



HAL
open science

Revalidation of *Caridina natalensis* De Man, 1908 (Crustacea: Decapoda: Atyidae) in the South Western Indian Ocean

Valentin de Mazancourt, Magalie Castelin, Clementine Renneville, Musa
Mlambo, Gerard Marquet, Philippe Keith

► **To cite this version:**

Valentin de Mazancourt, Magalie Castelin, Clementine Renneville, Musa Mlambo, Gerard Marquet, et al.. Revalidation of *Caridina natalensis* De Man, 1908 (Crustacea: Decapoda: Atyidae) in the South Western Indian Ocean. *Zootaxa*, 2019, 4543 (3), pp.375-387. 10.11646/ZOOTAXA.4543.3.3 . hal-03635547

HAL Id: hal-03635547

<https://hal.science/hal-03635547>

Submitted on 8 Apr 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 REVALIDATION OF CARIDINA NATALENSIS

2
3 **Revalidation of *Caridina natalensis* De Man, 1908 (Crustacea: Decapoda: Atyidae) in the**
4 **South Western Indian Ocean.**

5 VALENTIN DE MAZANCOURT^{1*}, MAGALIE CASTELIN^{1,2}, CLEMENTINE RENNEVILLE¹, MUSA C.
6 MLAMBO³, GERARD MARQUET¹, AND PHILIPPE KEITH¹

7
8 ¹ Muséum national d'Histoire naturelle, Département Adaptations du Vivant, UMR 7208 BOREA, CP026, 57,
9 rue Cuvier, F-75231 Paris, Cedex 05.

10 ² Muséum national d'Histoire naturelle, Département Origines et Evolution, UMR 7205 ISYEB, CP026, 57, rue
11 Cuvier, F-75231 Paris, Cedex 05.

12 ³ Albany Museum, Department of Freshwater Invertebrates, Affiliated Research Institute of Rhodes University,
13 Somerset Street, Grahamstown, 6139.

14 * Corresponding author. E-mail: valentin.demazancourt@laposte.net

15
16 **Abstract**

17 Numerous specimens of a freshwater shrimp with small eggs belonging to the *Caridina nilotica* complex
18 collected in the South Western Indian Ocean were studied and compared with recent and old collection specimens
19 genetically (16S mitochondrial analysis for recent and type specimens) and morphologically. The results revealed
20 that, in the Indian Ocean, what has been identified by several authors under various species names of the complex
21 *C. nilotica*, was in fact *C. natalensis* De Man, 1908. This valid species is re-described and compared with closely
22 related species, often confused with it in this area: *C. brachydactyla* De Man, 1908, *C. brevidactyla* Roux, 1920,
23 *C. gracilipes* De Man, 1892 and *C. longirostris* H. Milne Edwards, 1837.

24
25 **Keywords:** *Caridina*, Integrative taxonomy, 16S, Morphology, South Africa, Seychelles, Comoros, Madagascar,
26 Mayotte

27
28 **Introduction**

29 From 1991 to 2010, several South West Indian Ocean islands were prospected by field trips conducted
30 by the Muséum national d'Histoire naturelle (MNHN) in Mascarenes archipelago (Reunion, Mauritius and
31 Rodrigues; see Keith *et al.* 1999 and Keith *et al.* 2006), in Comoros (Anjouan, Mohéli) and Mayotte (see Keith
32 *et al.* 2006) and in Seychelles (La Digue, Mahé, Praslin and Silhouette; see Keith *et al.* 2006). In 2008 and 2010
33 the MNHN conducted also freshwater inventories in the Northeastern rivers of Madagascar, for the DIAMSOI
34 (Diversité des AMphihalins du Sud-Ouest de l'Océan Indien) program. Recently two of us (GM and MM, in
35 February 2018) collected various *Caridina* from South Africa. During these prospectations, numerous specimens
36 of freshwater shrimps with small eggs belonging to the "*Caridina nilotica* complex" were collected.

37 De Man (1908) compared all the specimens he received from all the Indo-Pacific area, related to the *C.*
38 *nilotica* complex with type material and recognized nine varieties. Four of those with small eggs were then
39 reported as occurring in the Indian Ocean: *C. nilotica brachydactyla*, *C. n. longirostris*, *C. n. gracilipes* and *C. n.*

40 *natalensis*. Later, Roux (1920) described *C. n. brevidactyla* and reported it from the Indian Ocean (1929). The
41 first three are considered valid species (Cai & Shokita 2006; Cai & Ng, 2001; Richard & Clark 2014), respectively
42 *C. brachydactyla* De Man, 1908, *C. longirostris* H. Milne Edwards, 1837 and *C. gracilipes* De Man, 1892,
43 whereas *C. n. natalensis* and *C. n. brevidactyla* are currently junior synonyms of *C. brachydactyla* (Richard &
44 Clark, 2010).

45 *Caridina brachydactyla* was originally described from Mbawa (Flores) and from Palopo, (Celebes) (De
46 Man, 1908). According to Lenz (1910) *C. brachydactyla* occurs in Madagascar, Mohéli and Mayotte (Comoros
47 Islands). Costa (1980) identified *C. brachydactyla brachydactyla* from Seychelles, Mauritius, Comoros and
48 Reunion islands. More recently, Richard & Clark (2010) have identified *C. brachydactyla*, for the first time,
49 from Africa (Tanzania, South Africa).

50 *Caridina longirostris* was originally described supposedly from the river Macta, near Oran, Algeria,
51 however, authors like Bouvier (1925) have suggested that this locality indication is erroneous. The types would
52 more likely be coming from Egypt (unpublished data). Richters (1880) identified *C. longirostris* from
53 Seychelles; Holthuis (1965) identified *C. longirostris* from Madagascar, so did Gurney (1984) and Short &
54 Doumenq (2003). Keith *et al.* (2006) reported *C. longirostris* from Comoros, Mascarenes archipelago and
55 Seychelles.

56 *Caridina gracilipes* was originally described from Maros (Celebes). According to Lenz (1910) *C.*
57 *gracilipes* occurs in Mohéli and Madagascar.

58 *Caridina n. natalensis* De Man, 1908 was described from specimens collected in the river Umgeni,
59 Natal (South Africa) in November 1894. They were wrongly referred by Weber (1897) to *C. wyckii* (Hickson,
60 1888) and considered by De Man (1908) as a distinct variety of *C. nilotica*, *C. nilotica natalensis*. Lenz (1912)
61 also identified *C. nilotica var. natalensis* near Amawzentoti (Natal, correct spelling: Amanzimtoti) and Bouvier
62 (1925) in the river Tiwi, 20km south of Mombasa (Kenya) and in the river Imanambo in Madagascar. In his key
63 for the South African species and varieties, Barnard (1950) listed *C. nilotica var. natalensis* with small eggs
64 (0.42-0.46 mm major axis). Recently, according to Richard & Clark (2010), *C. n. natalensis* was not considered
65 as a valid species but as a junior synonym of *C. brachydactyla*. However, Klotz & De Grave (2015) predicted
66 that *C. n. natalensis* should be resurrected for certain African populations, but they were lacking data to
67 effectively do it.

68 *Caridina n. brevidactyla* Roux, 1920 described from the Aru Islands, Indonesia, occurs also in
69 Madagascar according to Roux (1929). Richard & Clark (2010) considered that *C. nilotica brevidactyla* was also
70 a junior synonym of *C. brachydactyla* in contrast of Cai & Ng (2001) who considered it as a valid species.

