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# Integrative taxonomy study of brackish water crabs of the genus *Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) from Polynesia, with description of two new species

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1 **Integrative taxonomy study of brackish water crabs of the genus**  
2 ***Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) from Polynesia, with**  
3 **description of two new species.**

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6

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14

15 **Abstract**

16 In the present contribution, five species of *Ptychognathus* Stimpson, 1858 are reported from  
17 Polynesia: *P. crassimanus* Finnegan, 1931, *P. easteranus* Rathbun, 1907, *P. riedelii* (A.  
18 Milne-Edwards, 1868) and two new species. The first new species named *P. ngankeeae* sp.  
19 nov. is close to *P. barbatus* (A. Milne-Edwards, 1873) from New Caledonia which is here  
20 redescribed for comparison purposes. The second new species named *P. similis* sp. nov. is  
21 close to *P. hachijoensis* Sakai, 1955.

22

23 **Key words:** genetic, morphology, DNA, COI, 16S

24

25 **Introduction**

26 *Ptychognathus* Stimpson, 1858 is a genus that encompasses 28 species, all of which are  
27 indigenous to the Indo-West Pacific region (DecaNet 2023). These crabs are commonly found  
28 inhabiting the undersides of stones or the gaps between pebbles along river mouths and in  
29 coastal areas influenced by freshwater. (Osawa & Ng 2006). Until recently, the taxonomy of  
30 *Ptychognathus* species was mainly based on morphological characters, with species that are  
31 very close morphologically. According to recent studies (Hsu & Shih 2020; Komai *et al.*  
32 2021), an integrative and standardized approach is necessary to resolve the taxonomy of this

33 genus, using informative morphological features and molecular characters (Page *et al.* 2005;  
34 Page & Hughes 2011; de Mazancourt *et al.* 2017). To illustrate this problem, we focus here on  
35 *Ptychognathus* species from the lower course of Polynesian rivers.

36 Polynesia forms a triangle between Hawaii, New Zealand and Easter Island (Figure 1).  
37 We can distinguish Northern Polynesia (Hawaii), Western Polynesia (Tuvalu, Tokelau, Wallis  
38 and Futuna, Tonga, Niue, Independent State of Samoa, Cook Islands) and Eastern Polynesia  
39 (French Polynesia, Pitcairn Island and Eastern Island). The occurrence of the genus  
40 *Ptychognathus* in Polynesia has been reported by Rathbun (1907), Finnegan (1931), Marquet  
41 (1988, 1991, 1993), Keith *et al.* (2002), Keith & Marquet (2011), Keith *et al.* (2013), Poupin  
42 (1996, 2003, 2005), Poupin & Juncker (2008, 2010), Poupin & Corbari (2012) and Salvat *et*  
43 *al.* (2016). Streams of Austral, Society and Marquesas Islands (French Polynesia) were  
44 prospected by the Muséum national d'Histoire naturelle (MNHN, Paris) from 1983 to 2001  
45 and recently in September and October 2017; rivers of Futuna (Territory of Wallis and Futuna  
46 islands) in October 2004; rivers of Rarotonga (Cook islands) in July 2010; rivers of Upolu  
47 (Independent State of Samoa) in July 2008, February 2013, July 2014 and Savai (Independent  
48 State of Samoa) in July 2014. Streams of Austral, Society and Marquesas Islands (French  
49 Polynesia) were prospected by Poupin from 1995 to 2012 and rivers of Futuna in October,  
50 2007. One of the aims of the MNHN is to carry out faunistic inventories of rivers in tropical  
51 islands in order to establish a better protection of these fragile ecosystems and, in this context,  
52 to clarify the taxonomy of poorly known organisms. As we collected more and more  
53 specimens from different Polynesian islands, we started to raise doubts regarding the exact  
54 identity of some *Ptychognathus* species in this area. The purpose of this study, therefore, is to  
55 re-analyze the specimens of these *Ptychognathus* species in Polynesia by using an integrative  
56 taxonomic approach and to assess the validity of these species and their geographical  
57 distributions in our studied area.

58

## 59 **Material and methods**

60 Specimens from Polynesia were collected by electrofishing (portable Dekka 3000 electric  
61 device, Germany or SAMUS 1000, Poland: <http://www.electro-fisher.net/>) or by hand. All  
62 material preserved in 75–95% alcohol has been deposited in the collections of the Muséum  
63 national d'Histoire naturelle in Paris (MNHN). Additional specimens were examined from  
64 Strasbourg Zoological Museum (MZS), National Museum of Natural History, Washington

65 D.C. (USNM) and from Naturalis Biodiversity Center, Leiden (RMNH). Specimens were  
66 measured using a digital slide-caliper (Mitsutoyo IP 66) to the nearest 0.1 mm.

67

### 68 *Morphological analyses*

69 Sizes of the specimens are indicated as carapace length (CL) and carapace width (CW) in  
70 mm, measured from the midpoint of the front to the midpoint of the posterior carapace margin  
71 and along the greatest width, respectively; G1 = male first gonopod; P2–P5 first to fourth  
72 ambulatory legs (pereiopods). Cheliped palm length measured dorsally from the insertion of  
73 the dactylus to the articulation with the carpus.

74

### 75 *DNA extraction, amplification and sequencing*

76 Molecular analyses were realized on mitochondrial DNA, the cytochrome oxidase subunit 1  
77 (COI) and the 16S ribosomal RNA (16S) fragments, to differentiate more finely each  
78 specimen by species and location by genomic difference. A total of 26 specimens of  
79 *Ptychognathus* were genetically studied (Table 1).

80 Total DNA was extracted from leg muscle samples using the NucleoSpin 96 Tissue  
81 Core (Macherey-Nagel) protocol. For each sample, PCR reactions contained: 15.44 µl of  
82 H<sub>2</sub>O, 2 µl of Taq buffer (15 mM + MgCl<sub>2</sub>), 1 µl of DMSO (1 ng/ml), 1 µl of BSA, 0.8 µl of  
83 dNTP (6.6 mM), 0.32 µl of Forward primer (16Sar-Lmod:  
84 TACTTCTGCCTGTTTATCAAAA; LCO1490:  
85 GGTCAACAAATCATAAAGATATTGG) and 0.32 µl of Reverse primer  
86 (16Sbmod:GGTCTGAACTCAAATCATGTAAA;HCO2198: TAAACTTCAGGGTGAC-  
87 CAAAAATCA), both at 10 pM, 0.12 µl of Taq polymerase (Qiagen), and 3 µl of purified  
88 DNA from extraction. PCR program was: 4 min at 94°C, then 35 cycles in three steps with 30  
89 sec at 94°C, 40 sec at 42°C (16S) or 48°C (COI) and 1 min at 72°C. The program finished  
90 with 7 min at 72°C. PCR products were sequenced using Sanger method in both directions to  
91 minimize mistakes.

92

### 93 *Molecular analysis*

94 Sequences alignments were performed using MEGA 11 (Tamura *et al.* 2021). In addition to  
95 the newly sequenced specimens, published sequences of *Ptychognathus* were retrieved from  
96 GenBank, namely two 16S from Komai *et al.* (2021), the whole COI dataset (25 sequences)  
97 from Hsu & Shih (2020) and 16S and COI sequences from three non-*Ptychognathus* varunid  
98 mitochondrial genomes produced by Xin *et al.* (2018) to serve as outgroups: *Varuna litterata*,  
99 *Helice latimera* and *Hemigrapsus sanguineus*. A multiple alignment was realized between all  
100 sequences with MUSCLE algorithm (Edgar, 2004) for each locus separately. The best  
101 substitution model was determined independently using Bayesian Information Criterion in  
102 PartitionFinder (Lanfear *et al.* 2012) for each marker and for each codon position. From this  
103 alignment and with the selected substitution models, a phylogenetic tree is produced by  
104 MrBayes 3.2.7 (Ronquist & Huelsenbeck, 2003), available on CIPRES Science Gateway V3.3  
105 server (Miller *et al.* 2010, <https://www.phylo.org>), running for 10,000,000 generations, a  
106 sampling frequency of 1,000 and a burn in of 10%. Support for nodes was determined using  
107 posterior probabilities calculated by MrBayes. With RaxML-NG (Kozlov *et al.* 2019), another  
108 phylogenetic tree was made by maximum likelihood using the same substitution models.  
109 Robustness of the nodes was assessed using non-parametric bootstrapping (Felsenstein 1985)  
110 with 1,000 bootstrap replicates. After verifying that there were no supported inconsistencies  
111 between topologies from each independent locus, both datasets were concatenated and the  
112 same analyses were performed.

113

## 114 **Results**

### 115 *Molecular analyses*

116 (Table 1)

117 (Figs. 2, 3)

118 The substitution models retained for the analyses were GTR+G+I for 16S, HKY+G for the  
119 COI first codon position, GTR+I for the COI second codon position and F81+I for the COI  
120 third codon position.

121 The molecular analysis of the concatenated (COI + 16S) dataset (Fig. 2) showed 17  
122 well-defined Operational Taxonomic Units (OTUs) in the ingroup. Among the newly  
123 produced sequences 5 OTUs occurred in Polynesia, identified as *Ptychognathus crassimanus*  
124 Finnegan, 1931, *P. easteranus* Rathbun, 1907, *P. riedelii* (A. Milne-Edwards, 1868) and two

125 new species described hereafter. One OTU occurred in New Caledonia, identified as *P.*  
126 *barbatus*, included in the present study for comparison and because of records of that species  
127 from Wallis and Futuna territory.

128 The deep nodes of the tree are poorly resolved, however 4 main supported (PP = 0.94–1)  
129 groups can be distinguished:

- 130 - The first one including only specimens identified as *P. ishii* Sakai, 1939
- 131 - The second one containing 9 species (*Ptychognathus sakaii* Hsu, Shih & Li, 2022, *P.*  
132 *insolitus* Osawa & Ng, 2006, *P. aff. barbatus*, *P. takahashii* Sakai, 1939, *P.*  
133 *hachijoensis* Sakai, 1955, *P. barbatus* (A. Milne- Edwards, 1873), *P. stimpsoni* Hsu &  
134 Shih, 2020 and the two newly described species. Within this group, one of the new  
135 species is sister to *P. hachijoensis* in a clade with *P. takahashii*, whereas the other is  
136 basal to a clade containing *P. barbatus* and *P. stimpsoni* as sister-species. The other  
137 relationships are not resolved.
- 138 - The third one contains *P. pilosus* De Man, 1892 and *P. riedelii*
- 139 - The last one contains *Varuna litterata* (Fabricius, 1798), as sister to a clade comprised  
140 of *P. makii* Hsu & Shih, 2020 and *P. altimanus* (Rathbun, 1914) as sister species on  
141 one hand and *P. crassimanus* and *P. easteranus* on the other.

142 The analysis of the 16S single-locus dataset (Fig. 3) allowed to include two extra species  
143 (*P. glaber* Stimpson, 1858 and *P. lipkei* Ng, 2010) for which the COI had not been sequenced  
144 in addition to the 6 species sequenced for the present study. These two species cluster together  
145 in a poorly supported group as the sister-clade to a well-supported group comprising *P.*  
146 *barbatus* and the two new species. Three other species are clustering in a well-supported  
147 clade: *P. crassimanus* and its sister-species *P. easteranus*, with *P. riedelii* clustering basally to  
148 them.

149

### 150 *Morphological comparison*

151 The morphological study of the specimens confirmed the results of the molecular study in  
152 recognizing each operational taxonomic unit as a distinct species.

153

154 *Taxonomy*

155 **Family Varunidae H. Milne-Edwards**

156 **Genus *Ptychognathus* Stimpson, 1858**

157 ***Ptychognathus crassimanus* Finnegan, 1931**

158 (Fig. 4A–I, 5A–D)

159

160 *Ptychognathus crassimanus* Finnegan, 1931: 549 [type locality: Marquesas Islands (French  
161 Polynesia)]

162 *Ptychognathus crassimanus* – Poupin 1996: 69; 2005: 28 [Lists].

