

A new Northeast Asian *Lynceus* (Crustacea: Branchiopoda: Laevicaudata) with uniquely modified thoracopods and an evaluation of DNA barcoding for clam shrimp species identification

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SUBMITTED 09 August 2019
ACCEPTED 20 January 2020
PUBLISHED 03 June 2020

DOI 10.1590/2358-2936e2020013



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Nauplius, 28: e2020013

ABSTRACT

A new species of smooth clam shrimp (Branchiopoda: Laevicaudata) from Mongolia and China is described here based on both morphological and genetic differences. The new species, *Lynceus grossipedia* n. sp., has unique features, including asymmetrically modified male thoracopods (left side thoracopods III–VI), male claspers “movable finger” (=endopod) with delicate setation, and broad, bicarinate male and female rostrum. *Lynceus grossipedia* n. sp. is compared with the genera *Paralimnetis* Gurney, 1931 and *Lynceiopsis* Daday, 1912 and a recently described *Lynceus* Müller, 1776 from China, also showing modified male thoracopods. *Lynceus mandsuricus* Daday, 1927 is declared *nomen inquirendum*. DNA barcoding has not previously been applied on smooth clam shrimp taxonomy, so we generated new cytochrome c oxidase (COX1) data for 10 *Lynceus* species in order to explore its usefulness for Laevicaudata. Previous Laevicaudata sequences in GenBank were scarce (~50) and biased, with 62% (n=31) being assigned to a single taxon (*i.e.*, *Lynceus macleayanus*) and 28% (n=14) not assigned to species. Based on the addition of new barcoding data and the comparison with GenBank data for other clam shrimps, we conclude that distance thresholds between species (=barcoding gap) are similar for all three suborders (Spinicaudata, Cyclestherida, and Laevicaudata).

KEYWORDS

Lynceus grossipedia n. sp., Asian Laevicaudata, smooth clam shrimps, thoracopod asymmetry, COX1.

INTRODUCTION

The suborder Laevicaudata Linder, 1945, or “smooth clam shrimps”, is a small group of less than 45 described species divided into three genera namely, *Lynceus* Müller, 1776, *Lynceiopsis* Daday, 1912, and *Paralimnetis* Gurney, 1931. Despite being globally distributed, the seasonally astatic nature of their freshwater habitat makes the group challenging to study because collecting fresh material is difficult. A few key authors have revised and described most Laevicaudata taxa (Daday, 1927; Martin and Belk, 1988; Timms, 2013), and minor revisions and single species descriptions have been produced in the last few years (Pessacq *et al.*, 2011; Rogers *et al.*, 2015, 2016; Olesen *et al.*, 2016; Sigvardt *et al.*, 2019; Shu *et al.*, 2019), including a catalogue summarizing current taxonomy (Rogers and Olesen, 2016). *Lynceus* species are morphologically similar but can typically be distinguished by a combination of characters including: male and female rostrum, male claspers (first pair of modified thoracopods), and female laminae abdominalis (lamellae used to support egg clutches). *Paralimnetis* and *Lynceiopsis* differ from *Lynceus* males in the clasper size and shape and in having strongly modified second thoracopods (Martin and Belk, 2006). Smooth clam shrimps follow the general branchiopod

pattern of pronounced serially similar thoracopod morphology, with a few exceptions (see Ferrari and Grygier, 2012). However, a recently discovered *Lynceus* from Southwestern China (*L. amplopedia* Shu, Sigvardt, Chen, Olesen, Rogers and Sanoamuang, 2019) bears remarkably modified thoracopods approximately in the middle of the limb series, different from what is seen in other laevicaudatan species (let alone the Branchiopoda). The functional implications of these modified thoracopods are not fully understood yet (Shu *et al.*, 2019). A new *Lynceus* species from Northeast Asia also with modified “middle” thoracopods is described here. The new species is related to *L. amplopedia* but shows clear differences.

Clam shrimp taxonomy (Spinicaudata Linder, 1945, Cyclestherida Sars, 1899, and Laevicaudata) has traditionally been challenging, with uncertainty at many taxonomic levels, particularly due to morphological ‘plasticity’ and lack of precision in early descriptions (*e.g.*, Daday, 1913; 1927). The recent application of molecular systematics and DNA barcoding has successfully solved long-standing questions on geographic variation and the taxonomical validity of Spinicaudata both at generic and family level (Schwentner *et al.*, 2009; 2011; 2015). Despite many previous studies on Laevicaudata, the genetic diversity and evolutionary systematics of this distinct

group of clam shrimps are largely unknown (but see Sigvardt *et al.*, 2019).

DNA barcoding has gained popularity in the last decades for a number of reasons (Hebert *et al.*, 2003). First, COX1 barcodes provide supplementary diagnostic characters, allowing for the identification of potential new species, and establishing molecular thresholds for species delimitation. It also simplifies assignment of biological material to species already described and classified and allows for specimen identification regardless of life stage (Palero *et al.*, 2011; Torres *et al.*, 2014). The efficacy of this approach is based on the presence of higher genetic variation between species rather than within species and relies on sufficient sampling (Hebert *et al.*, 2004; Meyer and Paulay, 2005). Nevertheless, the clam shrimp data currently available in GenBank are highly skewed towards Spinicaudata, with more than 1,600 sequences, compared to less than 120 sequences for Cyclestherida and Laevicaudata together. Furthermore, out of 50 Laevicaudata COX1 sequences, 62% (31) are assigned to a single taxon (*i.e.*, *Lynceus macleayanus* (King, 1855)) and 28% (14) have not been assigned to a particular species. The efficiency of DNA barcoding is highly dependent on the completeness and quality of reference databases, and mistakes during morphological identification, labelling of samples, molecular lab work (*e.g.*, PCR or sequencing) or database annotation can invalidate the definition of an adequate genetic threshold (=barcoding gap).

In this paper, a new species of smooth clam shrimp from Mongolia and Northeast China with uniquely modified “middle” thoracopods is described. At the same time, we explore the validity of DNA barcoding methods for smooth clam shrimps by obtaining new COX1 barcoding data for 10 Laevicaudata taxa, including the new species described here.

MATERIALS AND METHODS

Collecting, specimens and morphology

Specimens were collected with a hand held dip net (0.5 mm mesh size), from four different localities in Mongolia (three in the Dundgovi Province, Mongolian Gobi Desert) and one in the Tuv Province, close to Ulaanbaatar) in August 2017 (~35 individuals) and from three different localities in Northeast China (two in Jilin Province and one in Inner Mongolia

Autonomous Region) in September 2017 (~37 individuals). Specimens were fixed either in 4% formaldehyde for morphology or in 95% ethanol for molecular studies. The animals were examined using a stereo microscope (Olympus SZX10 or Zeiss Stemi 508) and a compound microscope (Olympus CX31) and drawings were made using a camera lucida. Eight specimens of the Mongolian population, including the holotype and allotype, were photographed at different focal planes with an Olympus DP73 camera (operated by Olympus CellSens microscope imaging software), before further treatment/dissection. Four paratypes (an intact male, a dissected male, an intact female, and a dissected female) were prepared for scanning electron microscopy (SEM) (following Sigvardt *et al.*, 2017) and photographed with a JEOL JSM-6335-F (FE) SEM (located at the Natural History Museum of Denmark, Copenhagen).

Appendages of two paratypes (male and female) were dissected off and mounted on microscopy slides in 100% glycerol and sealed with nail polish. The appendages were photographed with a DP80 camera in an inverted Olympus IX 83 microscope, using both stacking (increased depth) and stitching (increased magnification). Dissection and light microscope photos were stacked using Zerene Stacker 1.04. All images were digitally processed with CorelDRAW X7 and Corel PHOTO-PAINT X7.

Terminology follows Kaji *et al.* (2014), Sigvardt and Olesen (2014), Rogers and Olesen (2016), and Sigvardt *et al.*, (2019). Specimens of the new species are deposited in the collections of the Natural History Museum of Denmark, Copenhagen, as well as in Kunming Institute of Zoology, Chinese Academy of Sciences (see details in Results).

The new species was compared to *Lynceus* species from Asia, Africa, America, Australia and Europe, including specimens of *Paralimnetis* and *Lynceiopsis*. Original descriptions and figures were used to supplement the material examined. The following collections were studied directly: BMNH = British Museum (Natural History), London, United Kingdom; DCR = personal collection of D. Christopher Rogers; KIZ = Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China; KKU = Khon Kaen University (Applied Taxonomic Research Center), Thailand; MNHB = Museum für Naturkunde, Leibniz Institut für Evolutions- und Biodiversitätsforschung

an der Humboldt-Universität zu Berlin, Germany; MNHN = Muséum national d'Histoire naturelle, Paris, France; NHMD = Natural History Museum of Denmark, Copenhagen, Denmark; USNM = United States Natural History Museum, Washington D.C., USA; ZMUC = Zoological Museum, University of Copenhagen (now NHMD).

Comparative material

Lynceiopsis perrieri Daday, 1912. AFRICA: Niger: Simbidissi, date unknown, det. and ded. E. Daday, 2 males, 2 females (MNHB 18 365).

Lynceus aequatorialis Daday, 1927. VENEZUELA: Apure State: Arichuna Road, G. Pereira, Id. D. Belk, Belk Collection, ~90 specimens, mostly females (USNM 1143987). Apure State: between Rio Apure and Rio Arauca, October 1894, F. Geay, 11 males, 4 females (MNHN-IU-2007-764). Apure State: Guanaparo, 1899, F. Geay, Dad. Auct., 13 males, 11 females (MNHN-IU-2007-763). Apure State: Guanaparo, 1899, F. Geay, Dad. Auct., 2 males, 2 females (MNHN-IU-2007-766).

Lynceus amplopedia Shu, Sigvardt, Chen, Olesen, Rogers and Sanoamuang, 2019. CHINA: Yunnan Province: Qiubei County: Tianxing Township: Longtao Village: Shuiyantang temporary pond near Road No. S206, 23°55'36.13"N 104°14'17.04"E, altitude 1553 m a.s.l., 5 Oct 2015, H.F. Yang, holotype, male (KIZ-2015010); allotype, female (KIZ-2015011); paratypes, 17 males, 22 females (KIZ-2015012 – KIZ-2015050); paratypes, 5 males, 5 females (KKU-CS2015001); paratypes, 2 males, 2 females (NHMD-615845).

Lynceus baylyi Timms, 2013. AUSTRALIA: Western Australia: 12 km N of Trayning Pit Gnamma Nr. 3, 19 May 2016, B.V. Timms; 27 females (NHMD-615846). Western Australia: Beacon: Yellari Pit, 19 May 2016, B.V. Timms; 15 males, 9 females (NHMD-615847).

Lynceus bififormis (Ishikawa, 1895). JAPAN: Shiga Prefecture: Kusatsu-Shi: Kataoka-Cho, 26 May 2004, M.J. Grygier, 5 males (NHMD-615848, additional material: DCR-611). Shiga Prefecture: Kusatsu-Shi: Kataoka-Cho: Rice paddies, 21 May 2001, M.J. Grygier, 16 males, 3 females (NHMD-81868/ZMUC-CRU-4020). Osaka Prefecture: Takatsuki City: irrigated paddy field, 34°57'18.4"N 135°35'23.7"E, 31 May 2018, S. Ishida, 2 males, 3 females (NHMD-615843). TAIWAN: Taipei: Yangminshan National Park, 2015, C.C. Wang, 1 male, 4 females (NHMD-615844).

Lynceus brachyurus Müller, 1776. DENMARK: Klampenborg: Deer Garden: pond close to "Trepilelågen", 28 April 2017, J. Olesen, 1 male, 4 females (NHMD-232312). USA: California: Sacramento County: Sloughhouse, 1 April 2008, D.C. Rogers, 8 males, 14 females (NHMD-265530, additional material: DCR-696). California: San Joaquin County: Large vernal pool south of Buena Vista Road, 14 February 1997, D.C. Rogers, 2 males, 3 females (NHMD-265529, additional material: DCR-103). Montana: Deer Lodge County: Pinter Lake pool, 23 July 1995, D.L. Gustafson, det. D.C. Rogers, 2 males, 1 female (NHMD-265531, additional material: DCR-574).