71 Comparing the new material collected by the MNHN in the South West Indian Ocean to the old collections, the
72 first aim of the present work is to review the status of *C. n. natalensis*, currently a junior synonym of *C.*
73 *brachydactyla*, and provide additional taxonomic information about their respective morphologies and
74 distributions. The second aim of this study is to re-examine existing material and descriptions related to all the
75 species of the *C. nilotica* complex that have historically been reported as occurring in the Western Indian Ocean.

76

77 **Material and Methods**

78 **Field collection data**

79 All specimens were collected in Indian Ocean islands by electrofishing (portable Dekka 3,000 electric device,
80 Germany) and by hand nets in South Africa. In the field, caught specimens were fixed in 75%. All material has
81 been deposited in the collections of the Muséum national d'Histoire naturelle (MNHN) or Albany Museum in
82 Grahamstown (South Africa).

83

84 **Abbreviations for museums.** Muséum national d'Histoire naturelle, Paris: MNHN; Naturhistorisches Museum
85 Basel, Basel: NMB; Rijksmuseum van Natuurlijke Historie (now in the Naturalis Biodiversity Center, Leiden):
86 RMNH; Zoological Museum Amsterdam (now in the Naturalis Biodiversity Center, Leiden): ZMA.

87

88 **Abbreviations for morphological analyses.** The following abbreviations are used in the present text: cl, carapace
89 length (mm): measured from the post-orbital margin to the posterior margin of the carapace. P1: first pereopod.
90 P2: second pereopod. P3: third pereopod. P5: fifth pereopod. P11: first pleopod. P112: second pleopod.

91

92 **Morphological comparison.** The rostrum, the general cephalon, the pereopods 1, 2, 3 and 5 and the abdomen
93 were observed using a stereoscopic microscope. The proportions of the various joints of the appendages were
94 measured using microphotographs and the AnalySIS Works software (Olympus). Drawings were made using the
95 “Digital Inking” method (Coleman, 2003, 2006) by tracing vectorial paths on high-resolution photographs using
96 Adobe Illustrator (CS6) and a WACOM MPTZ-1230 graphic tablet.

97

98 **DNA extraction, amplification and sequencing.** For recent specimens, DNA was extracted from abdominal
99 tissues using the semi-automatic Ependorf ep-Motion 5075 robot. Fragments of the mitochondrial 16S rRNA (~
100 520 bp) were amplified using the newly designed primers 16Sar-Lmod (TACTTCTGCCTGTTTATCAAAAA)
101 and 16Sbmod (GGTCTGAACTCAAATCATGTAAA). DNA amplification was performed in 20µl PCR
102 reactions, containing approximately 3 ng of template DNA, 2.5 mM MgCl₂, 0.26 mM of each nucleotide, 0.3
103 µM of each primer, 5% DMSO, 1 ng of BSA and 1.5 units of QBIOTAQ polymerase (MPBiomedicals).
104 Amplification products were generated by an initial denaturation step of 4 min at 94°C followed by 35 cycles of
105 denaturation at 94°C for 30 sec, annealing at 52°C for 40 sec, extension at 72°C for 60 sec and a final extension
106 step at 72°C for 7 min.

107 For old collection specimens (Type and non-type specimens of *C. brachydactyla*, *C. brevidactyla*, *C. gracilipes*,
108 *C. longirostris* and *C. natalensis*), a CTAB protocol was used to extract DNA from pleopods. A shorter fragment
109 of the 16S rRNA (332 bp) was amplified using the newly designed primers 16S-Car-81F
110 (AGGTAGCATAATAAATAGTC) and 16S-Car-413R (CTGTTATCCCTAAAGTAAC). If these primers
111 could not amplify successfully, another Reverse primer was designed and used to try amplifying a shorter
112 fragment (141 bp): 16S-Car-222R (CTTTATAGGGTCTTATCGT). DNA amplification was performed in 20µl
113 PCR reactions, containing 2.5 mM MgCl₂, 0.26 mM of each nucleotide, 0.3 µM of each primer, 1 ng of BSA
114 and 1.5 units of QBIOTAQ polymerase (MPBiomedicals). Amplification products were generated by an initial
115 denaturation step of 4 min at 94°C followed by 45 cycles of denaturation at 94°C for 30 sec, annealing at 55°C
116 for 30 sec, extension at 72°C for 40 sec and a final extension step at 72°C for 7 min.

117 PCR products were sequenced using the same primers and in both directions to insure the accuracy of base calls.
118 Chromatograms were edited using Geneious v.8 software (<http://www.geneious.com/> Kears e *et al.* 2012). All
119 new sequences were deposited in GenBank (Table 1, Numbers MH644413 to MH644429).

120

121 (Table 1)

122

123 **Molecular analyses** DNA sequences were aligned using MEGA7 software (Kumar *et al.* 2016) with Muscle
124 algorithm (Edgar, 2004). Using Bayesian information criterion in jModelTest (Darriba *et al.* 2012; Guindon and
125 Gascuel, 2003) we retained the GTR + G model. Best-scoring ML trees were estimated using RAxML HPC2
126 v.8.2.10 (Stamatakis, 2014) and best-scoring Bayesian Inference trees were estimated using MrBayes v.3.2.6
127 (Ronquist and Huelsenbeck, 2003), both methods implemented in the Cyber Infrastructure for Phylogenetic
128 Research (CIPRES) portal v.3.1. (Miller *et al.* 2010) (<https://www.phylo.org/>) with the previously determined
129 model, running for 10,000,000 generations, a sampling frequency of 2,000 and a burn in of 25%. Support for
130 nodes was determined using posterior probabilities calculated by MrBayes implemented in CIPRES. One
131 hundred independent searches, each starting from distinct random trees, were conducted. Robustness of the
132 nodes was assessed using non-parametric bootstrapping (Felsenstein, 1985) with 1,000 bootstrap replicates. We
133 considered a group to be ‘moderately supported’ if it had a bootstrap support value (B) between 75 and 89% or a
134 posterior probability (PP) between 0.80 and 0.94 and ‘highly supported’ when $B \geq 90\%$ or $PP \geq 0.95$.

135

136 **Results**

137 **Molecular results**

138 Due to their old age, no DNA in sufficient quantity and quality could be extracted using our method for the type
139 specimens of *C. brachydactyla*, *C. brevidactyla*, *C. longirostris* and *C. natalensis*, thus, no 16S sequence was
140 amplified for these specimens. However, the approach was successful for type specimens of *C. gracilipes* and
141 non-type specimen of *C. brachydactyla*. Furthermore, we tried to obtain recent specimens as close as possible to
142 the type locality for *C. brachydactyla* (Palopo, Sulawesi, Indonesia) and *C. natalensis* (Durban, South Africa).
143 Four major clades can be separated in the 16S tree. The first one (A in Fig. 1), highly supported ($B = 95\%$ $PP =$
144 0.99) comprises the specimens of *C. brevidactyla* and is separated from all the others grouped in a moderately
145 supported clade ($PP = 0.89$). Within this clade, the specimens of *C. brachydactyla* (B) cluster together in a
146 highly supported clade ($B = 99\%$ $PP = 1$) away from the others grouped in a moderately supported clade ($PP =$
147 0.84). This clade is split in two, the first one (C), highly supported ($B = 100\%$ $PP = 1$), comprises the type and
148 non-type specimens of *C. gracilipes* and the other one (D), moderately supported ($PP = 0.84$) with all the
149 specimens of *C. natalensis* from different Indian Ocean localities.

