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1 **Revision of freshwater shrimps belonging to *Caridina weberi* complex**
2 **(Crustacea: Decapoda: Atyidae) from Polynesia with discussion on their**
3 **biogeography.**

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**Revision of freshwater shrimps belonging to *Caridina weberi* complex
(Crustacea: Decapoda: Atyidae) from Polynesia with discussion on their
biogeography.**

Caridina weberi, an emblematic species of the ‘*C. weberi* complex’, was described by De Man in 1892 from different localities in Indonesia. Until now, this species was thought to have a wide distribution in Polynesia. Numerous specimens identified as *C. weberi* were collected recently from various Polynesian islands. In the context of an integrative taxonomy, they were morphologically and genetically studied. Three new species allied to *C. weberi* are here described: *C. marquesensis* n. sp., *C. futunensis* n. sp. and *C. tupaia* n. sp.. The occurrence of *C. rapaensis*, another species part of the ‘*C. weberi*’ complex is confirmed. Descriptions or redescription of these species are given as well as their geographical and ecological distributions. The position of these species in the complex is clarified. A key is provided to facilitate identification.

Keywords: 16S, genetic, morphology, integrative taxonomy, freshwater shrimp.

Introduction

The freshwater shrimp genus *Caridina*, comprising 298 species (WoRMS database, as of May 2018) and mostly present in the Indo-Pacific region, is the most diversified genus of the Atyidae (De Grave et al. 2015) and an important ecological component in the tropical streams (Covich et al. 1999; Pringle et al. 1993). Its high diversity combined with the lack of informative morphological characters has led to a confused taxonomy (Richard and Clark 2009). Indeed, until recently, the taxonomy of the genus was mainly based on morphological characters. Some 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 (Rintelen and Cai 2009; 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).

To illustrate this problem, we focus here on species of the troublesome '*C. weberi* complex'. The taxonomic complexity within the genus *Caridina* has led previous authors to create groups of species based on morphological characters they share. For example, Bouvier (1925) defined 5 species group: *C. nilotica* group, *C. laevis* group, *C. africana* group, *C. brevis* group and *C. typus* group. Some of these groups have been split to create new ones as new species were described, such as *C. serrata* (Cai and Ng 1999; Karge and Klotz 2007), *C. gracilirostris* (Cai and Ng 2007) and *C. weberi* (Cai and Anker 2004; Cai et al. 2009) while others still exist to this day, like *C. nilotica* and *C. typus* groups (Karge and Klotz 2007).

Polynesia forms a triangle between Hawaii, New Zealand and Easter Island (Figure 1). We can distinguish Northern Polynesia (Hawaii), Western Polynesia (Tuvalu, Tokelau, Wallis and Futuna, Tonga, Niue, Samoa islands, Cook Islands) and Eastern Polynesia (French Polynesia, Pitcairn Island and Easter Island). The occurrence of *C. weberi* in Polynesia has been reported by Edmondson (1935), Adamson (1935, 1939), Marquet (1988, 1991), Fossati and Marquet (1998), Keith and Vigneux (2002), Keith et al. (2002), Keith and Marquet (2011), and Keith et al. (2013).

Streams of Austral, Society and Marquesas Islands (French Polynesia) were prospected by the Muséum national d'Histoire naturelle (MNHN, Paris) from 1983 to 2001 and recently in September and October 2017, rivers of Futuna (Territory of Wallis and Futuna islands) in October 2004, rivers of Rarotonga (Cook islands) in July 2010, rivers of Upolu (Samoa) in July 2008 and 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 we collected more and more specimens from different islands from Polynesia, we started to raise doubts regarding the validity of *C. weberi* in this area. Thereby, in combining morphological data with a 16S mtDNA analysis, we identified three new species and confirmed the presence of *C. rapaensis*. The aim of this study is to describe or re-describe them and to compare them to type specimens of species belonging to the *C. weberi* complex.

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). A total of 42 recent specimens (33 identified as *C. weberi* from various Polynesian islands and 9 identified as *C. rapaensis* from Rapa and Rurutu islands) were morphologically studied. As comparative material, syntypes of *C. weberi* (MNHN-IU-2015-1755) and *C. parvirostris* (MNHN-IU-2015-1748 and MNHN-IU-2015-1754) preserved in the MNHN collections and type specimens of *C. rapaensis* (Holotype BPBM 53933 and paratype BPBM 53694) preserved in the Bernice Pauahi Bishop Museum collections (BPBM, Hawaii, USA) were examined.

DNA extraction, amplification and sequencing

DNA was extracted from abdominal tissues from 29 specimens using the semi-automatic Eppendorf ep-Motion 5075 robot with the Nucleospin[®] Tissue kit (Macherey-Nagel, Düren, Germany), following the manufacturer's instructions. Extracted DNA was

stored at -20°C. Fragments of the mitochondrial 16S rRNA (~ 520 bp) were amplified using primers, adapted from Palumbi (1996) to our taxa: 16Sar-Lmod (5'-TACTTCTGCCTGTTTATCAAAAA-3') and 16Sbmod (5'-GGTCTGAACTCAAATCATGTAAA-3'). DNA amplification was performed in 20µl PCR reactions, containing approximately 3ng of template DNA, 2.5mM MgCl₂, 0.26mM of each nucleotide, 0.3µM of each primer, 5% DMSO, 1ng of BSA and 1.5 units of QBIOTAQ polymerase (MPBiomedicals). Amplification products were generated by an initial denaturation step of 4min at 94°C followed by 35 cycles of denaturation at 94°C for 30s, annealing at 52°C for 40s, extension at 72°C for 60s and a final extension step at 72°C for 7 min. PCR products were sequenced using the same primers and in both directions to ensure the accuracy of base calls. Chromatograms were edited using Geneious v.8 software (<http://www.geneious.com/> Kearse et al. 2012). All sequences were deposited in GenBank (Accession numbers XXXXXXXXXXXX to XXXXXXXXXXXX, Table 1).

Phylogenetic analyses

DNA sequences were aligned using MEGA7 software (Kumar et al. 2016) with Muscle algorithm (Edgar 2004). Best-fit molecular evolution model was selected using Bayesian information criterion in jModelTest (Darriba et al. 2012; Guindon and Gascuel 2003). Molecular p-distances among aligned sequences were calculated with MEGA7. Best-scoring ML trees were estimated using RAxML HPC2 v.8.2.10 (Stamatakis 2014) and best-scoring Bayesian Inference trees were estimated using MrBayes v.3.2.6 (Ronquist and Huelsenbeck 2003), both methods implemented in the Cyber Infrastructure for Phylogenetic Research (CIPRES) portal v.3.1. (Miller et al. 2010, <https://www.phylo.org/>) with the previously determined model, running two separate analyses for 5,000,000 generations, a sampling frequency of 1,000 and a burn in of 25%. Convergence was assessed by comparing

the two runs in Tracer v.1.6 (<http://tree.bio.ed.ac.uk/software/tracer/>). Support for nodes was determined using posterior probabilities (PP) calculated by MrBayes implemented CIPRES. For ML trees, one hundred independent searches, each starting from distinct random trees, were conducted to assess robustness of the nodes using non-parametric bootstrapping (Felsenstein 1985) with 1,000 bootstrap replicates (B). A total of 30 specimens were included in the analysis, 27 initially identified as *C. weberi* collected in various Polynesian islands and 3 identified as *C. rapaensis* from Rapa (Table 1), plus a sequence from *Macrobrachium australe* published by Page et al. (2007a) to root the tree (Accession number: DQ681290).

(Table 1 near here)

Automatic species delimitation methods

Three different methods were used. First, ABGD (Puillandre et al. 2012) implemented on the web server <http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html>, for which a pairwise distances matrix was built from the sequences alignment using JC69 Jukes-Cantor model. We used $P_{min} = 0.001$ and $P_{max} = 0.4$ with 20 steps and $X = 1.5$. A graphical representation of the distribution of the distances showed a barcoding gap between 0.03 and 0.1 divergence. Second, we ran a bPTP analysis (Zhang et al. 2013) from the web server <http://species.h-its.org/ptp/> using the ML tree as input specifying *M. australe* as outgroup. Other parameters were left as default. Finally, we used the GMYC method (Pons et al. 2006) implemented in the web server <https://species.h-its.org/gmyc/> using only the single threshold method (phylogeny composed of several species with one coalescent time value) as species studied are phylogenetically close to each other. To run this analysis, an ultrametric tree is required, which was constructed using BEAST v. 1.8.3 (Drummond and Rambaut 2007). We used a relaxed lognormal clock with a coalescent tree prior as these have been identified as

best prior parameters for GMYC analyses (Esselstyn et al. 2012; Monaghan et al. 2009). Monte Carlo Markov chains (MCMC) ran for 35,000,000 generations, sampling every 1000 generations. Chains convergence was assessed using Tracer v.1.6 (Rambaut et al. 2014). The consensus tree (maximum clade credibility tree; 10% burn in; tree not presented) was constructed with TreeAnnotator v.1.8.3 (Rambaut and Drummond 2016).

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. Pl1: first pleopod. Pl2: second pleopod.

Morphological comparison

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 (CS3) and a WACOM PTZ-1230 graphic tablet.

Results

Phylogenetic analyses

Following the analysis by jModelTest, we retained the GTR + G model as the best to fit our data. As the trees obtained from the two methods were congruent for the main clusters, we present here the one obtained from the Bayesian Inference analysis with the posterior

probabilities and the bootstrap numbers obtained from the Maximum Likelihood analysis (Figure 2, see Supplementary material for ML tree).

Automatic species delimitation methods

ABGD: The analysis proposed two partitions of the dataset, one with 5 clusters (plus the outgroup) (ABGD1 in Figure 2) for prior intraspecific divergences ($P < 0.0048$) and the other with 4 clusters (plus the outgroup) (ABGD2 in Figure 2) for P between 0.0066 and 0.0827.

bPTP: The analysis determined 4 clusters (plus the outgroup) (PTP in Figure 2) having each a Bayesian probability > 0.97 .

GMYC: The single threshold model was preferred over the null model (single species phylogeny with only coalescent processes; $P < 0.05$). This model identified 6 ML entities (95% confidence interval: 3–20): 5 ML clusters (95% confidence interval: 2–9) and 1 singleton (the outgroup) (GMYC in Figure 2).

Each of the clusters identified by the species delimitation methods corresponded to robust Bayesian clades.