163 *Ptychognathus easteranus* – Poupin 1996: 66 (in part, Marquesas only). – Poupin & Corbari  
164 2012: 8 [Marquesas]. – Salvat *et al.* 2016: 244 [Marquesas]. – All not *P. easteranus* Rathbun,  
165 1907 but *P. crassimanus* Finnegan, 1931.

166

167 **Material examined.** *FRENCH POLYNESIA. Marquesas Islands. Fatu Hiva:* MNHN-IU-  
168 2011-9062, (DNA voucher: CA2646), 1 ♀, 14.0 mm × 11.8 mm, Baie des Vierges, Stn  
169 MQ16-M, 10°27.84'S, 138°39.97'W, January 17–18, 2012, coll. Expedition PAKAIHI I TE  
170 MOANA, Coll. MNHN-AAMP. – MNHN-IU-2022-4082, (DNA voucher: CA2647), 1 ♀  
171 ovig., 13.7 mm × 12.4 mm, same collection data as previous one. *Hiva Oa:* MNHN-IU-2022-  
172 4083, (DNA voucher: CA2668), 1 ♂, 13.0 mm × 12.5 mm, Ta'aoa river, February 13, 2000,  
173 coll. E. Feunteun, P. Keith, E. Vigneux. – MNHN-IU-2022-4084 (DNA voucher: CA2669), 1  
174 ♂, 14.0 mm × 13.2 mm, Ta'aoa river, February 13, 2000, coll. E. Feunteun, P. Keith, E.  
175 Vigneux. – MNHN-IU-2019-180 (DNA voucher: CA2465), 1 ♂, 9.4 mm × 8.4 mm, Ta'aoa  
176 river, 9° 50.101'S, 139° 03.725'W, October 9, 2017, coll. E. Feunteun, P. Gerbeaux, G.  
177 Marquet, P. Tiberghien. – MNHN-IU-2019-183, (DNA voucher: CA2464), 1 ♂, 18.2 mm ×  
178 15.4 mm, Faakuaa river, 09° 46.097'S, 139° 01.768'W, October 10, 2017, coll. E. Feunteun,  
179 P. Gerbeaux, G. Marquet, P. Tiberghien. *Ua Pou:* MNHN-IU-2019-182, (DNA voucher:  
180 CA2466), 1 ♂, 16.2 mm × 13.8 mm, Hakahetau river, 09° 21.600'S, 1140° 06.313'W,  
181 October 16, 2017, coll. E. Feunteun, P. Gerbeaux, G. Marquet, P. Tiberghien. – MNHN-IU-  
182 2022-4085 (DNA voucher: CA2665), 1 ♂, 9.6 mm × 8.4 mm, Hakahau Bay, February 12,

183 1996, coll. J. Poupin. – MNHN-IU-2022-4086, (DNA voucher: CA2666), 1 ♀ ovig., 9.2 mm  
184 × 8.5 mm, Hakahau Bay, February 12, 1996, coll. J. Poupin.

185

186 **Diagnosis.** Carapace quadrate, dorsal surface smooth and flat. Front broad, anterior margin  
187 straight to faintly sinuous, breadth of front 0.37–0.42 times as long as CW. Anterolateral  
188 margin with three teeth including orbital tooth. Third maxillipeds with a auriculiform merus  
189 and an exopod broad, inflated, greatest width 1.3–1.6 times of median width of ischium.  
190 Chelipeds stout, symmetrical in males; Inner angle of carpus with single blunt spine only in  
191 females. Fingers glabrous. Ambulatory legs slender, somewhat compressed laterally. Merus  
192 with single spine on anterior margins near carpus in P2–P4, spine indistinct or absent in P5.

193

194 **Description.** Carapace (Fig. 4A) quadrate, slightly broader than long, 1.1 times as broad as  
195 long, flat, dorsal surface smooth and glabrous; regions poorly defined: presence of clearly  
196 discernible, H-shaped. Front broad, anterior margin faintly sinuous. Breadth of front 0.37–  
197 0.42 times as long as CW, Breadth of fronto-orbit 0.91–0.96 times as long as CW. Upper  
198 border of orbit S-shaped, inner angle with distinct slit. Anterolateral margins and supraorbital  
199 margins lined with small granules, anterolateral margins with tree teeth including orbital  
200 tooth, first tooth most distinct and acute, slightly sloping forward, second and third teeth,  
201 clearly visible, blunt. Posterolateral margins divergent posteriorly, moderately sloping  
202 outwards. Lateral and posterolateral margins furnished with short soft setae.

203 Third maxillipeds (Fig. 4B) with ischium subequal in proximal and distal widths,  
204 lateral margin concave, ventral surface with longitudinal median ridge. Merus very broad,  
205 with antero-lateral angle strongly inflated, auriculiform; ventral surface with oblique ridge on  
206 mesial part. Exopod broad, inflated, greatest width 1.4–1.6 times (male), 1.3–1.4 (female) of  
207 median width of ischium.

208 Male chelipeds (Fig. 4C) symmetrical, not granular at all. Merus longer than broad  
209 (length to width ratio 1.8–2.1, anterior and posterior proximal margins with long soft setae,  
210 posterior distal margins bluntly carinate. Carpus strongly inflated, slightly longer than wide  
211 (length to width ratio 1.0–1.2); anterior distal angle with single blunt spine only in females.  
212 Palm very much inflated (*crassimanus* means stout palm), outer surface smooth, without  
213 distinct granules; inner surface glabrous. Fingers glabrous. Dactylus about as long as palm,



214 terminating in small, hoof shaped corneous claw, bearing 8 to 12 small teeth , pollex with  
215 only faint indication of longitudinal groove, with 4 to 8 more conical teeth, larger than those  
216 of dactylus. No pulvinus at base of fingers.

217 Female chelipeds (Fig. 4D, 4E) distinctly smaller than those of male, chela much  
218 narrower than that of male. Palm not strongly inflated; movable finger distinctly shorter than  
219 palm. Carpus with small blunt spine at inner distal angle (Fig. 4E). Narrow hiatus between  
220 fingers. Pollex with ridge consisting of large granules toward palm.

221 Ambulatory legs (P2 to P5 pereopods), slender, somewhat compressed laterally; P4  
222 longest (male: length 1.4–1.9 times carapace width, female: length 1.2–1.4 times carapace  
223 width); P5 shortest. Meri elongated, subrectangular in lateral view. Merus with single spine  
224 on anterior margins near carpus in P2–P4, spine indistinct or absent in P5. Anterior margins of  
225 meri of P2, P3 P4 and P5 with long soft setae; posterior margins glabrous. Anterior border of  
226 carpus with dense short setae, posterior margins glabrous. Propodus with dense short setae on  
227 anterior margins and dense short setae with sparse long setae on posterior margins. Dactylus  
228 terminating in subacute corneous claw, with dense short setae on anterior and posterior  
229 margins; ventral surface with rows of short setae. P3 (Fig. 4F) with merus 3.2–3.9 as long as  
230 wide, carpus 1.5–2.1 as long as wide, propodus 2.1–2.3 as long as wide, dactylus 3.7–5.2 as  
231 long as wide, dactylus 1.0–1.2 times as long as propodus. P5 (Fig. 4G) with merus 2.2–2.8 as  
232 long as wide, carpus 1.6–2.5 as long as wide, propodus 1.2–1.6 as long as wide, dactylus 2.5–  
233 3.0 as long as wide, dactylus 0.7–0.9 times as long as propodus.

234 Male pleon (Fig. 4H) narrow, broadly triangular, nearly smooth, distinctly narrowed at  
235 base of telson; margins covered with short setae, setae on margins of telson longer; tongue  
236 shaped, terminal margin broadly rounded. Length 1.0–1.2 times basal breadth, 1.1–1.3 times  
237 long as sixth somite, sixth somite 1.1–1.4 times longer than fifth somite.

238 Female pleon (Fig. 4I, 5C) very broad, covering most of thoracic sternum; telson  
239 broadly subtriangular, terminal margin broadly rounded, 0.25 length of basal breadth, 0.8–0.9  
240 times longer than sixth somite, sixth somite 1.0–1.2 times longer than fifth somite, measured  
241 on midline. Small round eggs 0.25–0.31 mm in diameter.

242 Male G1 (Fig. 4J) slender, 8 times as long as wide, slightly curving dorsally; tip  
243 bluntly rounded, forming short chitinous structure; subdistal lobe obtuse, partially obscured  
244 by stiff setae.

245

246 **Colouration in life.** The colour of the carapace (Fig. 5A) is bluish brownish; the chelipeds  
247 (Fig. 5B) are bluish brownish on their superior part and orange on their inferior part. The  
248 fingers tips are whitish. The ambulatory legs are bluish brownish with orange parts.

249

250 **Size.** This is a medium-sized species, the largest male specimen examined is 18.2 mm × 15.4  
251 mm and the largest female 14.0 mm × 11.8 mm.

252

253 **Habitat.** This species is found in brackish water, near estuaries (Fig. 5D).

254

255 **Distribution.** *Ptychognathus crassimanus* Finnegan, 1931 (Fig. 6) is endemic to the  
256 Marquesas Islands (French Polynesia).

257

258 **Remarks.** This species looks like *P. easteranus*, *P. makii* Hsu & Shih, 2020 and *P. altimanus*  
259 (Rathbun, 1914) by its broad front, anterolateral margins of carapace with 3 teeth clearly  
260 visible, its P2–P4 merus with a single small spine on anterior margin near carpus. *P.*  
261 *crassimanus* differs from *P. altimanus* by having a shorter frontal region (vs longer) and  
262 posterolateral margins of carapace distinctly divergent posteriorly (vs almost parallel, not  
263 divergent posteriorly) (Naruse *et al.* 2005, fig. 1A). It differs from *P. makii* by having fewer  
264 teeth on the dactylus 8–12 (vs 15) and on the pollex 4–8 (vs 10) (see Hsu & Shih 2020: Fig.  
265 3D) and merus of ambulatory legs with their posterior margins glabrous (vs with short setae  
266 densely and long setae sparsely (see Hsu & Shih 2020: Fig. 3F). *P. crassimanus* differs from  
267 *P. easteranus* by its stouter P5 dactylus 2.5–3.0 as long as wide (vs 3.0–3.9) and its propodus  
268 0.7–1.1 times as long as dactylus (vs 0.9–1.4).

269 For the present study, the type specimen preserved in the Natural History Museum,  
270 London (Catalogue no. NHM 1932.12.19.221) was not examined.

271

272 ***Ptychognathus easteranus* Rathbun, 1907**

273 (Figs. 7A–I, 8A–B, 16A, B, D)

274

275 *Ptychognathus easterana* Rathbun, 1907: 31, pl. 2, fig. 4, pl. 7: 4,4a; [type locality: Easter  
276 Island]

277 *Ptychognathus easteranus* - Tesch, 1918: 86; Garth: 1973; Poupin, 2003: 31; Keith *et al.*,  
278 2002: 70–71 (partim); 2013: 122–123 (partim); Poupin & Juncker, 2010: 74–75.

279 Not *Ptychognathus easteranus* – All Marquesas Islands records, attributed herein to *P.*  
280 *crassimanus* (see under that species).

281 *Ptychognathus intermedius* – Ortmann, 1894: 711 (Tahiti) – Not *Ptychognathus intermedius*  
282 (De Man, 1879)

283

284 **Material examined.** Type material: Holotype: *CHILE. Easter Island.* Holotype, 1 ♂, 10.8  
285 mm × 12.6 mm, coll. R/V Albatross, December 20, 1904, USNM 32845 (Fig. 16D).