150

151 (Figure 1)

152

153 **Morphological comparison**

154 Our morphological study, confirming the molecular study results, reveals that what has been attributed by
155 several authors to various species names is in fact *C. natalensis* De Man, 1908. Until now, *C. natalensis* was
156 considered a synonym of *C. brachydactyla*.

157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195

(Figure 2)

Detailed description.

Infraorder Caridea Dana, 1852

Family Atyidae De Haan, 1849

Genus *Caridina* H. Milne Edwards, 1837

***Caridina natalensis* De Man, 1908**

Caridina nilotica var. *natalensis* De Man, 1908: 262–263 pl.20, fig.3, 3a, 3b; Lenz, 1912: 5; Bouvier, 1925: 154–155 fig. 320; Barnard, 1950: 655 (key).

Caridina longirostris Richters, 1880:162–163 ; Holthuis, 1965: 20–23 fig. 6 ; Keith *et al.* 2006: 50–51.

Caridina nilotica var. *brachydactyla* Lenz, 1910: 568; Roux, 1929: 303–304 tab.1 no.15.

Caridina nilotica var. *gracilipes* Lenz, 1910: 568.

Caridina brachydactyla brachydactyla Costa 1980: 673–700.

Material examined

Type material:

Caridina nilotica natalensis De Man, 1908: **SOUTH AFRICA**. Lectotype. ZMA.CRUS.D.102886, 1♀ ovig. cl 6.4mm; Umgeni River, Durban, Natal, coll. M. Weber, 1898, det. J.G. De Man. Paralectotypes. ZMA.CRUS.D.102886, 2♀ ovig. cl 5.7–6.4mm; same data.

Caridina nilotica var. *brachydactyla* De Man, 1908: **INDONESIA**. Lectotype. RMNH.CRUS.D.977, 1♀ ovig. cl 4.8mm; Near Reo, Flores, coll. M. Weber. Paralectotypes. RMNH.CRUS.D.2552, 2♀ ovig. cl 5.3–5.4mm; river near Palopo Luwu, Sulawesi, coll. M. Weber..

Caridina brevidactyla Roux, 1920: **INDONESIA**. Lectotype. NMB 4.VI.b 1, 1♂ cl 4,8mm; Sungai Manumbai, Wokam Island, Aru, April 14–15,1908. Paralectotypes. NMB 4.VI.a, 1♂ cl 3.3mm; Aru, Udjir Island, April 15, 1908, NMB 4.VI.b, 2♀ cl 5.8–6.4mm; Sungai Manumbai, Wokam Island, Aru, April 14–15,1908. NMB 00004 VIc, Wokamar, Wokam Island, Aru, April 17, 1908, 1♀ ovig. 5,7mm; NMB 4.VI.d; 2♀ ovig. cl 5.7mm, Seltutti, Kobroor Island, Aru, May 2, 1908.

Caridina gracilipes De Man, 1892: **INDONESIA**. Paralectotypes. ZMA.CRUS.D.102635, 1♂ cl 4.1mm (DNA: CA025), 1♀ ovig. cl 5.9mm (DNA: CA023), 3♀ cl 5.1mm (DNA: CA027), 5.2mm (DNA:CA024) and 5.6mm; in a rice field, Makassar, Sulawesi, coll. M. Weber, 1888. NMB 1061e, 1♂ 3.8mm; 2♀ cl 5.8–5.9mm; same data.

Caridina longirostris H. Milne Edwards, 1837: **ALGERIA**. Paralectotypes. MNHN-IU-2013-19419, 3♂ cl 2.9–3.1mm; from the river Macta, near Oran. MNHN IU-2013-19418, 2♂ 3.2–3.6mm; same data.

Non- types :

Caridina natalensis **KENYA**. MNHN-IU-2015-1854, Tiwi river, 20km south of Mombasa. **TANZANIA**. NHM 1982.576, 3♀ ovig. cl 5.5–7.2mm, Ruo Lukuledi, Tanganyika. **SOUTH AFRICA**. MNHN-IU-2018-61, 1♂ cl 3.3mm (DNA: CA2079) and MNHN-IU-2018-62, 1♀ ovig. cl 6.0mm, River Mbanyana, 32°13.123'S