Four well-supported groups could be identified. The most basal one (A in Figure 2; $PP = 0.9$; $B = 48$; 0.6% p-distances intra-group maximum divergence) containing all the specimens from Futuna is separated (9.3% p-distance from the closest sequence) from the group containing all the others ($PP = 0.97$; $B = 48$). The second one (B in Figure 2; $PP = 1$; $B = 100$; 0.6% p-distances intra-group maximum divergence) clusters the three specimens of *C. rapaensis* from Rapa Island and is sister group (11.1% p-distance from the closest sequence) to a clade containing the two last ones ($PP = 1$; $B = 79$), one containing the specimens from Marquesas (Hiva Oa, Ua Pou and Nuku Hiva) (C in Figure 2; $PP = 1$; $B = 99$; 0.4% p-distances intra-group maximum divergence) and another containing specimens from Samoa,

Cook and Society Islands (D in Figure 2; PP = 1; B = 99; 2.4% p-distances intra-group maximum divergence), separated by 12.1% (p-distance between the two the closest sequences). Within clade D, there seems to be a geographical structuration, with the specimens from Samoa all clustered in a well-supported group (PP = 1; B = 99), suggesting a genetic isolation of this population, and considered as a distinct species by two out of the four automatic partitions (Figure 2). Since no clear morphological character could separate these specimens from the others of the Clade D, we chose the conservative approach of considering them both as part the same species.

Considering all the molecular analyses, we chose to recognise 4 distinct species in the islands of Polynesia, that we described below.

(Figure 2 near here)

Morphological analyses

Measures and observations made on the specimens allowed us to confirm the molecular results in recognising 6 species including 3 new ones: *C. futunensis* n. sp., *C. marquesensis* n. sp., *C. tupaia* n. sp., *C. rapaensis* Edmondson, 1935, *C. parvirostris* De Man, 1892, and *C. weberi* De Man, 1892. No molecular data could be obtained from specimens of *C. weberi* and *C. parvirostris* of which only type specimens were examined, but morphological studies allowed us to confidently consider them distinct. The descriptions (or re-descriptions) of the species present in Polynesia, as well as their identification key follow.

Taxonomy

Family Atyidae De Haan, 1849

Genus *Caridina* H. Milne Edwards, 1837

Caridina futunensis n. sp.

(Figure 3)

(Figure 3 near here)

Caridina weberi – Keith and Marquet 2011: 42–43; Mary et al. 2006: 33.

Material examined

Type material. Holotype: 1 ♀ ovig, cl 2.8 mm, 14 October 2004, 14°17.278'S 178°09.037'W, Leava river, Futuna, altitude 97m, G. Marquet, P. Keith & N. Mary coll., MNHN-IU-2018-195 (DNA: CA2118).

Paratypes: 1 ♀ ovig, cl 2.6 mm, same data as for holotype, MNHN-IU-2018-208 (DNA: CA2119); 1 ♀ ovig, cl 2.9 mm, same data as for holotype, MNHN-IU-2018-209 (DNA: CA2116); 1 ♀ ovig, cl 3.1 mm, same data as for holotype, MNHN-IU-2017-1460 (DNA: CA2032); 1 ♀ ovig, 3.1 mm, same data as for holotype, MNHN-IU-2017-64 (DNA: CA2117); 1 ♀, cl 3.0 mm, same data as for holotype, MNHN-IU-2017-1459 (DNA: CA2031); 1 ♀, cl 3.6 mm, 12 October 2004, 14°17.738'S 178°08.423'W, Vainifao river, Futuna, altitude 150m, G. Marquet, P. Keith & N. Mary coll., MNHN-IU-2017-65 (DNA: CA2033).

Comparative material. Type material

Caridina parvirostris De Man, 1892.

232 Syntypes: 2 ♀, cl. 3.1–3.2 mm, river near Bombang, Flores Island, Indonesia, M. Weber coll.,
233 MNHN-IU-2015-1748; 1 ♀, cl. 4.2 mm, same data as for previous, MNHN-IU-2015-1754.

234 *Caridina weberi* De Man, 1892.

235 Syntypes: 2 ♂, cl 4.4–4.5 mm and 1 ♀ ovig, cl 6.1 mm, Kotting, Flores Island, Indonesia, M.
236 Weber coll., MNHN-IU-2015-1755.

237

238 *Description*

239 *Cephalothorax*. Rostrum (Figures 3h and 7F): always bent down, short, 0.2–0.3 of cl,
240 reaching to base of first segment of antennular peduncle, armed dorsally with 5–10 teeth, 0 of
241 them on carapace posterior to orbital margin, ventral margin with 0–3 teeth. Rostrum formula
242 (0) 5–10/0–3. Suborbital angle indistinguishably fused with antennal spine. Pterygostomian
243 margin rectangularly rounded..

244 Eyes well developed, anterior end reaching to 0.73 length of antennular peduncle basal
245 segment. Antennular peduncle 0.47 times as long as carapace. Anterolateral angle reaching
246 0.20 length of second segment, second segment subequal to third. Stylocerite reaching to 0.90
247 length of antennular peduncle basal segment. Scaphocerite distinctly overreaching tip of
248 antennular peduncle, about 2.1 times longer than wide.

249 *Mouthparts*. Left mandible, right mandible, first maxilla, second maxilla, first maxilliped,
250 second maxilliped and third maxilliped typical of genus.

251 *Pereiopods*. Epipods on first four pereiopods.

252 Pereiopod 1 (Figure 3a): chela about 1.9–2.2 times as long as wide, movable finger 2.3–2.9
253 times as long as wide, 0.7–1.0 times length of palm, carpus 1.3–1.5 times as long as wide.

254 Pereiopod 2 (Figure 3b) More slender and longer than first pereiopod with chela 2.4–2.6 times
255 as long as wide: movable finger 4.0–5.0 times as long as wide, 1.5–1.9 times length of palm,
256 carpus slender 5.5–6.2 times as long as wide.

257 Pereiopod 3 (Figure 3c, e): stout, dactylus 2.6–3.9 times as long as wide (terminal spine
258 included) with 5 spines on flexor margin including terminal spine, propodus 8.8–13.1 times as
259 long as wide, 3.7–4.5 times as long as dactylus.

260 Pereiopod 5 (Figure 3d, f): dactylus 2.9–3.7 as long as wide with 25–38 spiniform setae on
261 flexor margin, propodus 12.2–13.8 times as long as wide, 4.3–4.9 times as long as dactylus.

262 *Abdomen.* Third abdominal somite with moderately convex dorsal profile. Sixth abdominal
263 somite about 0.5 of carapace length, 1.3 times as long as fifth somite, shorter than telson.

264 Telson (Figure 3k) 2 times as long as wide, with four to six pairs of dorsal spinules and one
265 pair of dorsolateral spinules, posterior margin with median process, rounded with 5
266 intermediate plumose setae longer than lateral spines.

267 First male pleopod: Unknown (no males in the collections).

268 Second male pleopod: Unknown (no males in the collections).

269 Preanal carina (Figure 3g): High, unarmed.

270 Uropodal diaeresis (Figure 3j) with 17–22 spinules.

271 Eggs (Figure 3i): Size $0.43\text{--}0.53 \times 0.25\text{--}0.30\text{mm}$.

272

273 *Habitat* (Figure 7G)

274 This new species prefers fresh and well-oxygenated running waters from the lower
275 course to the higher course.

276

277 *Etymology*

278 This new species is named *futunensis*, from the name of the island, Futuna, where this
279 new species occurs.

280

281 *Colour pattern*

282 Unknown

283

284 *Distribution* (Figure 8)

285 This species is known only from Futuna so far and seems to be endemic.

286

287 *Remarks*

288 This species looks like *C. parvirostris* by its bent rostrum with 5-10 dorsal teeth and

289 no post orbital teeth (vs bent rostrum with 8–10 dorsal teeth and no postorbital teeth in *C.*

290 *parvirostris*) but the P2 carpus is shorter 5.5-6.2 times as long as wide (vs 6.0–7.4 in *C.*

291 *parvirostris*) and so is P2 chela 2.4–2.6 times as long as wide (vs 2.6–3.0 in *C. parvirostris*).

292 This species differs from *C. marquesensis* n. sp. and *C. tupaia* n. sp. by its shorter rostrum

293 0.2–0.3 of cl (vs 0.3–0.4 in *C. marquesensis* n. sp. and *C. tupaia* n. sp.), fewer dorsal teeth on

294 the rostrum 5–10 (vs 10–13 in *C. marquesensis* n. sp. and 8–14 in *C. tupaia* n. sp.) and P5

295 dactylus with fewer spiniform setae on flexor margin 25–38 spines (vs 32–55 in *C.*

296 *marquesensis* n. sp. and 29–54 in *C. tupaia* n. sp.) and by its telson with 5 intermediate setae

297 longer than lateral spines (vs 6–14 in *C. marquesensis* n. sp. and 6–10 in *C. tupaia* n. sp.).

298 This species differs from *C. rapaensis* by its bent rostrum with more dorsal teeth (5–

299 10) (vs bent rostrum with 0–5 in *C. rapaensis*) and its P5 dactylus ending in two large claws

300 (vs one large claw in *C. rapaensis*).

301

302

303 ***Caridina marquesensis* n. sp.**

304 (Figure 4)

305

306 (Figure 4 near here)

307

308 *Caridina weberi* – Edmondson 1935: 10, fig. 4h; Adamson 1935: 16; 1939: 36; Marquet 1988
309 (partim); 1991: 129-130 (partim); Poupin 1998: 9 (partim); Keith & Vigneux 2002: 126
310 (partim), photo 7 & 8; Keith et al. 2002: 44–45 (partim); 2013: 84–85 (partim).

311

312 *Material examined*

313 *Type material.* Holotype: 1 ♂, cl 2.9 mm, 9 October 2017, 09°49.750'S 135°04.418'W, Ta'ooa
314 river, Hiva Oa Island, French Polynesia, altitude 220m, G. Marquet, P. Tiberghien, E.
315 Feunteun, P. Gerbeaux & M. Gerbeaux coll., MNHN-IU-2017-66.

316 Paratypes: 1 ♀ ovig, cl 3.3 mm, same data as holotype, MNHN-IU-2017-67 (DNA: CA2067);
317 1 ♀, cl 2.8 mm, same data as holotype, MNHN-IU-2017-68 (DNA: CA2066); 1 ♀ ovig, cl 4.7
318 mm, 18 October 2017, 08°51.126'S 140°06.066'W, Taipivai river, Nuku Hiva Island, French
319 Polynesia, altitude 130m, G. Marquet, P. Tiberghien, P. Keith & H. Lucien-Brun coll.,
320 MNHN-IU-2017-69 (DNA: CA2075); 1 ♀ ovig, cl 4.8mm, same data as previous, MNHN-
321 IU-2017-70 (DNA: CA2074); 1 ♀, cl 3.2 mm, 14 October 2017, 09°25.452'S 140°03.409'W,
322 unnamed rivulet, Ua Pou Island, French Polynesia, altitude 130m, G. Marquet, P. Tiberghien,
323 P. Keith & H. Lucien-Brun coll., MNHN-IU-2017-71 (DNA: CA2071); 1 ♀, cl 3.4 mm, same
324 data as previous, MNHN-IU-2018-257 (DNA: CA2070); 1 ♀ ovig, cl 5.2 mm, 21 February
325 2000, 09°24.180'S 140°03.060'W, Paaumea river, Ua Pou Island, French Polynesia, altitude
326 200m, P. Keith & E. Vigneux coll., MNHN-IU-2018-258; 1 ♀, cl 4.6 mm, same data as
327 previous, MNHN-IU-2018-259.