286 Other material: *COOK ISLANDS. Rarotonga* (no specimens collected, observations  
287 only): Avana river, station 7, 21°14.808'S, 159°43.796'W, July 13, 2010. – Aratiu river,  
288 21°12.562'S, 159°47.280'W, July 14, 2010. – Takavainé river, 21°12.562'S, 159°46.485'W,  
289 July 14, 2010. – Murivai river, 21°14.802'S, 159°49.726'W, July 15, 2010. *FRENCH*  
290 *POLYNESIA. Gambier archipelago. Mangareva:* MNHN-IU-2022-4087 (DNA voucher:  
291 CA2670), 1 ♂, 15.0 mm × 12.2 mm. – MNHN-IU-2022-4088 (DNA voucher: CA2671), 1  
292 ♀ ovig, 9.4 mm × 7.5 mm. – MNHN-IU-2022-4089, 8 ♂, 8.4 mm – 13.9 mm × 7.2 mm –  
293 11.9 mm. – 2 ♀ ovig, 8.4 mm – 8.5 mm × 7.0 mm – 7.1 mm. *Austral archipelago. Rapa:*  
294 MNHN-IU-2022-4090 (DNA voucher: CA2654), 1 ♂, 13.5 mm × 12.1 mm. – MNHN-IU-  
295 2022-4091, 1 ♂, 14.3 mm × 12.7 mm (DNA voucher: CA2655). – MNHN-IU-2022-4092, 5  
296 ♂, 10.7 mm – 13.7 mm × 9.1 mm – 11.8 mm. – 5 ♀, 6.2 mm – 9.1 mm × 5.6 mm – 8.1  
297 mm. – 1 ♀ ovig, 11.4 mm × 9.7 mm, Ahurei Bay, November 8, 2002, coll. J. Poupin. –  
298 MNHN-IU-2022-4093, 3 ♂, 8.0 mm – 14.7 mm × 7.4 mm – 14.2 mm, July 2001, coll. J.C.  
299 Guéry, G. Marquet. – MNHN-IU-2022-4094 (DNA voucher: CA2672), 1 ♂, 11.1 mm ×  
300 10.5 mm. – MNHN-IU-2022-4095 (DNA voucher: CA2673), 1 ♂, 9.4 mm × 8.4 mm. – 7 ♂  
301, 9.8 mm – 12.2 mm × 8.3 mm – 10.6 mm. – 3 ♀, 6.9 mm – 8.1 mm × 5.8 mm – 7.01 mm,  
302 Ahurei Bay, March 19–21, 1995, coll. J. Poupin. – MNHN-IU-2022-4096, 8 ♂, 7.1 mm –

303 14.0 mm × 6.3 mm – 12.4 mm. – 2 ♀ ovig, 10.8 mm – 12.5 mm × 9.9 mm – 11.2 mm. – 4  
304 ♀, 6.6 mm – 8.8 mm × 5.8 mm – 7.4 mm, November 8, 2002, coll. J. Poupin. – MNHN-IU-  
305 2022-4097 (DNA voucher: CA2667), 1 ♂, 13.7 mm × 14.6 mm. – MNHN-IU-2022-4098, 3  
306 ♂, 8.4 mm – 14.0 mm × 7.2 mm – 11.3 mm. – 2 ♀, 7.9 mm – 11.6 mm × 7.3 mm – 10.5  
307 mm, July 2001, coll. J. C. Guéry & G. Marquet. *Rurutu*: MNHN-IU-2019-179 (DNA  
308 voucher: CA2478), 1 ♂, 14.9 mm × 12.2 mm. – MNHN-IU-2022-4099, 4 ♂, 8.1 mm – 13.8  
309 mm × 6.5 mm – 11.2 mm. – 3 ♀, 8.3 mm – 10.41 mm × 7.3 mm – 9.0 mm, "two rivers,"  
310 July 14, 2007, coll. T. Robinet. *Society Archipelago. Tahiti*: MNHN-IU-2022-4100, 10 ♂,  
311 6.4 mm – 15.4 mm × 5.7 mm – 13.8 mm, Papenoo river, sample 11, February 6, 2019, coll.  
312 V. Mazel. – MNHN-IU-2022-4101 (DNA voucher: CA2717), 1 ♂, 17.1 mm × 14.5 mm. –  
313 MNHN-IU-2022-4102, 6 ♂, 8.4 mm – 12.4 mm × 7.6 mm – 11.1 mm. – 2 ♀, 8.5 mm – 9.1  
314 mm × 7.5 mm – 8.1 mm, Papenoo river, sample 9, February 7, 2019, coll. V. Mazel. –  
315 MNHN-IU-2022-4103 (DNA voucher: CA2716), 1 ♂, 13.9 mm × 11.7 mm, Papenoo river,  
316 sample 1, January 28, 2020, coll. V. Mazel. – MNHN-IU-2022-4104, 2 ♂, 9.4 mm – 12.4  
317 mm × 8.7 mm – 11.2 mm. – 3 ♀, 7.3 mm – 9.2 mm × 6.7 mm – 8.1 mm, Papenoo river,  
318 sample 5, January 26, 2020, coll. V. Mazel. – MNHN-IU-2022-4105, 2, 14.0 mm – 15.0 mm  
319 × 11.9 mm – 11.9 mm, Papenoo river, sample 4, January 24, 2020, coll. V. Mazel. MNHN-  
320 IU-2022-4106, 7 ♂, 8.3 mm – 15.3 mm × 7.5 mm – 14.2 mm. – 2 ♀, 6.5 mm – 8.9 mm ×  
321 5.4 mm – 7.7 mm, Papenoo river, sample 9, January 22, 2020, coll. V. Mazel. – MNHN-IU-  
322 2016-11891, 1 ♂, 9.6 mm × 12.5 mm and 1 ♀, 14.8 mm × 12.5 mm, Papenoo river,  
323 sample 2, March 11, 2019, coll. V. Mazel. – MNHN-IU-2022-4107, 1 ♂, 13.5 mm × 11.4  
324 mm, Papenoo river, sample 1, January 12, 2020, coll. V. Mazel. – MNHN-IU-2022-4108, 2  
325 ♂, 8.5 mm – 11.2 mm × 7.6 mm – 10.3 mm, Papenoo river, sample 2, November 11, 2020,  
326 coll. V. Mazel. – MNHN-IU-2016-11889, 1 ♂, 17.2 mm × 14.8 mm, Papenoo river, sample  
327 1, March 12, 2021, coll. V. Mazel. – MNHN-IU-2022-4109 (DNA voucher: CA2645), 1 ♂,  
328 16.5 mm × 14.7 mm. – MNHN-IU-2022-4110, 1 ♂, 6.0 mm × 5.3 mm and 1 ♀, 6.9 mm  
329 × 5.9 mm, Papenoo river, sample 3, March 14, 2021, coll. V. Mazel. – MNHN-IU-2022-  
330 4111, 2 ♂, 13.4 mm – 15.7 mm × 11.8 mm – 13.7 mm, Papenoo river, sample 9, January 11,  
331 2021, coll. V. Mazel. – MNHN-IU-2022-4112, 1 ♂, 12.0 mm × 10.6 mm, Papenoo river,  
332 sample 1, December 18, 2020, coll. V. Mazel. – MNHN-IU-2022-4113 (DNA voucher:

333 CA2644), 1 ♂, 15.0 mm × 12.0 mm, Papenoo river, sample 11, January 15, 2021, coll. V.  
334 Mazel.

335 Comparative material: *Ptychognathus intermedius* De Man, 1879 – Syntype male 55.2  
336 × 46.9 mm, Moluccas (Indonesia), RMNH.CRUS.D.194 (photo only, fig. 16C).

337

338 **Diagnosis.** Carapace quadrate, dorsal surface smooth and flat. Front broad, anterior margin  
339 faintly sinuous, breadth of front 0.37–0.42 times as long as CW. Anterolateral margin with  
340 three teeth including orbital tooth. Third maxillipeds with auriculiform merus and exopod  
341 broad, inflated, greatest width 1.3–1.6 times of median width of ischium. Chelipeds stout,  
342 symmetrical in males; Inner angle of carpus with single blunt spine only in females. Fingers  
343 glabrous. Ambulatory legs slender, somewhat compressed laterally. Merus with single spine  
344 on anterior margins near carpus in P2–P4, spine indistinct or absent in P5.

345

346 **Description.** Carapace (Fig. 7A) quadrate, slightly broader than long, 1.1 times as broad as  
347 long, flat, dorsal surface smooth and glabrous. Regions poorly defined; presence of clearly  
348 discernible, H-shaped. Front broad, anterior margin faintly sinuous. Breadth of front 0.37–  
349 0.42 times as long as CW. Breadth of fronto-orbit 0.89–0.96 times as long as CW. Upper  
350 border of orbit S-shaped, inner angle with distinct slit. Anterolateral margins and supraorbital  
351 margins lined with small granules, anterolateral margins with three teeth including orbital  
352 tooth, first tooth most distinct and acute, slightly sloping forward, second and third teeth,  
353 clearly visible, blunt. Posterolateral margins divergent posteriorly, moderately sloping  
354 outwards. Lateral and posterolateral margins furnished with short soft setae.

355 Third maxillipeds (Fig. 7B) with ischium subequal in proximal and distal widths,  
356 lateral margin concave, ventral surface with longitudinal median ridge. Merus very broad,  
357 with antero-lateral angle strongly inflated, auriculiform; ventral surface with oblique ridge on  
358 mesial part. Exopod broad, inflated, greatest width 1.7–1.9 times (male), 1.4–1.6 (female) of  
359 median width of ischium.

360 Male chelipeds (Fig. 7C) symmetrical, not granular at all. Merus longer than broad  
361 (length to width ratio 1.8–2.0, anterior and posterior proximal margins with long soft setae,  
362 posterior distal margins bluntly carinate. Carpus strongly inflated, slightly longer than wide  
363 (length to width ratio 1.0–1.4); anterior distal angle with single blunt spine only in females.

364 Palm inflated outer surface smooth, without distinct granules; inner surface glabrous. Fingers  
365 glabrous. Dactylus about as long as palm terminating in small, hoof shaped corneous claw,  
366 bearing 8 to 10 small teeth , pollex with 4 to 5 more conical teeth, larger than those of  
367 dactylus. No pulvinus at base of fingers.

368 Female chelipeds (Fig. 7D) distinctly smaller than those of male, chela much narrower  
369 than that of male. Palm not strongly inflated; dactylus distinctly shorter than palm Carpus  
370 with small blunt spine at dorsodistal angle. Narrow hiatus between fingers. Distally numerous  
371 short setae on the fingers. Distinct rows of granules on the fingers and palm.

372 Ambulatory legs (P2 to P5 pereopods), slender, somewhat compressed laterally; P4  
373 longest (male: length 1.4–1.5 times carapace width, female: length 1.5 times carapace width);  
374 P5 shortest. Meri elongated, subrectangular in lateral view. Merus with single spine on  
375 anterior margins near carpus in P2–P4, spine indistinct or absent in P5. Anterior margins of  
376 meri of P2, P3 P4 and P5 with long soft setae; posterior margins with long setae sparsely.  
377 Anterior margins of carpus with dense short setae and long setae sparsely, posterior margins  
378 glabrous. Propodus with dense short setae and sparse long setae on anterior margins and only  
379 dense short setae on posterior margins. Ventral surface with rows of short setae Dactylus  
380 terminating in subacute corneous claw, with dense short setae on anterior and posterior  
381 margins; ventral surface with rows of short setae. P3 with merus (Fig. 7F) 2.8–3.9 as long as  
382 wide, carpus 1.6–2.0 as long as wide, propodus 2.1–2.5 as long as wide, dactylus 3.4–5.9 as  
383 long as wide and 1.1–1.3 times as long as propodus. P5 with merus (Fig. 7G) 2.6–2.9 as long  
384 as wide, carpus 1.5–2.0 as long as wide, propodus 1.4–1.6 as long as wide dactylus 3.0–3.9 as  
385 long as wide and 0.9–1.4 times as long as propodus.