196 28°55.031'E, altitude 9m, coll. Maliwa L., Mlambo M., Marquet G. & Tiberghien, P., February 11, 2018;
197 MNHN-IU-2018-63, 1♀ ovig. cl 6.9mm and MNHN-IU-2018-64, 1♀ ovig. cl 6.8mm, River Umtata, altitude
198 2m, 31°34.144'S, 28°45.523'E, coll. Maliwa L., Mlambo M., Marquet G. & Tiberghien, P., February 13, 2018;
199 MNHN-IU-2018-65, 1♀ ovig. cl 6.3mm and MNHN-IU-2018-66, 1♀ ovig. cl 6.3mm (DNA: CA2083), River
200 Mzumbe, altitude 6m, 30°36.151'S 30°32.817'E, coll. Maliwa L., Mlambo M., Marquet G. & Tiberghien, P.,
201 February 16, 2018; MNHN-IU-2018-67, 1♀ ovig. cl 6.8mm and MNHN-IU-2018-68, 1♀ ovig. cl 7.0mm, River
202 iLovu, altitude 8m, 17°05.858'S 30°49.390'E, coll. Maliwa L., Mlambo M., Marquet G. & Tiberghien, P.,
203 February 17, 2018. **MAYOTTE.** MNHN-IU-2018-69, 1♀ ovig cl 6.1mm, River Bouyoni, altitude 14m,
204 12°43.966'S 45°8.250'E, coll. ARDA, May 15, 2006; MNHN-IU-2018-70, 1♀ cl 4.5mm and MNHN-IU-2018-
205 71, 1♀ cl 6.0mm, River Dembeni, altitude 19m, 12°50.402'S 45°10.461'E, coll. ARDA, November 12, 2003;
206 MNHN-IU-2018-72, River Kwalé, altitude 39m, 12°48'092'S 45°11.520'E, coll. ARDA, November 10, 2003;
207 MNHN-IU-2018-73, 1♀ cl 4.6mm, MNHN-IU-2018-74, MNHN-IU-2018-76 and MNHN-IU-2018-75, 1♀ cl
208 5.2mm, River Soulou, altitude 14m, 12°45.812'S 45°5.951'E, coll. ARDA, November 9, 2003. **COMOROS.**
209 MNHN-IU-2018-77, 1♀ ovig. cl 3.8mm (DNA: CA1344), River Bwanifunge, Moheli Island, altitude 39m,
210 12°19.642'S, 43°40.240'E, coll. A. Abdou December 30, 2013; MNHN-IU-2018-78, 1♀ ovig. cl 4.5mm (DNA:
211 CA1343), River Mdjawashe, Moheli Island altitude 18m, 12°21.386'S, 43°41.944'E, coll. A. Abdou, December
212 31, 2013. **MADAGASCAR.** MNHN-IU-2018-79, 1♀ ovig. cl 4.1mm (DNA: CA1035), MNHN-IU-2018-80, 1♀
213 ovig. 4.8mm (DNA: CA1037), MNHN-IU-2018-81, 1♀ cl 4.3mm and MNHN-IU-2018-82, 1♂ cl 4.8mm, River
214 Ambodiforaha, altitude 9m, 15°43.054'S 49°57.637'E, coll. R. Fara, H. Grondin, G. Marquet, T. Robinet, May
215 15, 2010; MNHN-IU-2018-87, 1♀ ovig cl 3.5mm, MNHN-IU-2018-83, 1♀ ovig cl 5.2mm, MNHN-IU-2018-88
216 1♀ cl 4.0mm, MNHN-IU-2018-85, 1♀ cl 4.0mm, MNHN-IU-2018-86, 1♀ cl 4.3mm and MNHN-IU-2018-84,
217 1♂ cl 4.0mm, River Andempona, Ampanasanovy estuary, altitude 0m, 14°35.298'S 50°10.105'E, coll. C. Ellien,
218 R. Fara, E. Feunteun, N. Mary, T. Robinet, July 04, 2008; MNHN-IU-2018-89, 1♀ ovig. cl 4.7mm, MNHN-IU-
219 2018-90, 1♀ cl 4.7mm, MNHN-IU-2018-92, 1♀ cl 4.9mm, MNHN-IU-2018-91, 1♀ cl 5.5mm, MNHN-IU-
220 2018-93, 1♂ cl 3.8mm and MNHN-IU-2018-94, 1♂ cl 4.0mm, River Ankavia, altitude 23m, 14°59.488'S
221 50°11.095'E, coll. C. Ellien, R. Fara, E. Feunteun, N. Mary, T. Robinet, July 03, 2008; MNHN-IU-2018-95, 1♀
222 ovig. cl 4.0mm, MNHN-IU-2018-96, 1♀ cl 4.8mm, MNHN-IU-2018-97, 1♀ cl 5.5mm and MNHN-IU-2018-98,
223 1♂ cl 3.0mm, River Fanambana, altitude 11m, 14°33.517'S 50°10.017'E, coll. C. Ellien, R. Fara, E. Feunteun, N.
224 Mary, T. Robinet, July 4, 2008; MNHN-IU-2018-99, 1♀ ovig cl 3.9mm (DNA: CA1184) and MNHN-IU-2018-
225 100, 1♀ cl 4.8mm (DNA: CA1185), unknown locality, coll. C. Ellien, R. Fara, E. Feunteun, N. Mary, T.
226 Robinet. **SEYCHELLES ISLANDS.** MNHN-IU-2017-1445, 1♀ ovig. cl 4.8mm (DNA: CA1195) and MNHN-IU-
227 2017-1446, 1♀ cl 4.8mm (DNA: CA1194), unknown river, Mahé Island, coll. ARDA, November 24, 2004;
228 MNHN-IU-2017-1447, 1♀ ovig. cl 4.5mm (DNA: CA1186) and MNHN-IU-2017-1448, 1♂ cl 4mm (DNA:
229 CA1187), River Nouvelle Découverte, Praslin Island, altitude 8m, 4°19.304'S 55°42.351'E, coll. ARDA, October
230 08, 2003.; MNHN-IU-2017-1449, 1♀ ovig. cl 4.9mm (DNA: CA1197) and MNHN-IU-2017-1450, 1♂ cl
231 4.1mm (DNA: CA1196), River Grande Barbe, Silhouette Island, 4°30.052'S 55°13.537'E, coll. ARDA,
232 November 20, 2004. **MAURITIUS.** MNHN-IU-2017-1451, 1♀ ovig. cl 4.2mm, MNHN-IU-2017-1452, 1 juvenile
233 cl 2.3mm, MNHN-IU-2017-1454, 1 juvenile cl 2.4mm and MNHN-IU-2017-1453, 1 juvenile cl 2.6mm;

234 Forested lake, saline, near Camp Poorun, altitude 11m, 20°10.517'S 57°45.767'E, coll. C. R. Turner, December
235 11, 2005.

236

237 **Diagnosis.**

238 Carapace (Fig. 2m, n, o) smooth, glabrous, with sharp antennal spine placed at lower orbital angle.
239 Pterygostomian margin rounded. Rostrum rather constantly long, 0.8–1.3 of cl, straight or curved up distally,
240 reaching well beyond scaphocerite. 15–26 dorsal teeth, leaving distally unarmed part of rostrum 0.4–1.2 times
241 that of armed part, except for one to three subapical tooth, 1 to 2 post-orbital teeth present. 7–23 teeth present on
242 the ventral margin extending from highest part of the rostrum either to tip or with short distal part unarmed.
243 Number of dorsal teeth on the rostrum before the most proximal ventral tooth 10–14. Rostral formula: (1–2) 15–
244 26 + 1–3 / 7–23.

245 First pereopod (Fig. 2a): Stout, chela about 1.8–2.4 times as long as wide, dactylus 2.5–6.0 times as long as
246 wide, 0.8–1.6 length of palm; carpus 1.7–3.3 times as long as wide with shallow excavation on anterior margin.

247 Second pereopod (Fig. 2b): More slender and longer than first pereopod. Chela 1.9–3.0 times as long as wide,
248 dactylus 3.5–7.0 times as long as wide, 1.1–1.9 times length of palm; carpus 4.3–6.0 times as long as wide.

249 Third pereopod (Fig. 2c): Dactylus (Fig. 2d): 2.9–4.0 times as long as wide (terminal spine included) with 6–9
250 spines on flexor margin in addition to the terminal one; propodus 12.7–18.6 times as long as wide, 4.1–6.6 times
251 as long as dactylus.

252 Fifth pereopod (Fig. 2e): Dactylus (Fig. 2f): 3.0–6.01 times as long as wide with 31–61 spiniform setae on
253 flexor margin; propodus 15.2–22.0 times as long as wide, 4.3–5.7 as long as dactylus.

254 First male pleopod (Fig. 2k): Endopod leaf-like with a developed appendix interna in males.

255 Second male pleopod (Fig. 2l): Appendix masculina on second pleopod reaching 0.52 times length of endopod;
256 appendix interna reaching about 0.84 times length of appendix masculina.

257 Egg size (Fig. 2j): 0.35–0.46 × 0.22–0.29 mm.

258 Preanal carina (Fig. 2h): with a strong spine.

259 Telson (Fig. 2i): ending triangular with a posteromedian projection; 1 pair of longer lateral simple setae and 2 to
260 3 pairs of shorter intermediate simple setae shorter or slightly longer.

261 Uropodal diaeresis (Fig. 2g): with 9–14 short spinules.

262

263

264 **Colour pattern.** Colours (Fig. 3) vary and tend to match the substrate the shrimp lives on. The body can vary
265 from hyaline to brownish with red dots, with sometimes a large red border on the ventral side of the rostrum. An
266 oblique brown or carmine red band on the cephalothorax is very characteristic. The coloration is lost on
267 preserved animals.

268

269 (Figure 3)

270

271 **Habitat.** All specimens were collected in the lower course of rivers, (altitude 5–25 m), among macrophytes in
272 running water.

273

274 **Distribution.** *C. natalensis* occurs in Comoros (Anjouan, Mohéli), Mayotte, Seychelles (La Digue, Mahé,
 275 Praslin and Silhouette), Mauritius, in Madagascar and South Africa. Present before in Reunion Island (Costa
 276 1980; Kiener & Duchochois 1981) this species seems now absent despite extensive prospections made there
 277 since (Fig. 4).

