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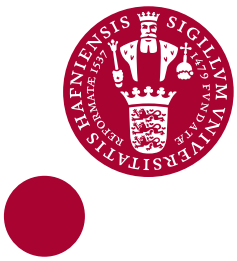

Lynceus amplopedia sp. nov., A New Laevicaudatan Clam Shrimp with Asymmetrically Modified Thoracopods from Yunnan, China (Crustacea: Branchiopoda)

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Lynceus amplopedia sp. nov., A New Laevicaudatan Clam Shrimp with Asymmetrically Modified Thoracopods from Yunnan, China (Crustacea: Branchiopoda)

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Laevicaudata has a nearly global distribution, but only a few records from China. We present a new *Lynceus* (Crustacea: Branchiopoda: Laevicaudata) species, *Lynceus amplopedia* sp. nov., from Yunnan, China, which shows significant left-right differences in some non-clasper thoracopods. It can be distinguished from all congeners by asymmetrically modified thoracopods III–VI. In the 'explanate modified' side (usually the left side, occasionally the right) the following modifications are present: endites 4, 5, and endopod enlarged (explanate) (thoracopods III and IV); exopod with 14–15 digitiform processes dorsomedially (thoracopods V and VI); and broad muscular basis (thoracopods III–V). The following modifications are seen in the thoracopods of the opposing 'spinose modified' side (usually the right side, occasionally the left): endite 4 with robust, specialized spines medially (thoracopods V and VI); endite 3 elongate protruding (thoracopod VI), and broad muscular basis (thoracopod V). Other unique characters of the new species include: male and female rostrum sinuate, compound eyes protruding, male claspers with endopod constricted, and endite 3 with two scale patches. We suggest the modified thoracopods may be involved in mating and/or respiration. The diversity of Chinese *Lynceus* is also discussed.

Key words: Laevicaudata, Diversity, New species, Modified thoracopods, Lateral asymmetry.

BACKGROUND

Most metazoans are fundamentally bilaterally symmetrical, although many taxa display well-known examples of the opposite condition, such as the assymmetrical arrangement of internal organs in vertebrates, or the shell coiling of gastropod mollusks. Within Crustacea the unequal chelae in decapod crabs (Palmer 1996) are classical examples of assymmetry, but also within Laevicaudata (Branchiopoda) assymmetry is seen; most well-documented is its presence in *Paralimnetis*, *Lynceiopsis*, *Lynceus gracilicornis* (Packard, 1871), and *L. aequatorialis* Daday, 1927, where male claspers and thoracopods II show clear differences between left and right sides (Martin and Belk 1988).

The smooth clam shrimps, Laevicaudata Linder, 1945, are a small, monophyletic group of branchiopod

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crustaceans, sister to the Onychocaudata (Olesen 1998; Richter et al. 2007; Richter and Olesen 2013; Rogers and Olesen 2016; Schwentner et al. 2018). Laevicaudatan diversity was first reviewed by Daday (1913 1927), and Brtek (1997 2002), and most recently by Rogers and Olesen (2016) who provided an updated diagnosis and discussed synapomorphies. The diversity of Asian Laevicaudata was reviewed by Rogers et al. (2016), who recognised seven distinct species and one species complex. *Lynceus simiaefacies* Harding, 1941 is only known from Yemen. *Lynceus planifascius* Rogers et al., 2016 and *L. spinimanus* Rogers et al., 2016 occur in Thailand. *Lynceus indicus* Daday, 1927 and the *L. denticulatus* species complex occur in India and Sri Lanka. *Lynceus mandsuricus* Daday, 1927 and *L. biformis* (Ishikawa, 1895) are reported from northern China, Japan, and Korea (Rogers et al. 2016; Rogers and Olesen 2016). Here, we supplement the knowledge of bilaterally assymmetry in Laevicaudata by describing a new species of *Lynceus* (Branchiopoda: Laevicaudata) from Yunnan Province, China, characterised by uniquely modified and asymmetrical thoracopods III–IV.

MATERIALS AND METHODS

Specimens were collected in the field using a handheld dip net, and were preserved in 95% alcohol. Specimens were examined under a stereo microscope (Zeiss Stemi 508) and a compound microscope (Olympus CX31) in the laboratory. All drawings were made using a camera lucida, and light microscope images were taken with a ToupCam microscope digital camera on a compound microscope. Specimens were also photographed with an Olympus DP73 camera mounted on an Olympus SZX10 dissecting microscope and operated by Olympus CellSens microscope imaging software. Images were stacked using Zerene Stacker 1.04 (Zerene Systems LLC). A male and a female were prepared for SEM (Sigvardt et al. 2017) and examined with a JEOL JSM-6335-F (FE) housed at the Natural History Museum of Denmark, Copenhagen. Images were processed digitally with Photoshop CS and Corel PHOTO-PAINT X7 (Corel Corporation). Terminology follows Rogers and Olesen (2016), Olesen et al. (2016), and Sigvardt and Olesen (2014).

Examined specimens are deposited in the following institutions: Kunming Natural History Museum of Zoology, Kunming Institute of Zoology (KIZ), Chinese Academy of Sciences; Natural History Museum of Denmark (NHMD); and the Applied Taxonomic Research Center, Khon Kaen University, Thailand (KKU).

Comparative material

Comparisons were made with *Lynceus* species from Asia and other continents, both from the literature and by direct examination of the material below. Acronyms: BMNH = British Museum (Natural History), London, United Kingdom; DCR = collection of D. Christopher Rogers; 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 = US Natural History Museum, Washington D.C., USA; ZMUC = Zoological Museum, University of Copenhagen, old catalogue numbers at NHMD).

Lynceus aequatorialis Daday, 1927. VENEZUELA: Apure state: Arichuna Road. Date unknown, 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 biformis (Ishikawa, 1895). JAPAN: Shiga-Ken: Kusatsu-Shi: Kataoka-Cho. 26 May 2004, M.J. Grygier; 5 males (NHMD-615848, additional material: DCR-611). Shiga: Livsatsu: Kataoka-Cho: Rice paddies. 21 May 2001, M.J. Grygier; 16 males, 3 females (NHMD-81868/ZMUC-CRU-4020). Tano-Hanakuma: Takatsuki City: Osaka Prefecture, 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. Year and collector unknown; 1 male, 3 females (MNHB 18 363).