328

329 *Comparative material.* Type material

330 *Caridina weberi* De Man, 1892.

331 Syntypes: 2 ♂, cl 4.4–4.5 mm and 1 ♀ ovig, cl 6.1 mm, Kotting, Flores Island, Indonesia, M.
332 Weber coll., MNHN-IU-2015-1755.

333

334 *Description*

335 *Cephalothorax*. Rostrum (Figure 4h): always bent down, short, 0.3–0.4 of cl, reaching to base
336 or middle of second segment of antennular peduncle, armed dorsally with 10–13 teeth, 0–3
337 teeth on carapace posterior to orbital margin (mostly 2–3), ventral margin with 0–3 teeth.
338 Rostral formula (0–3) 10–13/0–3. Suborbital angle indistinguishably fused with antennular
339 tooth. Pterygostomian margin rectangularly rounded.

340 Eyes well developed, anterior end reaching to 0.62 length of antennular peduncle basal
341 segment. Antennular peduncle 0.50 times as long as carapace. Anterolateral angle reaching
342 0.20 length of second segment, second segment subequal to third. Stylocerite reaching to 0.9
343 length of antennular peduncle basal segment. Scaphocerite reaches just slightly beyond tip of
344 antennular peduncle, about 2.1 times longer than wide.

345 *Mouthparts*. Left mandible, right mandible, first maxilla, second maxilla, first maxilliped,
346 second maxilliped and third maxilliped typical of genus.

347 *Pereiopods*. Epipods on first four pereiopods.

348 Pereiopod 1 (Figure 4a): chela about 2.0–2.2 times as long as wide, movable finger 2.2–3.1
349 times as long as wide, 0.6–0.9 times length of palm, carpus 1.3–1.7 times as long as wide.
350 Tips of both fingers with prominent claws (Figure 4b).

351 Pereiopod 2 (Figure 4c) more slender and long than first pereiopod with chela 2.5–3.3 times
352 as long as wide: movable finger 4.2–5.2 times as long as wide, 1.5–1.8 times length of palm,
353 carpus slender 5.5–6.6 times as long as wide.

Pereiopod 3 (Figure 4d, g): stout, dactylus 2.7–3.1 times as long as wide including terminal spine) with 6–7 spines including terminal spine, propodus with numerous spines on ventral margin, 8.0–9.3 times as long as wide, 3.4–4.3 times as long as dactylus.

Pereiopod 5 (Figure 4e, f): dactylus 3.4–5.5 as long as wide, ending in two large claws with 32–55 spiniform setae on flexor margin, propodus 13.0–17.7 times as long as wide, 3.8–5.2 times as long as dactylus.

Abdomen. Third abdominal somite with moderately convex dorsal profile. Sixth abdominal somite about 0.37 of carapace, 0.7 times as long as fifth somite, shorter than telson. Telson (Figure 4l) 2.1 times as long as wide, with four to six pairs of dorsal spines and one pair of dorsolateral spines, posterior margin with a median process, rounded with 6–14 intermediate plumose setae longer than lateral spines.

First male pleopod (Figure 4m): Endopod extending to half length of exopod, elongate, with a developed appendix interna near distal end of endopod.

Second male pleopod (Figure 4n): Appendix masculina reaching 0.72 times length of endopod, appendix interna reaching about 0.50 times appendix masculina length.

Preanal carina (Figure 4i): High, unarmed.

Uropodal diaeresis (Figure 4k): with 16–22 spinules.

Eggs (Figure 4j): Size $0.39\text{--}0.47 \times 0.23\text{--}0.27\text{mm}$.

Habitat

This new species prefers fresh and well-oxygenated running waters from the lower course to the higher course. In Nuku Hiva (Marquesas islands) *C. marquesensis* n. sp. lives in lentic habitat of the lower course, associated with accumulations of leaves, where it collects small detritus and eventually is able to swim (Fossati et al. 2002).

379 *Etymology*

380 This new species is named *marquesensis*, from the name of the archipelago,
381 Marquesas Islands, where it occurs.

382

383 *Colour pattern* (Figure 7C)

384 The live general colour of the body is bluish to greenish and slightly translucent.
385 Numerous red spots are visible all over the body.

386

387 *Distribution* (Figure 8)

388 This species is known only from Marquesas islands (Nuku Hiva, Hiva Oa, Ua Pou
389 Islands) so far and seems to be endemic.

390

391 *Remarks*

392 This new species was identified as *C. weberi* several times: Edmondson (1935),
393 Adamson (1935, 1939), Marquet (1988), Marquet (1991), Poupin (1998), Keith & Vigneux
394 (2002), Keith et al. (2002), Keith et al. (2013). Indeed this species looks like *C. weberi sensu*
395 *stricto* by its straight or bent down rostrum, 0.3–0.4 of cl, (vs 0.4 in *C. weberi*) reaching to the
396 base or middle of second segment of antennular peduncle with numerous dorsal teeth 10–13
397 (vs 10–19 in *C. weberi*), but differs by the presence of 0–3 dorsal teeth situated on carapace
398 behind orbital margin (vs 0 in *C. weberi*). Also its P1 movable finger is shorter 0.6–0.9 times
399 length of palm (vs 1.2–1.3 in *C. weberi*) as is its P1 carpus 1.3–1.7 times as long as wide (vs
400 1.9–2.0 in *C. weberi*), and its P2 carpus is longer, 5.5–6.6 times as long as wide (vs 4.9–5.0 in
401 *C. weberi*). Furthermore, the posterior margin of the telson always shows only one pair of
402 lateral spines (vs 2 in *C. weberi*).

This species differs from *C. tupaia* n. sp. by its rostrum with mostly 2–3 teeth on carapace posterior to orbital margin (vs mostly 0 in *C. tupaia* n. sp.), its tips of both P1 fingers with prominent claws (vs not in *C. tupaia* n. sp.) and its P5 dactylus ending in two large claws (vs one claw in *C. tupaia* n. sp.).

Caridina tupaia n. sp.

(Figure 5)

(Figure 5 near here)

Caridina weberi – Edmondson 1935 : 8-9, fig. 3 (a-f) page 11, fig. 4g page 13; Marquet 1988 (partim); 1991: 129-130 (partim); Poupin 1998: 9 (partim); Keith & Vigneux 2002: 126 (partim), Keith et al. 2002: 44–45 (partim); 2013: 84–85 (partim).

Caridina cf. weberi – Page et al. 2007b: specimen voucher GU-993, sequence DQ478493.

Caridina cf. weberi sp. 3 – Mazancourt et al. 2018.

Material examined

Type material. Holotype: 1 ♀, cl 4.1 mm, 23 October 2017, 17°49.719'S 149°17.067'W, Papehere river, Tahiti Island, French Polynesia, G. Marquet & P. Tiberghien coll., MNHN-IU-2018-260 (DNA: CA2058).

Paratypes: 1 ♂, cl 3.9 mm, 11 July 2010, 21°14.806'S 159°43.795'W, Avana river, Rarotonga Island, Cook Islands, altitude 5–10m, P. Keith, P. Gerbeaux & G. Marquet coll., MNHN-IU-2018-261 (DNA: CA1048); 1 ♂, cl 4.1 mm, same data as previous, MNHN-IU-2018-262 (DNA: CA1046); 1 ♂, cl 4.2 mm, same data as previous, MNHN-IU-2018-263 (DNA: CA1047); 1 ♀ ovig, cl 3.8 mm, same data as previous, MNHN-IU-2018-264 (DNA:

428 CA1049); 1 ♂, cl 2.5 mm, 26 September 2017, 22°27.009'S 151°21.061'W, Puputa river,
 429 Rurutu Island, French Polynesia, G. Marquet & P. Tiberghien coll., MNHN-IU-2018-265
 430 (DNA: CA2054); 1 ♀, cl 3.5 mm, same data as previous, MNHN-IU-2018-266 (DNA:
 431 CA2055); 1 ♀, cl 4.1 mm, same data as holotype, MNHN-IU-2018-267 (DNA: CA2059); 1 ♀
 432 ovig, cl 4.2 mm, 1 July 2001, Mahidi river, Huahiné Island, French Polynesia, P. Keith & E.
 433 Vigneux coll., MNHN-IU-2018-268; 1 ♀, cl 4.5 mm, same data as previous, MNHN-IU-
 434 2018-269; 1 ♀, cl 2.8 mm, 5 October 2017, 17°32.785'S 149°48.484'W, Afareaitu river,
 435 Moorea Island, French Polynesia, altitude 109m, G. Marquet & P. Tiberghien coll., MNHN-
 436 IU-2018-270 (DNA: CA2062); 1 ♀ ovig, cl 3.9 mm, same data as previous, MNHN-IU-2016-
 437 11762 (DNA: CA2063); 1 ♀ ovig, cl 6.2 mm, 10 July 2014, 13°54.543'S 171°35.300'W,
 438 Falefa river, Upolu Island, Samoa, altitude <50m, P. Gerbeaux coll., MNHN-IU-2016-11763
 439 (DNA: CA1410); 1 ♀ ovig, cl 5.5 mm, 8 July 2014, 13°53.642'S 171°39.913'W, Tuafaleloa
 440 river, Upolu Island, Samoa, altitude 100m, P. Gerbeaux coll., MNHN-IU-2016-11764 (DNA:
 441 CA1411); 1 ♀ ovig, cl 4.4 mm, 8 July 2014, 13°53.788'S 171°40.031'W, Tuafaleloa river,
 442 Upolu Island, Samoa, altitude 250m, P. Gerbeaux coll., MNHN-IU-2016-11765 (DNA:
 443 CA1412); 1 ♀, cl 5.0 mm, 12 July 2014, 13°43.741'S 172°18.832'W, Faleata river, Savaii
 444 Island, Samoa, altitude 195m, P. Gerbeaux coll., MNHN-IU-2016-11766 (DNA: CA1413); 1
 445 ♀ ovig, cl 5.0 mm, 7 July 2014, 13°51.900'S 171° 41.196'W, Ma'epu river, Savaii Island,
 446 Samoa, altitude 20–50m, P. Gerbeaux coll., MNHN-IU-2016-11767 (DNA: CA1918).
 447
 448 *Comparative material.* Type material
 449 *Caridina weberi* De Man, 1892.
 450 Syntypes: 2 ♂, cl 4.4–4.5 mm and 1 ♀ ovig, cl 6.1 mm, Kotting, Flores Island, Indonesia, M.
 451 Weber coll., MNHN-IU-2015-1755.
 452

453 *Description*

454 *Cephalothorax*. Rostrum (Figure 5g): rarely straight, mostly bent down, short, 0.3–0.4 of cl,
455 reaching to base or middle of second segment of antennular peduncle, armed dorsally with 8–
456 14 teeth, 0–3 of them situated on carapace posterior to orbital margin (mostly 0), ventral
457 margin with 1–3 teeth. Rostral formula (0–3) 8–14/1–3. Suborbital angle indistinguishably
458 fused with antennular tooth. Pterygostomian margin rectangularly rounded.