278
 279 (Figure 4)

280
 281 **Key for studied species**

- 282 1.1 Preanal carina with spine.....2
 283 1.2 Preanal carina unarmed.....*C. brevidactyla*
 284
 285 2.1 P1 carpus greater than 1.9 times as long as wide and P2 carpus mostly than
 286 4.3.....3
 287 2.2 P1 carpus less than 1.8 (1.4–1.8) times as long as wide and P2 carpus than
 288 4.2.....*C. longirostris*
 289
 290 3.1 P1 Chela greater than 2.1 times (2.1–2.3) as long as wide; P3 dactylus with mostly 5-6 spines (5–7) on flexor
 291 margin in addition to the terminal one.....*C. brachydactyla*
 292 P1 Chela less than 2.1 times as long; P3 dactylus with mostly 6–9 spines on flexor margin in addition to the
 293 terminal one..... 4
 294
 295 4.1 P5 propodus 4.3–5.7 as long as dactylus.....*C. natalensis*
 296 4.2 P5 propodus mostly 3.4–4.1 (3.4–5.8) as long as dactylus.....*C. gracilipes*

297
 298
 299
 300 **Discussion**

301
 302 ***Caridina natalensis*, not a junior synonym of *C. brachydactyla***

303 The molecular and morphological analyses of specimens collected from a large geographic range,
 304 covering the entire known distribution of *C. brachydactyla* (*sensu* Richard & Clark (2010)) in the
 305 Indian Ocean and including localities close to most of the type localities of its synonyms, suggest that
 306 *C. n. natalensis* is a valid species. These results disprove Richard and Clark (2010) study, which based
 307 on old collection specimens (from which molecular studies are difficult to do), thus using morphology
 308 only, recognized *C. n. natalensis* and *C. n. brevidactyla* as junior synonyms of *C. brachydactyla*.
 309 Indeed, Richard and Clark (2010) found that the dactylus to propodus ratios of the first and second
 310 pereopods in *C. n. natalensis* fell into the range calculated for *C. brachydactyla*. They also showed
 311 that the Natal specimens differed from topotypical specimens of *C. brachydactyla* in having the
 312 appendix interna slightly turned down towards the exopod, whereas it was straight in the Indonesian

313 material. This was regarded by the authors as a non-significant character for the separation of species.
314 Here, the molecular results show that the specimens from the Southwestern Indian Ocean (here
315 attributed to *C. natalensis* - type locality: Umgeni River, Durban, South Africa) are genetically highly
316 distinct from the specimens collected in Indonesia (here attributed to *C. brachydactyla* - type locality:
317 Sulawesi, Indonesia) and to specimens from Melanesia (here attributed to *C. brevidactyla* - type
318 locality: Aru Island, Indonesia). The morphological examination of the specimens used in the
319 molecular tree allowed finding new characters that are stable within genetic clusters but clearly
320 different among clusters. Having examined the type specimens of *C. brachydactyla*, we show that it
321 can be separated from *C. natalensis* by P1 chela greater than 2.1 times as long as wide (vs mostly 1.8–
322 2.1) and P3 dactylus with mostly 5–6 spines on flexor margin in addition to the terminal one (vs 6–9).
323 Having also examined the type specimens of *C. n. brevidactyla*, we show that it can be separated from
324 *C. natalensis* by the tooth on the preanal carina that is present in *C. natalensis* but absent in *C.*
325 *brevidactyla*. Indeed, in a not yet published work, we show based on many specimens from the Pacific
326 Ocean that *C. brevidactyla* is also a valid species (see de Mazancourt *et al.* unpublished).

327

328 ***Taxonomy of Caridina nilotica complex in the Indian Ocean***

329 Of the 298 known species of *Caridina* (WoRMs database as of May 2018), the complex *C. nilotica*,
330 which includes 22 described varieties and/or species (Karge & Klotz 2007) has a very confuse
331 systematic (Johnson 1963). Although, assumed to be broadly distributed across the Indo-West Pacific
332 (from Africa to Fiji), *C. nilotica* complex remains ill defined and subject to many confusions. In this
333 study, we focussed on the Indian Ocean members of the *C. nilotica* complex. Since the studies of De
334 Man (1908) and Roux (1920), six varieties were generally reported in the Western Indian Ocean: *C. n.*
335 *brachydactyla*; *C. n. longirostris*; *C. n. gracilipes*; *C. n. natalensis* and *C. n. brevidactyla*. Here, based
336 on a large geographic range, covering the entire known distribution of *C. nilotica* complex in the
337 Indian Ocean and including localities close to most of the type localities of its varieties, molecular and
338 morphological analyses suggest that the only variety of *C. nilotica* that occurs in the Indian Ocean is
339 *C. n. natalensis*, that we here resurrect as a valid species.

340 As demonstrated above, the 16S molecular tree showed that *C. brachydactyla* only occurs in
341 Indonesia, and *C. brevidactyla* only occurs in the West Pacific. Moreover, the inclusion of the
342 paralectotypes of *C. gracilipes* in the molecular tree also suggested that this species is absent from the
343 Western Indian Ocean. Indeed, in this study, none of the specimens collected in the Indian Ocean and
344 morphologically resembling *C. brachydactyla*, *C. brevidactyla* or *C. gracilipes*, fell into the genetic
345 clusters containing specimens of each of these three species. On the contrary, all of these specimens
346 collected in the Indian Ocean formed a single clade, genetically highly differentiated from *C.*
347 *brachydactyla*, *C. brevidactyla* and *C. gracilipes*, and morphologically close to the type specimen of
348 *C. natalensis*.

349 In this study, we have compared the specimens of *C. natalensis* with all the species of the *C.*
350 *nilotica* complex that have been historically reported as occurring in the Western Indian Ocean,
351 namely: *C. n. gracilipes*, *C. n. brevidactyla*, *C. n. brachydactyla* and *C. n. longirostris*. These
352 comparisons showed that not only these species do not occur in the Western Indian Ocean, but they
353 also are distinguishable from *C. natalensis*. Morphologically, *C. gracilipes*, can be separated from *C.*
354 *natalensis* by the P5 propodus mostly 3.3–4.1 as long as dactylus (vs 4.3–5.7). As mentioned earlier,
355 *C. brevidactyla* and *C. brachydactyla* can be morphologically separated from *C. natalensis*. Finally,
356 although the type specimens of *C. n. longirostris* could not be genetically analyzed, they were
357 morphologically easy to separate from *C. natalensis* (or from other variants of *C. nilotica* complex)
358 because of their P1 and P2 carpus respectively 1.7–2.3 (vs 1.4–1.8) and 4.3–8.0 (vs 3.9–4.7), P3
359 dactylus stouter, dactylus 2.9–4.0 (vs 4.0–4.8) times as long as wide, with propodus 4.1–6.6 (vs 3.4–
360 4.0) times as long as dactylus, and P5 dactylus stouter with propodus 4.3–5.7 (vs 3.2–3.7) times as
361 long as dactylus.

362

363 **Conclusion**

364 Further studies should be led on a larger geographic coverage in the Indian Ocean to determine more
365 precisely the northern limit of *C. natalensis* distribution range. This species is abundant in lower
366 course of rivers from South Africa, Madagascar, Comoros, Mayotte and Seychelles, however, it has a
367 critical status in Mascarene archipelago. Indeed *C. natalensis* seems to have now disappeared from
368 Reunion Island (Keith *et al.* 2006) like *Macrobrachium hirtimanus* (Olivier, 1811).