Lynceus planifascius Rogers, Saengphan,

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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; 12 males, 44 females, topotypes (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, 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), male and female thoracopods on 3 slides, paratypes (BMNH1940.7.23.1, 1940.7.23.2 and 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-82062/ZMUC-CRU-8218), 2 paratype females (NHMD-86114/ZMUC-CRU-8270), respectively.

RESULTS

TAXONOMY

Suborder Laevicaudata Linder, 1945
Family Lynceidae Baird, 1845
Genus *Lynceus* Müller, 1776 (*Sensu* Rogers and Olesen, 2016)

Lynceus amplopedia sp. nov.

(Figs. 1–8)

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Type locality: 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 asl.

Type material: Holotype, male (KIZ-2015010). Allotype, female (KIZ-2015011). Paratypes: five males and five females (KKU-CS2015001), two males and two females, (NHMD-615845), 18 males and 23 females (KIZ-2015012-50). All collected 5 October 2015, by H. F. Yang from the type locality.

Etymology: The specific epithet *amplopedia* is a combination of the Latin "amplus", meaning "wide", and the Latin "ped", meaning "foot". It refers to the unique, explanate modifications of endites 4 and 5 in male thoracopods III and IV. The gender is feminine.

Specific Diagnosis: *Both sexes*: Rostrum bicarinate. Head in lateral view with anterior margin sinuate, compound eyes on an ocular tubercle and frontal setal fields in deep concavity (Figs. 1, 3, 5, 7, 8).

Male: Left and right thoracopods asymmetrically modified. One side, termed 'explanate modified side' (usually left side, occasionally right), with endites 4, 5, and endopod explanate (thoracopods III and IV); exopod with 14–15 digitiform processes dorsomedially (thoracopods V and VI); broad muscular basis (thoracopods III–V). Opposite side, termed 'spinose modified side' (usually right side, occasionally left), with endite 4 with robust, specialized spines medially (thoracopods V and VI); endite 3 elongate protruding (thoracopod VI) broad muscular basis (thoracopod V). Clasper palm with two scale patches (one laterally, one posteriorly), clasper endopod (movable finger) with constriction near articulation, endite 5 (large palp) dorsoventrally flattened with dorsal sulcus bearing setae (Figs. 1–6).

Female: Rostrum distal margin broadly rounded and smooth, lacking serrations or lateral spines. Lamina abdominalis with four dorsal extensions and three marginal extensions (Figs. 1, 7, 8).

Description: Male: Length range: 5.9–6.8 mm (Figs. 1A, 3A, B). Head (Figs. 1B, 3B, E, 5C) ~0.50 of body length. Occipital condyle round. Head anterior margin sinuate in lateral view, with three protrusions along rostrum: dorsal most the ocular tubercle, the second just distad to the setal fields (setal fields in deep concavity), and distal most approximately mid-length of rostrum. Dorsal organ oval, elongate, near occipital condyle. Compound eye sub-circular. Setal fields smaller than compound eyes, circular, with short dense setae, separated by rostral carinae proximal ends (Figs. 1B, C, 3D, 5A).

Rostrum (Figs. 1C, 3D, 5A, B) with two medial carinae, extending distally from near setal fields. Carinae parallel in proximal third, diverging approximately 20° at distal two thirds, terminating before rostral apex. Rostrum truncate with acute apicolateral corners. Truncated rostral distal margin shallowly, evenly concave, with dense row of setae, denticles absent (Figs. 5A, B, D). Rostral apex in lateral view dorsoventrally flattened distally (Figs. 1B, 5D). Rostrum in anterior view broadest at apicolateral corners with constriction approximately 50% of rostral length. Rostrum greatest

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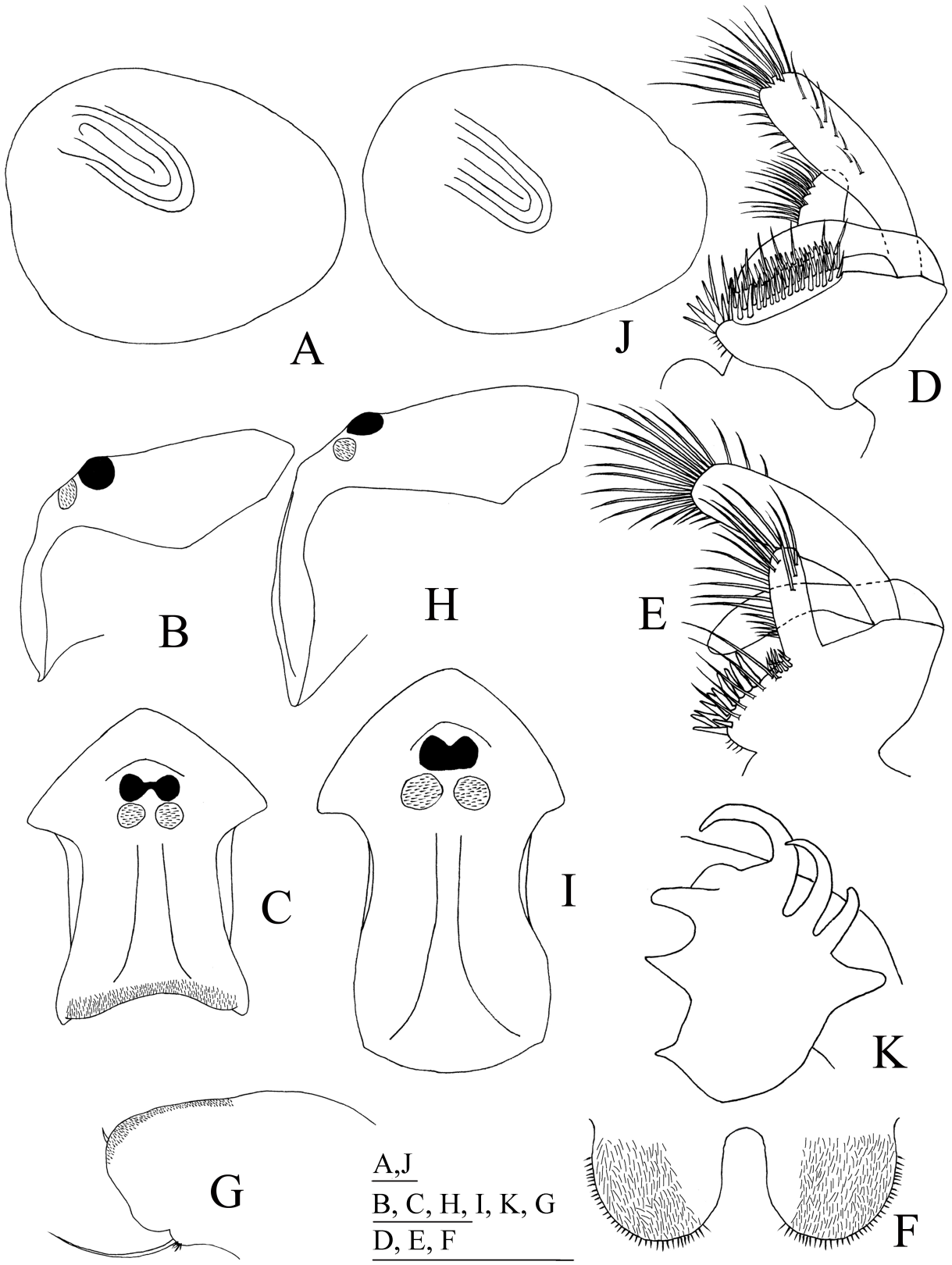