459 Eyes well developed, anterior end reaching to 0.77 length of antennular peduncle basal
460 segment. Antennular peduncle 0.55 times as long as carapace. Anterolateral angle of basal
461 segment reaching 0.20 length of second segment, second segment twice as long as third.

462 Stylocerite reaching to 0.90 length of antennular peduncle basal segment. Scaphocerite
463 reaching just slightly beyond the tip of antennular peduncle, about 3 times longer than wide.

464 *Mouthparts*. Left mandible, right mandible, first maxilla, second maxilla, first maxilliped,
465 second maxilliped and third maxilliped typical of genus.

466 *Pereiopods*. Epipods on first four pereiopods.

467 Pereiopod 1 (Figure 5a): chela about 1.9–2.1 times as long as wide, movable finger 2.2–3.3
468 times as long as wide, 0.7–1.0 times length of palm, carpus 1.3–1.7 times as long as wide.

469 Pereiopod 2 (Figure 5b) more slender and longer than first pereiopod with chela 2.4–2.8 times
470 as long as wide: movable finger 3.8–4.9 times as long as wide, 1.3–1.7 times length of palm,
471 carpus slender 4.7–6.1 times as long as wide.

472 Pereiopod 3 (Figure 5c, f): stout, dactylus 2.6–4.2 times as long as wide including terminal
473 spine with 5–7 spines including terminal spine, propodus with numerous spines on ventral
474 margin, 7.6–10.6 times as long as wide, 3.4–5.2 times as long as dactylus.

475 Pereiopod 5 (Figure 5d, e): dactylus 3.5–4.7 times as long as wide with 29–54 spiniform setae
476 on flexor margin, propodus 11.6–16.0 times as long as wide, 3.7–4.4 times as long as
477 dactylus.

478 *Abdomen*. Third abdominal somite with moderately convex dorsal profile. Sixth abdominal
479 somite about 0.46 times carapace length, as long as fifth somite, shorter than telson. Telson
480 (Figure 5k): 2.3 times as long as wide, with four or five pairs of dorsal spines and one pair of
481 dorsolateral spines, posterior margin with median process, rounded with 6–10 intermediate
482 plumose setae longer than lateral spines.

483 First male pleopod (Figure 5l): Endopod extending to half length of exopod, elongate, with
484 developed appendix interna near distal end of endopod.

485 Second male pleopod (Figure 5m): Appendix masculina reaching 0.68 times length of
486 endopod, appendix interna reaching about 0.40 times appendix masculina length

487 Preanal carina (Figure 5h): High, unarmed.

488 Uropodal diaeresis (Fig.5j): With 16–20 spinules.

489 Eggs (Figure 5i): Size 0.38–0.47 × 0.20–0.30 mm.

490

491 *Habitat*

492 This new species prefers fresh and well-oxygenated running waters from the lower
493 course to the higher courses. Under the name of *C. weberi*, its microhabitat was intensely
494 studied in Opunohu river (Moorea) with that of another sympatric species *Atyoida pilipes*
495 (Newport, 1847) (Resh et al. 1990). *C. tupaia* n. sp. were often found near leaf litter, tending
496 to aggregate in on the bottom of pools where detritus accumulated. Both their leaf litter
497 habitat and their ability to consume it in the laboratory indicate the possibility that this scraper
498 increase rates of litter decomposition (Williams 1999). Cheliped morphology and,
499 consequently, differences in feeding methods are the main factors determining the
500 microdistribution of *A. pilipes* and *C. tupaia*. *A. pilipes* is filter feeding in faster flowing
501 habitats, while *C. tupaia* are scraping and sweeping detritus within and on leaf surfaces and
502 also in other microhabitats on the stream channel bed (Resh et al. 1990). *C. tupaia*, whose

microhabitat is in pools and slow water, may be less able to grasp the substrate in high velocity water, while *A. pilipes* which is often found in the faster moving water of riffles may be better able to grasp the substrate (Feldman 1996). These differences are likely a contributing factor in their distribution above and below barriers such as waterfalls and culverts, which require fighting current to move farther upstream. The climbing ability of these two species was tested by Falvo (2013) in rivers of Moorea (Opunohu and Afareaitu). *C. tupaia* had the highest success rate and *A. pilipes* was the fastest climber. The latter species is found at higher reaches of the streams than *C. tupaia*. These species exhibited different climbing behaviours. *C. tupaia* would consistently take breaks while climbing, only moving a few centimetres at a time, while *A. pilipes* would rarely stop once it started climbing. An examination of the distal portions of the pereopods of *A. pilipes* and *C. tupaia* indicates that *A. pilipes* is more strongly built and its appendages may also be better suited for gripping substrate and with standing current, explaining its ability to reach higher altitudes.

Etymology

This new species is named in honour of Tupaia, the Polynesian pilot of James Cook, on board of H.M.S. Endeavour for its ability to cross long distances between Polynesian islands.

Colour pattern (Figure 7A, B)

The live general colour of the body is yellowish and slightly translucent. Numerous red spots are visible all over the body. Sometimes, a lighter longitudinal dorsal band is present stretching from the rostrum to the telson.

Distribution (Figure 8)

Among the species studied here, this species seems to have the widest distribution in Polynesia (Upolu, Savaii (Samoa), Rarotonga (Cook Islands), Rurutu, Tahiti, Moorea, and Huahine (French Polynesia)).

Remarks

This new species was identified as *C. weberi* several times: Edmondson (1935), Adamson (1935, 1939), Marquet (1988), Marquet (1991), Poupin (1998), Keith and Vigneux (2002), Keith et al. (2002), Page et al. (2007b), Keith et al. (2013). Indeed this species looks like *C. weberi sensu stricto* by its straight or bent down rostrum, 0.3–0.4 of cl, (vs 0.4 in *C. weberi*) reaching to the base or middle of second segment of antennular peduncle with numerous dorsal teeth 8–14 (vs 10–19 in *C. weberi*), but differs by the presence of 0–3 dorsal teeth situated on carapace behind orbital margin (vs 0 in *C. weberi*). Also its P1 movable finger is shorter 0.7–1.0 times length of palm (vs 1.2–1.3 in *C. weberi*) as is its P1 carpus 1.3–1.7 times as long as wide (vs 1.9–2.0 in *C. weberi*). Furthermore, the posterior margin of the telson shows always only one pair of lateral spines (vs 2 in *C. weberi*).

This species is easily separated from *C. marquesensis* n. sp. by numerous characters (see previously).

***Caridina rapaensis* Edmondson, 1935**

(Figure 6)

(Figure 6 near here)

553 *Caridina rapaensis* Edmondson 1935: 12, 14, fig. 5(a-h) page 15; Marquet 1988; 1991: 130;
 554 Poupin 1998: 8; Keith & Vigneux 2002: 125, photo 3 & 4; Keith et al. 2002: 40–41; 2013:
 555 78–79.
 556
 557 *Material observed*
 558 *Type material.* Holotype: 1 ♀, cl 4.7 mm, 1934, a freshwater stream, Rapa Island, French
 559 Polynesia, Mangarevan Expedition coll., BPBM 53933.
 560 Paratype: 1 ♀, cl 5.0 mm, same data as holotype, BPBM 53694.
 561
 562 *Other material.* 1 ♂, cl 3.3 mm, 15 June 2001, 27°35.919'S 144°20.392'W, Panui stream,
 563 Rapa Island, French Polynesia, altitude 18m, G. Marquet coll., MNHN-IU-2016-11768; 1 ♂,
 564 cl 3.4 mm, same data as previous, MNHN-IU-2016-11769 (DNA: CA2114); 1 ♀, cl 4.8 mm,
 565 same data as previous, MNHN-IU-2016-11770; 1 ♀, cl 5.2 mm, same data as previous,
 566 MNHN-IU-2016-11771 (DNA: CA2115); 1 ♀, cl 6.0 mm, same data as previous, MNHN-IU-
 567 2016-11772 (DNA: CA2111); 2 ♂, cl 2.5–2.9 mm and 2 ♀ ovig, cl 4.0–4.6 mm, 2 May 1986,
 568 22°26.240'S 151°22.243'W, Tevaovai stream, Rurutu Island, French Polynesia, altitude 52m,
 569 G. Marquet coll., MNHN-IU-2015-1921.
 570
 571 *Comparative material.* Type material
 572 *Caridina parvirostris* De Man, 1892.
 573 Syntypes: 2 ♀, cl. 3.1–3.2 mm, river near Bombang, Flores Island, Indonesia, M. Weber coll.,
 574 MNHN-IU-2015-1748; 1 ♀, cl. 4.2 mm, same data as for previous, MNHN-IU-2015-1754.
 575 *Caridina weberi* var. *keiensis* Roux, 1911
 576 Lectotype: 1 ♀ ovig. cl 5.7mm, 5 June 1908, Warka, Grand Kei Island, Indonesia, H. Merton
 577 coll., NMB 6.IV.b.

578 Paralectotypes: 2 ♂ cl 2.6mm, 1 ♂ 6.IV.b, same data as for lectotype, NMB 6.IV.a; 1 ♀, cl
579 5.5mm and 1 ♂, cl 3.4mm, same data as for lectotype, NMB 6.IV.b.

580 *Caridina weberi* De Man, 1892.

581 Syntypes: 2 ♂, cl 4.4–4.5 mm and 1 ♀ ovig, cl 6.1 mm, Kotting, Flores Island, Indonesia, M.
582 Weber coll., MNHN-IU-2015-1755.

583

584 *Description*

585 *Cephalothorax*. Rostrum (Figure 6h): always bent down, short, 0.3–0.5 of cl, reaching to base
586 of second segment of antennular peduncle, armed dorsally with 0-5 teeth, occupying distal
587 fourth of border, none situated on carapace posterior to orbital margin, ventral margin with 1-
588 6 teeth. Rostral formula (0) 0–5/1–6. Suborbital angle indistinguishably fused with antennular
589 tooth. Pterygostomian margin rounded.

590 Eyes well developed, anterior end reaching to 0.77 length of antennular peduncle basal
591 segment. Antennular peduncle 0.44 times as long as carapace. Anterolateral angle of basal
592 antennular segment reaching 0.20 length of second antennular segment, second antennular
593 segment distinctly longer than third. Stylocerite reaching to end of antennular peduncle basal
594 segment. Scaphocerite reaching just slightly beyond tip of antennular peduncle, about 3.1
595 times longer than wide.

596 *Mouthparts*. Left mandible, right mandible, first maxilla, second maxilla, first maxilliped,
597 second maxilliped and third maxilliped typical of genus.

598 *Pereiopods*. Epipods on first four pereiopods.

599 Pereiopod 1 (Figure 6a): chela about 1.5–2.5 times as long as wide, movable finger 1.5–4.4
600 times as long as wide, 0.5–1.4 times length of palm, carpus 1.2–1.7 times as long as wide.
601 Tips of both fingers with prominent claws (Figure 6b).