369

370 **Acknowledgements**

371 The authors wish to thank Dr Urs Wuest and Edi Stöckli (NMB), Paula Martin-Lefèvre and Dr Laure Corbari
372 (MNHN), Dr Charles Franssen and Karen van Dorp (ZMA) for providing the specimens used in this study

373 Comoros archipelago: thanks to Yaya, Abdallah Ahmed Soilihi and Halidi Ahmed Ben Ali. We are also grateful
374 to Conservation International (CI) and particularly to F. Hawkins and CI Madagascar.

375 Mayotte: Thanks to DAF (Direction de l'agriculture et de la forêt) and ARDA (Association Réunionnaise de
376 Développement de l'Aquaculture).

377 Seychelles: We thank P. Grondin of ARDA (Association Réunionnaise de Développement de l'Aquaculture) in
378 Reunion Island for giving us specimens from this archipelago.

379 Madagascar: We thank the DIAMSOI team (The IH-SM from Tuléar with Dr Man-Wai Rabenevanana and the
380 MNHN from Paris with E. Feunteun, P. Keith and T. Robinet) and the ARDA team (P. Bosc, H. Grondin and P.
381 Valade). We are grateful to Joe Aride from Madagascar National Parcs (MNP-ANGAP) and to the manager of
382 Masoala National Parc at Maroantsetra. Lastly, we want to thank all the Responsible Chiefs of the areas
383 concerned for their kind permission, and the villages and communities who have always heartily received us and
384 helped us in our prospecting of rivers. This research was financed by the Institut Français de la Biodiversité
385 (IFB) for the DIAMSOI program (2007-2010).

386 South Africa: We are grateful to Patrick Kubheka and Helen James for facilitating collecting permits for us with
387 provincial conservation urgencies in KwaZulu-Natal and Eastern Cape (permit no. CRO69/17CR), respectively.
388 We thank Nick and Tim McClurg, Patrick Kubheka, Lazola Maliwa and Pascal Tiberghien for their help in the
389 field and Albert Chakona (SAIAB) for lending us his electric fishing gear.

390

391

392 **References**

393

394 Barnard, K.H. (1950) Descriptive Catalogue of South African Decapod Crustacea. *Annals of the South African*
395 *Museum*, 38, 1–864.

396

397 Bouvier, E.L. (1913) The Percy Sladen Trust Expedition, n° XXVIII. Les Caridines des Seychelles.
398 *Transactions of the Linnean Society of London*, 15 (4), 447–472.

399

400 Bouvier, E. L. (1925) Recherches sur la morphologie, les variations, la distribution géographique des crevettes
401 de la famille des Atyidae. *Encyclopédie entomologique*, 4, 1–370.

402

403 Cai, Y. & Ng P. (2001) The freshwater decapod crustaceans of Halmahera, Indonesia. *Journal of Crustacean*
404 *Biology*, 21 (3), 665–695.

405

406 Cai, Y. & Shokita S. (2006) Report on a collection of freshwater shrimps (Crustacea: Decapoda: Caridea) from
407 the Philippines with descriptions of four new species. *The Raffles Bulletin of Zoology*, 54 (2), 245–270.

408

409 Coleman, C.O. (2003) "Digital inking": How to make perfect line drawings on computers. *Organisms Diversity*
410 *and Evolution*, 3 (4), 303.

411

412 Coleman, C.O. (2006) Substituting time-consuming pencil drawings in arthropod taxonomy using stacks of
413 digital photographs. *Zootaxa*, 1360 (1), 61–68.

414

415 Costa, H.H. (1980) Results of the Austrian-Indian Hydrobiological Mission 1974 to the Seychelles-,Comores
416 and Mascarene-Archipelagos: Part III: The Ecology and the Distribution of Decapoda Caridea in the Indian
417 Ocean Islands of Seychelles, Mauritius, Comores & Réunion. *Annalen des Naturhistorischen Museums in Wien*,
418 83, 673–700.

419

420 Darriba, D., Taboada, G.L., Doallo, R., and Posada, D. (2012) jModelTest 2: more models, new heuristics and
421 parallel computing. *Nature Methods*, 9 (8), 772.

422

423 De Man, J.G. (1908) On *Caridina nilotica* and its varieties. *Records of the Indian Museum*, 2, 255–283.

424

425 Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic*
426 *Acids Research*, 32, 1792.

427

428 Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783–
429 791.

430

431 Guindon, S. & Gascuel, O. (2003) A simple, fast and accurate method to estimate large phylogenies by
432 maximum-likelihood". *Systematic Biology*, 52, 696–704.

433

434 Gurney, A.R. (1984) Freshwater shrimps genera *Caridina* and *Parisia* (Decapoda: Caridea: Atyidae) from
435 Madagascar, with descriptions of four new species. *Journal of Natural History*, 18, 567–590.

436

437 Holthuis, L.B. (1965) The Atyidae of Madagascar. *Mémoires du Muséum National d'Histoire Naturelle, séries A*
438 *(Zoologie)*, 33 (1), 1–48.

439

440 Johnson, D. S. (1963) Distribution and other notes on some freshwater prawns (Atyidae and Palaemonidae)
441 mainly from the Indo-West Pacific region. *Bulletin of the National museum of Singapore*, 32, 5–30.

442

443 Karge, A., & Klotz, W. (2007). *Süßwassergarnelen aus aller Welt*. Dähne Verlag: Ettligen, Germany, 216p.

444

445 Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A.,
446 Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P., & Drummond, A. (2012) Geneious Basic: an
447 integrated and extendable desktop software platform for the organization and analysis of sequence data.
448 *Bioinformatics*, 28 (12), 1647–1649.

449

450 Keith, P. Vigneux, E. Bosc P. (1999) *Atlas des poissons et des crustacés d'eau douce de la Réunion*. Muséum
451 national d'Histoire naturelle, Patrimoines naturels, 39, Paris, France, 136p.

452

453 Keith, P., Marquet G., Valade P., Bosc P. & Vigneux E. (2006) *Atlas des poissons et des crustacés d'eau douce*
454 *des Comores, Mascareignes et Seychelles*. Muséum national d'Histoire naturelle, *Patrimoines naturels*, 65, Paris,
455 France, 250p.

456

457 Kiener, A. & Duchochois, P. (1981) *Etude des problèmes piscicoles des eaux intérieures de la Réunion*.
458 CEMAGREF. Report. Section Qualité des eaux de pêche et pisciculture, Study n°25, Aix en Provence, France,
459 140p

460

461 Klotz, W. & De Grave, S. (2015) *Elephantis jaggeri*, a replacement name for *Elephantis natalensis* (Bouvier,
462 1925), a junior primary homonym of *Caridina nilotica* var. *natalensis* De Man, 1908. *Crustaceana*, 88, 1463–
463 1465.

464

465 Kumar, S., Stecher, G., & Tamura, K. (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for
466 bigger datasets. *Molecular biology and evolution*, 33 (7), 1870–1874.

467

468 Lenz, H. (1910) Crustaceen von Madagaskar, Ostafrika and Ceylon. In: Voeltzkow, A. (Ed.), *Reise in Ostafrika*
469 *in den Jahren 1903-1905 mit Mitteln der Hermann und Elise geb.Heckmann Wentzel-Stiftung ausgeführt*, 2,
470 539–576.

471

472 Lenz, H. (1912) Afrikanische Crustaceen aus schwedischen sammlungen. *Arkiv für Zoologi*, 7 (29), 1–10.

473

474 de Mazancourt, V., Marquet, G., Rogers, D.C., & Keith, P. (2018) Description of a new species of *Caridina*
475 (Crustacea: Decapoda: Atyidae) from two Micronesian islands (Guam and Babeldaob). *Zootaxa*, 4377 (1), 39–
476 50.