386 Male pleon (Fig. 7H) narrow, broadly triangular, nearly smooth, distinctly narrowed at  
387 base of telson; margins covered with short setae, setae on margins of telson longer; tongue  
388 shaped, terminal margin broadly rounded. Length 1.0–1.1 times basal breadth, 1.1–1.2 times  
389 long as sixth somite, sixth somite 1.1–1.2 times longer than fifth somite.

390 Female pleon (Fig. 7I) very broad, covering most of thoracic sternum, fourth?? somite  
391 broadest, telson broadly subtriangular, terminal margin broadly rounded, 0.29 length of basal  
392 breadth, 1.0 times longer than sixth somite, sixth somite 1.0–1.2 times longer than fifth  
393 somite, measured on midline. Small round eggs 0.27–0.30 mm in diameter.

394 Male G1 (Fig. 7J) slender, 6 times as long as wide, straight; tip slightly acute, forming  
395 short chitinous structure; subdistal lobe obtuse, partially obscured by stiff setae.

396

397 **Colouration in life.** The colour of the carapace (Fig. 8A) is bluish brownish; the chelipeds  
398 (Fig. 8B) are bluish brownish on their superior part and orange on their inferior part. The  
399 fingers tips are whitish. The ambulatory legs are bluish brownish with orange parts.

400

401 **Size.** This is a medium-sized species, the largest male specimen examined measures 17.2 mm  
402 × 14.8 mm and the largest female 14.8 mm × 12.5 mm.

403

404 **Habitat.** In French Polynesia and in Rarotonga, this species (Fig. 8C) is found in brackish  
405 water, near estuary.

406

407 **Distribution.** *Ptychognathus easteranus* occurs (Fig. 6) in Cook Islands (Rarotonga), French  
408 Polynesia (Mangareva in Gambier archipelago; Rapa and Rurutu in Austral archipelago,  
409 Tahiti and Moorea in Society archipelago) and Easter Island.

410

411 **Remarks.** This species looks like *P. crassimanus*, *P. makii* Hsu & Shih, 2020 and *P.*  
412 *altimanus* (Rathbun, 1914) by its broad front, anterolateral margins of carapace with 3 teeth  
413 clearly visible, its P2–P4 meri with single small spine on anterior margin near carpus. *P.*  
414 *easteranus* differs from *P. altimanus* by having a shorter frontal region (vs longer) and  
415 posterolateral margins of carapace distinctly divergent posteriorly (vs almost parallel, not  
416 divergent posteriorly) (Naruse *et al.* 2005, fig. 1A). It differ from *P. makii* by its fewer and  
417 stronger teeth on the fingers: 9–10 for the mobile finger (vs 15: Hsu & Shih 2020: fig. 3D), 4–  
418 5 for the fixed finger (vs 10 Hsu & Shih 2020: fig. 3D). For the difference with *P.*  
419 *crassimanus* see above.

420 Ortmann (1894: 711) has reported a specimen of *Ptychognathus intermedius* (De Man,  
421 1879) from Tahiti. This specimen deposited in Strasbourg Zoological Museum (MZS) has  
422 been reexamined and compared herein with the type specimen of *P. intermedius* (Fig. 16C)  
423 from Moluccas). It appears to be in fact a typical *P. easteranus*, with its type illustrated  
424 alongside in the same figure (fig. 16D). Therefore, *P. intermedius* is removed from the  
425 Polynesian fauna, its distribution being limited to its type locality in Moluccas (Indonesia).

426

427 *Ptychognathus riedelii* (A. Milne-Edwards, 1868)

428 (Fig. 9A–H, 10A–B)

429

430 *Gnathograpsus Riedelii* A. Milne-Edwards, 1868: 182, pl. 27, figs 1–5. [type locality:  
431 Sulawesi (Celebes), Indonesia]

432 *Ptychognathus riedelii riedelii* – De Man, 1892: 323.

433 *Ptychognathus riedelii* – Tesch, 1918: 87; Cai & Ng 2001: 686, fig. 16.

434 *Ptychognathus andamanica* Alcock, 1900: 404, pl. LXV, figs 3, 3a.

435

436 **Material examined.** Type material: *INDONESIA. Sulawesi.* Syntypes: MNHN-IU-2000-3402  
437 (= MNHN-B3402): 1 ♂, dry specimen, 23.2 mm × 20.4 mm, coll. M. Riedel. – MNHN-IU-  
438 2000-3627 (= MNHN-B MNHN-3627): 2 ♂ and 1 ♀, dry specimens, coll. M. Riedel.

439 Other material: *SAMOA. Upolu:* MNHN-IU-2022-4114 (DNA voucher: CA2660): 1  
440 ♂, 26.7 mm × 26.27. – MNHN-IU-2019-8 (DNA voucher: CA2492): 1 ♂, 20.8 mm × 17.9  
441 mm, Pineula river, 14° 01.780'S, 171° 37.003'W, July 25, 2004, 20m a.s.l., coll. P.  
442 Gerbeaux, G. Marquet & P. Keith. *INDONESIA. Papua:* MNHN-IU-2018-2965 (DNA  
443 voucher: CA2491): 1 ♂, 19.5 mm × 16.9 mm, SIG 99. – MNHN-IU-2018-2643 (DNA  
444 voucher: CA2490): 1 ♂, 17.3 mm × 15.1 mm, SIG11. *PAPUA NEW GUINEA. New Britain:*  
445 MNHN-IU-2018-2967 (DNA voucher: CA2456): 1 ♀, 14.2 mm × 12.6 mm, Gavuvu river,  
446 05° 28.733'S, 150° 23.557'E, October 27, 2018, coll. R. Causse, P. Keith, C. Lord, P.  
447 Amick. *SOLOMON ISLANDS. Choiseul:* MNHN-IU-2018-4124 (DNA voucher: CA2489): 1  
448 ♂, 16.2 mm × 14.6 mm. – MNHN-IU-2022-4115: 1 ♂, 13.3 mm × 10.8 mm, Lopakare, 07  
449 ° 01.613'S, 156° 46.567'E, October 20, 2014, coll. P. Gerbeaux, P. Keith, G. Marquet. –  
450 MNHN-IU-2018-4132 (DNA voucher: CA2482): 1 ♂, 22.4 mm × 18.8 mm. – MNHN-IU-  
451 2022-4116: 2 ♂, 10.3–21.0 mm × 9.4–17.8 mm and 2 ♀, 13.7–17.6 mm × 12.7–15.6 mm,  
452 Lopakare, 07° 01.834'S, 156° 45.789'E, October 21, 2014, coll. P. Gerbeaux, P. Keith, G.  
453 Marquet. *Kolombangara:* MNHN-IU-2018-2647 (DNA voucher: CA2483): 1 ♂, 10.0 mm ×



454 8.9 mm, Pointete river, 07° 52.413'S, 157° 07.982'E, November 15, 2015, coll. P. Keith, C.  
455 Lord, G. Marquet. – MNHN-IU-2018-4129 (DNA voucher: CA2486): 1 ♂, 21.3 mm × 16.6  
456 mm, Vanga 1 river, 07° 55.172'S, 156° 57.798'E, November 18, 2015, coll. P. Keith, C.  
457 Lord, G. Marquet. – MNHN-IU-2018-4120 (DNA voucher: CA2488): 1 ♂, 19.2 mm × 17.1  
458 mm. – MNHN-IU-2022-4117: 1 ♂, 11.7 mm × 10.5 mm and 1 ♀, 11.8 mm × 10.7 mm,  
459 Liva river, 08° 03.881'S, 157° 10.421'E, November 11, 2015, coll. P. Keith, C. Lord, G.  
460 Marquet. – MNHN-IU-2018-2651 (DNA voucher: CA2487): 1 ♂, 11.8 mm × 9.6 mm,  
461 Pipiro river, 07° 53.083'S, 157° 08.195'E, November 13, 2015, coll. P. Keith, C. Lord, G.  
462 Marquet. *Vella Lavella*: MNHN-IU-2018-2645 (DNA voucher: CA2484): 1 ♀, 10.8 mm ×  
463 10.0 mm. – MNHN-IU-2022-4118: 1 ♀, 9.7 mm × 9.2 mm, Vala Kadju river, 07° 49.860'S,  
464 156° 42.644'E, October 28, 2016, coll. C. Lord & P. Keith. – MNHN-IU-2018-4128 (DNA  
465 voucher: CA2485): 1 ♂, 18.6 mm × 17.1 mm. – MNHN-IU-2022-4119: 1 ♀, 12.7 mm ×  
466 12.1 mm, Maravai river, 07° 51.703'S, 156° 41.648'E, October 31, 2016, coll. C. Lord & P.  
467 Keith. *VANUATU. Efate*: MNHN-IU-2018-41.768'E (DNA voucher: CA2493): 1 ♂, 20.1  
468 mm × 16.7 mm, Epaule river, 17° 33.992'S, 168° 27.609'E, February 4, 2010, coll. P.  
469 Feutry, P. Keith, D. Kalfatak, C. Lord, L. Taillebois. *Pentecost*: MNHN-IU-2019 (DNA  
470 voucher: CA2494): 1 ♂, 17.6 mm × 15.1 mm. – MNHN-IU-2022-4120: 2 ♂, 12.1–14.9  
471 mm × 11.1–13.0 mm, Bay Omo river, January 26, 2010, coll. P. Feutry, P. Keith, D.  
472 Kalfatak, C. Lord, L. Taillebois. *Santo*: MNHN-IU-2022-4121 (DNA voucher: CA2456): 1  
473 ♂, 14.6 mm × 12.8 mm. – MNHN-IU-2022-4122 (DNA voucher: CA2457): 1 ♀, 14.6 mm  
474 × 12.8 mm. – MNHN-IU-2022-4123: 1 ♀, 14.9 mm × 13.0 mm, Sarataka river, 15°  
475 30.060'S, 167° 9.259'W, July 25, 2003, coll. D. Kalfatak, P. Keith & G. Marquet.

476

477 **Diagnosis.** Carapace quadrate, dorsal surface smooth and flat. Front broad, anterior margin  
478 slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third  
479 maxilliped merus, with antero-lateral angle strongly inflated, auriculiform, exopod, 1.6–2.6  
480 times broader than ischium. Chelipeds large, glabrous, symmetrical in males, fingers with a  
481 small tuft of setae at tips of pollex. Ambulatory legs with margins setose.

482

483 **Description.** Carapace (Fig. 9A) quadrate, slightly broader than long, 1.1 times as broad as  
484 long, flat, dorsal surface smooth and glabrous. Regions poorly defined with usual H-shaped  
485 mark in middle quite distinct. Front broad, sinuous, slightly concave medially. Front broad,  
486 anterior margin faintly sinuous. Breadth of front 0.39–0.45 times as long as CW. Breadth of  
487 fronto-orbit 0.79–0.86 times as long as CW. Upper margin of orbit sinuous. Anterolateral  
488 margins and supraorbital margins lined with small granules, Anterolateral margins each with  
489 3 teeth including orbital tooth; blunt first tooth, largest and more distinct, second and third  
490 teeth, less distinct especially the third. Posterolateral margins divergent posteriorly,  
491 moderately sloping outwards.

