A new species of *Lynceus* Müller, 1776 from New Caledonia (Crustacea: Branchiopoda: Laevicaudata) from dolines, with remarks on zoogeography

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Abstract. A new species of laevicaudatan branchiopod, *Lynceus insularis* sp. nov., is described. It is reported from five sinkholes (dolines) in the southern part of New Caledonia. *Lynceus insularis* sp. nov. is closest to *Lynceus* species from Australia, but can be separated from these on the basis of clasper morphology and the form of the lamina abdominalis. *Lynceus insularis* sp. nov. is the first record of a remote insular endemic laevicaudatan. The habitats of the species may be threatened due to hydrological changes, reduction of water supply, acidification of fresh water, invasive species, and/or mining activities in the vicinity.

Keywords. Clam shrimp, large Branchiopoda, sinkholes, “Conchostraca”.


Introduction

The Laevicaudata, or “smooth clam shrimp”, is a taxon of bivalved branchiopod crustaceans with a peculiar adult appearance (e.g., an enormous head) and bizarre flattened larvae (Martin 1992; Olesen & Martin 2014). The Laevicaudata are branchiopods, but their precise phylogenetic position within the Branchiopoda has been under some debate (Richter et al. 2007; Olesen 2009; Pessacq et al. 2011; Olesen
& Richter 2013). The Laevicaudata contains a single family, Lynceidae, which has three genera and approximately 42 species worldwide (Martin & Belk 1988; Pessacq et al. 2011; Timms 2013; Rogers et al. 2015, 2016). Lynceus, like other large branchiopod crustaceans, is rarely found on remote islands. The majority of species are found on continents, with the few insular species on large, nearshore, “mainland-like” island systems: Lynceus bifurmis (Ishikawa, 1895) from Japan and Taiwan; L. decaryi Gauthier, 1936, L. dovei Daday, 1927 and L. rotundus Thiele, 1907 from Madagascar. Few large branchiopod crustaceans are known to occur on small islands (e.g., Linder 1960; Smith & Wier 1999; MacKay 2009), and even fewer on remote insular locations such as the Galapagos Islands (Brendonck et al. 1990).

We present a new species of Lynceus that represents the first record from New Caledonia and the first of a remote insular endemic laevicaudatan. New Caledonia (NC) and New Zealand (NZ) were part of “Zealandia”, a Gondwana-derived microcontinent that sank (except NC and NZ) after having separated from the northeastern margin of Australia ca 80 Ma. It has been discussed whether New Caledonia’s biodiversity is that of an ancient continental island, which has retained ancient groups since its separation from the northeastern margin of Australia, or whether it is an oceanic island with a composite biota dominated by more recent colonization and neo-endemism, a so-called ‘Darwinian’ island (Gillespie & Roderick 2002; Grandcolas et al. 2008). The discovery of a new endemic, doline-inhabiting Lynceus is interesting in this context. The new species was found during a biological survey undertaken in connection with a nickel and cobalt mining project in the southern part of New Caledonia.

Material and methods

Collecting and description

Material was collected from southern New Caledonia (Fig. 1). The specimens were collected with a hand net and preserved in 90% alcohol. Specimens were photographed with an Olympus DP73 fitted to an Olympus SZX10 dissecting microscope. To increase the depth of focus of each final illustration, several photographs (about 10) were taken at different focal planes and combined in Zerene Stacker 1.04 (Figs 2, 6, 7). Several males and females were prepared for scanning electron microscopy (SEM), which involved dehydration in a graded alcohol series, critical point drying, mounting on stubs, and coating with a mixture of palladium and platinum; the SEM used was a JEOL JSM-6335-F (FE) housed at the Natural History Museum of Denmark.