Lynceus indicus Daday, 1927. INDIA: Bhowali Bazar: Kumaon, date and collector unknown, 1 male, 3 females (MNHB 18 363).

Lynceus macleayanus (King, 1855) (sensu Timms 2013). AUSTRALIA: New South Wales: Bloodwood: Sue's Pan, 26 July 2015, D.C. Rogers, 4 males, 4 females (NHMD-232861, additional material: DCR-916).

Lynceus mucronatus (Packard, 1875). CANADA: Alberta: 1.6 km E and 1.6 km S of Hussar. 22 May 1963, R. Hartland-Rouse, 3 males, 5 females (BMNH 1968.8.9.11). USA: Montana: Madison County: Hidden Lake Area Pond, 30 June 1990, D.L. Gustafson, det. D.C. Rogers, 2 males, 1 female (NHMD-265546, additional material: DCR-576).

Lynceus planifascius Rogers, Saengphan, Thaimuangphol and Sanoamuang, 2016. THAILAND: Khon Kaen Province: south of Don Han: roadside ditch on northeast side of Highway 208 flooded by rainwater, 16°18'45.88"N 102°52'31.37"E, 19 June 2015, D.C. Rogers and L. Sanoamuang, topotypes, 12 males, 44 females (NHMD-615849, additional material: DCR-889). Khon Kaen Province: south of Don Han: rice paddies on southwest side of Highway 208 flooded by rainwater, 16°19'18.08"N 102°51'44.63"E, 19 June 2015, D.C. Rogers and P. Dabseepai, 10 males, 11 females (NHMD-615850, additional material: DCR-891). Udon Thani Province: table drain on Highway 2 (Mittraphap Road), south of Rual Road 100, 17°07'27.48"N 102°58'25.22"E, 20 June 2015, D.C. Rogers and P. Dabseepai, 12 males, 14 females (NHMD-615851, additional material: DCR-898).

Lynceus simiaefacies Harding, 1941. YEMEN: Jebel Jihaf: Aden: 7100 ft., 1 September 1937, E.B.

Britton, 1 male in ethanol (BMNH 1948.9.28.1); paratypes, male and female thoracopods on 3 slides (BMNH 1940.7.23.1, BMNH 1940.7.23.2 and BMNH 1940.7.23.3).

Lynceus spinimanus Rogers, Saengphan, Thaimuangphol and Sanoamuang, 2016. THAILAND: Suphan Buri: Donchedi District, between Thap Luang and Sra Krachom, roadside ditch flooded by rainwater, 14°40'N 99°50'E, 12 May 2012, N. Saengphan, holotype, female (NHMD-86057/ZMUC-CRU-8213); allotype, male (NHMD-86062/ZMUC-CRU-8218); paratypes, 2 females (NHMD-86114/ZMUC-CRU-8270).

Lynceus susanneae Timms, 2013. AUSTRALIA: Western Australia: Cocklebiddy gnamma Nullarbor Plain, B.V: Timms, 16 May 2016, 15 males, 12 females (NMHD-615888).

Paralimnetis mapimi Maeda-Martinez, 1987. MEXICO: Chihuahua: de la carretera federal No. 49, 16 July 1983, A.M. Maeda-Martínez, paratypes, 5 males, 4 females (USNM 222990).

Paralimnetis rapax Gurney, 1931. ARGENTINA: Chaco: Salta: 12 March 1987, P. Caballo, 1 male, 1 female (NHMD-615852). PARAGUAY: Makthlawaiya: 23°25'S 58°19'W, 11 December 1926, G.S. Carter, Esq., holotype, male (BMNH 1928.2.23.21-23).

Paralimnetis texana Martin and Belk, 1988. USA: Texas: Llano County: natural drainage dammed by road, east side of Ranch Road 2323, 8 km south of Texas Highway 16 at Llano, 30°48'N 98°30'W, 7 November 1984, D. Belk, paratypes, 1 male, 6 females (USNM 234416).

DNA extraction and COX1 sequencing

Total genomic DNA extraction was performed using the DNAeasy kit (QIAGEN, Valencia, California) following the manufacturer instructions. The standard universal primers for the COX1 gene were used for DNA barcoding, since this marker shows a high amplification success in a wide range of taxa (Folmer *et al.*, 1994; Palero *et al.*, 2014). The polymerase chain reaction (PCR) thermal profile used was 94°C for 4 min for initial denaturation, followed by 30 cycles of 94°C for 30 s, 50°C for 30 s, 72°C for 30 s and a final extension at 72°C for 4 min. Amplified PCR products were purified with QIAquick PCR Purification Kit (QIAGEN, Valencia, California) before direct

sequencing of the product on an ABI Prism 3770. The chromatograms for each DNA sequence were checked using the software BioEdit ver. 7.2.5 (Hall, 1999). All sequences were translated to amino acids to detect insertions, deletions and/or in-frame stop codons in order to discard presence of pseudogenes (Beltrà *et al.*, 2015). Sequence alignment was conducted using the program Muscle v3.6 (Edgar 2004) with default parameters.

Genetic distance analyses: Barcoding gap

The COX1 gene has been suggested to be an informative molecular marker at several taxonomic scales, but particularly at the species level. New COX1 sequences were obtained for 10 Laevicaudata samples (see Tab. 1), and data available in GenBank for Spinicaudata, Laevicaudata, and Cycletherida were downloaded (accession date: 11/11/2018) to explore the presence of a DNA barcoding gap in clam shrimps. In order to allow for comparison with previous estimates, p-distance and K2P genetic distances were obtained for the COX1 datasets using MEGA v7 (Kumar *et al.*, 2016). Stacked histograms, chosen to approximate an underlying smooth distribution, for both p-distance and K2P genetic distances were plotted using the Histogram function in Mathematica v11.3.0.0 (<http://www.wolfram.com/mathematica/>). The presence/absence of phylogenetic signal saturation was checked by plotting p-distance versus K2P genetic distances for each clam shrimp dataset (Spinicaudata, Laevicaudata, and Cycletherida).

SYSTEMATICS

Class Branchiopoda Latreille, 1817

Order Diplostraca Gerstaecker, 1866

Suborder Laevicaudata Linder, 1945

Family Lynceidae Stebbing, 1902

Genus *Lynceus* Müller, 1776 (*sensu* Rogers and Olesen, 2016)

***Lynceus grossipedia* n. sp.**
(Figs. 1–9)

Zoobank: [urn:lsid:zoobank.org:act:B0FBCC1D-782A-4FE3-8946-3E58AC73EE51](https://zoobank.org/urn:lsid:zoobank.org:act:B0FBCC1D-782A-4FE3-8946-3E58AC73EE51)

Table 1. New COX1 sequences generated in the present study and used for DNA barcoding analyses. The material of the new species, *Lynceus grossipedia* n. sp., is highlighted in bold.

Species	Continent	Locality	Collector and date	Museum voucher/ genetic identifier	GenBank Accession number
<i>Lynceus baylyi</i> Timms, 2013	Australia	Australia, Western Australia: 12 km North of Trayning Pit Gnamma Nr. 3	B.V. Timms, 19 May 2016	NHMD-615846 ZS 002	MN515424
<i>Lynceus bififormis</i> (Ishikawa, 1895)	Asia	Japan: Shiga, Livsatsu, rice paddies of Kataoka-Cho	M.J. Grygier, 21 May 2001	NHMD-81868/ ZMUC-CRU-4020 ZS 017	MN515425
<i>Lynceus brachyurus</i> Müller, 1776	Europe	Denmark: Pond close to "Trepiløgen", Deer Garden, North of Copenhagen	J. Olesen, 28 April 2017	NHMD-232312 BRP2/CS88	MN515426
<i>Lynceus brachyurus</i> Müller, 1776	America	USA, California: Sacramento County, Sloughhouse	D.C. Rogers, 01 April 2008	NHMD-265530 (DCR-696) ZS 006	MN515427
<i>Lynceus grossipedia</i> n. sp.	Asia	Mongolia: Dundgovi Province, Khar debriin khudagiin toirom (lagoon); 45.516833, 105.833436	M. Alonso, August 2017	NHMD-616088 ZS 055, 578 DUG*	MN515428
<i>Lynceus grossipedia</i> n. sp.	Asia	Mongolia: Tuv province, Uguu nuur (Lake), 47.673917, 108.356333	M. Alonso, August 2017	NHMD-616086 ZS 056, 554 TU*	MN515429
<i>Lynceus macleayanus</i> (King, 1855)	Australia	Australia, New South Wales: Bloodwood, Sue's Pan	D.C. Rogers, 26 July 2015	NHMD-232861 (DCR-916) ZS 008	MN515430
<i>Lynceus magdaleanae</i> Timms, 2013	Australia	Australia, South Australia: Peela Rock, Pit 1 via Wudinna	B.V. Timms, 13 May 2016	NHMD-232860 BRP4/CS90	MN515431
<i>Lynceus susanneae</i> Timms, 2013	Australia	Australia, Western Australia: Cocklebidy gnamma Nullarbor Plain	B.V. Timms, 16 May 2016	NHMD-615888 ZS 003	MN515432
<i>Lynceus tatei</i> (Brady, 1886)	Australia	Australia, Western Australia: large central pool, Wanarra Rock, via Perenjori, 50km ESE; -29.523194, 116.793917	B.V. Timms, 20 August 2011	WAM C51608 ZS 010	MN515433

ZS/BRP/CS = molecular extraction numbers.

* Numbers from the Limnological Catalogue of Mongolian Lakes (see website: http://oslo.geodata.es/mongolian_lakes).

Etymology. The species epithet *grossipedia* is a combination of the word "grosso" from Italian meaning "big/fat" and the Latin word *pedes* meaning "legs", referring to the male's left side thoracopods III–VI, which have enlarged muscular bases.

Type locality. MONGOLIA: Tuv Province: Uguu nuur (Lake), 47°40'26.1"N 108°21'22.8"E, 1307 m a.s.l., coll. Miguel Alonso, 24 August 2017.

Type material. Holotype: Male, from type locality (NHMD-615874). Allotype: Female, from type locality (NHMD-616085). Paratypes: 11 males and 7 females, same collecting data as for holotype: 2 males and 2 females prepared on SEM stubs; 1 male and 1 females prepared on microscope slides (few larger parts still in ethanol); 2 males used for DNA extraction (voucher specimens); remaining 6 males and 4 females in ethanol (NHMD-616086, 554 TU [TU and DUG codes from the Limnological Catalogue of Mongolian Lakes (see website: http://oslo.geodata.es/mongolian_lakes)]).

Other material examined. MONGOLIA: Dundgovi Province: Khar debrin khudagiin toirom (lagoon), 45°31'00.6"N 105°50'00.4"E, 1398 m a.s.l., 1 male (NHMD-616088, 578 DUG). Delgerekhiin toirom (lagoon) 15, 46°28'03.0"N 107°55'07.0"E, 1250 m a.s.l., 5 males and 6 females (NHMD-616087, 1197 DUG). Delgerekhiin toirom (lagoon) 14, 46°28'04.0"N 107°54'56.0"E, 1240 m a.s.l., 1 male and 2 females (NHMD-615923, 1196 DUG). All specimens collected by Miguel Alonso, August 2017. CHINA: Jilin Province: Qianguo County: Songyuan City: Chaganhua Town: Dongpao Lake, 44°36'10.6"N 124°15'38.2"E, 177 m a.s.l., 14 September 2017, 10 males, 12 females (8 males, 10 females in KIZ; 2 males, 2 females NHMD-615880). Qian'an County: Daozixiang Town: Busu Lake, 44°53'38.8"N 123°44'45.3"E, 138 m a.s.l., 16 September 2017, 5 females (KIZ). Inner Mongolia Autonomous Region: Keyou Zhongqi County: Xing'anmeng City: Haoyaosumu Town: a pond near the road of G111, 44°30'47.6"N 122°02'26.3"E, 174 m a.s.l., 19 September 2017, 2 males, 8 females (KIZ). All specimens collected by S. Shu.