602 Pereiopod 2 (Figure 6c): more slender and long than first pereiopod with chela 2.0–2.7 times
603 as long as wide: movable finger 3.2–4.7 times as long as wide, 1.3–1.9 times length of palm,
604 carpus slender 4.2–5.2 times as long as wide.

605 Pereiopod 3 (Figure 6d, g): stout, dactylus 2.7–3.9 times as long as wide including terminal
606 spine with 6–8 spines including terminal spine, propodus 9.0–12.8 times as long as wide, 3.9–
607 4.9 times as long as dactylus.

608 Pereiopod 5 (Figure 6e, f): dactylus 3.1–4.9 as long as wide, ending in two large claws with
609 30–45 spiniform setae on flexor margin, propodus 11.7–19.0 times as long as wide, with
610 numerous spines on ventral margin, 4.5–5.4 times as long as dactylus.

611 *Abdomen.* Third abdominal somite with moderately convex dorsal profile. Sixth abdominal
612 somite about 0.4 times carapace length, 1.2 times as long as fifth somite, shorter than telson.

613 Telson (Figure 6k): 2.9 times as long as wide, with five or six pairs of dorsal spines and one
614 pair of dorsolateral spines, posterior margin with small median process, rounded with 5–13
615 intermediate plumose setae much longer than lateral spines.

616 First male pleopod (Figure 6m): Endopod extending to 0.42 times length of exopod,
617 rectangular, with a short appendix interna near distal end of endopod.

618 Second male pleopod (Figure 6n): Appendix masculina reaching 0.83 times length of
619 endopod, appendix interna reaching about 0.34 times appendix masculina length

620 Preanal carina (Figure 6i): High, unarmed.

621 Uropodal diaeresis (Figure 6k): with 15–20 spinules.

622 Eggs (Figure 6j): Size 0.44–0.49 × 0.26–0.29mm.

623

624 *Habitat*

625 This new species prefers fresh and well-oxygenated running waters from the lower
626 course to the middle course.

627

628 *Colour pattern* (Figure 7D, E)

629 The live general colour of the body is yellowish to greenish and slightly translucent.

630 Numerous red spots are visible all over the body.

631

632 *Distribution* (Figure 8)

633 This species is known only from Austral Islands (Rurutu and Rapa islands) so far and

634 seems to be endemic.

635

636 *Remarks*

637 Our specimens look like those described by Edmondson (1935): Rostrum always bent

638 down, short, 0.3–0.5 of cl, reaching to base of second segment of of antennular peduncle (vs

639 rostrum slender, slightly turned down, reaching to the middle of the second segment of the

640 antennular peduncle for Edmondson (1935)), rostrum armed with 0–5 teeth on dorsal margin,

641 occupying the distal fourth of the border, ventral margin with 1–6 teeth. (vs rostral teeth small

642 and few, stronger above than below, those above occupying the distal fourth of the border, the

643 first (basal) tooth below being posterior to the first one of the upper border for Edmondson

644 (1935)), P1 finger 0.5–1.4 times length of palm (vs dactylus as long as upper border of palm

645 for Edmondson (1935)), P3 dactylus with 6–8 spines on flexor margin in addition to the

646 terminal spine (vs border dactylus provided with a stout tooth just proximal of the tip, and

647 four other small spines for Edmondson (1935)), P5 dactylus ending in two large claws with

648 30–45 spiniform setae on flexor margin (vs dactylus of fifth leg bearing numerous short hairs

649 and a strong supplementary tooth near the tip for Edmondson (1935)), posterior margin of the

650 telson with a little median process, rounded with 5–13 intermediate plumose setae much

651 longer than lateral spines (vs telson with 6 pairs of small spines on upper border, its posterior

margin bearing a small median tooth for Edmondson (1935)), and uropodal diaeresis with 15–20 spinules (vs uropodal spinelets 20 in number for Edmondson (1935)).

This species differs from *C. parvirostris* by its bent rostrum with fewer dorsal teeth (0–5) (vs bent rostrum with 8–10 dorsal teeth in *C. parvirostris*) and its P2 carpus shorter 4.2–5.2 times as long as wide (vs 6.0–7.4 in *C. parvirostris*) and so is P2 chela 2.0–2.7 times as long as wide (vs 2.6–3.0 in *C. parvirostris*).

This species differs from *C. futunensis* n. sp. by its bent rostrum with fewer dorsal teeth (0–5) (vs bent rostrum with 5–10 in *C. futunensis* n. sp.) and its P5 dactylus ending in two large claws (vs one large claw in *C. futunensis* n. sp.).

C. rapaensis was reported by Shokita (2003) from Ryukyu Islands, but according to Cai and Shokita (2006), these specimens actually belong to *C. prashadi* Tiwari & Pilai, 1971 described from the Andaman Islands. Indeed, even if the rostrum formula is similar (0) 0–5/1–6 (vs (0)1–6/3–6 in *C. prashadi*), *C. rapaensis* can be distinguished easily from *C. prashadi* by its prominent claws on the tips of both P1 fingers (vs no prominent claws in *C. prashadi*) and by its P5 dactylus ending in two large claws (vs one claw in *C. prashadi*) with 30–45 spiniform setae on flexor margin (vs 29 in *C. prashadi*).

C. rapaensis looks like *C. weberi* var. *keiensis* from Kei Islands (Indonesia) by its bent and short rostrum, its P1 chela bearing prominent claws and its P5 dactylus being biunguiculate. However, they can be distinguished by the number of dorsal teeth on the rostrum 0–5 (vs 2–13 in *C. weberi* var. *keiensis*). Furthermore, considering the distance between Kei Islands and Polynesia and that *C. weberi* var. *keiensis* has never been collected in between, we consider it to be a distinct species.

(Figure 7 near here)

677 **Key of the Polynesian species of the *C. weberi* complex**

- 678 1. Rostrum armed dorsally with many teeth (10–19), relatively long (0.3–0.4 of cl, reaching to
679 base or middle of antennular peduncle second segment).....2
680 - Rostrum armed dorsally with few teeth (0–10), mostly relatively short (0.2–0.3 of cl,
681 reaching to end of antennular peduncle basal segment).....3
682
683 2 Mostly 2–3 dorsal rostrum teeth situated on carapace behind orbital margin, tips of both P1
684 fingers with prominent claws, P5 dactylus ending in two large
685 claws.....*C. marquesensis* n. sp.
686 - Mostly no dorsal rostrum teeth, tips of both P1 fingers without prominent claws, P5 dactylus
687 ending in one large claw.....*C. tupaia* n. sp.
688
689 3 Rostrum armed dorsally with 5–10 teeth, 0.2–0.3 of cl, reaching to end of antennular
690 peduncle basal segment, tips of both P1 fingers without prominent claws....*C. futunensis* n. sp.
691 - Rostrum armed dorsally with 0–5 teeth on dorsal margin, 0.3–0.5 of cl, reaching to base or
692 middle of antennular peduncle second segment), tips of both P1 fingers with prominent
693 claws.....*C. rapaensis*
694

695 **Discussion**

696 **Systematics**

697 The taxonomy of the *C. weberi* complex is problematic because it is based essentially
698 on the rostrum (variable in length and shape) and on teeth (number of dorsal teeth, dorsal
699 teeth situated on carapace behind orbital margin). Curiously, *C. weberi* is reported from
700 numerous localities in Indonesia, Philippines, Micronesia and Melanesia, but in the literature,
701 put apart specimens described by Bouvier (1925) and Edmondson (1935), only two

702 publications detailed the morphological characters of this species, the first one by Roux
 703 (1928), and the second one by Cai and Ng (2001). Specimens from Ceram (Indonesia)
 704 described as *C. weberi* by Roux (1928) look like our specimens of *C. tupaia* n. sp. by its P1
 705 chela about 1.9–2.1 times as long as wide (vs 2–2.2 in *C. tupaia* n. sp.), P1 movable finger
 706 0.7–1.0 times length of palm; (vs 0.9–1.2 in *C. tupaia* n. sp.), its P2 carpus slender 4.7–6.1
 707 times as long as wide (vs 5.5–7.5 in *C. tupaia* n. sp.), its P3 dactylus 2.6–4.2 times as long as
 708 wide (terminal spine included) (vs 3.1–3.8 in *C. tupaia* n. sp.) with 5–7 spines on flexor
 709 margin in addition to the terminal one (vs 6–7 in *C. tupaia* n. sp.), P3 propodus, 3.7–5.2 times
 710 as long as dactylus (vs 4.5–5.4 in *C. tupaia* n. sp.), its P5 dactylus 3.5–4.7 as long as wide (vs
 711 4.4–5.0 in *C. tupaia* n. sp.) and its P5 propodus 11.6–16.0 times as long as wide (vs 11–15 in
 712 *C. tupaia* n. sp.), but its rostral formula is different: (0–3) 8–14/ 1–3 (vs (0–2)12–19/2–6 in *C.*
 713 *tupaia* n. sp.), its P1 carpus is shorter 1.3–1.7 times as long as wide.(vs 1.5–2.1 in *C. tupaia* n.
 714 sp.), so is its P2 chela 2.4–2.8 times as long as wide: (vs 2.8–3.1 in *C. tupaia* n. sp.), and its
 715 P3 propodus 7.6–10.7 times as long as wide (vs 11–16 in *C. tupaia* n. sp.), its P5 dactylus
 716 bears fewer spiniform setae on flexor margin 29–54 (vs 62–70 in *C. tupaia* n. sp.), and finally,
 717 its eggs are larger $0.38\text{--}0.47 \times 0.20\text{--}0.30$ mm (vs $0.35\text{--}0.38 \times 0.2\text{--}0.21$ in *C. tupaia* n. sp.).
 718 Our specimens of *C. tupaia* n. sp. also look like those from Halmahera described by Cai and
 719 Ng (2001) as *C. weberi* by its rostral formula (0–3) 8–14/1–3 (vs (0–2) 13–14/2–3 for Cai and
 720 Ng (2001)), P1 movable finger 0.7–1.0 times length of palm (vs 1.0 for Cai and Ng (2001)),
 721 carpus 1.3–1.7 times as long as wide (vs 1.3 for Cai and Ng (2001)), P5 dactylus with 29–54
 722 spiniform setae on flexor margin (vs 55 for Cai and Ng (2001)) and P5 propodus 3.7–4.4
 723 times as long as dactylus (vs 5 for Cai and Ng (2001)), and its eggs size $0.38\text{--}0.47 \times 0.20\text{--}0.$
 724 30 mm (vs 0.4×0.2 for Cai and Ng (2001)). They differ from these specimens by the
 725 posterior margin of the telson that always shows one pair of lateral spines (vs 2 for Cai and
 726 Ng (2001); see Figure 3C, D, E, like *C. weberi* sensu stricto).

In this complex, as for others, it is necessary to always combine genetics with morphology and to collect specimens from the type locality in order to do a genetic study.