Comparative material

We compared our material to other species in the genus from Asia and Australia, either by direct comparisons or to original descriptions in the literature. The following material was studied (DCR = the collections of D.C. Rogers; ZMUC = Zoological Museum, Natural History Museum of Denmark, Copenhagen):

Lynceus bifurmis (Ishikawa, 1895)

Lynceus macleayanus (King, 1855)
Fig. 1. Aerial photographs of the distribution area of *Lynceus insularis* sp. nov. in New Caledonia and photographs of the type locality. A. Overview of New Caledonia. B. Close-up of southern part of New Caledonia with position of localities where *L. insularis* sp. nov. has been found. C. Overview of mining area with four out of the five sinkholes where *L. insularis* sp. nov. has been found. The type locality is DOL-03. The fifth locality (DOL-16) is approximately 9 km NE of DOL-03, outside of the area shown. D–E. Type locality (DOL-03) of *L. insularis* sp. nov. F–G. Additional localities of *D. insularis* sp. nov., DOL-02 and DOL-07, respectively. A–C modified from Google Earth.
Lynceus magdaleanae Timms, 2013

Lynceus planifascius Rogers, Saengphan, Thaimuangphol & Sanoamuang, 2016

Lynceus spinimanus Rogers, Saengphan, Thaimuangphol & Sanoamuang, 2016

Lynceus tatei (Brady, 1866)

Results

Class Branchiopoda Latreille, 1817
Order Laevicaudata Linder, 1945
Family Lynceidae Baird, 1845
Genus Lynceus Müller, 1776

Lynceus insularis sp. nov.
Figs 2–8

Material examined
Holotype

Allotype
NEW CALEDONIA: ♀, same collection data as holotype (ZMUC-CRU-4784).

Paratypes
NEW CALEDONIA: 2 spec., same collection data as holotype (ZMUC-CRU-4785); 8 ♂♂, 6 ♀♀, same location as holotype, 14 May 2010 (ZMUC-CRU-4786); 2 ♂♂, 1 ♀, same location as holotype, 14 May 2010, prepared for SEM (ZMUC-CRU-4787).

Etymology
The species epithet ‘insularis’ is the genitive form of the Latin word for ‘island’ (insula), literally ‘of an island’ in reference to the insular distribution of this species.

Description
Male (holotype; Figs 2–3, 5A, 6)
LENGTH RANGE. 4.8–5.9 mm.

HEAD. 0.75 to 0.80 of body length. Occipital condyle rounded, longitudinal. Fornices broad posteriorly, rounded above second antennae, folded anteriorly over sides of rostrum base. Fornices project anteriorly...
as sharp ridges on each side of rostral constriction and extend to ends of rostral carina bifurcation. Ocular tubercle somewhat prominent, with shallow concavity posterolaterally between tubercle and occipital condyle. Frontal setal fields subcircular, separated by rostral carina, about ¾ size of compound eye. Dorsal organ narrowly oval, elongate. Rostrum constricted basally, bearing pronounced medial carina. Greatest rostral width 0.8 times rostral length. Rostral carina simple, projecting and narrow along margin. Rostral carina bifurcated distally, with each branch continuing to fornices. Rostrum distal of carina bifurcation bent nearly 90° posteriorly. Carina bifurcations and rostral anterior surface

**Fig. 2.** *Lynceus insularis* sp. nov., ♂, light microscopy (holotype, ZMUC-CRU-4783). A. Right lateral view with carapace valve removed. B. Head. C. Second antenna, right side. D. Carapace from ventral with body inside. E. Carapace, right lateral view. F. Carapace, left side half seen from inside.
to apex densely setose. Rostrum apex subequal in width to distance between compound eyes and rostral constriction. Apex margin projecting slightly, lacking setae and arcing between fornix margins.

**First antenna.** With two antennomeres. Proximal antennomere cylindrical, twice as long as broad. Distal antennomere cylindrical, 5 times as long as broad, with apex rounded and bearing numerous short sensory setae (olfactory papillae sensu Martin *et al.* 1986) in a fringe around anterior surface.

**Second antenna.** Peduncle with proximal coxa with transverse row of 10–12 plumose setae directed anteriorly. Peduncle basis with three or four short, acute setae between endopod and exopod (flagellae). Exopod (anterior flagellum) with 26 flagellomeres, each bearing a dorsolateral, pectinate, natatory seta bearing numerous setulae. Endopod (posterior flagellum) with 38 flagellomeres, with lateral, pectinate natatory seta bearing numerous setulae.