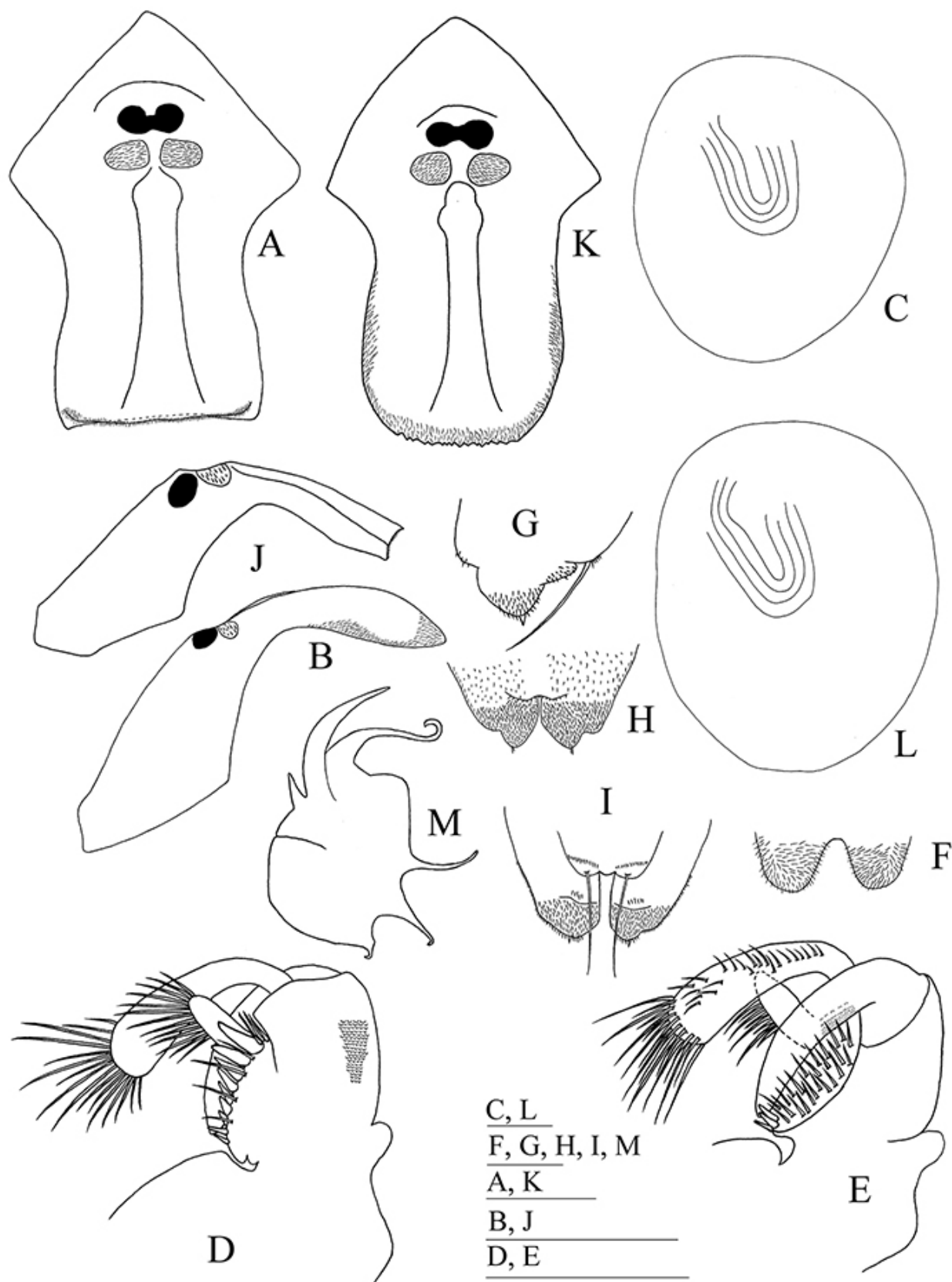


Figure 1. Line drawings of *Lynceus grossipedia* n. sp., A–G: male, H–M: female. A. Head, anterior view. B. Head, left lateral view. C. Carapace, left lateral view. D. Left clasper, posterior view. E. Right clasper, anterior view. F. Opercular lamella, ventral view. G. Telson, left lateral view. H. Telson, ventral view. I. Telson, dorsal view. J. Head, left lateral view. K. Head, anterior view. L. Carapace, left lateral view. M. Lamina abdominalis, left lateral view. Scale bars 1 mm.

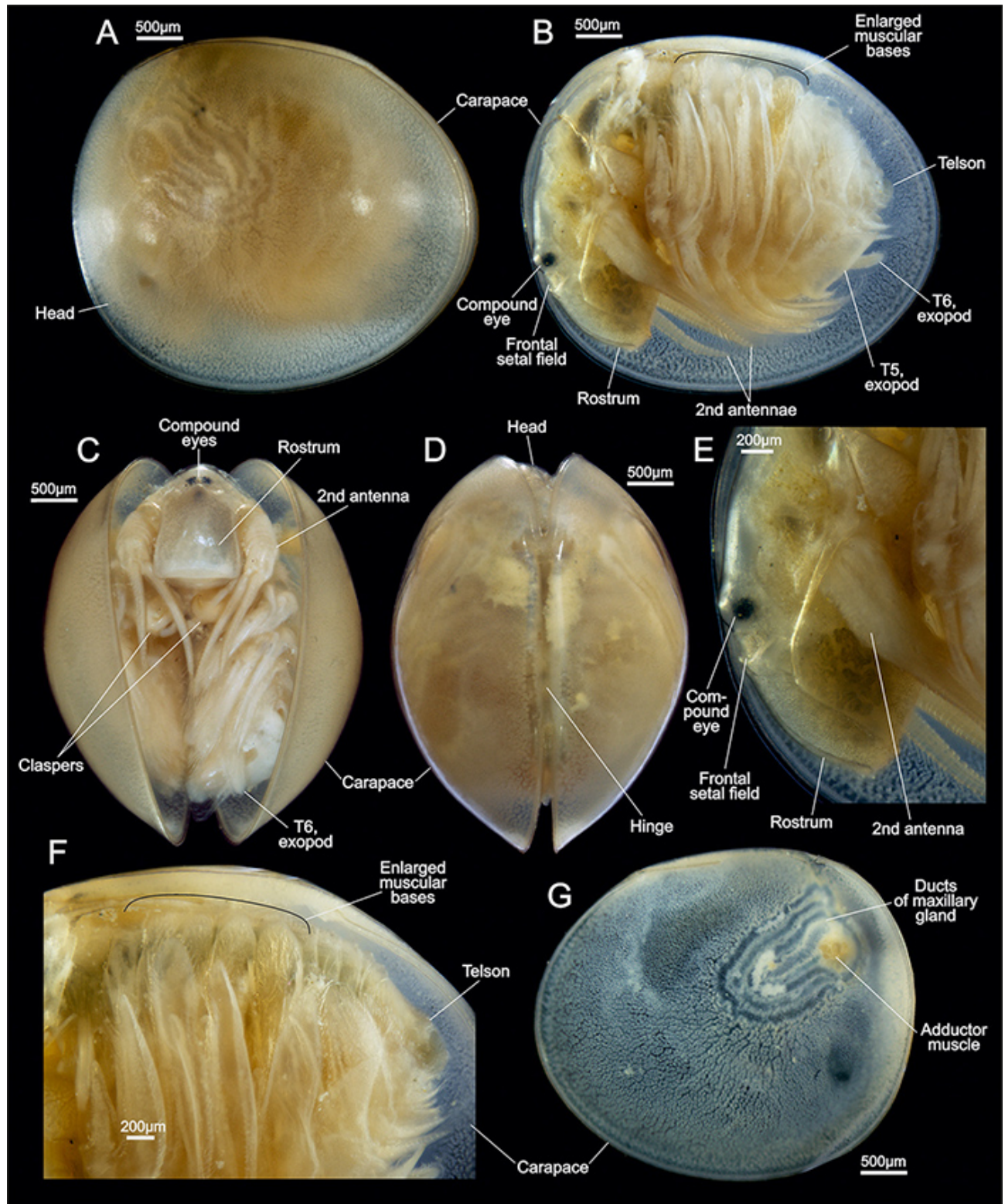


Figure 2. *Lynceus grossipedia* n. sp., male, stereo microscopy (holotype, NHMD-615874). **A.** Left lateral view, intact animal. **B.** Left lateral view, carapace valve removed. **C.** Ventral view, carapace valves apart. **D.** Dorsal view, carapace valves slightly apart. **E.** Head close-up (from B). **F.** Left side thoracopods, showing enlarged muscular bases. **G.** Carapace, left valve interior.

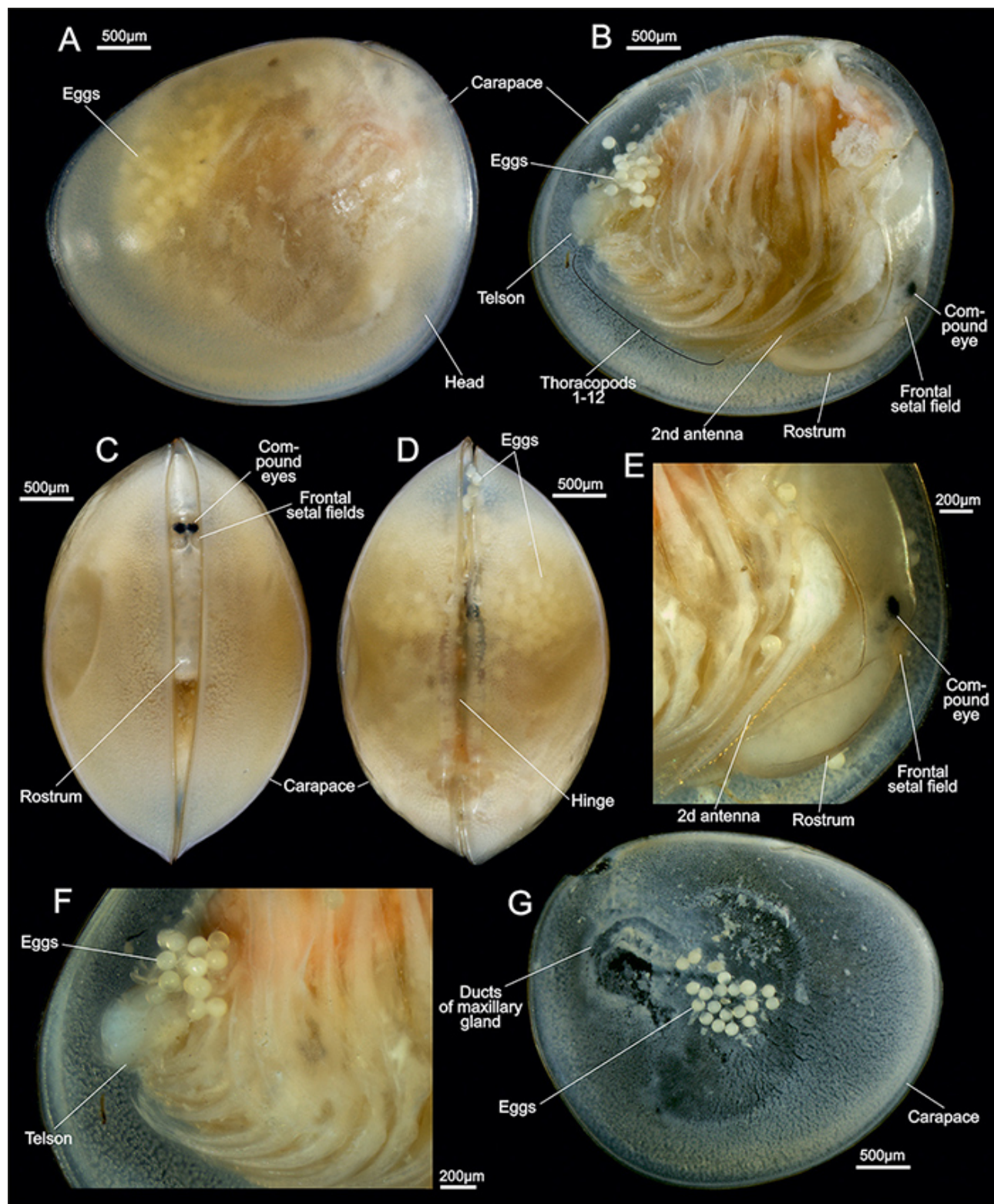


Figure 3. *Lynceus grossipedia* n. sp., female, stereo microscopy (allotype, NHMD-616085). **A.** Right lateral view, intact animal. **B.** Right lateral view, carapace valve removed. **C.** Ventral view, carapace valves slightly apart. **D.** Dorsal view. **E.** Head close-up (from B). **F.** Telson close-up (from B). **G.** Carapace, right valve interior.