Fig. 1. *Lynceus amplopedia* sp. nov., A–G: male: A, carapace, left lateral view; B, head, left lateral view; C, head, anterior view; D, right clasper, anterior view; E, left clasper, posterior view; F, opercular lamella, ventral view; G, telson, left lateral view. H–K: female: H, head, left lateral view; I, head, anterior view; J, carapace, left lateral view; K, lamina abdominalis, left lateral view. Scale bar = 1 mm.

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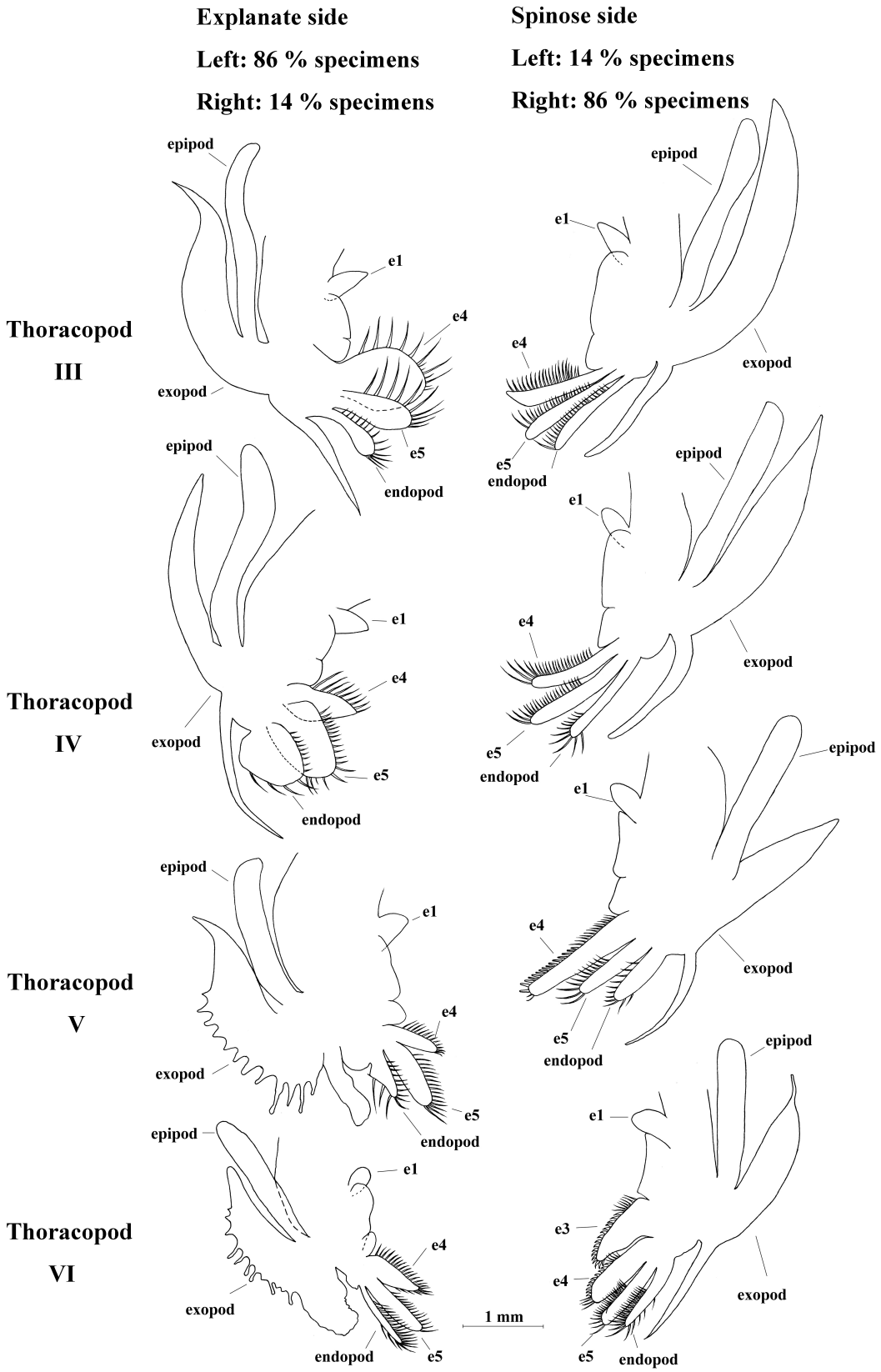

Fig. 2. Asymmetry and modified thoracopods III–VI of *Lynceus amplopedia* sp. nov., setae and spines are presented only on endites 4, 5 and endopod. Abbreviations: e1–e5 = endites 1–5.

