediate setae distinctly longer than lateral ones.

P11 (Fig. 4k): Endopod of male subtriangular, 2.6 times as long as wide, reaching 0.75 times of endopod, with a distinct appendix interna near distal end of endopod.

P12 (Fig. 4l): Appendix masculina of male reaching 0.78 times length of endopod, inner and distal surface densely lined with long spines; appendix interna at basal 0.36 times length of appendix masculina, extending to distal 0.36 length of appendix interna.

Triangular preanal carina (Fig. 4h) without spine.

Uropodal diaeresis (Fig. 4i) with 11-18 spinules.

Eggs (Fig. 4l): developed (visible eyes): 0.32-0.54 × 0.57-0.72mm; undeveloped: 0.33-0.39 × 0.55-0.57mm.

Habitat

The habitat of *A. tahitensis* (named *A. pilipes* in the papers cited below) has been particularly studied in Oponuhu Valley watershed (Moorea island) by Resh *et al.* (1990), Feldman (1996), Falvo (2013) and Goldstein (2016). *A. tahitensis* covers a broad elevation range from 2 to 335m (Resh *et al.* 1992). In this study, it represented only 5% of the shrimps found at three low elevation sites, 11% at three middle elevation sites and 30% at three high elevation sites. This distribution range is positively correlated with elevation and distance from stream mouth (Goldstein 2016). According to Falvo (2013), it is more strongly built and its appendages may also be better suited for gripping substrate and for withstanding strong current, explaining its ability to reach higher altitudes. Of the *A. tahitensis* caught, 143 were caught in leaf packs, 79 in riffles, 47 in banks without vegetation, 35 in pools, 26 in runs, and 6 in banks with vegetation.

Colour pattern

The body is blackish on its back, ornamented on its flanks with numerous bluish dots and longitudinal stripes (Fig. 6).

Distribution

See remarks below. This species (Fig. 7) is restricted to Cook Islands (Rarotonga) and in French Polynesia to Austral, Gambier and Society archipelagoes. Rapa in Austral archipelago and Mangareva in Gambier archipelago correspond respectively to the most southerly (27°35'S) and easterly extension (135°W) of the genus *Atyoida*, with *A. tahitensis* being present.

Remarks.

Atyoida tahitensis looks like *A. pilipes* by its short, unarmed, and bent rostrum, by the proportions between the joints of pereopods and the egg size. Due to their high morphological variability, finding diagnostic characters to separate *A. tahitensis* from *A. pilipes* turned out to

be a difficult task (see Table 2), so much that they could be considered to be cryptic species, as they can only be distinguished by the telson: 2 to 3 pairs of dorsal spinules, often in pairs for *A. tahitensis* (vs 1 to 5 pairs of dorsal spinules, often not in pairs for *A. pilipes*); posterior margin rounded with 6 to 13 plumose intermediate setae distinctly longer than lateral ones (vs posterior margin rounded with 4 to 9 plumose intermediate setae distinctly longer than lateral ones) and by their uropodal diaeresis with 11-18 spinules (vs 15-22 spinules). Nevertheless, following the integrative taxonomy framework, their genetic distinctiveness coupled with their discrete geographical distribution provides enough evidence to distinguish the two species as distinct taxa, as it was the case for other species of freshwater shrimps (e.g. Christodoulou *et al.* 2012; de Mazancourt *et al.* 2019; Choy *et al.* 2019a, b). One of us (GM) captured numerous specimens of “*Atyoida pilipes*” from Mangareva in 1986, which were deposited in the USNM (USNM 231705). Some specimens were re-examined. All have a telson with more than nine plumose intermediate setae on its posterior margin and less than 18 spinules on its uropodial margin. We can conclude that *A. tahitensis* occurs in Mangareva but not *A. pilipes*. In Rapa and Mangareva islands “*Atya serrata*” were collected by the Mangarevan Expedition of Bernice Bishop Museum in 1934 (Edmondson 1935). We can affirm that it is *A. tahitensis* that is found at Rapa Island instead of *A. serrata*, which occurs in Indian Ocean (Chace 1983).