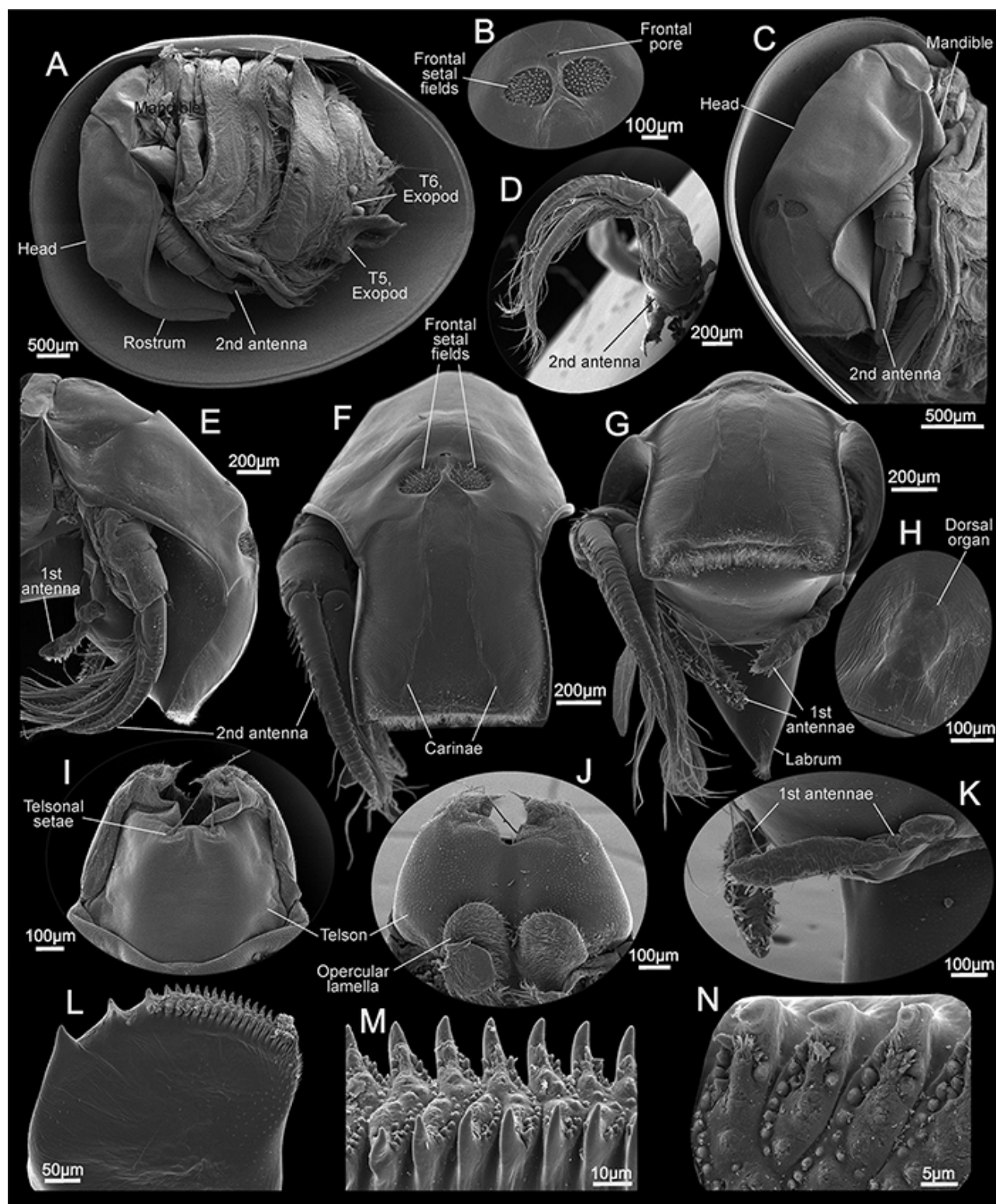


Figure 4. *Lynceus grossipedia* n. sp., male, scanning electron microscopy (paratype, NHMD-616086). **A.** Left lateral view, carapace valve removed. **B.** Frontal setal fields. **C.** Left ventrolateral view. **D.** Left second antenna. **E.** Head, lateral view. **F.** Head, anterior view. **G.** Head, anteroventral view. **H.** Dorsal organ. **I.** Telson, dorsal view. **J.** Telson, ventral view. **K.** First antennae. **L.** Left mandible, lateral view. **M.** Mandible close-up, dorsolateral view. **N.** Mandible close-up, dorsal view.

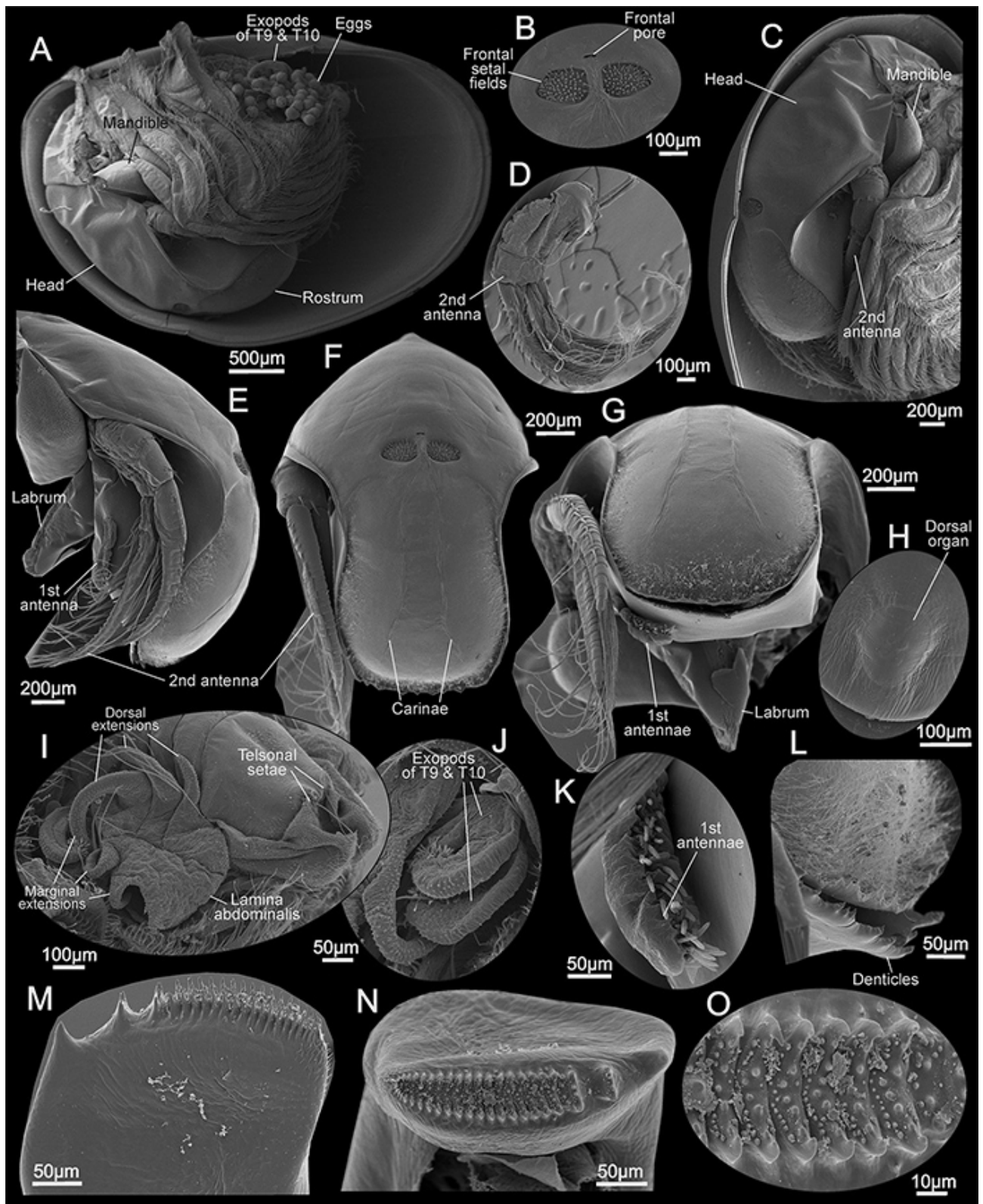


Figure 5. *Lynceus grossipedia* n. sp., female, scanning electron microscopy (paratype, NHMD-616086). **A.** Left lateral view, carapace valve removed. **B.** Frontal setal fields. **C.** Left ventrolateral view. **D.** Left second antenna. **E.** Head, lateral view. **F.** Head, anterior view. **G.** Head, anteroventral view. **H.** Dorsal organ. **I.** Telson and lamina abdominalis, dorsolateral view. **J.** Egg-carrying exopods of thoracopods IX and X. **K.** Distal part of right first antenna. **L.** Serration of rostral distal margin, lateral view (gap at edge likely due to drying artifact). **M.** Left mandible, lateral view. **N.** Left mandible, dorsal view. **O.** Mandible close-up (from N).