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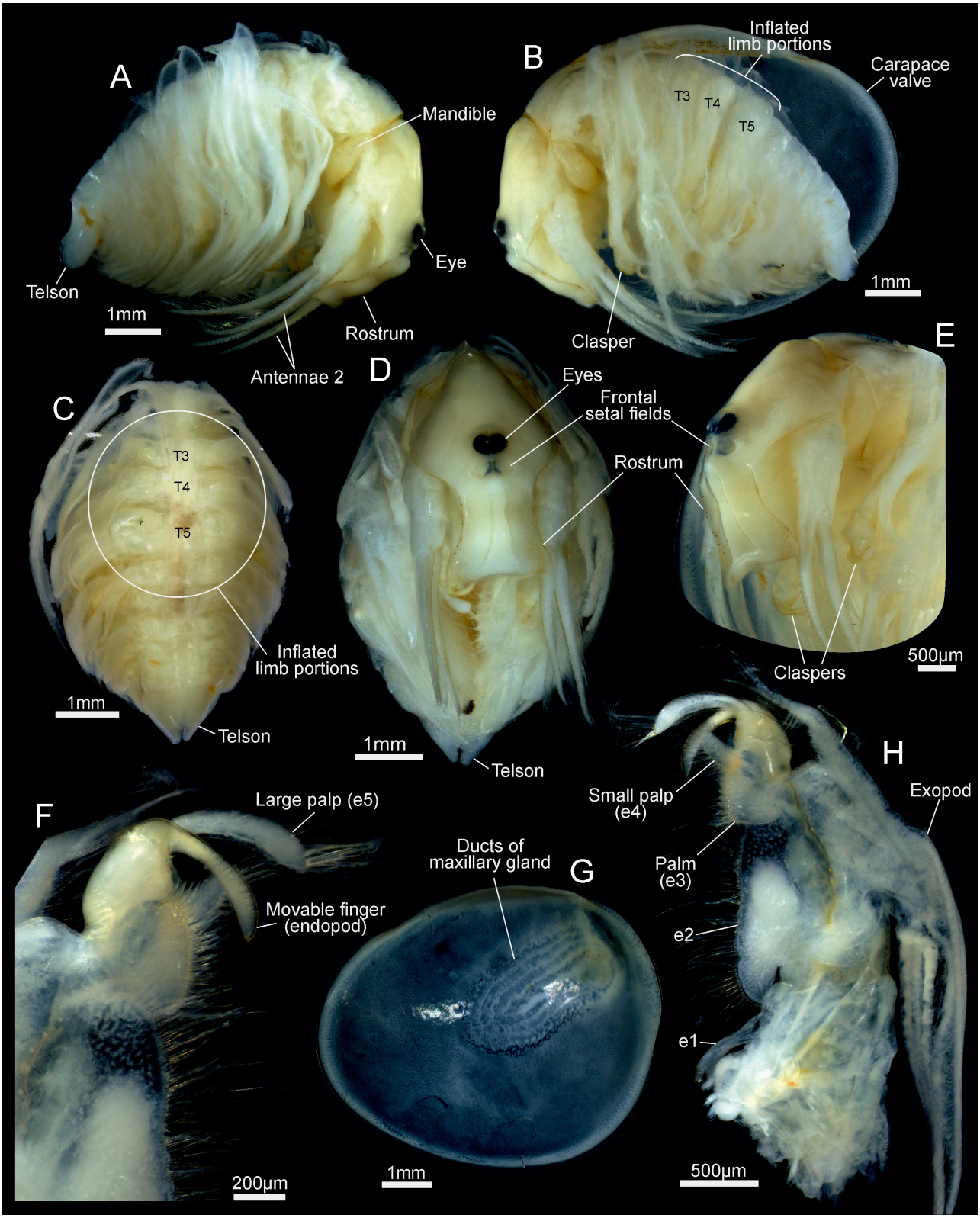

Fig. 3. *Lynceus amplopedia* sp. nov., male, stereo microscopy (paratype NHMD-615845). A, right lateral view (carapace valves removed); B, left lateral view (left carapace valve removed); C, dorsal view (head removed); D, ventral view; E, rostrum and claspers, ventrolateral view; F, left clasper, anterior view; G, carapace, right valve, exterior; H, left clasper, posterior view. Abbreviations: e1–e5 = endites 1–5, T3–T5 = thoracopods III–V.

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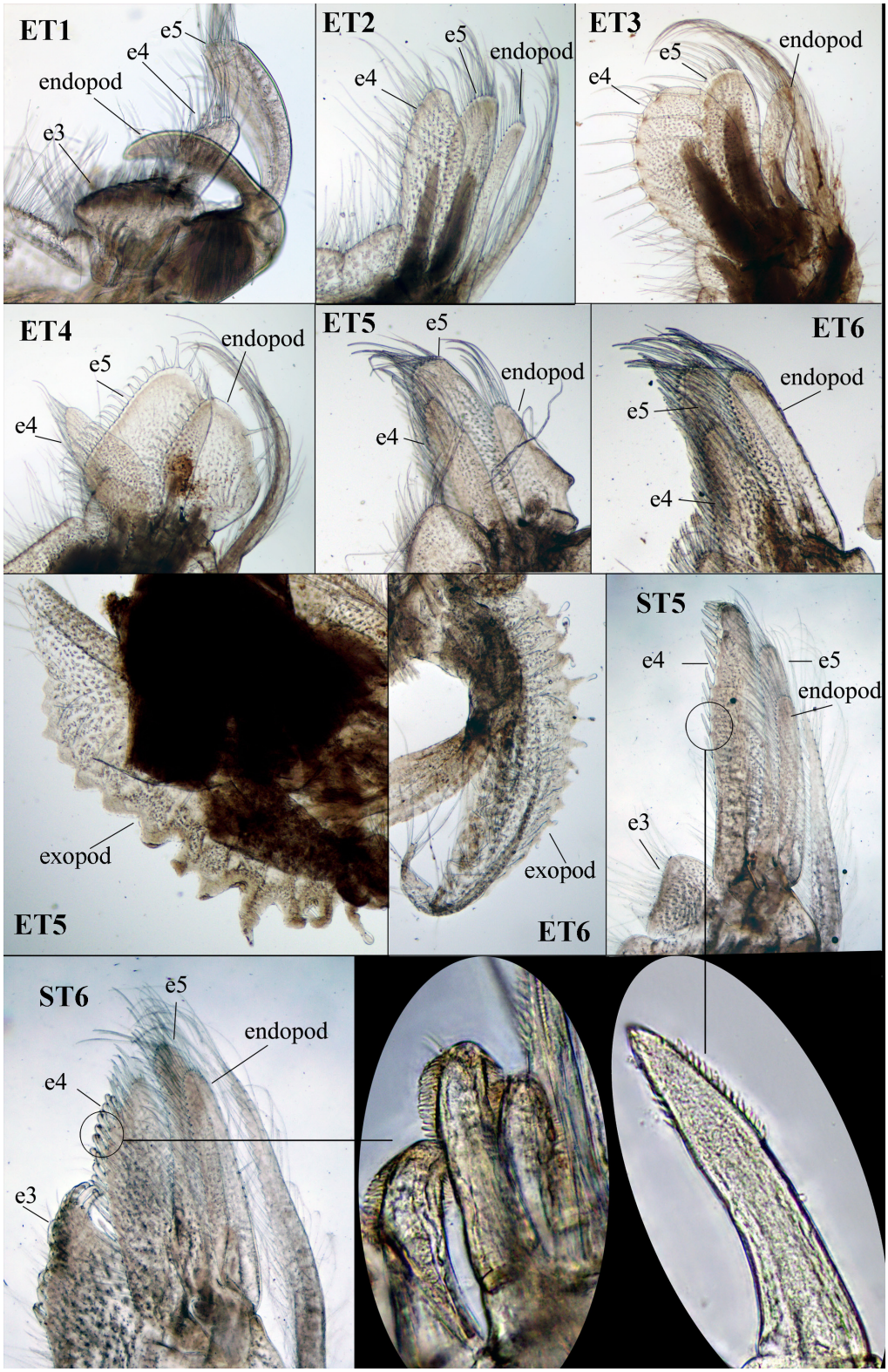