492 Third maxillipeds (Fig. 9B) with ischium subequal in proximal and distal widths,  
493 lateral margin concave, ventral surface with longitudinal median ridge. Merus very broad,  
494 with antero-lateral angle strongly inflated, auriculiform; ventral surface with oblique ridge on  
495 mesial part. Exopod very broad, inflated, greatest width 2.1–2.6 times (♂), 1.6–1.9 (♀) of  
496 median width of ischium.

497 Male chelipeds (Fig. 9C) symmetrical, not granular at all. Merus longer than broad  
498 (length to width ratio 1.3–1.7), anterior and posterior margins glabrous, posterior distal  
499 margins bluntly carinate, directed outward. Carpus, unarmed, strongly inflated, slightly longer  
500 than wide (length to width ratio 1.0–1.2). Palm inflated outer surface smooth, without  
501 distinct granules; inner surface glabrous. Fingers glabrous except a very characteristic small  
502 tuft of setae at tip of pollex. Dactylus distinctly longer than palm, terminating in small, hoof  
503 shaped corneous claw, bearing 10 to 12 small teeth. pollex with 5 to 6 more conical teeth,  
504 which are larger than those of the dactylus. No pulvinus at base of fingers;

505 Female chelipeds (Fig. 9D) distinctly smaller than those of male, chela much narrower  
506 than that of male. Dactylus distinctly shorter than palm, terminating in small, hoof shaped  
507 corneous claw. The fingers have smaller and less large teeth. Palm not strongly inflated. Their  
508 outer surface is very reticulate-granular. The outer surface of the palm and pollex is outlined  
509 near its lower border, by a fine raised granular line. Like for the male a very characteristic  
510 small tuft of setae at tips of pollex.

511 Ambulatory legs (P2 to P5 pereopods), slender, somewhat compressed laterally; P4  
512 longest (♂: length 1.4–1.6 times carapace width, ♀: length 1.4–1.5 times carapace width); P5  
513 shortest. Meri elongated, subrectangular in lateral view, unarmed. Anterior margins of merus  
514 of P2, P3 P4 and P5 with long soft setae; posterior margins with sparsely long setae. Anterior

515 margins of carpus with dense short setae, posterior margins glabrous. Propodus with dense  
516 short setae and sparsely long setae on anterior margins and posterior margins. Ventral surface  
517 with rows of short setae. Dactylus terminating in subacute corneous claw, with short setae on  
518 anterior and posterior margins ventral surface with rows of short setae. P3 with merus (Fig.  
519 9E) 3.6–4.2 as long as wide, carpus 1.9–2.1 as long as wide, propodus 1.9–2.6 as long as wide  
520 dactylus 5.5–7.4 as long as wide, dactylus 0.9–1.2 times as long as propodus. P5 with merus  
521 (Fig. 9F) 3.3–3.5 as long as wide, carpus 1.7–2.7 as long as wide; propodus 1.2–2.0 as long as  
522 wide dactylus 3.3–5.1 as long as wide, dactylus 0.6–0.9 times as long as propodus.

523 Male pleon (Fig. 9G) narrow, broadly triangular, nearly smooth, distinctly narrowed at  
524 base of telson; margins covered with short setae, setae on margins of telson longer; tongue  
525 shaped, terminal margin broadly rounded. Length 0.9–1.1 times basal breadth, 0.9–1.0 times  
526 long as sixth somite, sixth somite 1.1–1.2 times longer than fifth somite.

527 Female pleon (Fig. 9H) very broad, covering most of thoracic sternum, four somite  
528 broadest, telson broadly subtriangular, terminal margin broadly rounded, 0.6–0.7 length of  
529 basal breadth, 0.9–1.0 times longer than sixth somite, sixth somite 1.1–1.2 times longer than  
530 fifth somite, measured on midline.

531 Male G1 (Fig. 9I) slender, 6 times as long as wide, slightly curving dorsally; tip  
532 bluntly rounded, forming short chitinous structure; subdistal lobe obtuse, partially obscured  
533 by stiff setae.

534

535 **Colouration in life.** The body (Fig. 10A) is brownish green to dark brown, the chelipeds (Fig.  
536 10B) rather reddish.

537

538 **Size.** This is a large-sized species, the largest male specimen examined is 22.4 mm × 18.8 mm  
539 and the largest non-ovigerous female 14.2 mm × 22.6 mm.

540

541 **Habitat.** Among *Ptychognathus* species, it is a true fresh water species, not collected in  
542 brackish waters.

543

544 **Distribution.** *Ptychognathus riedelii* occurs (Fig. 6) in Indonesia, Philippines, Papua New  
545 Guinea (New Britain), Solomon Islands, Vanuatu and Samoa Independent State (Upolu).

546

547 **Remarks.** This large species is easily recognizable by its very characteristic small tuft of  
548 setae at tips of pollex, both in males and females.

549

550 ***Ptychognathus barbatus* (A. Milne-Edwards, 1873)**

551 (Fig. 11A–H, 12A–B)

552

553 *Gnathograpsus barbatus* A. Milne-Edwards, 1873: 316, pl. 17: 4.

554 *Ptychognathus barbatus* – De Man, 1895: 105; Fransen *et al.*, 1997: 127.

555

556 **Material examined.** Type material: *NEW CALEDONIA*. Syntypes: MNHN-IU-2000-10877  
557 (= MNHN-B10877): 3 ♂ (dry material, mounted on board) 9.0–9.8 mm × 11.0–12.7 mm,  
558 coll. B. Balansa. – MNHN-IU-2000-3395 (= MNHN-B3395): 1 ♂ (dry material), coll. B.  
559 Balansa. – MNHN-IU-2000-3401 (= MNHN-B3401): 2 ♂ (dry material), coll. B. Balansa. –  
560 MNHN-IU-2000-3394 (= MNHN-B3394): 2 ♂ (dry material), ♂ 10.0 mm × 12.0 mm, ♂ 9.6  
561 × 11.6 mm, coll. B. Balansa. – MNHN-IU-2008-10675 (= MNHN-B12605): 1 ♂ (in ethanol,  
562 regenerated dry material), coll. B. Balansa. – RMNH-D192: 1 ♂ (12.3 mm × 10.0 mm), coll.  
563 B. Balansa. – USNM-20308: 3 ♂ (9.5–11.9 mm × 8.0–9.8 mm), 2 ♀ (9.4–9.6 mm × 7.8  
564 mm), coll. B. Balansa.

565 Other material: *NEW CALEDONIA*. MNHN-IU-2019-210 (DNA voucher: CA2467): 1  
566 ♂, 9.6 mm × 8.0 mm, Wadjana waterfall, 22° 17.603'S, 167° 0.859'E, September 13, 2018,  
567 coll. G. Marquet & V. de Mazancourt. – MNHN-IU-2022-4124: 1 ♂, 8.8 mm × 7.7 mm,  
568 Wadjana waterfall, 22° 17.603'S, 167° 0.859'E, September 13, 2018, coll. G. Marquet & V.  
569 de Mazancourt. –MNHN-IU-2017-8250: 3 ♂, 9.4–9.8 mm × 8.0–9.1 mm and 2 ♀, 8.7–9.0  
570 mm × 7.7–7.9 mm, coll. B. Balansa.

571

572 **Diagnosis.** Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior  
573 margin slightly concave medially. Anterolateral margin with three teeth including orbital  
574 tooth. Merus of third maxilliped with antero-external angle broad, exopod, 0.7–1.2 times  
575 broader than ischium. Chelipeds large, symmetrical in males, fingers with a small tuft of setae  
576 at tips of pollex. A single pulvinus at base of fingers. Merus and carpus of ambulatory legs  
577 glabrous.

578

579 **Description.** Carapace (Fig. 11A) subquadrate, slightly broader than long, 1.2 times as broad  
580 as long, flat, dorsal surface smooth and glabrous. Regions poorly defined with the usual H-  
581 shaped mark in the middle quite distinct and epigastric cristae barely visible. Front broad,  
582 anterior margin, divided into two lobes, slightly concave medially. Breadth of front 0.47–0.51  
583 times as long as CW, Breadth of fronto-orbit 0.84–0.90 times as long as CW. Anterolateral  
584 margins and supraorbital margins lined with small granules. Upper margin of orbit weakly  
585 sinuous. Anterolateral margins each with 3 teeth including orbital tooth; first tooth largest and  
586 more distinct, second and third blunt, third tooth indistinct or notch.. Posterolateral margins  
587 divergent posteriorly, moderately sloping outwards. Lateral and posterolateral margins  
588 regularly furnished with short, soft setae.

589 Third maxillipeds (Fig. 11B) with ischium subequal in proximal and distal widths,  
590 lateral margin concave, ventral surface with longitudinal median ridge. Merus with antero-  
591 lateral angle broad; ventral surface with oblique ridge on mesial part. Exopod broad, inflated,  
592 greatest width 0.9–1.2 (♂), 0.7–1.0 (♀) times of median width of ischium.

593 Male chelipeds (Fig. 11C) symmetrical, not granular at all. Merus longer than broad  
594 (length to width ratio 1.1–2.2. anterior and posterior margins glabrous, posterior distal  
595 margins bluntly carinate. Carpus, unarmed, strongly inflated, slightly shorter than wide  
596 (length to width ratio 0.8–1.0). Palm inflated, smooth, without distinct granules; inner  
597 surface glabrous. Fingers with a tuft of long setae on outer surface restricted at the base of  
598 fingers. Dactylus shorter than palm, 0.7–1.0 times as long as palm, terminating in small, hoof  
599 shaped corneous claw bearing 9 to 10 small blunt teeth pollex, with 4–5 larger blunt teeth.  
600 Proximal half of fingers with long dense soft setae, a single pulvinus at base of fingers.

601 Female chelipeds (Fig. 11D) distinctly smaller than those of male, chela much  
602 narrower than that of male. The fingers have smaller and less large teeth. Proximal half of

603 fingers with no long dense soft setae and no pulvinus at base of fingers; pollex with ridge  
604 consisting of large granules toward palm and ending with a distal tuft of setae.

605 Ambulatory legs (P2 to P5 pereopods) comparatively long, slender, somewhat  
606 compressed laterally; P4 longest (male: length 1.3–1.4 times carapace width) P5 shortest.  
607 Meri elongated, subrectangular in lateral view, unarmed. Anterior margins and posterior  
608 margins of merus of P2, P3 P4 and P5 glabrous. Anterior margin of carpus with scarce short  
609 setae, posterior margin glabrous. Propodus with dense short setae on anterior margins and  
610 dense short setae and long setae on posterior margins. Ventral surface with rows of short  
611 setae. Dactylus terminating in subacute corneous claw, with dense short setae on anterior and  
612 posterior margins; dorsal and ventral surface with rows of short setae. P3 with merus (Fig.  
613 11E) length to width ratio 1.9–3.3, carpus length to width ratio 1.8–2.1, propodus length to  
614 width ratio 1.3–2.0, dactylus length to width ratio 4.1–4.5, dactylus 0.7–1.3 times as long as  
615 propodus. P5 with merus (Fig. 11F) length to width ratio 2.2–3.3, carpus length to width ratio  
616 1.6–2.6, propodus length to width ratio 1.1–1.9, dactylus length to width ratio 2.6–  
617 3.9, dactylus 0.7–0.9 times as long as propodus.

618 Male pleon (Fig. 11G) narrow, broadly triangular, nearly smooth, distinctly narrowed  
619 at base of telson; lateral margins of first to fifth somites nearly straight; margins covered with  
620 short setae, distal margin of telson with tuft of setae; telson tongue shaped, terminal margin  
621 broadly rounded. Length 1.1 times basal breadth, 1.0–1.4 times longer than sixth somite, sixth  
622 somite 1.1–1.7 times longer than fifth somite.

623 Female pleon (Fig. 11H) very broad, covering most of thoracic sternum, four somite  
624 broadest, telson broadly subtriangular, terminal margin broadly rounded, 0.43–0.51 length of  
625 basal breadth, 1.1 times longer than sixth somite, sixth somite 1.0–1.1 times longer than fifth  
626 somite, measured on midline.