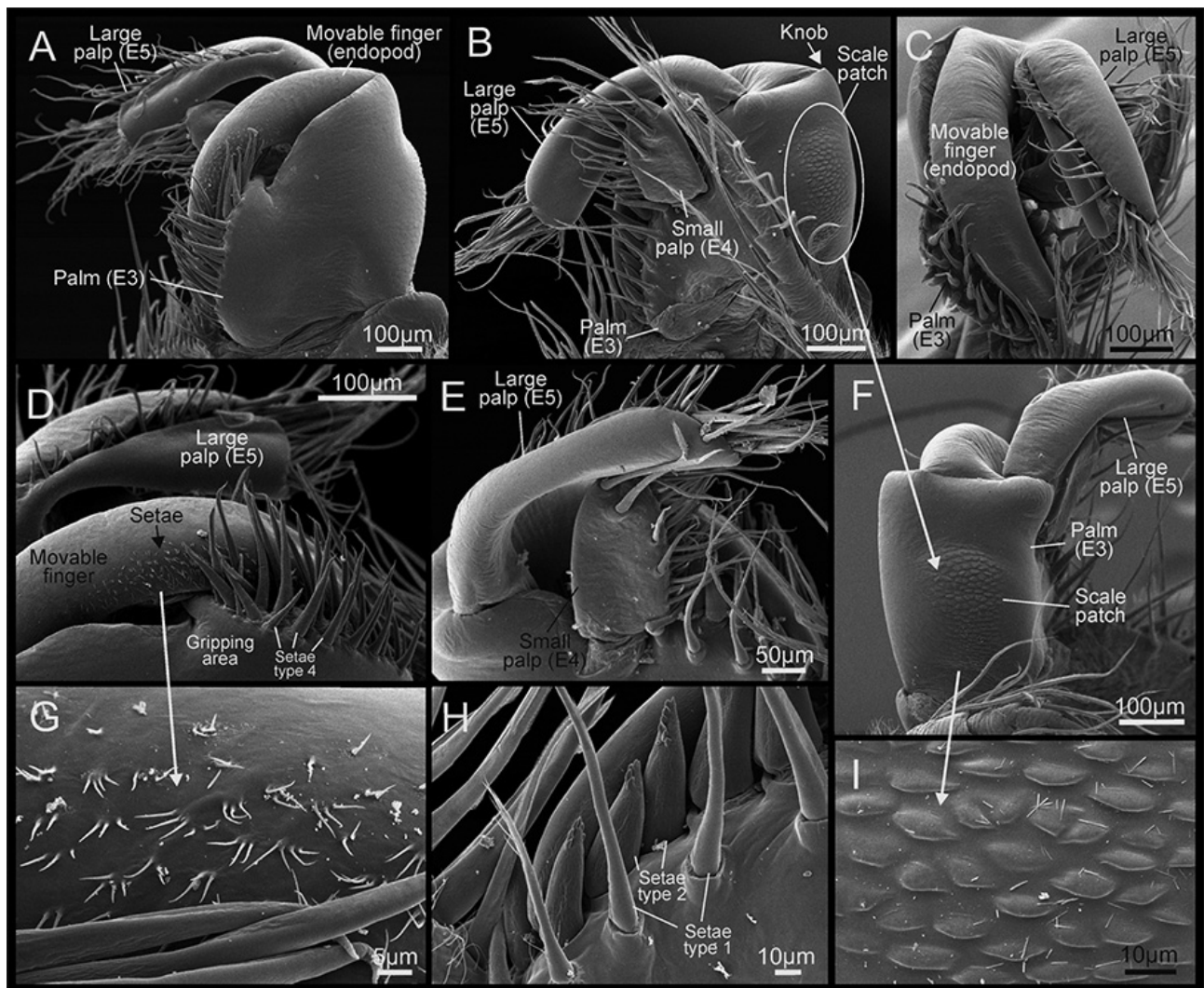


Figure 6. *Lynceus grossipedia* n. sp., male, scanning electron microscopy of claspers (same specimen as on Figs. 4, 7; paratype, NHMD-616086). **A.** Right clasper, anterior view. **B.** Left clasper, posterior view. **C.** Movable finger (endopod), large palp (endite 5), and gripping area (part of palm, endite 3), left clasper, apical view. **D.** Movable finger with band of minute setae, gripping area with type 4 setae, left clasper. **E.** Small palp (endite 4) and large palp (endite 5), right clasper. **F.** Palm with scales (encircled area in B), lateral view, right clasper. **G.** Setation on movable finger (endopod). **H.** Setation on posterior side of gripping area. **I.** Magnification of scales on clasper palm.

Diagnosis

Male. Left side thoracopods III–VI modified as follows: thoracopods III–VI with broad muscular bases; thoracopod V with endopod and distal part of exopod explanate; exopod lamellar, biramal; thoracopod VI with endopod, endite 4 and 5 posteriorly directed (on limb posterior side), and exopod flabelliform, margin with ~7 lobiform processes (further details in description). Right side thoracopods unmodified (= right–left asymmetry). Male claspers: palm with scale patch laterally; movable finger (endopod) base

with small knob, anteriorly with band of minute setae; two prominent bumps/protrusions laterally between “palm” and exopod. Rostrum bicarinate, distal margin truncate with setal row and minor distolateral corners.

Female. Rostrum bicarinate and distally broadly rounded with marginal denticles, distolateral corners indistinct. Lamina abdominalis with three dorsal extensions and three marginal extensions.

Both sexes: Rostral shape broad. Head in lateral view smoothly curving with compound eyes on ocular tubercle; compound eyes smaller than frontal setal fields.

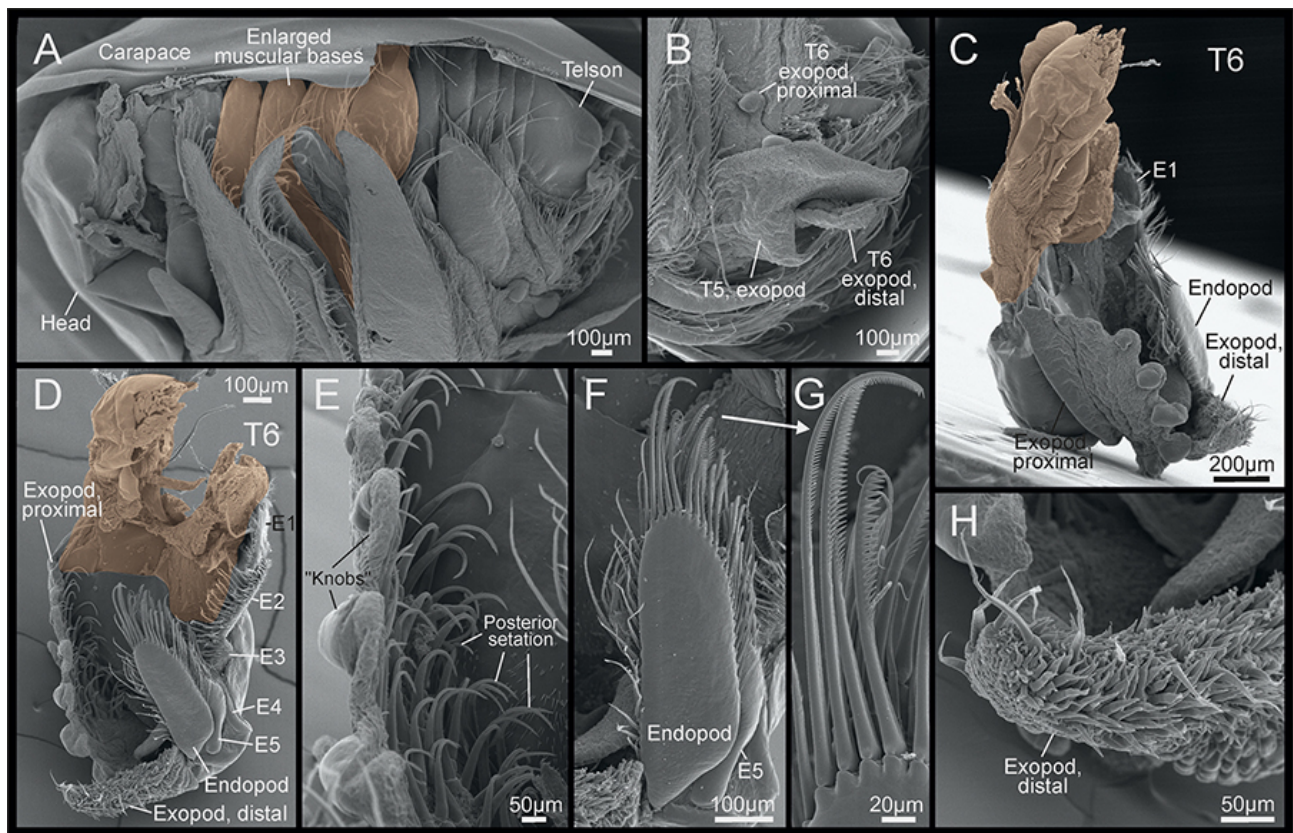


Figure 7. *Lynceus grossipedia* n. sp., male, scanning electron microscopy of modified thoracopods, broad muscular bases highlighted by coloring (same specimen as on Figs. 4, 6; paratype, NHMD-616086). **A.** Dorsolateral view of thoracopods, broad muscular bases of thoracopods III–VI colored. **B.** Modified exopods of thoracopod V and VI. **C–H:** all of thoracopod VI. **C.** Thoracopod VI in posterolateral view, note exopod with ~7 knob-shaped processes. **D.** Thoracopod VI in posterior view with endites, endopod and exopod labelled. **E.** Exopod, knob-shaped processes and posterior surface with long setae (magnification of D). **F.** Endopod, broadly lobiform (magnification of D). **G.** Setae of endopod (magnification of F). Distal part of exopod densely setose.

Description

Male (holotype, 4.2 mm, Fig. 2; paratypes Figs. 1, 4, 6–9).

Length range. Mongolian material: 3.4–4.7 mm (based on 10 specimens). Chinese material: 4.3–5.2 mm (based on 10 specimens).

Head (Figs. 1A, B, 2B, C, E, 4A–C, E–H). Large, ~25–30% of body, rostrum extending to thoracopod I. Head in lateral view arcuate, evenly curving with region of compound eyes protruding on ocular tubercle. Dorsal organ oval, near occipital condyle. Frontal setal fields oval, distally narrower, with short, dense setation, frontal pore dorsal. Compound eyes subcircular, ~50% smaller than setal fields. Rostrum bicarinate, protruding distally between frontal setal fields. Carinae parallel in proximal half, diverging in distal half, each branch terminating near rostral apex, but not reaching it. Rostral apex truncate with distal transverse setal row, distolateral corners not projecting,

denticles absent. Rostrum in anterior view broad with minor constriction approximately at second antennae insertion. Fornices present where rostral marginal rims bend anteriolaterally, from above second antenna insertion to distolateral corners. Rostral apex broad in lateral (and apical) view.

First antenna (Fig. 4E, G, K). With two antennomeres. Proximal antennomere short, about twice as long as broad. Distal antennomere cylindrical, length ~5x > breadth, with numerous simple setae in two longitudinal rows.

Second antenna (Figs. 2B, C, 4C–G). Biramous, extending to around thoracopod IX. Peduncle proximal coxa with transverse row of ~4–5 long plumose setae ventrally and transverse row of ~4 short setae dorsally. Peduncle basis with 6–8 short setae dorsally. Exopod (anterior flagellum) with ~20–22 flagellomeres; short acute seta dorsally and long, plumose seta ventrally. Endopod (posterior flagellum) longer than exopod,

with ~24–26 flagellomeres; long, plumose seta ventrally.

Labrum (Fig. 4G). Large, lobiform. With fine setae around apex and posteriorly. Minute setae in clusters of 1–3, most dense around apex.

Mandible (Fig. 4L–N). Molar surface with ~21–22 transverse ridges. Posteriormost three ridges broadly spaced. Distalmost ridge projecting as single spine, previous two ridges bispinose without ornamentation (maybe due to wear). Remaining ridges closely placed, bispinose with hamulate spines and anterior transverse rows of tubercles (see female description). Ridges broadest around mandible middle, decreasing in size anteriorly. Fine setae present anteriorly, longer ones in cluster near ridges, shorter ones scattered on anterior surface.

Paragnath. Posterior to maxilla I, posterior surface covered with fine setae.

Maxilla I. Elongate, distally semicircular. Posterior surface covered with fine setae. Medially with ~10 long plumose setae, distalmost surface with 2–3 short robust setae with denticulae.

Maxilla II. Absent.

Carapace (Figs. 1C, 2A–D, G, 4A, C). Shape subspherical, longer than broad, smooth, without ornamentation. Rounded anteriorly (near attachment of adductor muscle), more arcuate posteriorly. Ducts of maxillary gland transversely surrounding adductor muscle. Oval in dorsal and ventral view, dorsally with depression at attachment site. [Open space around the body within the carapace on SEM images (Figs. 4A, 5A) is likely an artefact of drying].

Thoracopods (Figs. 6–9). 10 pairs, becoming smaller from anterior to posterior. First pair modified as claspers, left side thoracopods III–VI modified (see further below).

Thoracopod I (clasper limb) (Figs. 6, 8A, B, 9A): claspers equal in size and shape, with parts as typical for *Lynceus* present: endite 3 = “palm” with “gripping area”, endite 4 = small palp, endite 5 = large palp, and endopod = “movable finger”. Endite 1 lobiform, elongate, dorsal margin with multiple (~12) long setae, apex with 3–5 pectinate spines and ventrally a single long seta (similar found on remaining thoracopods). Endite 2 transverse, broad, long setae along margin. Endite 3 (palm with gripping area) suboval, in close proximity to endite 2; small protrusion (“knob”) near base of endopod (movable finger) (Figs. 6B, 8B, 9B); laterally with larger

area with scales (Fig. 6B, F, I); posteriomedially with minor, discrete area with scales (difficult to see on images). Endite 3 medially with longitudinal gripping area with diverse setation (setae types *sensu* Sigvardt and Olesen, 2014): anterior margin with numerous (>25) long, robust setae (type 4); posterior margin with two rows of setae: five long setae, distally plumose (type 1), 7–8 conical peg-like spines (type 2), apex with prominent denticles in two parallel rows. Setae type 3 and 5 absent. Endite 4 (small palp) lobiform, anterioposteriorly flattened. Distal half with 3–4 long setae, some setae distally with bipectinate setulae; margined with >25 long (varying length), simple setae without setulae. Endite 5 (large palp) around twice as long as endite 4, clavate, becoming broader towards apex; long simple setae at apex (a few with setules) extending in dorsal sulcus; dorsal setae (>20) decreasing in size towards termination of sulcus (near palp basis). Endopod (movable finger) digitiform, curved; tapering towards apex, extending to proximal margin of endite 3 (gripping area); anterior side distal half with elongate band of minute setae clustering together 1–4 (Fig. 6D, G). Lateral part between palm and exopod bilobed with two prominent protrusions, basal width ~3x> medial length (Figs. 8A, B, 9A, B). Exopod proximal lobe broadly oval, distal lobe elongate with acute apex, both with long setae along margin, either simple or with setules. Epipod elongate, lacking setation.