**Labrum.** Large, smooth, apically tapering to elongated spine. Labrum apex with ventral surface bearing fine setae. Mandible broadly spatulate, molar surface with 18 transverse ridges becoming larger in size posteriorly. Posteriormost three ridges more broadly spaced than other ridges, with penultimate ridge separated from previous ridge by its basal width and projecting as two spines, posteriormost ridge separated by twice its basal width and prolonged into a single spine; semicircularly arranged row of 7 bent spines present anterior to anteriormost small ridge. Possible paragnaths posterior to mandibles: lobiform, with dense setae.

**Maxilla I.** Typical for the genus (Martin *et al.* 1986; Martin & Belk 1989; Fryer & Boxshall 2009), elongate, broad-margined, distally with 10–15 stout setae, each with double pectinate row in proximal half and densely plumose in distal half. With three posterior, intermediate-length, robust setae lacking plumose portion, but with two rows of spiniform denticles, and one short robust seta terminating in 4–5 spines. Posterior margin fringed with fine setae.

**Maxilla II.** Absent.

**Carapace.** 8–10 mm in length, globose, subspherical, smooth and without ornamentation, subtriangular in lateral outline, with anterior margin being less arcuate than other margins. Maxillary gland ducts arranged transversely, posterior to adductor muscle scar.

**Thoracopods.** 10 pairs, first pair modified as claspers. Right and left claspers equal in size and shape, of typical *Lynceus* form (clasper terminology follows Sigvardt & Olesen 2014 and Kaji *et al.* 2014). Endite 1 of clasper limb typical for genus, lobiform, margined with short setae. Endite 2 broadly transverse, margined with several stout, long (~100–700 μm) setae, each margined with sparse setules separated by at least half their length. Endite 3 broad, oval, laterally compressed, with proximal anterior margin bearing patch of fine plumose setae. Median margin or “palm” region (“gripping area”) of clasper with slender, relatively short setae (~100 μm) bearing sparse lateral setulae (type 3 or 4 setae of Sigvardt & Olesen 2014). Endite 4 (small palp) lobiform proximally, with dorsal branch bearing five long (~100–400 μm) setae, each margined with sparse long setules along anterior margin to apex, and additional ~20 setae of varying length along posterior margin. Endite 5 (large palp) 50% longer than endite 4, subcylindrical, straight in proximal half, with medial bend, straight in distal half. Posterior margin of distal half with row of long (~100–400 μm) setae, each margined with sparse setules separated by at least half their length. Setae continue to dorsal surface of rounded apex. Endopod (movable finger) stout, straight in proximal half, with distal half abruptly decurved, tapering to subacute apex. Endopod apex extending ¼ to ½ of endite 3 “palmar” region (“gripping area”). Remaining thoracopods and body typical for the genus (Martin *et al.* 1986; Martin &
Fig. 3. *Lynceus insularis* sp. nov., ♂♂, scanning electron microscopy (paratypes, ZMUC-CRU-4787).
Belk 1989). Remaining nine thoracopod pairs in general serially similar, becoming gradually smaller posteriorly (significant differences between limbs in the series mentioned below). General aspects of setation of anterior thoracopods are as follows. Margin of endites 1–5 with two rows of setae, margined on distal and proximal sides with smaller setulae. Marginal setae encompass a posterior row of elongate plumose setae, a row of shorter pectinate scraping setae and fine, short, scattered setae. Posterior row of plumose setae three or four times longer than anterior pectinate row. Endite 1 oval, with two to four large pectinate spines at apex. Endite 2 broadly transverse. Endite 3 transverse and lobiform on distolateral margin. Endite 4 projecting, elongate, digitiform. Endite 5 elongate, digitiform, straight. Endopod elongate, digitiform, straight, with stout setae along dorsal margin and apically, similar in form to setae of endite 5. Endites 4–5 and distal margin of endopod with scattered fine, filiform setae, with pectinate scraping setae present apically. Exopod distally elongate, digitiform and apically acute. Exopod proximolaterally broadly oval. Epipod projecting dorsally, truncated. Significant variation in limb components between thoracopods from anterior to posterior as follows. One epipod per appendage present in thoracopods 1 through 7, becoming gradually longer posteriorly, reaching maximum length in thoracopod 4, after which they become smaller until thoracopod 7; epipod absent in thoracopods 8–10. Proximolateral part of exopod broadly oval in thoracopods 2 through 4, from thoracopod 5 gradually more narrow and curved distally; thoracopod 10 lacks a proximolateral part. Endites 4–5 and endopod project significantly, digitiform in thoracopods 2 through 6, from thoracopod 7 gradually shorter and more lobate posteriad.