627 Male G1 (Fig. 11I) slender, 6 times as long as wide, slightly curving dorsally; tip  
628 bluntly rounded, forming short chitinous structure; subdistal lobe obtuse, partially obscured  
629 by stiff setae.

630

631 **Colouration in life.** The body, chelipeds and legs are orange (Fig. 12A and B).

632

633 **Size.** This is a small-sized species, the largest male specimen examined is 9.6 mm × 8.0 mm  
634 and the largest female 9.0 mm × 7.9 mm.

635

636 **Habitat.** *Ptychognathus barbatus* lives in seashores influenced by flows of freshwater.  
637 Indeed, it was found under rocks on a beach next to the estuary of the Wadjana waterfall in  
638 the South Province of New Caledonia (Fig. 12D).

639

640 **Distribution.** *Ptychognathus barbatus* (Fig. 6) seems endemic to New Caledonia.

641

642 **Remarks.** This species is not reported from Polynesia but re-described herein for comparison  
643 purposes. It was reported from Aceh (Sumatra) and Penang Island (Malaysia) by De Man,  
644 1895 (see pages 105–111, fig. 23), from Japan by Sakai, 1939 (see page 638–639, text-fig.  
645 348 and from Madagascar by Crosnier, 1965 (see pages 36–38, Figs 42–45). This species  
646 seems to be in fact restricted to New Caledonia. It can be distinguished from the other crabs  
647 reported under this name by the frontal region, setae on ambulatory legs and telson of male  
648 (see next species).

649

650 ***Ptychognathus ngankeae* sp. nov.**

651 (Fig. 12C, 13A–H)

652

653 *Ptychognathus barbatus* – Poupin & Juncker, 2008:36; Keith & Marquet, 2011: 62–63 (partim:  
654 picture on page 62 only); Keith *et al.*, 2013: 120–121 (partim: picture on page 120 only).

655

656 **Material examined.** Type material: *WALLIS AND FUTUNA TERRITORY*. *Futuna*: MNHN-  
657 IU-2019-411: Holotype: 1 ♂, 6.7 mm × 5.8 mm, DNA voucher CA2653, Vainifao, Station  
658 13, 14° 18.461'S, 178° 8.564'W; October 14, 2007, coll. J. Poupin & M. Juncker. – MNHN-  
659 IU-2019-412: Paratype: 1 ♂, 5.5 mm × 4.7 mm, DNA voucher CA2652, Leava, Station 15,  
660 14° 17.593'S, 178° 9.531'W, October 15, 2007, coll. J. Poupin & M. Juncker.

661 Comparative material: *Ptychognathus barbatus* (A. Milne-Edwards, 1873): examined  
662 herein from New Caledonia (See list of studied specimens above).

663

664 **Diagnosis.** Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior  
665 margin slightly concave medially. Anterolateral margin with three teeth including orbital  
666 tooth. Merus of third maxilliped with antero-external angle broad, exopod, 1.1–1.3 times  
667 broader than ischium. Chelipeds large, symmetrical in males, fingers with a small tuft of setae  
668 at tips of pollex. No pulvinus at base of fingers. Merus and Carpus of ambulatory legs  
669 glabrous.

670

671 **Description.** Carapace (Fig. 13A) subquadrate, slightly broader than long, 1.2 in haplotype  
672 (1.2 in paratype) times as broad, flat, dorsal surface smooth, glabrous, regions poorly defined,  
673 only with an usual H-shaped mark in the middle quite distinct and noticeable epigastric  
674 cristae. Front broad, anterior margin divided into two lobes, slightly concave medially.  
675 Breadth of front 0.50 (0.47) times as long as CW, Breadth of fronto-orbit 0.89 (0.88) times as  
676 long as CW. Upper margin of orbit not sinuous. Anterolateral margins and supraorbital  
677 margins lined with small granules, Anterolateral margins each with 3 teeth including orbital  
678 tooth; first tooth largest and more distinct, second and third blunt, third tooth indistinct or  
679 notch Posterolateral margins divergent posteriorly, moderately sloping outwards; lateral and  
680 posterolateral margins regularly furnished with short, soft setae.

681 Infraorbital ridge consisting of 17 (14) small round granules.

682 Epistome broad, median part triangular, margin with tiny granules (Fig. 13B).

683 Third maxillipeds (Fig. 13C) with ischium subequal in proximal and distal widths,  
684 lateral margin concave, ventral surface with longitudinal median ridge. Merus with antero-  
685 lateral angle broad; ventral surface with oblique ridge on mesial part. Exopod broad, inflated,  
686 greatest width 1.1–1.3, times of median width of ischium.

687 Chelipeds (Fig. 13D) symmetrical in male, not granular at all. Merus without spines  
688 longer than broad 2.1 in holotype (1.7 in paratype) times as long as wide, outer lower margin  
689 bluntly carinate, smooth. Carpus unarmed, strongly inflated, slightly shorter than wide 1.0  
690 (0.8) times as long as wide; surface of carpus smooth. Outer surface of palm in male smooth,  
691 without distinct granules or horizontal ridge, inner surface glabrous, middle part convex.



692 Dactylus distinctly shorter than palm 1.0 (0.7) times as long as palm, inner surface glabrous,  
693 terminating in small, hoof shaped corneous claw, bearing 10 (7) small blunt teeth, pollex,  
694 with 4 larger blunt teeth (the two middle teeth are bigger). Proximal half of fingers with long  
695 dense soft setae in male. No pulvinus at base of fingers.

696 Ambulatory legs (P2 to P5 pereopods) comparatively long, slender, somewhat  
697 compressed laterally; P4 longest (male: length 1.4 times as long as CW): P5 shortest. Meri  
698 elongated, subrectangular in lateral view, unarmed. Anterior and posterior margins of merus  
699 of P2, P3 P4 and P5 glabrous. Anterior and posterior margins of carpus glabrous. Propodus  
700 with dense short setae on anterior margins. Ventral surface with no rows of short setae.  
701 Dactylus terminating in subacute corneous claw, with dense short setae on anterior margins,  
702 short and long setae on posterior margins, dorsal and ventral surface with no rows of short  
703 setae. P3 (Fig. 13E) with merus 2.5 in holotype (2.6 in paratype) times as long as wide, carpus  
704 2.4 (1.6) times as long as wide, propodus 2.0 (1.5) times as long as wide, dactylus 3.7 (3.3)  
705 times as long as wide), dactylus 1.0 (1.3) times as long as propodus. P5 (Fig. 13F) with  
706 merus 2.5 in holotype (2.1 in paratype) times as long as wide, carpus 1.9 (1.5) times as long as  
707 wide, propodus 1.3 (1.4) times as long as wide, dactylus 2.5 (2.6) times as long as wide),  
708 dactylus 0.8 times as long as propodus.

709 Male pleon (Fig. 13G) narrow, broadly triangular, nearly smooth, distinctly narrowed  
710 at base of telson; lateral margins of first to fifth somites nearly straight; margins covered with  
711 short setae, distal margin of telson without tuft of setae; telson tongue shaped, terminal  
712 margin broadly rounded. length 1.2 times as long as basal breadth, 1.1 in haplotype (1.2 in  
713 paratype) times longer than sixth somite, sixth somite 1.3 (1.1) times longer than fifth somite.  
714 The female pleon is not known.

715 Male G1 (Fig. 13H) slender, 7.6 times as long as wide, slightly curving dorsally  
716 reaching suture between thoracic sternite 4 and 5; tip rounded, forming short chitinous  
717 structure; subdistal lobe obtuse, partially obscured by stiff setae.

718

719 **Habitat.** In Futuna Island, this species is found, with *P. similis* sp. nov. in rivers in brackish  
720 water, near estuaries.

721

722 **Colouration in life.** The body (Fig. 12C) and chelipeds are yellowish to brownish. The inside  
723 of the claws is whitish.

724

725 **Size.** This is a small-sized species, the largest male specimen examined is 6.7 mm × 5.8 mm.

726

727 **Distribution.** *Ptychognathus ngankeeae* sp. nov. is apparently endemic to Futuna Island  
728 (Wallis and Futuna Territory).

729

730 **Etymology.** Named after our late colleague Ngan Kee Ng who devoted her life to the study of  
731 varunid crabs.

732

733 **Remarks.** This new species is very similar to *P. barbatus* (A. Milne-Edwards, 1873) in  
734 morphology (see previously, under that species) but it can be distinguished by the absence of  
735 a pulvinus at base of fingers of chelipeds (vs presence of a pulvinus) and setae on ambulatory  
736 legs (dactylus with short and long setae on posterior margins, dorsal and ventral surface with  
737 no rows of short setae (vs dactylus with only dense short setae on posterior margins, dorsal  
738 and ventral surface with rows of short setae)).

739 This new species is also similar to *P. stimpsoni* Hsu & Shih, 2020 in morphology, but  
740 they can be separated by the absence of a pulvinus at base of fingers of chelipeds (vs presence  
741 of a pulvinus, see Hsu & Shih 2020, fig. 4E) and setae on ambulatory legs (carpus of  
742 ambulatory legs glabrous on anterior margins (vs carpus covered with dense short setae, see  
743 Hsu & Shih 2020, figs. 4G and 4H).

744 *P. ngankeeae* sp. nov. seems to be less common in Futuna than the next new species  
745 (see below).

746

747 ***Ptychognathus similis* sp. nov.**

748 (Fig. 14A–J, 15A–B)

749

750 *Ptychognathus hachijoensis* – Poupin & Juncker, 2008: 36, Fig. 4c–d; 2010: 75, Fig. c; Keith  
751 & Marquet, 2011: 64–65; Keith *et al.*, 2013: 124–125.

752

753 **Material examined.** Type material: *WALLIS AND FUTUNA TERRITORY: Futuna:*  
754 Holotype: MNHN-IU-2022-4125 (DNA voucher CA2659), 1 ♂, 9.3 mm × 7.6 mm,  
755 Vainifao river, Station 13, 14° 18.461'S, 178° 8.564'W; October 14, 2007, coll. J. Poupin &  
756 M. Juncker. – Paratypes: MNHN-IU-2022-4126 (DNA voucher CA2658), 1 ♀, 7.3 mm × 6.1  
757 mm, and 5 ♂ 6.4–7.9 mm × 5.6–6.5 mm, 2 ♀ 7.0–7.2 mm × 5.9–6.3 mm, and 2 ♀ ovig.  
758 6.6–7.9 mm × 5.2–7.6 mm, same locality data as for holotype. – MNHN-IU-2022-4127, 4 ♂,  
759 6.5–15.2 × 5.8–13.2 mm, Vai river, Station 3, 14°15.229'S, 178° 9.192'W; August 6 2023,  
760 coll. N. Charpin & V. Mazel. – MNHN-IU-2022-4128, 2 ♂, 6.4–6.6 × 5.5–5.6 mm and 2 ♀  
761 ovig., 10.9–11.4 × 9.6–9.9 mm, Galoli river, Station 5 14°15.574'S, 178°8.305'W; August 6  
762 2023, coll. N. Charpin & V. Mazel. – MNHN-IU-2022-4129, 2 ♂, 13.7–15.3 × 12.5–11.6 mm  
763 and 1 ♀, 13.7 × 11.4 mm, Leava river, Station 10, 14°17.598'S, 178°9.543'W, August 8 2023,  
764 coll. N. Charpin & V. Mazel. – MNHN-IU-2022-4130, 1 ♂, 9.2 × 7.3 mm, Vainifao river,  
765 Station 11, 14°17.085'S 178°8.180'W, August 9 2023, coll. N. Charpin & V. Mazel. –  
766 MNHN-IU-2022-4131, 1 ♂, 14.5 × 12.5 mm, Leava river, Station 20, 14°17.498'S,  
767 178°9.305'W, August 14 2023, coll. N. Charpin & V. Mazel.