Thoracopod II (Fig. 8C): not modified, typical for genus (see Olesen *et al.*, 2016; Sigvardt *et al.*, 2019) however, endite 2 and 3 elongate rounded and epipod relatively long.

Thoracopods III and IV (Fig. 8D, E): left side modified with muscular bases enlarged. Exopod proximal part and epipod long. Remaining parts and right side typical for genus (Fig. 9C, D).

Thoracopod V (Figs. 7A, B, 8F): left side modified with muscular basis enlarged. Endites 4 and 5 adjacent. Endopod explanate, proximally with stout lobiform structure extending posteriorly, setation as follows: dorsally stout setae increasing in length towards apex, ventrally long filiform setae. Exopod distal lobe biramal (Fig. 8F), with lateral major part explanate, subquadrate with lateral margin undulating, setae absent; medial minor part triangular with setae distally. Remaining parts and right side typical for genus (Fig. 9E).

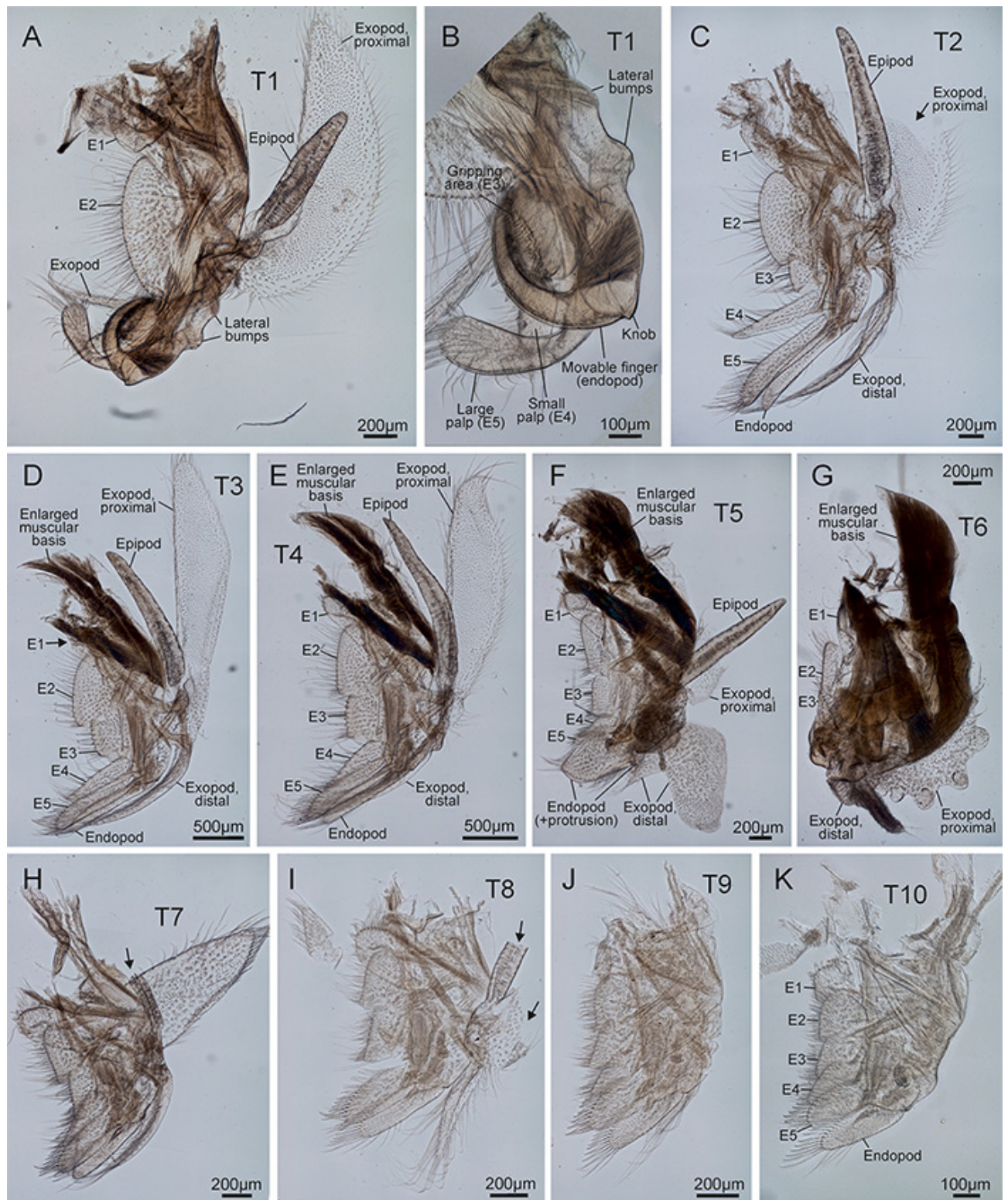


Figure 8. *Lynceus grossipedia* n. sp., male, light microscopy of left side thoracopods, seen from anterior (paratype, NHMD-616086). **A.** Thoracopod I (male clasper). **B.** Higher magnification of clasper. **C–K.** Thoracopods II–X of which III–VI (**D–G**) are modified, not least with notably enlarged muscular bases. **F.** Thoracopod V with endopod and distal part of exopod explanate. **G.** Thoracopod VI with exopod proximal part with ~7 knob-shaped processes and distal part highly setose (seen better on SEM images, Fig. 7H), endites 4–5 and endopod non-visible as folded behind thoracopod. Arrows indicate broken/hidden parts.

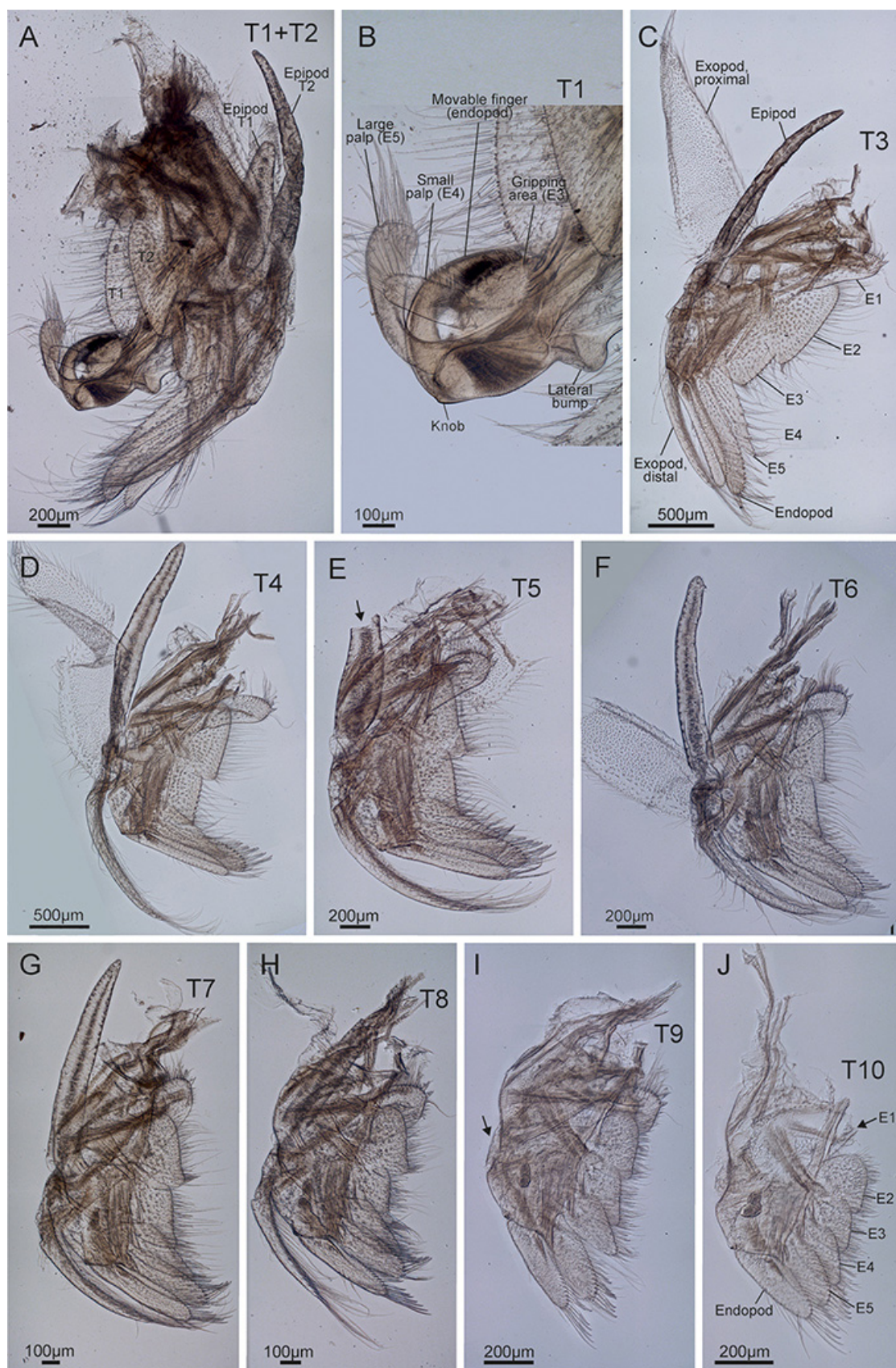


Figure 9. *Lynceus grossipedia* n. sp., male, light microscopy of right side thoracopods (unmodified) (paratype, NHMD-616086). **A.** Thoracopods I (male clasper) and II, seen from posterior. **B.** Higher magnification of clasper. **C–K.** Thoracopods III–X, seen from anterior; all of “regular” *Lynceus* type (= unmodified). Arrows indicate broken/hidden parts.

Thoracopod VI (Figs. 7C–H, 8G): left side highly modified with: (1) heavily enlarged musculature extending from basis to near apex (Fig. 8G), (2) endopod broadly lobiform, together with endite 4 and 5 directed posteriorly (on limb posterior side) (Figs. 7D, F), (3) exopod distal part transversely lamelliform, densely covered with robust setae tapering towards apex (Fig. 7C, D, H), few (~8) longer setae with setulae distally along margin (Fig. 7H). Exopod proximal part a large semicircular lamella with ~7 lobiform processes with deep invaginations between them (Figs. 7C, 8G); proximally with cluster of 5–6 long setae with setulae, posterior surface covered with robust elongate setae (Fig. 7D, E), anterior surface and margin lacking setation. Right side thoracopod VI typical for genus (Fig. 9F).

Thoracopods VII–X (Figs. 8H–K, 9G–J): left and right side typical for genus.

Unmodified structures of thoracopods II–X (Figs. 8, 9): endite 1 lamelliform, elongate, dorsal margin with multiple long setae, apex with ~3 pectinate stout spines, ventral margin with short setae and a single long prominent seta. Endite 2 transversely broad, with different setal types along margin, some long, slender with setules at distal half, others short, robust, without setulae. Endite 3 similar to endite 2, however less transversely broad. Endite 4 broadly digitiform, margin with ~6 prominent setae together with other setae of varying length. Endite 5 and endopod similar to endite 4, but distally with characteristic stout setae, distally pectinate serrate. Towards posterior thoracopods, all endites and endopod become of more similar shape. Epipod long, slender, without setation, present in thoracopods I–VIII. Exopod proximal lobe broadly oval, flattened, setation along entire margin; exopod distal lobe elongate with acute apex, setation along margin.

Telson (Figs. 1G). Broad, dorsal lobes with elongate, filiform telsonal setae. Ventral surface finely hirsute except medially. Opercular lamella (thin membranous fold under telson) cordate with minute setae covering surface and margin.