**Female** (Figs 4, 5B–F, 7–8)

**Length range.** 4.8–5.9 mm. Generally similar to male in appearance.

**Head.** Occipital condyle rounded, longitudinal. Fornices broad posteriorly, rounded above second antennae, folded anteriorly over sides of rostrum base. Fornices project anteriorly as sharp ridges on each side of rostral constriction, extend just short of distolateral rostral corners. Distal apices of forni rounded. Ocular tubercle less pronounced than in male. Setal fields subcircular, separated by rostral carina, about ⅔ size of compound eye. Dorsal organ as in male. Rostrum constricted basally, bearing pronounced medial carina. Greatest width of rostrum 0.8 times rostral length. Rostral carina simple, projecting, narrow along margin. Rostral carina not bifurcated distally. Apex margin rounded, projecting as a ridge, lacking setae.

**Antennae and mouthparts.** As in males.

**Carapace.** 8–10 mm in length, globose, subspherical, smooth, without ornamentation. Anterior margin nearly straight. Maxillary gland ducts as in male.

**Thoracopods.** Twelve pairs, claspers absent. General shape of many thoracopods and setal patterns of endites, endopod and exopod as in male. Epipod becoming gradually longer from thoracopod 1 through 4, in thoracopod 4 of maximum size, from thoracopod 5 through 7 decreasing in size, absent on thoracopods 8 through 12. Exopod increases in size posteriad from thoracopod 1 until thoracopod 3 or 4, after which it becomes smaller, entirely absent in thoracopods 11–12. Proximolateral part of exopod broadly oval in thoracopods 1–2, from thoracopod 3 gradually more narrow and curved distally; proximolateral part of exopod in thoracopods 9–10 distinctly modified into curved lobe with distal setation to which egg clusters are attached.
Fig. 4. *Lynceus insularis* sp. nov., ♀, scanning electron microscopy (ZMUC-CRU-4787). A. Left lateral view with carapace valve removed. B. Head/rostrum, anterior view. C. Rostrum, anterior view. D. Frontal sensory fields and pore leading to compound eyes. E–F. Lamella abdominalis and eggs of left side. G. Attachment of thoracopod 10 exopod to eggs.
Lamina abdominalis. Present, broad, directed laterally, bearing three marginal extensions and two dorsal extensions. Anterior marginal extension sinuate, longer than other marginal extensions by one fourth. Medial marginal extension tapering, nearly straight. Posterior marginal extension broadly triangular,

Fig. 5. Lynceus insularis sp. nov., scanning electron microscopy (paratypes, ZMUC-CRU-4787; A, ♂; B–F, ♀). A. Head, rostrum and labrum of right side. B. Second antenna, left side. C. Gnathal edge of mandible, left side. D. First maxillae from posterior. E. First maxilla, left side, from ventral. F. Posteriomedial spine bearing corner of first maxilla.
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Table 1. The five localities in the southern part of New Caledonia from where *Lynceus insularis* new species is known. Information on sampling dates, geographic position, and size of locality (surface m²) is included. The material used from this study is from locality DOL-03 (type locality).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Surface (m²)</th>
<th>Years Observed</th>
<th>Amount of material</th>
</tr>
</thead>
<tbody>
<tr>
<td>DOL-02</td>
<td>22°19’36.77” S</td>
<td>166°54’15.97” E</td>
<td>4412</td>
<td>2009</td>
<td>rare</td>
</tr>
<tr>
<td>DOL-04</td>
<td>22°19’41.18” S</td>
<td>166°54’04.67” E</td>
<td>5977</td>
<td>2009</td>
<td>rare</td>
</tr>
<tr>
<td>DOL-07</td>
<td>22°19’29.25” S</td>
<td>166°53’30.54” E</td>
<td>378</td>
<td>2008</td>
<td>empty carapaces</td>
</tr>
<tr>
<td>DOL-16</td>
<td>22°15’46.89” S</td>
<td>166°57’09.07” E</td>
<td>3118</td>
<td>2015</td>
<td>common</td>
</tr>
</tbody>
</table>