477

478 Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large
479 phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 1-8.

480

481 Palumbi, S.R. (1996) ‘Nucleic acids II: the polymerase chain reaction.’ In Hillis, D.M., Mable, B.K. & Moritz,
482 C. (Eds.), *Molecular systematics*. Sinauer Associates: Sunderland, USA, 205–247.

483

484 Richard, J. & Clark P.F. (2010). *Caridina* H. Milne Edwards, 1837 (Crustacea: Decapoda: Caridea: Atyoidea:
485 Atyidae) freshwater shrimps from eastern and southern Africa. *Zootaxa*, 2372, 305–337.

486

487 Richard, J. & Clark P.F. (2014) *Caridina simoni* Bouvier, 1904 (Crustacea: Decapoda: Caridea: Atyoidea:
488 Atyidae) and the synonymy by Johnson, 1963. *Zootaxa*, 3841 (3), 301–338.

489

490 Richters, F. (1880) *Beträge zur Meeresfauna der Insel Mauritius und der Seychellen*. *Decapoda*, 162–163.

491

492 Ronquist, F., and Huelsenbeck, J.P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models.
493 *Bioinformatics*, 19, 1572–1574.

494

495 Roux, J. (1920) Süßwasserdekapoden von den Aru- und Kei-Inseln. *Abhandlungen der Senckenbergischen*
496 *Naturforschenden Gesellschaft*, 35, 317–351.

497

498 Roux, J. (1929) Crustacea. III. Atyidae. In G. Petit, Contribution à l'étude de la faune de Madagascar. *Faune des*
499 *colonies françaises*, 3, 293–319.

500

501 Short, J.W., & Doumenq, E. (2003) Atyidae and Palaemonidae, freshwater shrimps. In: Goodman, S.M. &
502 Benstead, J.P. (Eds.), *The Natural History of Madagascar*, The University of Chicago. 603p.

503

- 504 Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies.
505 *Bioinformatics*, 30 (9), 1312–1313.
506
- 507 Weber, M. (1897). Beiträge zur Kenntniss der Fauna von Süd-Afrika. I. Zur Kenntniss der Süßwasser-Fauna
508 von Süd-Afrika. *Zoologische Jahrbucher supplement* 10, 135–199.
509

510 **Legends to figures:**

511

512 . - **FIGURE 1:** Bayesian 16S rRNA phylogenetic tree showing the relationships of some of the species discussed
513 in this study. Numbers above branches indicate bayesian posterior probabilities; numbers under branches
514 indicate Maximum Likelihood bootstrap values.

515

516 . - **FIGURE 2:** *Caridina natalensis*; a. first pereopod; b. second pereopod; c. third pereopod; d. fifth
517 pereopod; e. dactylus of fifth pereopod; f. dactylus of third pereopod; g. uropodal diaeresis; h. pre-anal carina;
518 i. telson; j. eggs; k. second male pleopod; l. first male pleopod; m. anterior region of cephalothorax; n, o. rostrum
519 variations.

520

521 . - **FIGURE 3:** a, b, c, d: Views of living specimens of *Caridina natalensis* showing their coloration; a.
522 Specimen from Madagascar (G. Marquet); b. Specimen from Seychelles (P. Keith); c, d. Specimen from South
523 Africa (G. Marquet). e: Example of habitat where *C. natalensis* lives; Iharaka river, Madagascar (G. Marquet).

524

525 . - **FIGURE 4:** Distribution of *Caridina natalensis* with sampling localities of the specimens of this species
526 examined for the study (black circles) and its type locality (white star).

| Species | Locality | DNA voucher | Museum n° | Type status | GenBank n° | Reference |
|-------------------------|-----------------|-------------|----------------------|---------------|------------|---------------------------------------|
| <i>C. brachydactyla</i> | Bali | CA037 | NMB 1054a | | MH497490 | de Mazancourt <i>et al</i> , in press |
| | Sulawesi | CA1129 | WK 63-10 | Topotypical | MH497500 | de Mazancourt <i>et al</i> , in press |
| | | CA1130 | WK 63-10-1 | Topotypical | MH497501 | de Mazancourt <i>et al</i> , in press |
| | | CA1131 | WK 64-10-3 | Topotypical | MH497502 | de Mazancourt <i>et al</i> , in press |
| <i>C. brevidactyla</i> | Solomon Islands | CA1302 | MNHN-IU-2018-175 | | MH497513 | de Mazancourt <i>et al</i> , in press |
| | Vanuatu | CA1232 | MNHN-IU-2018-191 | | MH497508 | de Mazancourt <i>et al</i> , in press |
| <i>C. gracilipes</i> | Borneo | CA1673 | MNHN-IU-2018-209 | | MH497535 | de Mazancourt <i>et al</i> , in press |
| | Flores | CA029 | NMB 1061f | | MH497489 | de Mazancourt <i>et al</i> , in press |
| | Sulawesi | CA023 | ZMA.CRUS.D .102635 1 | Paralectotype | MH497485 | de Mazancourt <i>et al</i> , in press |
| | | CA024 | ZMA.CRUS.D .102635 2 | Paralectotype | MH497486 | de Mazancourt <i>et al</i> , in press |
| | | CA025 | ZMA.CRUS.D .102635 3 | Paralectotype | MH497487 | de Mazancourt <i>et al</i> , in press |
| | | CA027 | ZMA.CRUS.D .102635 5 | Paralectotype | MH497488 | de Mazancourt <i>et al</i> , in press |
| | Taiwan | CA1674 | MNHN-IU-2018-208 | | MH497536 | de Mazancourt <i>et al</i> , in press |
| <i>C. natalensis</i> | Comoros | CA1343 | MNHN-IU-2018-78 | | MH644416 | This study |
| | | CA1344 | MNHN-IU-2018-77 | | MH644417 | This study |
| | Madagascar | CA1035 | MNHN-IU-2018-79 | | MH644413 | This study |
| | | CA1036 | MNHN-IU-2017-1455 | | MH644414 | This study |
| | | CA1037 | MNHN-IU-2018-80 | | MH644415 | This study |
| | | CA1184 | MNHN-IU-2018-99 | | MH644424 | This study |
| | | CA1185 | MNHN-IU-2018-100 | | MH644425 | This study |

| | | | | | |
|--------------|--------|-------------------|-------------|----------|------------|
| Mayotte | CA1206 | MNHN-IU-2017-1456 | | MH644418 | This study |
| | CA1207 | MNHN-IU-2017-1457 | | MH644419 | This study |
| Seychelles | CA1186 | MNHN-IU-2017-1447 | | MH644426 | This study |
| | CA1187 | MNHN-IU-2017-1448 | | MH644427 | This study |
| | CA1194 | MNHN-IU-2017-1446 | | MH644420 | This study |
| | CA1195 | MNHN-IU-2017-1445 | | MH644421 | This study |
| | CA1196 | MNHN-IU-2017-1450 | | MH644422 | This study |
| South Africa | CA1197 | MNHN-IU-2017-1449 | | MH644423 | This study |
| | CA2079 | MNHN-IU-2018-61 | Topotypical | MH644428 | This study |
| | CA2083 | MNHN-IU-2018-66 | Topotypical | MH644429 | This study |