Female (allotype, 3.9 mm, Fig. 3; paratypes Figs. 1, 5).

Length range. Mongolian material: 3.2–4.4 mm (based on 8 specimens). Chinese material: 4.2–5.3 mm (based on 23 specimens). Generally similar to male in appearance.

Head (Figs. 1K, J, 3B, E, 5A–C, E–H, L). Larger than male head, ~35–40% of body, rostrum extending to thoracopod III. Head in lateral view roundly/evenly curving with region of compound eyes extruding (on ocular tubercle). Dorsal organ oval, with 4 circular elevations. Frontal setal fields and compound eyes as in male. Rostrum bicarinate, carinae parallel around 2/3 proximally, expanding last 1/3 distally with branches terminating near rostral apex but not reaching apex. Rostral apex broadly rounded, almost truncated similarly to male, with denticles, distolateral corners obsolete. Rostrum in anterior view broad with fornices following constriction around second antenna insertion to rostral apex (as in male). Minute setae along rostral margin from lower constriction to apex. Rostral apex broad in lateral view.

Antennae, first and second (Figs. 3B, E, 5D–G, K). As in male.

Mandible (Fig. 5M–O). Similar to male, with all bispinose ridges ornamented with hamulate spines, anterior row of ~12–16 tubercles, middle row of ~6 larger tubercles, and posterior row of ~4 tubercles (can be due to lack of wear).

Remaining mouthparts. As in male.

Carapace (Figs. 1L, 3A–D, G, 5A, C). As in male.

Thoracopods (Figs. 3B, 5A, I, J). 12 pairs, serially similar, unmodified, claspers absent; typical for genus (see Olesen *et al.*, 2016; Sigvardt *et al.*, 2019). Thoracopods IX and X with exopods distally modified into curved lobes, dorsally with minute setae clustering together in groups of ~4, apex with tuft of setose setae used to attach egg clutches.

Lamina abdominalis (Fig. 5A, I). Broad lamellar structure dorsal to thoracopods X–XII. With three marginal extensions and three dorsal extensions, all with small dentiform spines in minor clusters. Dorsal extensions: digitiform, hamulate, tapering towards apex, anterior extension longest, posterior shortest; all

three directed anteriorly. Marginal extensions: anterior and medial extension similar to dorsal extensions but smaller, posterior extension broadly triangular, short; all directed anteriorly.

Eggs (Figs. 3A, B, F, G, 5A). Spherical, surface smooth, ~100 µm in diameter.

Telson (Figs. 1H, I, 3F, 5I). As in male.

Variation between populations

Only minor morphological variation was found between the Mongolian and Chinese populations, with male rostrum in the Chinese specimens being slightly constricted and apparently more elongate than in the Mongolian specimens. Male claspers were identical in the two populations.

Habitat

In Mongolia, *L. grossipedia* n. sp. was found in Tuv Province and Dundgovi Province. Both are steppe and desert areas with an extreme climate of less than 200 mm precipitation per year and completely frozen ground from November through April. *Lynceus grossipedia* n. sp. occurs in small temporary pools with low to moderately mineralized water (conductivity: 130–560 µS/cm) and high turbidity due to suspended clay particles caused from clay and sand substrates. Aquatic vegetation is very scarce or absent. Accompanying branchiopod fauna included *Branchiopodopsis affinis* Sars, 1901 and *Triops* sp.

In China, Jilin, *L. grossipedia* n. sp. is widely distributed on the Songhuajiang-Nenjiang plain in the Songliao Basin, which is in the frigid-temperate and temperate zones where the climate is semi-humid to humid (Lee, 1986). The basin is made of Paleozoic and Pre-paleozoic metamorphic, sedimentary, and volcanic rock (Lee, 1986). *Lynceus grossipedia* n. sp. commonly co-occurs with *Branchinella* (*Branchinellites*) *kugenumaensis* (Ishikawa, 1895), *Triops granarius* (Lucas, 1864), and *Leptestheria dahalacensis* (Ruppell, 1837). During sampling in this region in September 2017, average environmental measurements were: water temperature ~24 °C, pH ~8.63, conductivity ~460 µS/cm, and dissolved oxygen ~6.3 mg/L.

This information is just a snapshot in time, and not necessarily indicative of the species preferred ecological conditions. Songhuajiang-Nenjiang plain soils are alkaline with pH ranging from 8.06–10.21, carbonate ranging from 3.32–16.00 cmol/kg, and cations: K⁺: 0.2–1.27 cmol/kg; Na⁺: 1.77–46.96, Ca²⁺: 0.065–1.76 cmol/kg (Feng *et al.*, 2007).

Distributional range

Lynceus grossipedia n. sp. is found in Central Mongolia and widely distributed on the Songhuajiang-Nenjiang plain of Northeast China, including Jilin, Liaoning and Heilongjiang provinces and in the eastern part of Inner Mongolia. The type locality of *L. grossipedia* is more than 2,200 km apart from Shengyang, Liaoning (where *Lynceus mandsuricus* Daday, 1927 is described from, see Discussion), and separated by a mountain (Da Xing An Ling or Great Xing'an range). The Jilin populations of *L. grossipedia* are only about 300 km from Shengyang, without significant geographical barriers between them.

Genetic distance analyses: Barcoding gap

The alignment of DNA sequences obtained from the *Lynceus* specimens and GenBank data included 609 bp positions. Average p-distances between Laevicaudata species using GenBank data (0.120±0.076) increased ~17% after including the new *Lynceus* data (0.140±0.064), and ranged between those observed for Cyclestherida (0.083±0.078) and Spinicaudata (0.183±0.046) (Fig. 10). As expected, K2P genetic distances were slightly larger (Fig. 10A) and showed a similar pattern, both between Laevicaudata species (GenBank only = 0.138±0.091; including new data = 0.161±0.077), and for Cyclestherida (0.094±0.090) and Spinicaudata (0.215±0.0567). Indeed, K2P corrected distances were significantly correlated with p-distances and phylogenetic signal was not saturated within groups (Fig. 10B). All three suborders of clam shrimp showed the presence of a barcoding gap centred on genetic divergences around 5–10% (p-distance). Observed K2P genetic distance between the specimens recently collected from Mongolia and other *Lynceus* was always >10% suggesting they belong to a new species.

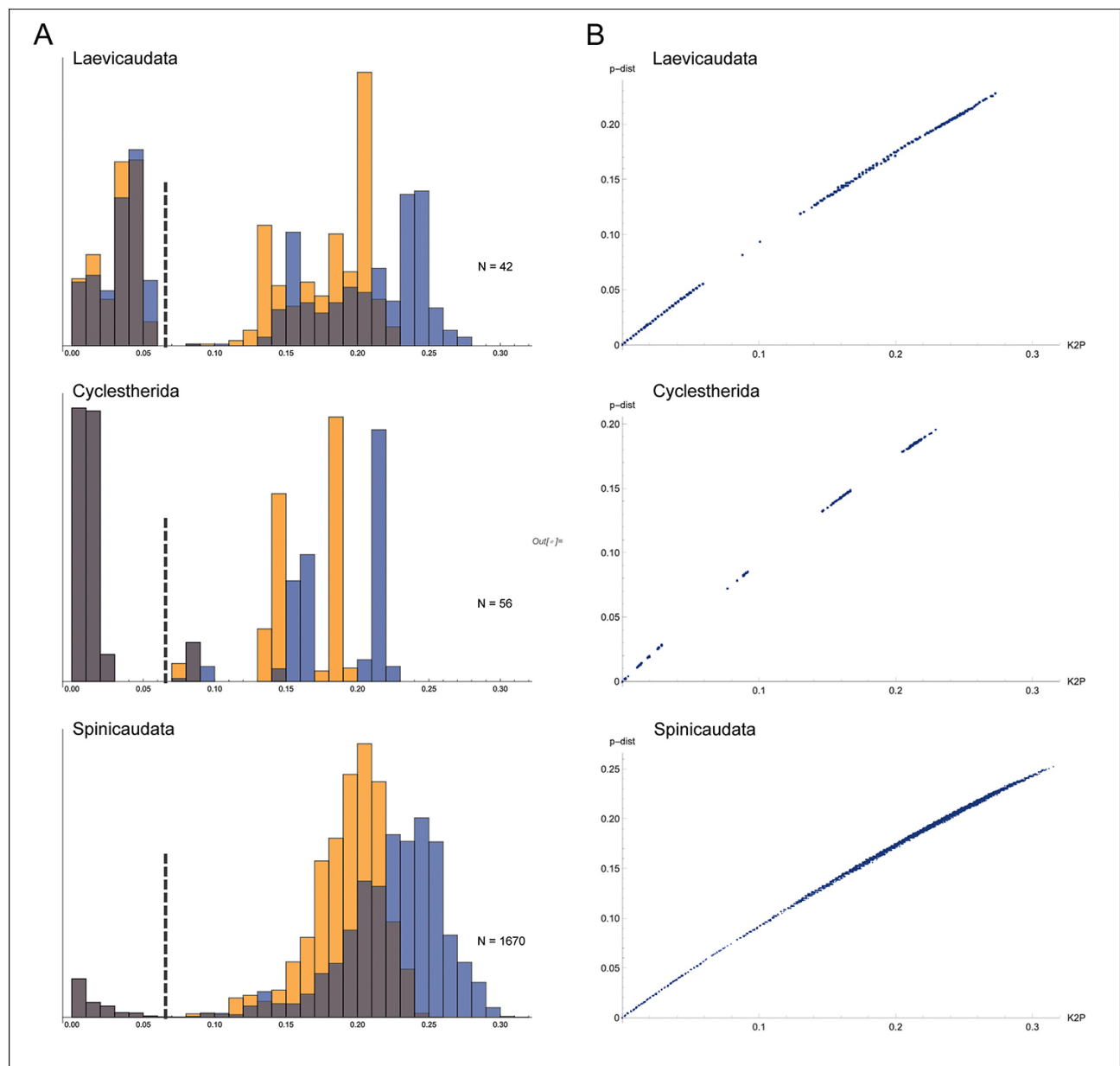


Figure 10. Genetic distances and DNA barcoding gaps in clam shrimps. **A.** Stacked histogram of p-distances (yellow) and K2P genetic distances (blue) between pairs of COX1 sequences available in GenBank (accession date: 11/11/2018) for every suborder of clam shrimp (Laevicaudata, Spinicaudata, and Cyclestherida). The presence of a DNA barcoding gap is highlighted with a dashed vertical line. **B.** Saturation plot showing the strong correlation between p-distances and corrected genetic distances (Kimura 2-parameter).

DISCUSSION

The new laevicaudatan species from Mongolia and China, *L. grossipedia* n. sp., is the 9th described species from Asia (Rogers et al., 2016; Shu et al., 2019), and the second from Mongolia. Naganawa and Zagas (2002) mention two *Lynceus* from the Gobi Steppe of Mongolia: *L. dauricus* Thiele, 1907, now synonymous with *L. biformis* (Yoon and Kim, 2000), and *Lynceus* sp. (Naganawa et al. 2001, indetermined). The *Lynceus* sp.

from Mongolia is also mentioned in the Laevicaudata catalogus (Rogers and Olesen, 2016) but with no material reported to be deposited, and no description or types designated, it is uncertain whether it is the same species as the one described here.

Lynceus grossipedia n. sp. displays multiple unique morphological traits (highlighted in the Diagnosis), which facilitate separation from its congeners. Of significant importance is the presence of: (1)

asymmetrically modified “middle” male thoracopods (Figs. 7, 8), only seen in another recently described *Lynceus* from China, but with a clearly distinct morphology (Shu *et al.*, 2019); (2) setation on the clasper endopod (movable finger), found in *Lynceus* for the first time (Fig. 6D, G); (3) broad rostral shape and double carina of both male and female (Figs. 4F, 5F). A double carina is previously found in several African Lynceidae such as *L. bicarinatus* Barbad, 1924, *L. dovei* Daday, 1927, *L. pachydactylus* Barnard, 1929, and *L. rotundus* Thiele, 1907 (see Daday, 1927; Barnard, 1924; 1929; Gauthier, 1936), as well as in other Asian species: *L. spinimanus* from Thailand (only the female) (Rogers *et al.*, 2016), most likely in the Chinese *L. manduricus* (see discussion below), and in the recently described *L. amplopedia* (see Shu *et al.*, 2019). However, the combination of the bicarination and the broad rostral shape gives *L. grossipedia* n. sp. a distinctive appearance.