* This is the type locality of *Lynceus insularis* sp. nov. It was found for the first time in April 2000 at the end of the rainy season.

with posterior margin arcing underneath lamina abdominalis. Dorsal extensions of lamina abdominalis directed anteriorly. Anterior dorsal extension sinuate, posterior dorsal extension digitiform, roughly \( \frac{3}{5} \) length of anterior extension. Eggs held between lamina abdominalis and exopods, attached to distal setae of modified exopods of thoracopods 9–10.

**Telson.** As in male.

**Type locality**

Temporary body of water (doline or sinkhole DOL-03; see Table 1, Fig. 1) with a perimeter at about 290 m, a surface area of about 3800 m² and a maximum depth at about 1.2 to 2.6 m. *Melaleuca quinquenervia* (Cav.) S.T. Blake trees grow both along the margin and in the deeper parts of the sink hole, and there are some scattered spots of *Eleocharis spiralis* (Rottb.) Roem. and Schult. and *Lepironia articulata* (Retz.) (both Cyperaceae); the muddy bottom is covered with smaller, submersed macrophytes like the New Caledonian endemic *Eriocaulon neocaledonicum* Schltr. *Lynceus insularis* sp. nov. occurs among vegetation or is free swimming.

**Habitat**

All sites where this species occurs are dolines (sinkholes) in Pliocene/Quaternary laterite deposits (Lillie & Brothers 1970) (Fig. 1). All localities have Cyperaceae growing on the bottom, sometimes being more than 2 m in length. The soil of the region is nutrient poor but rich in heavy metals (Mg, Fe, Cr, Co and Ni) and is ultrabasic.

**Distributional range**

This species is only known from New Caledonia. To date it is known from five sites, all in the Mont-Dore and Yaté communities of Southern Province. The species was first recognized in April 2000 (DOL-03). However, since it was not found in 2004, a larger survey of 17 additional, similar localities was undertaken in 2009, of which 5 had either empty carapaces or living *Lynceus* specimens. All localities are within a distance of 2 km from each other (in mining area), except one (DOL-16) which is situated approximately 9 km northeast of DOL-03 (the type locality).

**Activity Period**

The entire life cycle takes 3–4 months (from February to May/June). Larvae usually hatch in February, which is in the middle of the rainy season (from December to April). February is the warmest month, with average water temperatures ranging from 24–26°C. The highest population density and largest
mating intensity was observed at the end of April. From about June, Lynceus is absent from the ponds even if water still remains. The ponds are dry from about September to November.

**IUCN Red List status**

*Lynceus insularis* sp. nov. currently meets the red list definition (IUCN 2001) as a critically endangered species, with its distribution area being only about 1.7 ha. Furthermore, the distribution area of *L. insularis* sp. nov. is severely fragmented into small subpopulations, each of which shows extreme fluctuations in population size (IUCN Red List Criteria B2a, c). The probability of extinction is estimated to be at least 50% within 50 years due to a high risk of degradation of the biotope of the species which might result as a cumulative effect of a number of factors: hydrological changes, reduction of water supply, acidification of fresh water, invasive species (*Cervus timorensis rusa* Müller & Schlegel, 1845) and mining activities in the vicinity (less than 1 km).