Fig. 4. *Lynceus amplopedia* sp. nov., modified male thoracopods, light microscopy. Endites 3–5, and endopod of thoracopods I–VI and exopod of thoracopods V and VI. Explanate modified thoracopods (ET): thoracopod III with explanate endites 4 and 5, thoracopod IV with explanate endites 4, 5 and endopod, and thoracopods V and VI with exopods with digitiform processes. Spinose modified thoracopods (ST): thoracopod V with spinose endite 4 and thoracopod VI with spinose endites 3 and 4. Abbreviations: ET1–ET6 = explanate modified thoracopods 1–6; e3–e5 = endites 3–5. ST5,6 = spinose modified thoracopods V and VI.

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width 1.2x rostral length. Fornices extending from second antenna insertion to apicolateral corners (Figs. 1B, 3A, 3B).

First antenna (Fig. 5F) with two antennomeres. Proximal antennomere cylindrical, length 2x breadth. Distal antennomere cylindrical, narrower than proximal antennomere, length 5.5x breadth, with two longitudinal rows of short sensory setae (or olfactory papillae).

Second antenna (Fig. 5C) biramous, long, extending to thoracopod VIII. Peduncle coxa cylindrical and thick, with longitudinal row of 8–10 long plumose setae on posterior margin. Peduncle basis with two groups of short, acute setae on anterior margin: two setae at middle ventral margin and six setae distally at exopod base. Exopod (anterior flagellum) with approximately 29 flagellomeres, each bearing a posterior long, distally directed, plumose seta and a short, acute, anterior seta present in most flagellomeres (absent in distal two flagellomeres and eight setae on proximal flagellomere anterior margin). Endopod (posterior flagellum) with approximately 34 flagellomeres, each bearing posterior, distally plumose seta (as exopod). Flagellomere setal length about half of corresponding flagellum.

Labrum large, lobiform, apex flat with fine setae.

Mandible (Fig. 5E) broad, molar surface with 13 or 14 transverse bispinose ridges with moderate indentation between spines. Posteriormost four ridges larger, with last three more broadly spaced than remaining ridges, posterior most ridge projecting as spine. Anterior most ridges smaller with spines, cluster of setae anteriorly.

Maxilla I (Fig. 5C) typical for genus, semicircular, with 11 plumose setae at medial margin, with three short denticles, robust setae at distal end, but lacking terminal setae of spines, posterior margin with fine setae. Maxilla II absent.

Carapace (Figs. 1A, 3G) semitransparent, relatively thin, smooth (lacking growth lines), globose and suboval in lateral view. Length < width, broadest near adductor muscle attachment site. Carapace with a slightly depressed region at end of posterior hinge line. Carapace average dimensions: height 6.9 mm, length 7.5 mm, width 4.5 mm (n = 10).

Thoracopods, 10 pairs, first pair modified as claspers (Figs. 1D, E, 5H–N). Thoracopods III–VI not bilaterally symmetrical (Figs. 2, 3C, 4, 6). The modifications of one side are here termed "explanate modifications" due to the explanate shape of certain endites and the endopod (see below). The modifications of the opposing side thoracopods are here termed "spinose modifications" due to presence of greatly specialized spines on endite 4 (see below). In ~86% of specimens (19 of 22 specimens) the explanate modifications are on the left side thoracopods and the spinose modifications on the right side; in the remaining ~14% the pattern is opposite (n = 3 of 22 specimens, see below).

Thoracopod I (Figs. 1D, E, 3F, H, 5H–N) right and left clasper equal in size and shape. Endite 1 lobiform, elongate, margin with short setae and three pectinate spines. Endite 2 broadly transverse, margined with three setal types, (1) distal margin with ~50 long setae, each bearing dense, short setulae in distal half; (2) anterior surface submargin with ~40 short, smooth setae; (3) posterior surface submargin with ~20 long setae, each bearing sparse, long setulae in distal half. Endite 2 distal tenth slightly expanded, with six stout, long setae. Endite 3 (palm with gripping area) broadly transverse (Fig. 5K), length 1.5x width. Corm area 3 and 5 (*sensu* Kaji et al. 2014) covered with scales (Fig. 5I, M, N), medial margin with fine, type V setae (clasper setae types *sensu* Sigvardt and Olesen 2014). Gripping area with diverse setation: anterior margin with ~40 type IV setae (Figs. 1D, 5H), posterior margin with a row of ~seven long type I setae, a row of ~eight stout type II setae, and a group of six to eight type III setae (Figs. 1E, 5I–K, N). Endite 4 (small palp) digitiform, proximally expanded, length ~3x width, apex round, margined with ~15 long setae, endite 4 distal surface with four long setae, each bearing sparse, long setulae (Figs. 1E, 5I). Endite 5 (large palp) clavate, longer ~2x than endite 4, dorsoventrally flattened, proximal fifth arcuate, apex round, bearing ~20 simple setae; dorsal surface with sulcus with ~10–12 simple setae (Fig. 5L). Endopod (movable finger) digitiform, proximal fourth arcuate, diameter narrowing proximally distal to point of articulation, with sides diverging distally before apex (Figs. 1D, E, 5H, K). Endopod apex subacute, extending to one half of endite 3 medial surface. Clasper exopod elongate with setae along margin, mid-dorsal margin with three or four short, robust, spiniform setae, each with distal half bearing two rows of small denticles.