As the type locality of *A. tahitensis* described by Stimpson, is "In aquis dulcibus insulae Tahiti", we affirm that all specimens genetically and morphologically similar to those of Tahiti belong to this species. The description of one specimen of *A. tahitensis* by Stimpson is very succinct and therefore not informative: "A. bisulcatae valde similis (an diversa?) sed rostro paullo brevior, latiore et magis depresso; flagelle externa antennularum quam internum dimidia brevior; et angulo postero-inferiore segmenti abdominis quinti minus acuto". Chace (1983) considered *A. tahitensis* to be a junior synonym of *A. pilipes*. In this paper we demonstrate that *A. pilipes* and *A. tahitensis* are distinct species. Since the original type specimens were destroyed in the Great Chicago Fire of 1871, to prevent taxonomic confusion, we here designate an adult male specimen (cl 5.6mm) from Mahina river, Tahiti, as the neotype of *Atyoida tahitensis* (Stimpson 1860). It is deposited in the MNHN (collection number: MNHN-IU-2018-3290).

Key for Pacific *Atyoida* species

1.1 P1 and P2 polymorphic atyoid, caridinoid and ortmannoid (indifferently male or female);
Posterior margin of telson armed with 2-7 distinct fixed teeth.....***A. bisulcata*** (Hawaii)

- 1.2 P1 and P2 dimorphic atyoid (female) and caridinoid (male); Posterior margin of telson armed with indistinct fixed teeth.....2
- 2.1 From Vanuatu to Marquesas archipelago; living specimens with blue-black patterns of different shapes; telson with 1 to 5 pairs of dorsal spinules, often not in pairs); its posterior margin with 4 to 9 plumose intermediate setae distinctly longer than lateral ones; Uropodal diaeresis with 15-22 spinules.....*A. pilipes*
- 2.2 From Rarotonga, French Polynesia except Marquesas archipelago; living specimens with dark longitudinal stripes; telson with 2 to 3 pairs of dorsal spinules, often in pairs; its posterior margin 6 to 13 plumose intermediate setae distinctly longer than lateral ones; Uropodal diaeresis with 11-18 spinules.....*A. tahitensis*

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Legends for figures and tables:

Table 1: List of the sequences included in the phylogenetic analysis.

Table 2: Morphological values for *A. pilipes* and *A. tahitensis*. P5s, P3s, diaeresis, telson dorsal spines, telson setae and LT are counts and the others are in mm. Abbreviations: d = dactylus, ch = chela, ca = carpus, dp = palm, p = propodus, s = spine, CR = ratio between rostrum and carapce length, and LT = number of lap tooth, which are absent in these species.

Figure 1: Phylogenetic tree of the genus *Atyoida* from Pacific localities using Bayesian Inference. Values above branches indicate posterior probabilities, those below are bootstrap values. Scale represents the genetic distance

Figure 2: Histogram of pair-wise genetic distances by Jukes-Cantor model (shows the probability of all the nucleotide changes are equal) using ABGD method.

Figure 3: *Atyoida pilipes*. a. female first pereopod; b. chela of male first pereopod; c. female second pereopod; d. third pereopod; e. fifth pereopod; f. dactylus of third pereopod; g. dactylus of fifth pereopod; h. pre-anal carina; i. uropodal diaeresis; j. telson; k. male first pleopod; l. male second pleopod; m. undeveloped eggs; n. cephalothorax.

Figure 4: *Atyoida tahitensis*. a. female first pereopod; b. chela of male first pereopod; c. female second pereopod; d. third pereopod; e. fifth pereopod; f. dactylus of third pereopod; g. dactylus of fifth pereopod; h. pre-anal carina; i. uropodal diaeresis; j. telson; k. male first pleopod; l. male second pleopod; m. undeveloped eggs; n. cephalothorax.

Figure 5: A, B: Live coloration of *Atyoida pilipes* from Marquesas islands; C: Individuals of *A. pilipes* climbing a waterfall during a mass migration episode in Futuna Island (13/10/2004); D: Typical habitat of *A. pilipes* in Futuna, Vainifao river (Photos by E. Vigneux (A), G. Marquet (B) and A. Dutartre (C, D)).

Figure 6: A, B, C: Live coloration of *Atyoida tahitensis* from Society Islands; D: Typical habitat of *A. tahitensis* in Tahiti (Photos by E. Vigneux (A, B), G. Marquet (C)).

Figure 7: Distribution map of the three species of *Atyoida* present in Polynesia. Dots represent islands. Areas not coloured were either not prospected or lack freshwater streams (atolls).