**Discussion**

*Lynceus insularis* sp. nov. appears to be most closely related to members of the Australian fauna, and appears extraordinarily similar to the widespread *L. macleayanus* (King, 1855) and to *L. tatei* (Brady, 1886) in the general form of the head, rostrum, thoracopods and telson. In fact, using the key in Timms (2013), *L. insularis* sp. nov. would be identified as *L. macleayanus*. We compared *L. insularis* sp. nov. to the tropical Asian *Lynceus* taxa, but the similarities were limited to typical genus level characteristics. The tropical Asian species generally have a serrated distal margin on the rostrum and fine denticles covering the telson. These characters are absent in the Australian fauna and in *L. insularis* sp. nov.

The morphology of thoracopod 1 (the clasper) in *Lynceus insularis* sp. nov. is closest to that of *L. macleayanus*. *Lynceus insularis* sp. nov. only has four stout, cylindrical peg-like spines in the “palmar” region of endite 3, whereas *L. macleayanus* has a row of about nine such spines (see fig. 3c in Timms 2013); in *L. insularis* sp. nov. these spines are ‘hidden’ under the endopod (movable finger), while in *L. macleayanus* they are placed at the median side of endite 3 (the ‘palm’ of the clasper hand) and are therefore more easily visible. Furthermore, in *L. insularis* sp. nov. endite 4 (small palp) is branched, whereas in *L. macleayanus* that endite is palpiform. Yet another difference concerns endite 5 (large palp), which in *Lynceus insularis* sp. nov. is more slender than it is in *L. macleayanus*.

*Lynceus tatei* (Brady, 1886) also has more cylindrical peg-like spines in the “palmar” region of endite III than *L. insularis* sp. nov., as well as a palpiform endite 4. Additionally, *L. tatei* has endite 5 remarkably elongated, as opposed to *L. insularis* sp. nov., which has endite 5 subequal in length to the endopod.

Females of *Lynceus insularis* sp. nov. differ from *L. macleayanus* and *L. tatei* by the form of the lamina abdominalis, which has two dorsal projections in *L. insularis* sp. nov., versus one in *L. macleayanus* and *L. tatei* (see figs 2j and 5j, respectively, in Timms 2013).

As mentioned above, *Lynceus insularis* sp. nov. appears to be most similar to the Australian *L. macleayanus*. This species is the most widespread one in Australia, found across the continent in scattered areas in the west, but very common in South Australia, New South Wales and the eastern half of Queensland, as far north as Cairns, between 16˚ and 43˚ degrees of latitude (Timms 2013). New Caledonia lies roughly 1,200 km east of Australia, between 19˚ and 22˚ degrees latitude, well within the latitudinal range of *L. macleayanus*.

*Lynceus insularis* sp. nov. occurs in dolines (sinkholes) in Pliocene/Quaternary laterite deposits between 5 and 0.1 million years old (Lillie & Brothers 1970), which formed well after New Caledonia separated from Australia some 65 million years ago and before it achieved its present location around 50 million years ago (Coleman1980; Raven 1980).
The occurrence of a *Lynceus* species in New Caledonia, apparently having its closest relatives in Australia, can be explained in two fundamentally different ways. Either the distributional pattern is an ancient ‘Gondwana pattern’ from before the Gondwana-derived microcontinent ‘Zealandia’ (incl. New Caledonia and New Zealand) broke off from Australia (appr. 80 Ma, see Introduction), or the distribution is the result of more recent dispersal. New Caledonia has classically been considered a Gondwanan refuge with a fauna largely dating back to Gondwanan times, but this view was challenged by Grandcolas *et al.* (2007), who found evidence for a more recent colonization since 37 Ma. It has even been suggested that Zealandia has been fully submerged at various intervals, in which case a recolonization of all terrestrial and limnic fauna would have been required. The discovery of a new species of *Lynceus* does not in itself provide support to either of these two hypotheses. For this a more comprehensive phylogenetic study of a broad range of laevicaudatan species from, e.g., Australia and other nearby regions would be required. However, if dispersal indeed is the explanation for the occurrence of *Lynceus* in New Caledonia, it could have been from resting eggs dispersed from mainland Australia (Rogers 2014, 2015).

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