768 Comparative material: *Ptychognathus hachijoensis* Sakai, 1955 (TAIWAN): MNHN-  
769 IU-2022-4001, DNA voucher CA2866: 1 ♂, 9.6 mm × 7.9 mm, and 1 ♂, 8.8 mm × 7.3  
770 mm. – DNA voucher CA2865: 1 ♀, 10.2 mm × 9.0 mm, and 1 ♀, 10.8 mm × 9.2 mm,  
771 Gengfang River estuary, Toucheng, Yilan County, coll. J.-W. Hsu *et al.*

772

773 **Diagnosis.** Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior  
774 margin slightly concave, breadth of front 0.45–0.47 times as long as CW. Anterolateral  
775 margin with single orbital tooth, followed by a faint lobe. Third maxillipeds with a merus  
776 having its antero-lateral angle inflated and an exopod broad, inflated, greatest width 1.0–1.3  
777 times of median width of ischium. Chelipeds stout, symmetrical in males; Fingers with a tuft  
778 of long setae on outer surface restricted at the base of fingers. Pulvinus at base of fingers  
779 Ambulatory legs slender, somewhat compressed laterally. Propodus and dactylus with dense  
780 long setae on posterior margins and glabrous on anterior margins.

781

782 **Description.** Carapace (Fig. 14A) subquadrate, slightly broader than long, 1.1–1.2 times as  
783 broad as long, flat, dorsal surface smooth and glabrous. Regions poorly defined with the usual  
784 H-shaped mark in the middle quite distinct and epigastric cristae strong. Front broad, anterior  
785 margin slightly concave medially. Breadth of front 0.45–0.47 times as long as CW, Breadth of  
786 fronto-orbit 0.78–0.84 times as long as CW. Upper margin of orbit sinuous Anterolateral  
787 margins with single orbital tooth, followed by a faint lobe. Posterolateral margins divergent  
788 posteriorly, moderately sloping outwards.

789       Infraorbital ridge consisting of several small rounded granules, decreasing in size  
790 laterally.

791       Epistome broad (Fig. 14B), median part triangular, margin with tiny granules.

792       Third maxillipeds (Fig. 14C) with ischium subequal in proximal and distal widths,  
793 lateral margin concave, ventral surface with longitudinal median ridge. Merus broad, with  
794 antero-lateral angle inflated; ventral surface with oblique ridge on mesial part. Exopod broad,  
795 inflated, greatest width 1.2–1.3 times (male), 1.0 (female) of median width of ischium.

796       Chelipeds (Fig. 14D) symmetrical in male, not granular at all. Merus longer than broad  
797 (length to width ratio 1.6–1.7, anterior and posterior margins glabrous, posterior distal  
798 margins bluntly carinate. Carpus, unarmed, strongly inflated, slightly longer than wide (length  
799 to width ration 1.1–1.2). Palm much inflated, smooth, without distinct granules; inner surface  
800 glabrous. Fingers with a tuft of long setae on outer surface restricted at the base of fingers.  
801 Dactylus same length than palm, terminating in small, hoof shaped corneous claw, bearing 9  
802 to 10 small blunt teeth, pollex with only faint indication of longitudinal groove, with 4 to 5  
803 blunt teeth. Pulvinus at base of fingers.

804       Female chelipeds (Fig. 14E) distinctly smaller than those of male, chela much  
805 narrower than that of male. No tuft of setae on outer surface of fingers. Carpus unarmed. Palm  
806 not strongly inflated, dactylus distinctly shorter than palm; narrow hiatus between fingers.  
807 Two distinct rows of granules on the palm.

808       Ambulatory legs (P2 to P5 pereopods), slender, somewhat compressed laterally; P4  
809 longest (male: length 1.4–1.6 times carapace width, female: length 1.5 times carapace width);  
810 P5 shortest. Meri elongated, subrectangular in lateral view, unarmed. Anterior margins of  
811 merus of P2, P3 and P4 with long soft setae; posterior margins with sparsely long setae.

812 Anterior and posterior margins of carpus glabrous. Propodus with dense long setae distally on  
813 posterior margins and glabrous on anterior margins. Dactylus terminating in subacute  
814 corneous claw, with dense long setae on posterior margins and anterior margins glabrous;  
815 ventral surface with rows of short setae. P3 with merus (Fig. 14F) 2.9 in holotype (2.6–3.2 in  
816 paratypes) as long as wide, carpus 2.4 (1.7–2.4) as long as wide, propodus 1.9 (2.0–2.7) as  
817 long as wide dactylus 6.3 (4.4–5.4) as long as wide, dactylus 0.8 (0.8–0.9) times as long as  
818 propodus. P5 with merus (Fig. 14G) 2.2 in holotype (2.1–2.6 in paratypes) as long as wide,  
819 carpus 2.0 (1.9–2.3) as long as wide; propodus 1.3 (1.2–1.5) as long as wide dactylus 3.4  
820 (2.2–2.7) 4 as long as wide, dactylus 1.4 (0.9–1.1) times as long as propodus.

821 Male pleon (Fig. 14H) narrow, broadly triangular, nearly smooth, distinctly narrowed  
822 at base of telson; margins with no short setae, no setae on margins of telson which is tongue  
823 shaped, terminal margin broadly rounded. Telson length 1.2 in haplotype) (1.3 in paratypes)  
824 times basal breadth, 1.3 (1.4) times long as sixth somite, sixth somite 1.5 (1.3) times longer  
825 than fifth somite.

826 Female pleon (Fig. 14J) very broad, covering most of thoracic sternum, four somite  
827 broadest, telson broadly subtriangular, terminal margin broadly rounded, 0.42 length of basal  
828 breadth, 1.0 times longer than sixth somite. Sixth somite 1.2–1.3 times longer than fifth  
829 somite, measured on midline. Small round eggs 0.26–0.28 mm in diameter.

830 Male G1 (Fig. 14I) slender, 5 times as long as wide, slightly curving dorsally reaching  
831 suture between thoracic sternite 4 and 5; tip bluntly rounded, forming short chitinous  
832 structure; subdistal lobe obtuse, partially obscured by stiff setae.

833

834 **Colouration in life.** The body and chelipeds (Fig. 15A) are yellowish to brownish or greyish,  
835 sometimes reddish (Fig. 15B).

836

837 **Size.** This is a small-sized species, the largest male specimen examined is 9.3 mm × 7.6 mm  
838 and the largest ovigerous female 7.9 mm × 7.6 mm.

839

840 **Habitat.** In Futuna Island, this species is found in rivers in brackish water, near estuaries (Fig.  
841 15C).

842

843 **Distribution.** *Ptychognathus similis* sp. nov. seems endemic to Futuna Island (Wallis and  
844 Futuna Territory) (Fig. 6).

845

846 **Etymology.** This new species is named after its resemblance to *P. hachijoensis*.

847

848 **Remarks.** By the anterolateral margins of its carapace with a single orbital tooth, followed by  
849 a faint lobe and by the propodus and dactylus of its ambulatory legs with dense long setae on  
850 anterior margins, this species is very similar to *P. hachijoensis* Sakai, 1955 but it is possible  
851 to distinguish them by the breadth of front 0.45–0.47 times as long as CW (vs 0.55–0.56) and  
852 by its P5 dactylus 0.8 as long as propodus (vs 1.2).

853

#### 854 **Discussion**

855 In Polynesia, the genus *Ptychognathus* has never been reported from Hawaii nor New  
856 Zealand. It is however present in Samoa, Futuna, Cook Islands, French Polynesia and Easter  
857 Island.

858 Keith *et al.* (2013:129) report *P. pusillus* Heller, 1865 from Futuna and Samoa. Our  
859 survey, however, shows that this species is not present in these two islands. Indeed, in Futuna  
860 we have two new species *P. ngankeeae* sp. nov. and *P. similis* sp. nov., and in Samoa only  
861 one species *P. riedelii*.

862 *Ptychognathus intermedius* (de Man, 1879) was originally described from the  
863 Moluccas and recorded from Tahiti (Ortmann 1894: 711) by only one male. Keith *et al.*  
864 (2013: 127) follows the literature by indicating this species in Tahiti. The male specimen  
865 studied by Ortmann is deposited in the Strasbourg Zoological Museum. The photographs  
866 kindly sent by Marie Meister (Strasbourg University) show that it is not *P. intermedius* but in  
867 fact *P. easteranus*. Indeed in this specimen, outer surface of palm do not show the flat  
868 rounded granules (Fig. 16A), very characteristic of *P. intermedius*. Moreover, ambulatory legs  
869 do not show their margins densely setose (Fig. 16B), also characteristic of *P. intermedius*.  
870 (Fig. 16C).

871 Poupin & Corbari (2012) and Salvat *et al.* (2016) reported *Ptychognathus hachijoensis*  
872 Sakai, 1955 from the sample(s) and photographs (Figs. 17A–C) of J. Poupin and J. Starmer  
873 (Fatu Hiva, Baie des Vierges, estuary of Hanavave river, st. MQ16-M, January 17–18, 2012, -  
874 10.464033, 138.666167, accession number LC146). We were not able to locate these  
875 specimens in the MNHN collections. The examination of the photographed specimens alone  
876 does not allow to validate this species in French Polynesia that shows similarities (breadth of  
877 front 0.50 times as long as CW and by its short P5 dactylus 0.50 times length of propodus)  
878 with *P. similis* sp. nov. and is herein referred to "*P. aff. similis* from Marquesas" pending that  
879 the specimens are retrieved. The lack of these specimens prevents us from getting molecular  
880 data and thus applying our integrative taxonomic approach.

881 Within Polynesia, several biogeographic regions can be identified based on the  
882 distribution of freshwater species. Rivers of the Marquesas, being the most geographically  
883 isolated area, harbor a different fauna compared to neighbouring archipelagos: *Ptychognathus*  
884 *crassimanus* endemic to the Marquesas vs *Ptychognathus easteranus* with a wide distribution  
885 in Polynesia; *Caridina marquesensis* endemic to the Marquesas vs *Caridina tupaia* with a  
886 wider distribution in the Pacific (de Mazancourt *et al.* 2019); *Sicyopterus marquesensis*  
887 endemic to the Marquesas vs *Sicyopterus lagocephalus* with a wide distribution in the Indo-  
888 Pacific region (Keith *et al.* 2005), etc. This isolation is due to different factors, including  
889 distance and oceanic surface currents (see discussion in de Mazancourt *et al.* 2019).

890 Futuna is original in having several endemic species in its rivers, despite its less  
891 pronounced isolation compared to the Marquesas: *Ptychognathus similis* sp. nov.,  
892 *Ptychognathus ngankeae*, *Caridina futunensis*, *Smilosicyopus sasali*, *Akihito futuna*,  
893 *Stiphodon rubromaculatus*, etc. (see de Mazancourt *et al.* 2019; Keith & Taillebois 2014;  
894 Keith *et al.* 2007; Keith & Marquet 2007). Its isolation can be linked to the oceanic currents  
895 but also to the presence of a deep trench (see de Mazancourt *et al.* 2019).

896 Finally, Samoa Islands harbor an original fauna distinct from that of neighbouring  
897 archipelagos with a mix of Melanesian and Polynesian species: *Ptychognathus riedelii*, *Utica*  
898 *gracilipes*, *Atyoida pilipes*, *Australatya keithi* and *Caridina buehleri* are absent from the rest  
899 of Polynesia, whereas typical Polynesian species like *Caridina tupaia* occur there.