Thoracopod II not modified, endites 4 and 5 slightly expanded distally, digitiform.

Explanate modified side (holotype left side) (Figs. 2: ET3-ET6, 6A–C): Thoracopods III–V with greatly inflated, chitinous muscular bases. Thoracopod III endites 4 and 5 explanate; endite 4 length ~1.3x width, medial margin with sparse, long setae and apex with group of short setae; endite 5 length ~2x width, setae similar to endite 4 but apex with longer setae. Thoracopod IV endites 4, 5 and endopod explanate; endite 4 smaller than preceding endite 4, medial margin with long setae; endite 5 broadly ovate, medial margin with stout setae, apex with long setae; endopod subquadrate, medial margin with 12 stout setae and distally with four long, robust setae (Figs. 2, 6B).

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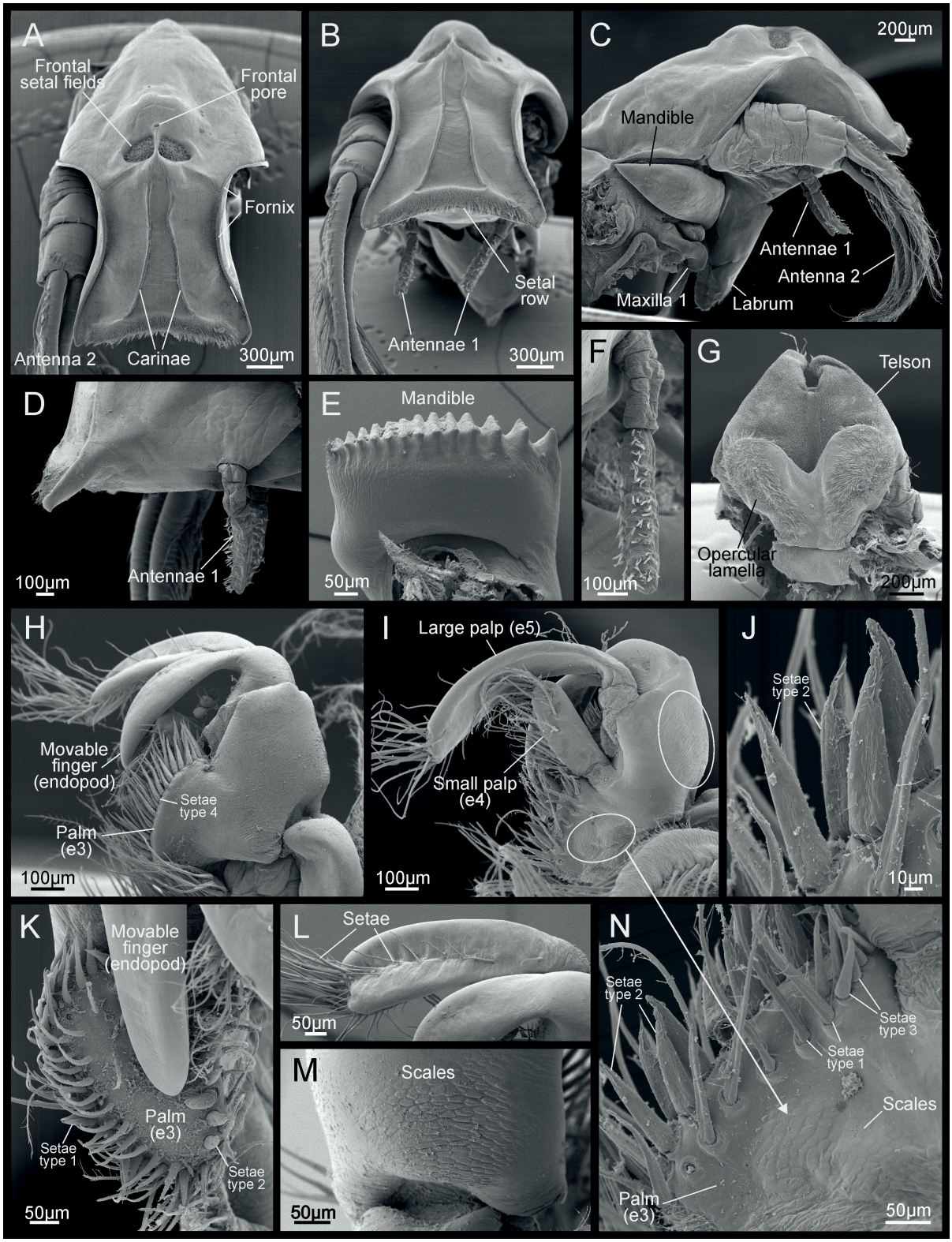

Fig. 5. *Lynceus amplopedia* sp. nov., male, scanning electron microscopy (paratype NMHD-615845). A, head, anterior view (left antenna removed); B, head, anteroventral view, left antenna removed; C, head, right lateral view; D, rostral apex, left lateral view; E, left mandible, lateral view; F, left first antennae; G, telson with opercular lamella, ventral view. H, right clasper, anterior view; I, left clasper, posterior view, encircled areas with scales; J, setae (magnification of I); K, clasper gripping area with setae, apical view; L, large palp (e5), right clasper, dorsal view; M, clasper palm (e3) with scales (upper encircled area in I), lateral view; N, setae and scales of clasper gripping area (magnification of I). Abbreviations: e3–e5 = endites 3–5.