Distribution

Endemism in the Marquesas and Austral archipelagos, and in Futuna

The high degree of freshwater endemism is well known in the Marquesas Islands where all the freshwater Gobiidae (Teleostei) are endemic (Keith et al. 2015). There is also one endemic freshwater palaemonid prawn (*Macrobrachium feunteuni* Keith and Vigneux, 2002) (Keith and Vigneux 2002), one endemic varunid (Decapoda: Brachyura) *Ptychognathus crassimanus* Finnegan, 1931 (NK Ng, pers. comm.) and now an endemic *Caridina* shrimp, *C. marquesensis* n. sp.. This high rate of endemism is also well known in the Austral archipelago, and particularly in Rapa Island, with its endemic Gobiidae (Teleostei): *Sicyopterus rapa* Parenti & Maciolek, 1996 and *Stiphodon julieni* Keith, Watson & Marquet, 2002. *Stenogobius randalli* Watson, 1991 is restricted to Austral archipelago, and *Stiphodon discotorquatus* Watson, 1995 is restricted to Rarotonga (Cook), Rurutu and Tubuai (Austral Islands). *Caridina rapaensis* is restricted to Rapa and Rurutu. Compared to Marquesas and Austral archipelagos, Society shows another different type of fauna. The type of life cycle for all native freshwater species in Polynesia is amphidromy. Indeed, river systems are colonised by crustaceans (Palaemonidae and Atyidae) with a life cycle typically adapted to the conditions that prevail in these distinctive insular habitats; i.e, young oligotrophic rivers, subject to extreme climatic and hydrological seasonal variations. These species spawn in freshwater, the free larvae drift downstream to the sea where they undergo a planktonic phase during several days to several months, before returning to the rivers to grow and reproduce. With this type of lifecycle, numerous authors suggest that some oceanic currents are biogeographic genetic barriers (Planes 1993; Mennesson 2016) and so generate

endemic species. This could partially explain the patterns observed in Marquesas and Austral Islands. There are in our study area (Figure 8) two main currents: the South Equatorial Current (SEC) and the South Equatorial countercurrent (SECC). SEC is caused by the influence of South-East trade winds and flows from east to west. More southward, the SECC flows from West to East. Under the influence of SEC and SECC, a gyre is formed. The global westward trend of the currents in the area could partially explain the distribution of *C. tupaia* n. sp. ranging from Society to Samoa through Cook and Rurutu (Austral) by carrying the larvae that would thus supposedly live in depths within the influence of those surface currents.

In French Polynesia, the Marquesas archipelago (Figure 8) is located in the Marquesas countercurrent (MCC), oriented from West to East. It is very regular throughout the year (Martinez et al. 2009). Tuamotu, Gambier and Society archipelagos are located in the South Equatorial Current (SEC) oriented from Northeast to Southwest. The Austral archipelago is located in the South Equatorial Countercurrent (SECC) oriented from west to east. This climatological scheme will be of major importance for the establishment of species that have a planktonic dispersive larval phase, such as species of the genus *Caridina*. Indeed the opposition (Figure 8) between the MCC and the SEC could explain the strong divergence of the Marquesas population, the border between these two currents (current in opposite direction and bodies of water having different characters) constituting a barrier for larvae (Vermeij 1987).

The same schema exists between the SEC and the SECC, explaining the divergence of the Austral population (Figure 8). So the two endemic areas in the north and south of French Polynesia could be explained by their provision of currents but also by their isolation. Indeed, the Marquesas Islands, which are almost exactly in the centre of the Pacific, are very isolated, some 4,828 km from the nearest American coast, 4,572 km from the western margin of the

Pacific depression and 1,287 km from the nearest high islands of the Society archipelago. The Marquesas Islands chain (Craig et al. 2001), with the putative hotspot to the southeast, comprises eleven islands from Eiao (average age 5.4 Ma) in the NW, to Fatu Hiva (average age 1.55 Ma) in the SE. Among all prospected islands of the Austral archipelago, Rurutu is the oldest: 12.8–0.3 Ma (see Craig et al. 2001), and Rapa is relatively young 5.0–4.1 Ma (Craig et al. 2001) but the most isolated (500 km from the nearest island Raivavae).

Contrarily to *C. futunensis* n. sp., *C. marquesensis* n. sp. or *C. rapaensis*, respectively endemic to Futuna, the Marquesas and Austral Islands, *C. tupaia* n. sp. has a wide distribution in Polynesia: Upolu (Samoa), Rarotonga (Cook Islands), Rurutu, Tahiti, Moorea, and Huahine (French Polynesia). Its larvae are supposedly transported by the southwestward currents of the gyre to colonize these different lineaments and *C. tupaia* n. sp. is likely to have a greater distribution and reach other islands to the West, like Tonga or Melanesia. Genetic studies are in progress on specimens belonging to the *C. weberi* complex from Fiji, New Caledonia, Vanuatu and Solomon Islands. Since *C. tupaia* n. sp. and *C. rapaensis* occur in sympatry in Rurutu Island but have different distribution areas, there must be biological differences explaining that they are not constrained in the same way by the currents, such as differences in larvae circulation depths between the two species, duration of the marine larval phase, differences in habitat preferences that restrict the distribution. The explication could also be of historical nature, one species having colonised the islands earlier, when the currents and conditions were different than at present, that prevent new species to arrive.

(Figure 8 near here)

Freshwater endemism is well known in Futuna Island with its endemic freshwater Gobiidae (Teleostei) (Keith et al. 2015): *Akihito futuna* Keith, Marquet and Watson, 2008,

Stenogobius keletaona Keith & Marquet, 2006, and *Smilosicyopus sasali* (Keith and Marquet, 2005) and with now an endemic *Caridina* shrimp, *C. futunensis* n. sp.. This endemism could be explained by the position of this island at the South of Vityaz trench, which would be – depending on the geological time – an obstacle to migration of larvae by its depth and by oceanic current variations. Indeed, Futuna (Keith et al. 2013) appeared as strong volcanic activity occurred in the contact zone between the Pacific and the Australian plates, at the South of fossil Vityaz subduction, in the junction area between the Lau and North Fiji basins, near the North Fiji transform zone (Figure 9).

(Figure 9 near here)

The absence of Caridina in the Further East and Further North of Polynesia

The Marquesas Islands represent the eastern limit in Polynesia of the *Caridina weberi* complex with the presence of *C. marquesensis* n. sp.. Further east, no species of *Caridina* occur (see Marquet 1991) as it seems to be absent from Mangareva (Gambier archipelago). Situated 1,600 km from Tahiti (Society archipelago) and 1,060 km from Rapa (Austral archipelago), Mangareva (6.26-5.66 Ma, see Craig et al. 2001), of the Gambier Islands, is a high island with small streams suitable for *Caridina* species, but none has been found so far (Keith et al. 2013). Further north, the Hawaiian Islands are biogeographically the most isolated in the world being about 3,500 to 4,000 km from the high islands of the Marquesas archipelago, but no *Caridina* species occurs in this archipelago. ‘*C. weberi*’ recorded by Devick (1991) as an introduced species, was a misidentification of *Neocaridina denticulata sinensis* (Kemp, 1918) (see Englund and Cai 1999). Among the Atyidae, only the genus *Atyoida* reaches both Mangareva and Hawaii.

Oceanic currents often act as dispersal barriers for organisms with planktonic larval stages (for example Lessios et al. 1999, Teske et al. 2008) and the position of Hawaii within the North Pacific gyre surrounded by westward currents makes it impossible for larvae coming from West Polynesia to reach the archipelago.

According to several authors studying the amphidromous lifecycle of different species, *Caridina gracilipes* De Man, 1892 (Zhang and Sun 1979), *C. gracilirostris* De Man, 1892 (Thomas et al. 1973; Pillai 1975; Heerbrandt and Lin 2006), *C. multidentata* Stimpson, 1860 from Japan (Hayashi & Hamano 1984; Nakahara et al. 2005), *C. typus* H. Milne Edwards, 1837 from Japan (Nakahara et al. 2005), *C. leucosticta* Stimpson, 1860 from Japan (Nakahara et al. 2005), and *C. 'weberi'* from India (Chinnaya 1974) we count 6 to 9 larval stages reared in the laboratory in 15 to 25.5% salt water with a larval development from 9 to 48 days. This short larval duration is related to that of other crustaceans like *Macrobrachium* species. For example, in *Macrobrachium australe* (Guérin-Méneville, 1838), Ito et al. (2002) managed to obtain 13 zoeal stages. The completion of the first 12 stages requires 50 to 69 days but the larvae can then survive to 150 days before dying for failing to find the environmental conditions required for their survival. For *Macrobrachium Lar* (Fabricius, 1798), Atkinson (1977) determined 11 zoeal stages representing a maximum duration of 89 days. Their relatively short larval duration could explain the absence of any *Caridina* in the far North and East of Polynesia. Indeed it does not allow the larvae to cross great distances from Tahiti or Rapa to Mangareva and from Marquesas islands to Hawaii without islands with permanent streams along their migration in this area of the Central Pacific. On the contrary, only robust crustacean species with supposedly long larval durations were able to reach Mangareva or Hawaii such as in genera *Atyoida* or *Macrobrachium* for Mangareva. Furthermore, Central Pacific waters are oligotrophic with little phytoplankton, which does not allow the larvae to get much food. Indeed, situated in 8° and 12° of latitude South, Marquesas archipelago still

benefits from a remnant of equatorial wealth (2 to 4 mmol/m³ of nitrates) but this effect is completely faded south of 15°S; the waters of the whole Tuamotu-Society-Austral archipelagos are oligotrophic with nitrate levels lower than 0.2 mmol/m³ (Rougerie and Wauthy 1993).

The larval durations of the species studied in this work are unknown but are probably different from one to another, judging from the differences in geographical ranges, with endemic species like *C. futunensis* n. sp. or *C. marquesensis* n. sp. having a shorter larval duration (and likely fewer larval stages) than *C. tupaia* n. sp.. It would be interesting to study the larval phases of these species by rearing them in the laboratory in order to clarify these points.

Management and conservation of freshwater crustaceans

This first review of *Caridina weberi* complex in Polynesia gives us an understanding of how diverse and unique its distribution is, with species having a very restricted distribution (*C. futunensis* n. sp. for example, endemic to Futuna Island) in contrast to others, more widely distributed (*C. tupaia* n. sp.). An assessment of the status of freshwater fish in Oceania was made at a Red List workshop held at the IUCN Oceania in September 2011, but crustaceans were not included in this assessment as not enough information is currently available to determine their conservation status. Complementary genetic studies on Palaemonidae and Atyidae in this region could fill this gap. An assessment of the status of freshwater crustaceans in Oceania becomes urgent, particularly for endemic species, by the development of nuisances on this fauna like culverts and fords (that assist with water flow passage across roads), dams (for water supply or electricity generation), weirs (for water abstraction), artificial channels (in urban areas), diversions of rivers by convenience or irrigation.

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References

Adamson, AM. 1935. Non-marine Invertebrate Fauna of the Marquesas (Exclusive of

901 insects). Occas. Pap. B. P. Bish. Mus. 11(10): 1–39.