900 The molecular study showed that the genus *Ptychognathus* may be paraphyletic, with  
901 *Varuna litterata* clustering near *P. makii*, *P. altimanus*, *P. crassimanus* and *P. easteranus*.  
902 This result partly confirms the conclusions of Rathbun (1914) who included *P. altimanus*

903 (among others) within the genus *Varuna*. The width of the exopod of the third maxilliped  
904 usually used to distinguish *Ptychognathus* from *Varuna* might not be a good character. Our  
905 results would need to be confirmed by more comprehensive analyses but it suggests that the  
906 taxonomy of varunid crabs is in need of a thorough revision.

907 A key to the Polynesian species of *Ptychognathus* is provided below.

908

909 Key for Polynesian *Ptychognathus* species:

910

911 1.1 Carpus of chelipeds with a spine at inner angle (female not in male); merus of P2, P3 and  
912 P4 armed with a spine on superior border distally (male and female); breadth of fronto-orbit  
913 0.89–0.96 times as long as CW (male and  
914 female).....2

915 1.2 Carpus of chelipeds without spine at inner angle (female and male); merus of P2, P3 and  
916 P4 without spine on superior border distally (male and female); breadth of fronto-orbit 0.78–  
917 0.90 times as long as CW (male and  
918 female).....3

919

920 2.1 Exopod of third maxilliped 1.4–1.6 (male), 1.3–1.4 (female) times as long as ischium; P5  
921 dactylus 2.5–3.0 times as long as broad (male and female). Endemic to Marquesas  
922 Islands.....***P.***

923 ***crassimanus***

924 2.2 Exopod of third maxilliped 1.7–1.9 (male), 1.4–1.6 (female) times as long as ischium; P5  
925 dactylus 3.0–3.9 times as long as broad (male and female). Occurs in Cook Islands, French  
926 Polynesia (Gambier, Austral and Society) and Easter Island.....***P.***

927 ***easteranus***

928

929 3.1 Chelipeds glabrous; exopod of third maxilliped 2.1–2.6 (male), 1.6–1.9 (female) times as  
930 long as ischium; a very characteristic small tuft of setae at tips of pollex.  
931 Widespread.....***P. riedelii***



932 3.2 Chelipeds setose; exopod of third maxilliped 0.9–1.3 (male and female) times as long as  
933 ischium; no small tuft of setae at tips of  
934 pollex.....4

935

936 4.1 Anterolateral margin of carapace with only a faint lobe after orbital tooth (male and  
937 female); exopod of third maxilliped 1.2–1.3 (male), 1.0 (female) times as long as ischium.  
938 Endemic to Futuna Island.....***P.***  
939 ***similis* sp. nov.**

940 4.2 Anterolateral margin of carapace with two distinct tooth after orbital tooth (male). Exopod  
941 of third maxilliped 0.9–1.0 (male) times as long as ischium. Endemic to Futuna  
942 Island.....***P. ngankeae* sp. nov.**

943

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954

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1115 <https://doi.org/10.3906/zoo-1703-46>
- 1116
- 1117 **Legends to figures and tables:**
- 1118 Fig. 1: Map of the Polynesian triangle and Polynesian sub-regions.
- 1119 Fig. 2: Phylogenetic tree obtained by Bayesian Inference from the concatenated 16S and COI  
1120 datasets. Numbers above branches indicate Bayesian posterior probabilities; numbers  
1121 under branches indicate Maximum Likelihood bootstrap values.
- 1122 Fig. 3: Phylogenetic tree obtained by Bayesian Inference from the single-locus 16S dataset.  
1123 Numbers above branches indicate Bayesian posterior probabilities; numbers under  
1124 branches indicate Maximum Likelihood bootstrap values.
- 1125 Fig. 4: *Ptychognathus crassimanus*. A: carapace; B: left third maxilliped; C: male cheliped; D  
1126 and E: female cheliped; F: third pereopod with inner view of dactylus; G: fifth  
1127 pereopod; H: male pleon; I: female pleon; J: male right first gonopod. MNHN-IU-  
1128 2019-182 (A, B, C, F, G, H) male from Ua Pou Island; MNHN-IU-2019-183 (J) male  
1129 from Hiva Oa Island; MNHN-IU-2011-9062 (E, D, I) female from Fatu Hiva Island.
- 1130 Fig. 5: *Ptychognathus crassimanus*. A: dorsal view of a living specimen; B: front view of a  
1131 living specimen; C: ventral view; D: typical habitat of the species, Faakuaa river, Hiva  
1132 Oa Island. Photo credits: É. Vigneux (A, B), J. Poupin (C) and G. Marquet (D).
- 1133 Fig. 6: Distribution map of the species studied. Stars indicate type localities.

- 1134 Fig. 7: *Ptychognathus easteranus*. A: carapace; B: left third maxilliped; C: male cheliped; D  
1135 and E: female cheliped; F: third pereopod; G: fifth pereopod; H: male pleon; I: female  
1136 pleon; J: male right first gonopod. MNHN-IU-2016-11889 (A, B, C, F, G, H) male;  
1137 MNHN-IU-2022-4090 (J); MNHN-IU-2016-11891 (E, D, I) female, both from Tahiti.
- 1138 Fig. 8: *Ptychognathus easteranus*. A: dorsal view of a specimen from Moorea; front view of a  
1139 living specimen; C: typical habitat of the species, Papenoo river, Tahiti. Photo credits: J.  
1140 Poupin, 2009 Moorea Biocode (A), É. Vigneux (B) and V. Mazel (C).
- 1141 Fig. 9: *Ptychognathus riedelii*. A: carapace; B: left third maxilliped; C: male cheliped; D:  
1142 female cheliped; E: third pereopod; F: fifth pereopod; G: male pleon; H: female pleon;  
1143 I: right male first gonopod. MNHN-IU-2022-4114 (A, B, C, E, F, G) male from Samoa;  
1144 MNHN-IU-2019-8 (I) male from Samoa; MNHN-IU-2018-2967 (D, H) female from  
1145 New Britain.
- 1146 Fig. 10: *Ptychognathus riedelii*. A: dorsal view of a living specimen from Kolombangara  
1147 Island; B: front view of the same. Photo credits: P. Keith.
- 1148 Fig. 11: *Ptychognathus barbatus*. A: carapace; B: left third maxilliped; C: male cheliped; D:  
1149 female cheliped; E: third pereopod; F: fifth pereopod; G: male pleon; H: female pleon;  
1150 I: right male first gonopod. MNHN-IU-2019-210 (A, B, C, E, F, G, I) male from New  
1151 Caledonia; MNHN-IU-2017-8250 (D, H) female from New Caledonia.
- 1152 Fig. 12: *Ptychognathus barbatus*. A: dorsal view of a living specimen from New Caledonia  
1153 (MNHN-IU-2019-210); B: ventral view of the same; D: typical habitat of the species,  
1154 Wadjana mouth of waterfall, New Caledonia. *Ptychognathus ngankeeae* sp. nov. C:  
1155 dorsal view of a living specimen from Futuna Island. Photo credits: V. de Mazancourt  
1156 (A, B, D) and J. Poupin (C).
- 1157 Fig. 13: *Ptychognathus ngankeeae* sp. nov. A: carapace; B: epistome, C: left third maxilliped,  
1158 D: male cheliped; E: third pereopod; F: fifth pereopod; G: male pleon; H: left first  
1159 gonopod. All from the holotype (MNHN-IU-2019-411).
- 1160 Fig. 14: *Ptychognathus similis* sp. nov. A: carapace; B: epistome, C: left third maxilliped, D:  
1161 male cheliped; E: female cheliped, F: third pereopod, G: fifth pereopod, H: male  
1162 pleon, I: left first gonopod, J: female pleon. Holotype MNHN-IU-2022-4125 (A, B, C,  
1163 D, F, G, H, I) male; Paratype MNHN-IU-2022-4126 (E, J) female, both from Futuna.



- 1164 Fig. 15: *Ptychognathus similis* sp. nov. A and B: dorsal views of specimens from Futuna, C:  
1165 typical habitat of the species, Vainifao river, Futuna. Photo credits: J. Poupin (A), P.  
1166 Keith (B) and A. Dutartre (C).
- 1167 Fig. 16: *Ptychognathus easteranus* from Strasbourg Zoological Museum (MZS Cru 1993).  
1168 Tahiti (reported by Ortmann, 1894 as *P. intermedius*): A: frontal view, B: dorsal view.  
1169 Male syntype (55.2 × 46.9 mm) of *Ptychognathus intermedius* from Moluccas  
1170 (Indonesia), RMNH.CRUS.D.194, C: dorsal view. *P. easteranus*, type specimen from  
1171 Easter Island (Chile), coll. R/V Albatross, shore, 20 December 1904, 1 M 10.8 × 12.6  
1172 mm (USNM 32845). Photo credits: M. Meister (A, B), Ng Ngan Kee (C), J. Poupin (D).
- 1173 Fig. 17: *Ptychognathus* aff. *similis*. A: dorsal view of a specimen from Fatu Hiva Island  
1174 (Virgin Bay, estuary of Hanavave river, st. MQ16-M, January 17–18, 2012, -10.464033,  
1175 -138.666167, sample accession number LC146), B: ventral view of the same specimen,  
1176 C: front view of the same specimen. Photo credits: J. Poupin.

1177 **Table 1: List of the specimens sequenced for the molecular study.**

Species	Country	Archipelago	Island	DNA No.	Collection No.	16S	COI	
<i>Ptychognathus barbatus</i>	New Caledonia (France)		Grande Terre	CA2467	MNHN-IU-2019-210	OR878435	OR864745	
<i>P. crassimanus</i>	French Polynesia (France)	Marquesas	Fatu Hiva	CA2646	MNHN-IU-2011-9062	OR878439	OR864750	
				CA2647	MNHN-IU-2022-4082	OR878440	OR864751	
			Hiva Oa	CA2464	MNHN-IU-2019-183		OR864742	
				CA2465	MNHN-IU-2019-180	OR878433	OR864743	
			Ua Pou	CA2466	MNHN-IU-2019-182	OR878434	OR864744	
				CA2665	MNHN-IU-2022-4085	OR878446	OR864759	
			CA2666	MNHN-IU-2022-4086	OR878447	OR864760		
<i>P. easteranus</i>	French Polynesia (France)	Austral	Rapa	CA2654	MNHN-IU-2022-4090		OR864754	
				CA2655	MNHN-IU-2022-4091	OR878442	OR864755	
				CA2667	MNHN-IU-2022-4097	OR878448	OR864761	
				CA2672	MNHN-IU-2022-4094	OR878450	OR864764	
				CA2673	MNHN-IU-2022-4095	OR878451	OR864765	
		Gambier	Rurutu	CA2478	MNHN-IU-2019-179	OR878436	OR864746	
				Mangareva	CA2670	MNHN-IU-2022-4087		OR864762
					CA2671	MNHN-IU-2022-4088	OR878449	OR864763
		Society	Tahiti	CA2644	MNHN-IU-2022-4113	OR878437	OR864748	
				CA2645	MNHN-IU-2022-4109	OR878438	OR864749	
				CA2674	MNHN-B30406		OR864766	
			CA2675	MNHN-B30406	OR878452	OR864767		
<i>P. ngankeae</i> sp. nov.	Wallis & Futuna (France)		Futuna	CA2652	MNHN-IU-2019-412		OR864752	
				CA2653	MNHN-IU-2019-411	OR878441	OR864753	
<i>P. similis</i> sp. nov.	Wallis & Futuna (France)		Futuna	CA2658	MNHN-IU-2022-4126	OR878443	OR864756	

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			CA2659	MNHN-IU-2022-4125	OR878444	OR864757
<i>P. riedelii</i>	Samoa	Upolu	CA2492	MNHN-IU-2019-8		OR864747
			CA2660	MNHN-IU-2022-4114	OR878445	OR864758

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