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Thoracopods V and VI endites 4, 5 and endopod slightly explanate, digitiform; exopod dorsomedial margin with 14–15 digitiform processes (Figs. 2, 4: ET5, ET6; 6C), apex with long setae becoming shorter posteriorly (Fig. 4).

Spinose modified side (holotype right side) (Figs. 2: 4ST5–ST6, 6D–G): Endites, endopod, and exopod of thoracopods II–IV of typical form for the genus. Thoracopod V with greatly inflated, chitinous muscular basis. Thoracopod V endite 4 digitiform, medial margin distal two third and apex with about 20 robust spines, each with two rows of small denticles in distal half. Thoracopod VI endite 3 protruding distally, elongate in similar way to endites 4, 5 and endopod; endite 3

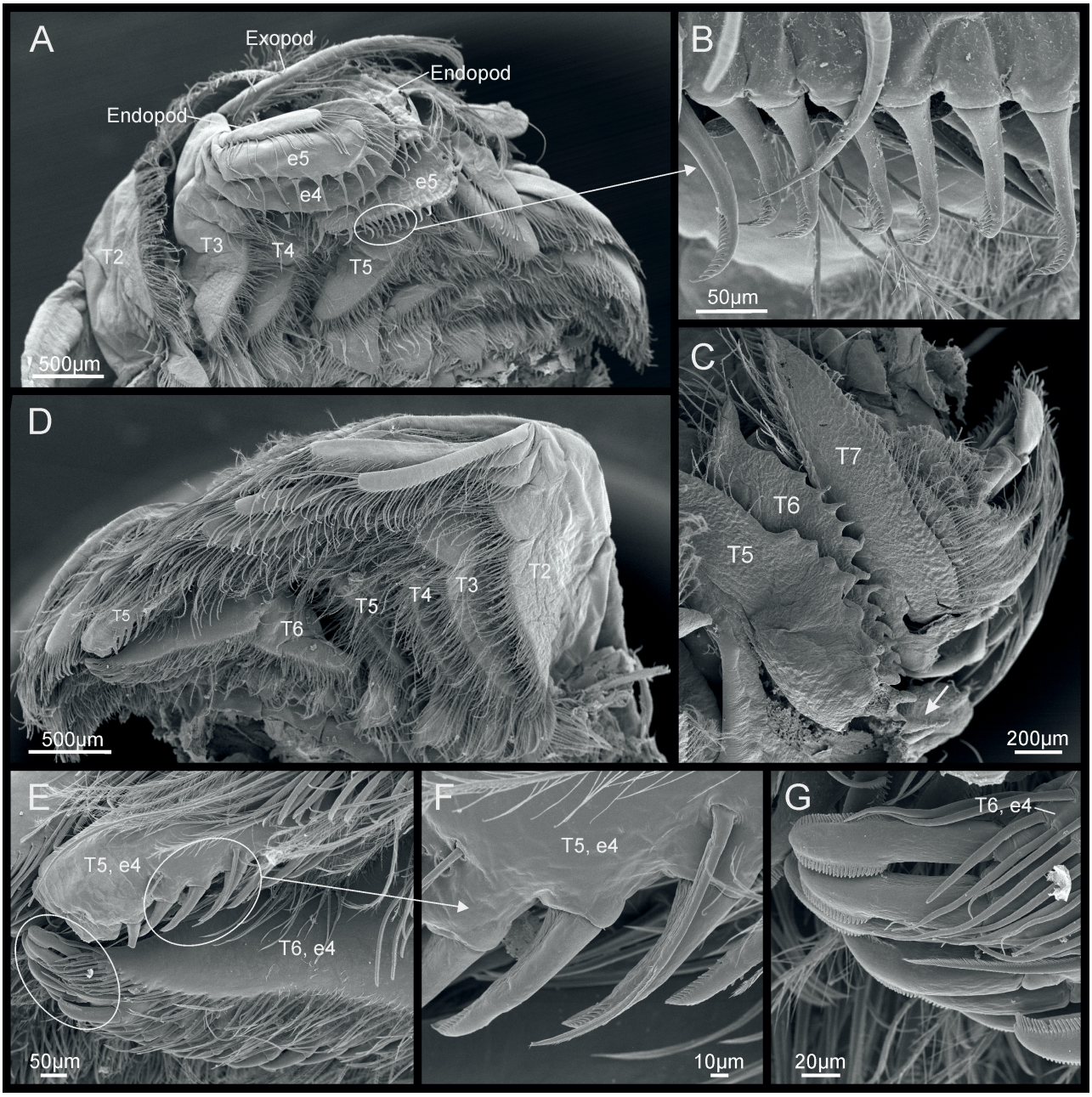

Fig. 6. *Lynceus amplopedia* sp. nov., modified male thoracopods, scanning electron microscopy (paratype NHMD-615845). A–C: explanate modified thoracopods (left side); D–G: spinose modified thoracopods (right side). A, thoracopods II-X, left side, median (inner) view, thoracopods III and IV with enlarged endites 4–5 (and endopod); B, magnification of setae on thoracopod V endite 5; C, lateral (outer) view, thoracopods V and VI with exopods with digitiform processes; D, thoracopods II-X, right side, median (inner) view, thoracopods V and VI with characteristic stout spines; E, higher magnification of endite 4 of thoracopods V and VI and their stout spines; F, spines on thoracopod V endite 4 (magnification of E); G, spines on thoracopod VI endite 4 (lower encircled area in E). Abbreviations: e4–e5 = endites 4–5, T2–T6 = thoracopods II–VI.

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distal half and endite 4 middle medial margin with characteristic stout spines, each with a broad apex turning backwards, with two parallel rows of strong denticles distally (Figs. 4, 6).

Thoracopods VII–X of typical form for the genus (Martin and Belk 1988; Olesen et al. 2016).

Opercular lamella (Figs. 1F, 5G) cordate, flattened, cleft medially, lobes separated by one third their width. Each lobe and ventral lateral surface margined with short dense setae directed distomedially.

Telson (Figs. 1G, 5G) broad, ventral surface with dense, fine pilosity. Dorsoposterior angles with spiniform cercopod. Dorsal lobes rounded, each terminating with a long filiform telsonal filament, base of telsonal filament with short fine setae, respectively.