902 Adamson AM. 1939. Review of the fauna of the Marquesas islands and discussion of its
 903 origin. Occas. Pap. B. P. Bish. Mus. 159: 93p.

904 Atkinson JM. 1977. Larval development of a freshwater prawn, *Macrobrachium lar*
 905 (Decapoda, Palaemonidae), reared in the laboratory. Crustaceana 33(2): 119–132.

906 Bouvier EL. 1925. Recherches sur la morphologie, les variations, la distribution géographique
 907 des crevettes de la famille des Atyidés. (Encyclopédie Entomologique de Roret, Paris,
 908 France.)

909 Cai Y, Anker A. 2004. On a collection of freshwater shrimps (Crustacea; Decapoda; Caridea)
 910 from the Philippines, with descriptions of five new species. Trop. Zool. 17: 233–266

911 Cai Y, Ng PKL. 1999. A revision of the *Caridina serrata* species group, with descriptions of
 912 five new species (Crustacea: Decapoda: Caridea: Atyidae). J. Nat. Hist. 33: 1603–
 913 1638.

914 Cai Y, Ng PKL. 2001. The freshwater Decapod Crustaceans of Halmahera. Indonesia. J.
 915 Crust. Biol. 21(3): 665–695.

916 Cai Y, Ng PKL. 2007. A revision of the *Caridina gracilirostris* De Man, 1892, species group,
 917 with descriptions of two new taxa (Decapoda; Caridea; Atyidae). J. Nat. Hist. 41(25–
 918 28): 1585–1602.

919 Cai Y, Choy S, Ng PKL. 2009. Epigean and hypogean freshwater shrimps of Bohol Island,
 920 central Philippines (Crustacea: Decapoda: Caridea). Raffles B. Zool. 57(1): 65–89.

921 Cai Y, Shokita S. 2006. Atyid shrimps (Crustacea: Decapoda: Caridea) of the Ryukyu Islands,
 922 southern Japan, with descriptions of two new species. J. Nat. Hist. 40(38–40): 2123–
 923 2172.

924 Chinnaya B. 1974. The embryonic and larval development of *Caridina weberi* De Man in the
 925 laboratory (Decapoda, Atyidae). Broteria. 43:119–134.

926 Coleman CO. 2003. 'Digital inking': How to make perfect line drawings on computers. Org.
 927 Divers. Evol. 3(Electronic Supplement 4): 1–14.

928 Coleman CO. 2006. Substituting time-consuming pencil drawings in arthropod taxonomy
 929 using stacks of digital photographs. Zootaxa. 1360: 61–68.

930 Covich AP, Palmer MA, Crowl TA. 1999. The role of benthic invertebrate species in
 931 freshwater ecosystems. BioScience. 49: 119–128

932 Craig DA., Currie DC., Joy DA. 2001. Geographical history of the central-western Pacific
 933 black fly subgenus *Inseliellum* (Diptera: Simuliidae: Simulium) based on a
 934 reconstructed phylogeny of the species, hot-spot archipelagoes and hydrological
 935 considerations. J. Biogeogr. 28: 1101–1127

936 Darriba D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: more models, new
 937 heuristics and parallel computing. Nat. Methods. 9(8): 772–772.

938 De Grave S, Smith KG, Adeler NA, Allen DJ, Alvarez F, Anker A, Cai Y, Carrizo SF, Klotz
 939 W, Mantelatto FL, et al. 2015. Dead Shrimp Blues: A Global Assessment of
 940 Extinction Risk in Freshwater Shrimps (Crustacea: Decapoda: Caridea). PLoS ONE
 941 10: e0120198.

942 De Man JG. 1892. Decapoden des Indischen Archipels. In: Weber, M, editor. Zoologische
 943 Ergebnisse einer Reise in Niederländisch Ost-Indien. Leiden (NL): Brill; p. 265–527.

944 Devick WS. 1991. Disturbances and fluctuations in the Wahiawa Reservoir Ecosystem.
 945 Hawaii Division of Aquatic Resource. F-14R-15.

946 Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees.
 947 BMC Evol. Biol. 7(1): 214.

948 Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high
 949 throughput. Nucleic Acids Res. 32(5): 1792.

- 950 Edmondson CH. 1935. Atyidae of Southern Polynesia. Occas. Pap. B. P. Bish. Mus. 10(24):
951 3–40.
- 952 Englund RA, Cai Y. 1999. The occurrence and description of *Neocaridina denticulata sinensis*
953 (Kemp, 1918) (Crustacea: Decapoda: Atyidae), a new introduction to the Hawaiian
954 Islands. Bish. Mus. Occas. Pap. 58: 58–65.
- 955 Esselstyn JA, Evans BJ, Sedlock JL, Anwarali Khan FA, Heaney LR. 2012. Single-locus
956 species delimitation: a test of the mixed Yule–coalescent model, with an empirical
957 application to Philippine round-leaf bats. Proc. R. Soc. B 279 (1743): 3678–3686.
- 958 Ito A, Fujita Y, Shokita S. 2002. Larval stages of *Macrobrachium australe* (Guerin
959 Meneville, 1838) (Decapoda: Palaemonidae), described from laboratory-reared
960 material Crus. Res. 31: 47–72.
- 961 Falvo CA. 2013. Overcoming barriers: the climbing ability and distribution of three species of
962 diadromous shrimp (*A. pilipes*, *C. weberi*, and *Macrobrachium spp.*) on Moorea,
963 French Polynesia. UC Press, Biology and Geomorphology of Tropical islands.
- 964 Feldman C. 1996. Distribution and ecology of freshwater shrimp (Decapoda) in the Opunohu
965 River, Moorea, French Polynesia. Biol. Geomor. Trop. Is. 5:151–162.
- 966 Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap.
967 Evolution, 39(4), 783–791.
- 968 Fossati O, Marquet G. 1998. Faune des eaux douces des îles Marquises: clé des
969 macroinvertébrés et des poissons. Paris: MNHN.
- 970 Fossati O, Mosseron M, Keith P. 2002. Distribution and habitat utilization in two atyid
971 shrimps (Crustaceae: Decapoda) in rivers of Nuka-Hiva Island (French Polynesia).
972 Hydrobiologia. 472:197–206
- 973 Guindon S, Gascuel O. 2003. A simple, fast, and accurate algorithm to estimate large
974 phylogenies by maximum likelihood. Syst. Biol. 52(5): 696–704.

975 Hayashi KI, Hamano T. 1984. The complete larval developpment of *Caridina japonica* De Man
 976 (Decapoda, Caridea, Atyidae) reared in the laboratory. Zool. Sci. 1: 571–589.

977 Heerbrandt TC, Lin J. 2006. Larviculture of red front shrimp, *Caridina gracilirostris*
 978 (Atyidae, Decapoda). J. World Aquacult. Soc. 37(2): 186–190.

979 Karge A, Klotz W. 2007. Süßwassergarnelen aus aller Welt. Etllingen (DE): Dähne Verlag.

980 Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A,
 981 Markowitz S, Duran C, et al. 2012. Geneious Basic: an integrated and extendable
 982 desktop software platform for the organization and analysis of sequence data.
 983 Bioinformatics, 28(12): 1647–1649.

984 Keith P, Vigneux E. 2002. Revue des crustacés Atyidae et Palaemonidae d'eau douce de
 985 Polynésie française avec description d'une nouvelle espèce de *Macrobrachium*. B. Fr.
 986 Pêche Piscic. 364: 121–145.

987 Keith P, Vigneux E, Marquet, G. 2002. Atlas des poissons et des crustacés d'eau douce de
 988 Polynésie française. Paris (FR): MNHN.

989 Keith P, Marquet G. 2011. Poissons et crustacés d'eau douce de Wallis et de Futuna. Paris
 990 (FR): Société Française d'Ichtyologie.

991 Keith P, Marquet G, Gerbeaux P, Vigneux E, Lord C. 2013. Poissons et crustacés d'eau douce
 992 de Polynésie. Taxonomie, écologie, biologie et gestion. Paris (FR): Société Française
 993 d'Ichtyologie.

994 Keith P, Lord C, Maeda K. 2015. Indo-Pacific Sicydiine Gobies. Biodiversity, life traits and
 995 conservation. Paris (FR): Société Française d'Ichtyologie.

996 Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis
 997 Version 7.0 for Bigger Datasets. Mol. Biol. Evol. 33(7): 1870–1874.

998 Lessios HA, Kessing BD, Robertson DR, Paulay G. 1999. Phylogeography of the pantropical
 999 sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution* 53(3):
 1000 806–817.

1001 Marquet G. 1988. Les eaux intérieures de la Polynésie française. Principales caractéristiques
 1002 physiques, chimiques et biologiques [dissertation]. Paris (FR): Paris VI University.

1003 Marquet G. 1991. Freshwater crustaceans of French Polynesia: Taxonomy, distribution and
 1004 biomass (Decapoda). *Crustaceana*. 61(2): 126–140.

1005 Martinez E, Ganachaud A, Lefevre J, Maamaatuaiahutapu K. 2009. Central South Pacific
 1006 thermocline water circulation from a high-resolution ocean model validated against
 1007 satellite data: Seasonal variability and El Nino 1997–1998 influence. *J. Geophys. Res.*
 1008 114: C05012.

1009 Mary N, Dutartre A, Keith P, Marquet G, Sasal P. 2006. Biodiversité des eaux douces de
 1010 Wallis et Futuna, Mission d'octobre 2004. Paris (FR): Ministère de l'Outre-Mer.

1011 Mazancourt V de, Marquet G, Keith P. 2017. The ‘Pinocchio-shrimp effect’: First evidence of
 1012 rostrum length variation with the Environment in *Caridina* H. Milne Edwards, 1837
 1013 (Crustacea: Decapoda: Atyidae). *J. Crus. Biol.* 37(3): 249–257.

1014 Mazancourt V de, Klotz W, Marquet G, Mos B, Rogers DC, Keith P. 2019. The complex
 1015 study of complexes: The first well-supported phylogeny of two species complexes
 1016 within genus *Caridina* (Decapoda: Caridea: Atyidae) sheds light on evolution,
 1017 biogeography, and habitat. *Mol. Phylogenet. Evol.* 131: 164–180

1018 Mennesson M. 2016. Taxonomie, Phylogénie et Dispersion du genre *Eleotris* (Teleostei :
 1019 Gobioidae : Eleotridae) dans l’Indo-Pacifique [dissertation]. Paris (FR): Muséum
 1020 national d'Histoire naturelle.

1021 Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for
 1022 inference of large phylogenetic trees. In: Proceedings of the Gateway Computing
 1023 Environments Workshop (GCE), New Orleans. p. 1–8.

1024 Monaghan MT, Wild R, Elliot M, Fujisawa T, Balke M, Inward DJG, Lees DC, Ranaivosolo
 1025 R, Eggleton P, Barraclough TG, Vogler AP. 2009. Accelerated species inventory on
 1026 Madagascar using coalescent-based models of species delineation. *Syst. Biol.* 58:
 1027 298–311.