Table 1: List of the specimens used in the genetic study

Figure 1

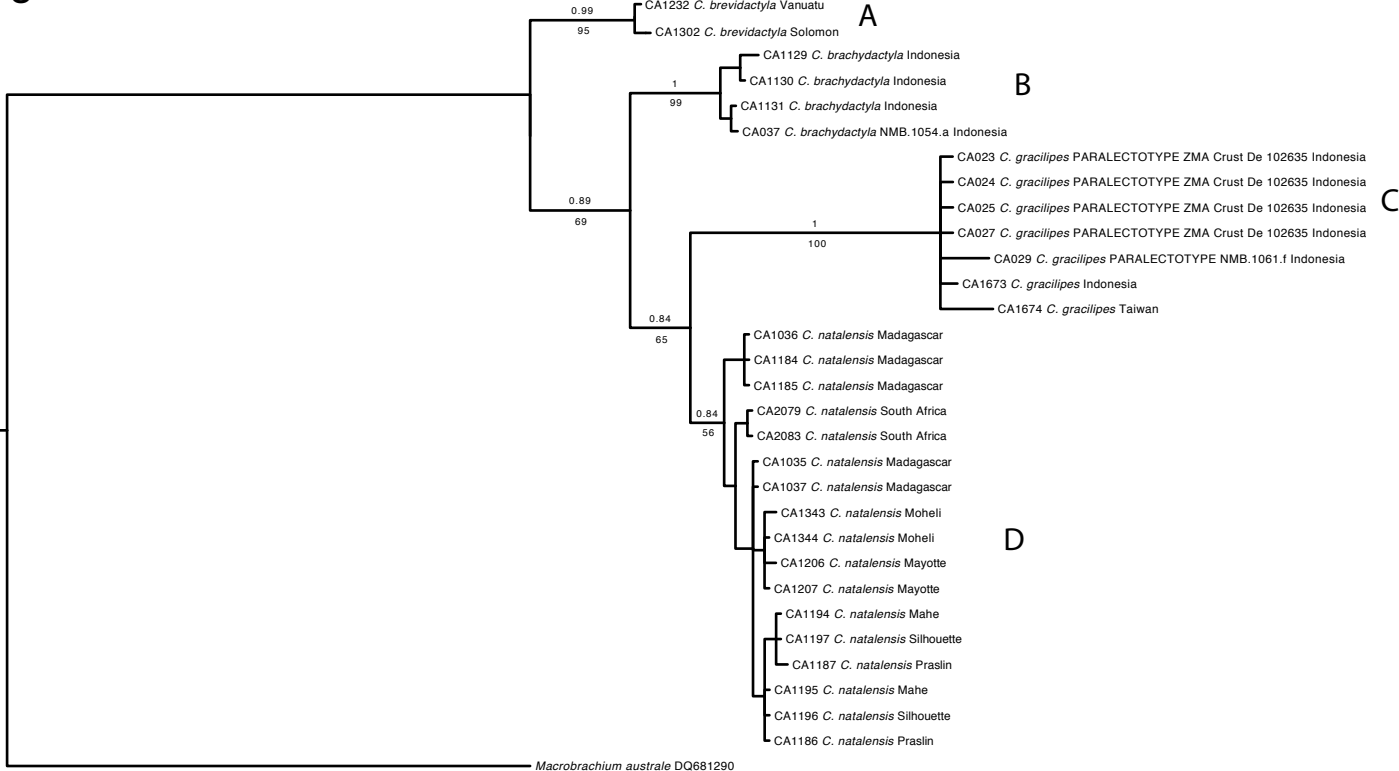


Figure 2

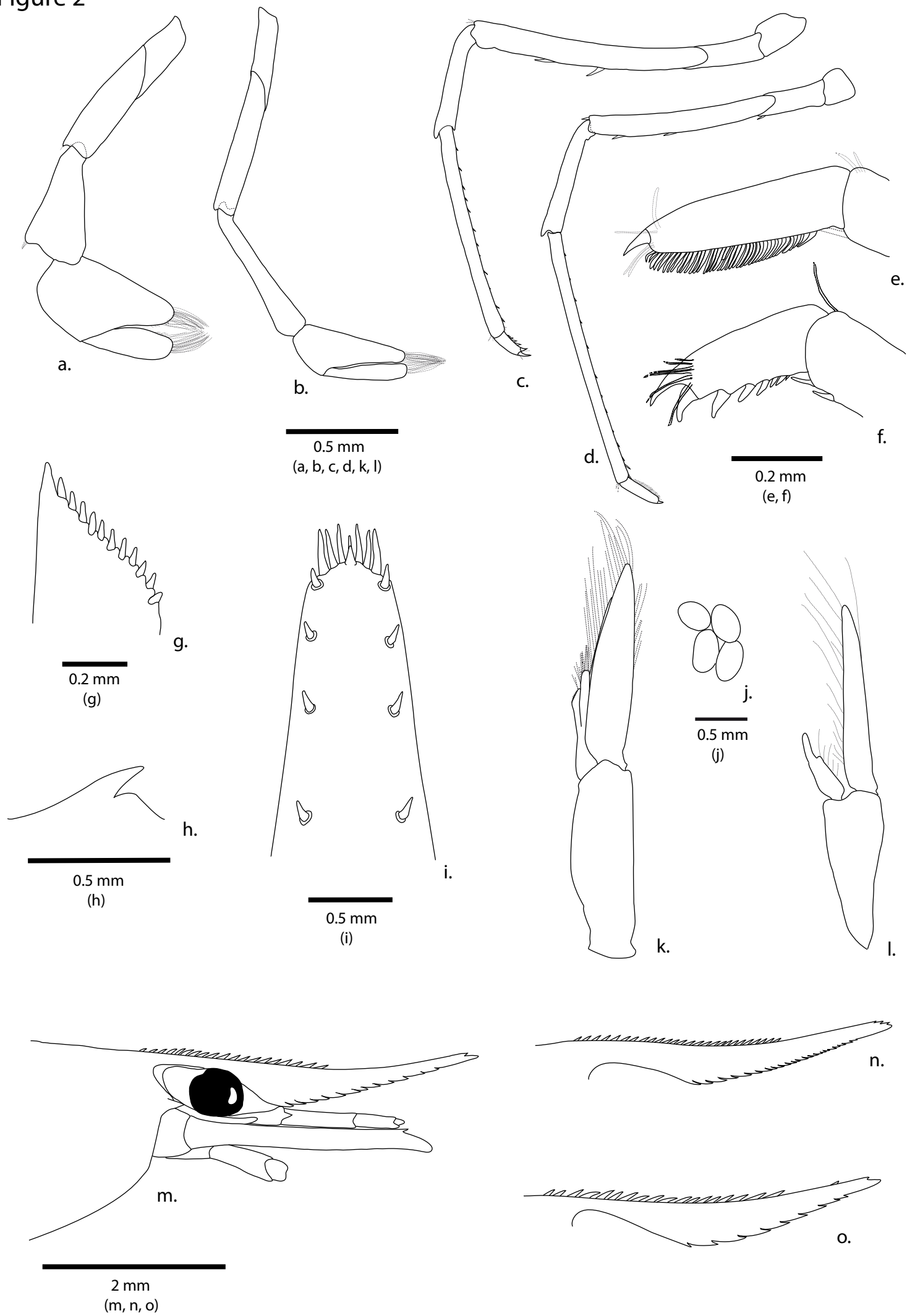


Figure 3



Figure 4