Lynceus grossipedia n. sp. is morphologically most similar to *L. amplopedia*, with the two species sharing several similarities such as: (1) modified thoracopods posterior to thoracopod II; (2) bicarinate rostrum; (3) clasper palm with setal patches; (4) clasper large palp with setae in sulcus; (5) compound eyes on an ocular tubercle.

Lynceus grossipedia n. sp. and *L. amplopedia* are distinguished from each other and all other *Lynceus* species by the following characters: (1) distribution and extent of thoracopod modifications (see details below); (2) mandibles, in *L. grossipedia* n. sp. with transverse ridges present in higher number being more hamulate and ornamented (presence of prominent spines and tubercles can be due to lack of wear) (Figs. 4L–N, 5M–O); (3) endopod length (movable finger), in *L. grossipedia* n. sp. extending to the tip of endite 3 (gripping area) (Figs. 8A, B, 9A, B), whereas in *L. amplopedia* it extends to approximately the middle; (4) female rostral margin, in *L. grossipedia* n. sp. with denticles (Fig. 5F, L), in *L. amplopedia* inerm; (5) head anterior margin in lateral view, in *L. grossipedia* n. sp. evenly curving (Figs. 4E, 5E), in *L. amplopedia* sinuate. The rostral anterior margin of the female *L. grossipedia* n. sp. shares its serration with the *L. denticulatus*-complex (Rogers and Padhye, 2015), which is in need of revision.

Modified “middle” thoracopods in L. grossipedia n. sp. vs. *L. amplopedia*

Despite the general perception of branchiopod trunk limbs displaying pronounced serial homology, laevicaudatans have long been known to bear different types of thoracopodal modifications along the limb series. Males of all species of the three known genera (*Lynceus*, *Paralimnetis*, and *Lynceiopsis*) have the first pair of thoracopods modified as clasper, which are used to amplex the female with during mating (=claspings) (Sigvardt and Olesen, 2014; Sigvardt *et al.*, 2017). In addition to these claspers, males of certain taxa (*Paralimnetis*, *Lynceiopsis*, and *Lynceus aequatorialis*) have strongly modified second thoracopods (Martin and Belk, 2006), probably also involved in claspings/mating, but their function has never been studied. A few other taxa (*L. simiaefacies*, *L. mucronatus*, and *L. spinimanus*) also have modified non-clasper thoracopods (Harding, 1941; Martin and Belk, 1988; Rogers *et al.*, 2016), but these modifications are less significant. However, modified thoracopods occurring in the “middle” limbs of the trunk limb series has, until the recent description of *L. amplopedia* (see Shu *et al.*, 2019), been unknown for laevicaudatan clam shrimps, and *L. grossipedia* n. sp. is the second case known so far. In both species only the male has its “middle” thoracopods modified, so the function can be assumed to be related to mating (this has not been studied). In the following the unique thoracopod modifications of these two clearly closely related species are compared and discussed.

Lynceus grossipedia n. sp. always has its left side thoracopods III–VI modified (Fig. 8), while its right side is unmodified (= the two sides being highly asymmetrical) (Fig. 9). This is significantly different from *L. amplopedia*, which has the thoracopods of both sides modified, but not in the same way in left and right side. Due to the type of thoracopodal modifications in *L. amplopedia* (Shu *et al.*, 2019) the two sides are described as being “explanate” and “spinose”, respectively and adding to the complications, it was found that the two types of modifications shift between left and right side of the animals in the examined population.

Overall the same types of thoracopodal modifications are present in the two species, but

interestingly these are often found on different structures and/or different thoracopods, which raise important questions on type of homology. For example, the characteristic enlarged muscular bases of certain thoracopods, likely to have a comparable (but unknown) function in the two species, do not involve the exact same limbs. Males of *L. grossipedia* n. sp. have these enlarged muscular bases in four thoracopods (III–VI, left side) (Figs. 2B, F, 7A, 8D–G), while *L. amplopedia* has them in three modified thoracopods (III–V) in one side and one in the other side (V). Another example of practically similar structures apparently “shifting position” between thoracopods in the two species concerns the so-called explanate lobes, which is a term used for endites, endopod, or exopod when they have a particularly extended and flattened shape (Shu *et al.*, 2019). In *L. grossipedia* n. sp., the endopod and the distal part of the exopod of only one thoracopod (V) are explanate (Figs. 7B, 8F), while in *L. amplopedia* endites 4–5 and the endopod of two thoracopods (III–IV) are explanate. Yet another comparable feature that appears on different limbs in the two species are distinctive processes on the distal part of the exopod: in *L. grossipedia* n. sp. there are ~7 lobiform processes (on exopod of thoracopod VI) (Figs. 7C–E, 8G), whereas in *L. amplopedia* there are 14–15 digitiform subacute processes (on exopod of thoracopods V–VI).

This “shifting around” of comparable structures between thoracopods that are not positionally homologous is very interesting from an evolutionary point of view. Despite thoracopods bearing uniquely enlarged muscular bases not being positioned similarly in the two species, we still consider these modifications homologous in the sense that they likely have an identical genetic background. Such duplication of structures is generally believed to have been important in arthropod evolution (Averof, 1997). Nevertheless, the different organization of various comparable structures in the “middle” of the thoracopodal series in *L. grossipedia* n. sp. and *L. amplopedia* may have specific functional implications that can only be clarified by much needed behavioral studies similar to those on the mating of *Lynceus brachyurus* (see Sigvardt and Olesen, 2014).

The case of Lynceus mandsuricus Daday, 1927 (nomen inquirendum)

Based on the literature, *L. grossipedia* n. sp. shares certain morphological traits with *Lynceus mandsuricus* (e.g., in the male claspers). We have therefore attempted to compare the two species, but we are hampered by the apparent lack of type material and inadequate descriptions (see below). According to Daday (1927), the type material of *L. mandsuricus* is deposited in the St. Petersburg Museum, but it was not recovered after extensive search in the collection and has probably been lost (pers. comm. Victor Alekseev, St. Petersburg Museum). *Lynceus mandsuricus* was first presented by Daday, 1913 as a *nomen nudum* in his *Lynceus* key and later described (Daday, 1927) based on type material from Mukden, Manchuria (now Shenyang City, Liaoning Province, China); approximately 2,400 km from the type locality of *L. grossipedia* n. sp. The spelling “*mandsuricus*” was corrected to “*manchuricus*” by Uéno (1940a; 1940b) since the collection site in Shenyang City is in Manchuria, not Mandsuria as stated in Daday’s (1927) original description. This has resulted in confusion concerning the name, as “*L. manchuricus*” subsequently became widely used, especially by Chinese researchers (and a single Danish researcher) (Røen, 1952; Dai, 1982; Hu, 1988; 1989; Han *et al.*, 1995), whereas “*mandsuricus*” was mainly used elsewhere (Yoon and Kim, 2000; Rogers and Olesen, 2016; Rogers *et al.*, 2016). According to article 32.5.1 of the ICZN, incorrect transliterations are not considered an inadvertent error. Furthermore, “*mandsuricus*” was not substituted, but was prevailing usage. To avoid the confusion of these two spellings, *mandsuricus* is the accepted *nomen* according to the ICZN.

Daday’s (1927) description of *L. mandsuricus* was based only on male specimens, while Uéno (1940b) gave a simple description of the female. Uéno’s work was published in a Japanese book and not widely disseminated. Some illustrations were quoted in various papers (Røen, 1952; Dai, 1982; Hu, 1986; Hu, 1989; Han *et al.*, 1995), but both illustrations and descriptions are inadequate (Yoon and Kim, 2000).

Uéno (1940b) noticed that his specimens deviated from Daday’s description in number of spines and setae on the clasper gripping area and in the shape of

the opercular lamella. The opercular lamella in our material has setation on the entire surface of both lobes (more proximally than on Daday's illustration), but the largest deviation is in size, as Daday (1927) illustrates the opercular lamella as larger, expanding to the lateral sides of the telson. Furthermore, the original description illustrates the male *L. mandsuricus* rostrum with an angular carina that first bifurcates around 1/3 towards distal end, and with prominent lateral corners, both of which differ from what we find in *L. grossipedia* n. sp. The male depicted in Uéno (1940b) shows a bicarinate rostrum more similar to our specimens, with the two carinae approximately parallel. However, they arise further below the setal fields, while the rostrum also has more prominent lateral corners.

Daday (1913; 1927) does not mention anything about modified thoracopods, but this is not a guarantee that his material did not have these structures present. He could have overlooked them or not found it of interest to describe the whole series of thoracopods, as there was no tradition in the descriptions of these animals at that time (but we highly recommend to do so in future studies of Laevicaudata). Together with other aspects discussed above, and the lack of type material, it is concluded that *L. grossipedia* n. sp. is indeed a new species and that *L. mandsuricus* should be declared *nomen inquirendum*.

Barcoding gaps in clam shrimps

Together with the description of a new species of *Lynceus*, we have explored the utility of DNA barcoding on smooth clam shrimps, contributing with new COX1 data for a range of *Lynceus* taxa from different continents. Barcoding gaps were observed in all three clam shrimp suborders, although Cyclestherida genetic distances showed a more ragged histogram than either Spinicaudata or Laevicaudata. This is most likely due to the smaller number of sequences for Cyclestherida available in GenBank and the fact that they correspond to a single large-scale study (Schwentner *et al.*, 2013). Previous studies have focused mostly on marine Crustacea, particularly decapods (da Silva *et al.*, 2011; Raupach *et al.*, 2015), but the presence of a DNA barcoding gap and the genetic threshold observed in clam shrimps are in agreement with those values suggested earlier for species delimitation in other taxa (Lefébure *et al.*, 2006). An accurate morphological

identification, combined with molecular methods, are fundamental to improve the completeness and quality of public reference databases and to contribute to the development of the DNA barcoding approach in clam shrimps.

ACKNOWLEDGEMENTS

We are grateful to those who provided material for molecular studies: Brian V. Timms and Andrew Hosie (Western Australian Museum, WAM) as well as for morphological comparisons: Miranda Lowe and Geoffrey Boxshall (Natural History Museum of London, UK, BMNH), Oliver Coleman (Museum für Naturkunde, Berlin, MNHB), Laure Corbari (Muséum national d'Histoire naturelle, Paris, France, MNHN), Rafael Lemaitre and Chad Walter (Smithsonian National Museum of Natural History, Washington DC, USA, USNM). Victor Alekseev (Zoological Institute, St. Petersburg, Russia) is thanked for providing information on the status of the type material of *L. mandsuricus* in the collection in St. Petersburg. We also thank Tom Gilbert, Stine Raith Richter, DNAMark, Danish reference database, and the Modern DNA laboratories at the Natural History Museum of Denmark, for their valuable assistance in DNA extraction and product generation. JO acknowledges financial support from the Villum Foundation for sequencing, and FP acknowledges a post-doctoral contract funded by the Beatriu de Pinós Programme of the Generalitat de Catalunya (2014-BPB-00038). The study is part of ZS's PhD studies financed by the Faculty of Science, University of Copenhagen as well as SS's PhD studies financed by Applied Taxonomic Research Center of Khon Kaen University, Southeast Asia Biodiversity Research Institute, the Chinese Academy of Sciences (Y4ZK111B01), and the National Natural Science Foundation of China (31702011).

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Erratum: Correction of Affiliation

In the published article: Sigvardt, Z. M. S.; Shu, S.; Alonso, M.; Ventura, M.; Sanoamuang, L.; Rogers, D. C.; Palero, F. and Olesen, J. 2020. A new Northeast Asian *Lynceus* (Crustacea: Branchiopoda: Laevicaudata) with uniquely modified thoracopods and an evaluation of DNA barcoding for clam shrimp species identification. *Nauplius*, 28: e2020013. doi: 10.1590/2358-2936e2020013,

on page 1, Authors Affiliation:

where it reads:

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should read:

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