1028 Nakahara Y, Hagiwara A, Miya Y, Hirayama K. 2005. Larval rearing of three amphidromous
 1029 shrimps species (Atyidae) under different feeding and salinity conditions. *Aquacult.*
 1030 *Sci.* 53(3): 305–310.

1031 Page TJ, Choy S, Hughes JM. 2005. The taxonomic feedback loop: symbiosis of morphology
 1032 and molecules. *Biol. Letters.* 1: 139–142.

1033 Page TJ, Rintelen K von, Hughes JM. 2007a. Phylogenetic and biogeographic relationships of
 1034 subterranean and surface genera of Australian Atyidae (Crustacea: Decapoda: Caridea)
 1035 inferred with mitochondrial DNA. *Invertebr. Syst.* 21(2): 137–145.

1036 Page TJ, Rintelen K von, Hughes JM. 2007b. An island in the stream: Australia's place in the
 1037 cosmopolitan world of Indo-West Pacific freshwater shrimp (Decapoda: Atyidae:
 1038 *Caridina*). *Mol. Phyl. Evol.* 43(2): 645–659.

1039 Page TJ, Hughes JM. 2011. Neither molecular nor morphological data have all the answers;
 1040 with an example from *Macrobrachium* (Decapoda: Palaemonidae) from Australia.
 1041 *Zootaxa.* 2874: 65–68.

1042 Palumbi SR. 1996. Nucleic acids II: the polymerase chain reaction. In: Hillis DM, Mable BK,
 1043 Moritz C, editors. *Molecular systematics*. Sunderland (MA): Sinauer Associates. p.
 1044 205–247.

1045 Pelletier B. 2003. Apport des travaux de géologie et de géophysique de l'équipe IRD (Ex.
 1046 ORSTOM) du centre de Nouméa à la compréhension de l'origine et de l'évolution des
 1047 archipels de Wallis et Futuna. Rev. Géol, 137: 81-88.

1048 Pillai NN. 1975. Larval development of *Caridina pseudogracilirostris* reared in the
 1049 laboratory. J. Mar. Biol. Assoc. India. 17: 1–17.

1050 Planes S. 1993. Genetic differentiation in relation to restricted larval dispersal of the convict
 1051 surgeon fish *Acanthurus triostegus* in French Polynesia. Mar. Ecol. Prog Ser. 98: 237–
 1052 246.

1053 Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S,
 1054 Sumlin WD, Vogler AP. 2006. Sequence-based species delimitation for the DNA
 1055 taxonomy of undescribed insects. Syst. Biol. 55: 595–609.

1056 Poupin J. 1998. Crustacea Decapoda and Stomatopoda of French Polynesia. Atoll Res. Bull.
 1057 451:1–62.

1058 Pringle CM, Blake GA, Covich AP, Buzby KM, Finley A. 1993. Effects of an omnivorous
 1059 shrimp in a montane tropical stream: sediment removal, disturbance of sessile
 1060 invertebrates and enhancement of understory algal biomass. Oecologia. 93: 1–11.

1061 Puillandre N, Lambert A, Brouillet S, Achaz G. 2012. ABGD, Automatic Barcode Gap
 1062 Discovery for primary species delimitation. Mol. Ecol. 21, 1864–1877.

1063 Rambaut A, Drummond AJ. 2016. TreeAnnotator v1. 8.3. URL:
 1064 <http://beast.bio.ed.ac.uk/treeannotator>.

1065 Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014. Tracer v1. 6. URL:
 1066 <http://beast.bio.ed.ac.uk/Tracer>.

1067 Resh VH, Barnes JR, Craig DA. 1990. Distribution and ecology of benthic
 1068 macroinvertebrates in the Opunohu river catchment, Moorea, French Polynesia. Ann.
 1069 Limnol. 26(2-3): 195–214.

- 1070 Richard J, Clark PF. 2009. African *Caridina* (Crustacea: Decapoda: Caridea: Atyidae):
 1071 redescrptions of *C. africana* Kingsley, 1882, *C. togoensis* Hilgendorf, 1893, *C.*
 1072 *natalensis* Bouvier, 1925 and *C. roubaudi* Bouvier, 1925 with descriptions of 14 new
 1073 species. Zootaxa. 1995: 1–75.
- 1074 Rintelen K von, Cai Y. 2009. Radiation of endemic species flocks in ancient lakes: systematic
 1075 revision of the freshwater shrimp *Caridina* H. Milne Edwards, 1837 (Crustacea:
 1076 Decapoda: Atyidae) from the ancient lakes of Sulawesi, Indonesia, with the
 1077 description of eight new species. Raffles B. Zool. 57(2): 343–452.
- 1078 Ronquist F, Huelsenbeck JP. 2003. MRBAYES 3: Bayesian phylogenetic inference under
 1079 mixed models. Bioinformatics. 19(12): 1572–1574.
- 1080 Rougerie F, Wauthy B. 1993. L'océanographie du Pacifique Central Sud. Encyclopédie de la
 1081 Polynésie française. Paris (FR): Editions de l'ORSTOM.
- 1082 Roux J, 1928. Notes carcinologiques de l'Archipel Indo-Australien. I. Décapodes macroures
 1083 d'eau douce de l'Archipel Indo-Australien. Treubia 10: 197-216.
- 1084 Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of
 1085 large phylogenies. Bioinformatics. 30(9): 1312–1313.
- 1086 Shokita S. 2003. Atyidae, pp 249–254. In: Nishida M, Shikatani N, Shokita S, editors. *The*
 1087 *flora and fauna of inland waters in the Ryukyu Islands*. Tokyo: Tokai University
 1088 Press. 572 [in Japanese].
- 1089 Teske PR, Papadopoulos I, Newman BK, Dworschak PC, McQuaid CD, Barker NP. 2008.
 1090 Oceanic dispersal barriers, adaptation and larval retention: an interdisciplinary
 1091 assessment of potential factors maintaining a phylogeographic break between sister
 1092 lineages of an African prawn. BMC Evol. Biol. 8(341): 1–14.
- 1093 Tiwari KK, Pillai RS. 1971. Atyid shrimps of the genus *Caridina* H. Milne Edwards, 1837,
 1094 from the Andaman islands (Decapoda, Caridea). Crustaceana. 21(1): 79–91.

1095 Thomas MM, Pillai VK, Pillai NN. 1973. *Caridina pseudogracilirostris* sp. nov. (Atyidae:
 1096 Caridina) from Cochin backwater. J. Mar. Biol. Assoc. India. 15: 871–873.

1097 Vermeij GJ. 1987. The dispersal barrier in the tropical Pacific: Implications for molluscan
 1098 speciation and extinction. Evolution. 41(5): 1046–1058.

1099 Williams JL. 1999. The feeding ecology and effects of flooding on the tropical freshwater
 1100 shrimp, *Caridina weberi*, (Atyidae). Biol. Geomor. Trop. Is. 8: 183–190.

1101 WoRMS. 2018. *Caridina* H. Milne Edwards, 1837 [in H. Milne Edwards, 1834-1840].
 1102 Accessed at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=240672> on
 1103 2018-05-15

1104 Zhang J, Sun X. 1979. Studies on the larval development of six freshwater prawn species in
 1105 the middle and lower Chang Jiang (Yangtze) Valley. Acta Zool. Sinica. 25: 143–153.

1106 Zhang J, Kapli P, Pavlidis P, Stamatakis A. 2013. A general species delimitation method with
 1107 applications to phylogenetic placements. Bioinformatics, 29(22), 2869-2876.

1108

1109 Table 1. List of the specimens used in the 16S phylogenetic study.

1110 Figure 1. Map of the Polynesian triangle.

1111 Figure 2. Bayesian Inference phylogenetic tree of the specimens studied. Numbers above
 1112 branches indicate BI posterior probabilities, numbers under branches indicate ML bootstrap.

1113 Figure 3. *Caridina futunensis* n. sp. Holotype (MNHN-IU-2018-195; DNA: CA2118), a, b, c
 1114 cephalothorax; d. first pereopod; e. second pereopod; f. third pereopod; g. dactylus of third
 1115 pereopod; h. fifth pereopod; i. dactylus of fifth pereopod; j. preanal carina; k. first pleopod;
 1116 l. second pleopod.

1117 Figure 4. *Caridina marquesensis* n. sp. Paratype (MNHN-IU-2017-71; DNA: CA2071), a.
 1118 first pereopod; b. first pereopod detail of the fingertips; c. second pereopod; d. third
 1119 pereopod; e. fifth pereopod; f. dactylus of fifth pereopod; g. dactylus of third pereopod; h.

1120 cephalothorax; i. preanal carina; k. uropodal diaeresis; l. telson. Paratype (MNHN-IU-2017-
 1121 69; DNA: CA2075), j. eggs. Holotype (MNHN-IU-2017-66), m. first pleopod; n. second
 1122 pleopod.

1123 Figure 5. *Caridina tupaia* n. sp. Holotype (MNHN-IU-2018-260; DNA: CA2058), a. first
 1124 pereopod; b. second pereopod; c. third pereopod; d. fifth pereopod; e. dactylus of fifth
 1125 pereopod; f. dactylus of third pereopod; g. cephalothorax; h. preanal carina; j. uropodal
 1126 diaeresis; k. telson. Paratype (MNHN-IU-2018-268), i. eggs. Paratype (MNHN-IU-2018-261;
 1127 DNA: CA1048), l. first pleopod; m. second pleopod.

1128 Figure 6. *Caridina rapaensis*. (MNHN-IU-2016-11771; DNA: CA2115), a. first pereopod; b.
 1129 first pereopod, detail of the fingertips; c. second pereopod; d. third pereopod; e. fifth
 1130 pereopod; f. dactylus of fifth pereopod; g. dactylus of third pereopod; h. cephalothorax; i.
 1131 preanal carina; k. uropodal diaeresis; l. telson. (MNHN-IU-2015-1921: ♀ ovig, 4.0 mm), j.
 1132 eggs. (MNHN-IU-2015-1921: ♂, cl 2.9 mm), m. first pleopod; n. second pleopod.

1133 Figure 7. Live colouration of the species: A, B. *C. tupaia* n. sp.. C. *C. marquesensis* n. sp.. D,
 1134 E. *C. rapaensis*. F. *C. futunensis* n. sp.. G. Habitat of *C. futunensis* n. sp. in Futuna. Credits:
 1135 A, B, C: G. Marquet; D, E: E. Vigneux; F: V. de Mazancourt; G: A. Dutartre.

1136 Figure 8. Distribution map of the four species studied with oceanic currents of Southern
 1137 Polynesia (from Martinez et al 2009) represented: SEC. South Equatorial Current. SECC.
 1138 South Equatorial Countercurrent. MCC. Marquesas Countercurrent. STCC. South Tropical
 1139 Countercurrent. GYRE. South Pacific Gyre.

1140 Figure 9. Map of the geology of the surroundings of Futuna Island (adapted from Pelletier
 1141 2003).