Female: Length range: 4.5–5.3 mm (Figs. 1J, 7A). Head (Figs. 1H, 7B, 8B). Head anterior margin in lateral view sinuate as in male, compound eyes on most prominent protrusion and setal fields placed in deepest concavity (Figs. 7A, B, 8B). Compound eyes proportionally smaller than in male (Fig. 7C). Rostrum (Figs. 1I, 7C, 8A) elongate, length about 2x distance from eyes to rostral constriction. Rostrum with two medial carinae extending distally from near setal fields. Carinae parallel in proximal half, diverging approximately 20° at distal half, extending towards rostral corners, terminating relatively far from apex. Rostral apex broadly rounded, smooth, apicolateral corners and denticulation absent (Figs. 1I, 8C).

Antennae and mouthparts as in male (Figs. 8E, F,

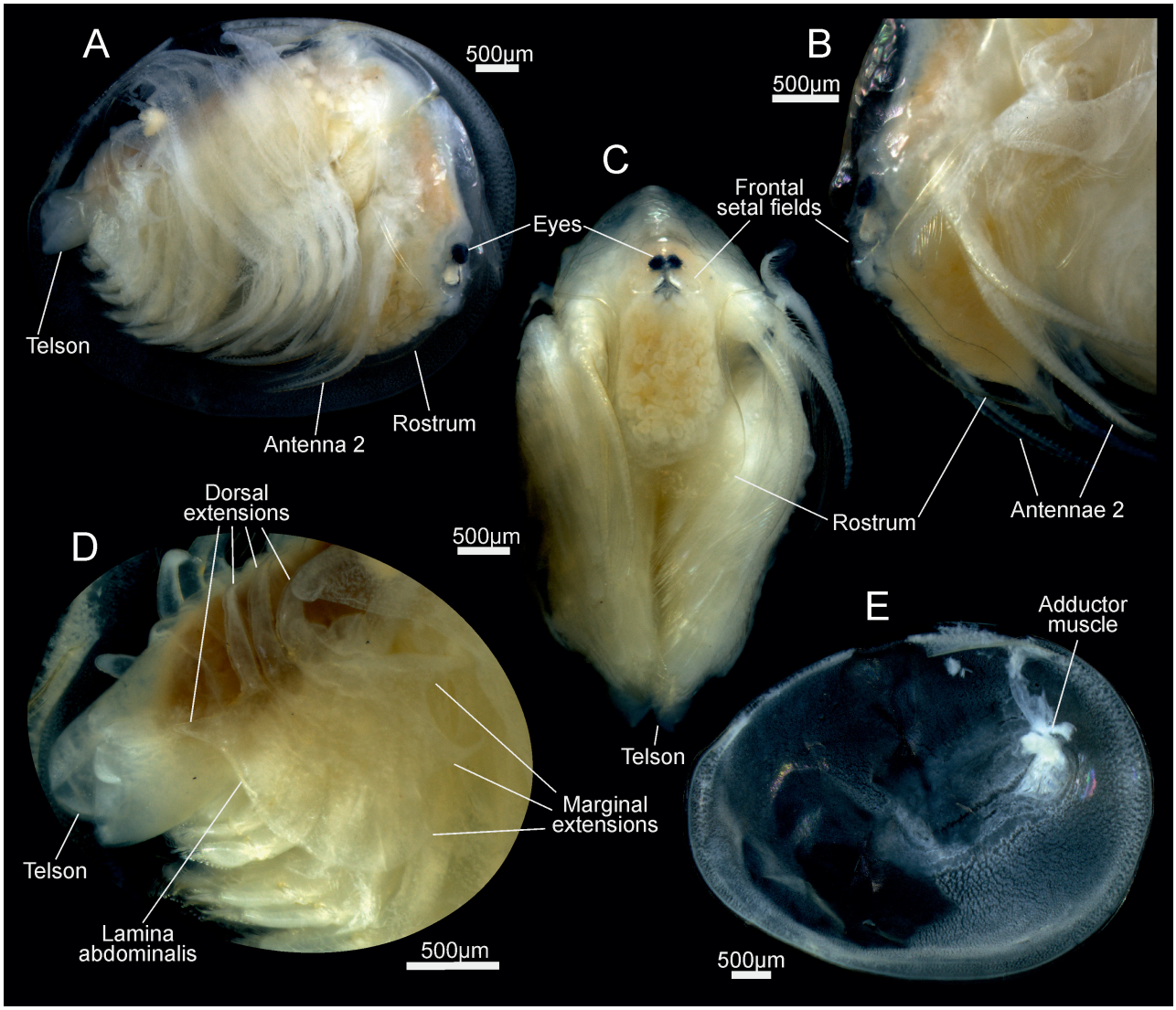

Fig. 7. *Lynceus amplopedia* sp. nov., female, stereo microscopy (paratype NHMD-615845). A, right lateral view (right carapace valve removed); B, rostrum, left lateral view; C, ventral view, valve removed; D, telson and right side posterior thoracopods with lamina abdominalis consisting of 4 dorsal and 3 marginal extensions; E, carapace, left valve, interior.

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H-K).

Carapace (Figs. 1J, 7E) in lateral view globose, smooth, thin, ovate. Carapace posteriodorsal margin sharply declivous, with distinct depressed region at posterior hinge line end. Carapace proportionately smaller than in male, average dimensions: height 6.5 mm, length 7.0 mm, width 4.4 mm (n = 10).

Thoracopods 12 pairs, unmodified, typical for genus. Thoracopod I endite 1 spine larger than in male. Endites 2 and 3 marginal setae short, dense and smooth, submarginal setae long and sparse, both with setulae, endites 4, 5 and endopod digitiform, with ventral marginal setae. Thoracopods II–VII serially homologous, with increasing number of short setae in endites 2 and 3, long seta shorter, endites 4 and 5 with scraping setae. Thoracopods VIII–XII, endites 4, 5 and endopod lobiform, without epipod. Thoracopods IX and X with modified exopods for carrying the eggs, with distodorsal curved lobe with fine setae.

Lamina abdominalis (Figs. 1K, 7D, 8G) broad,

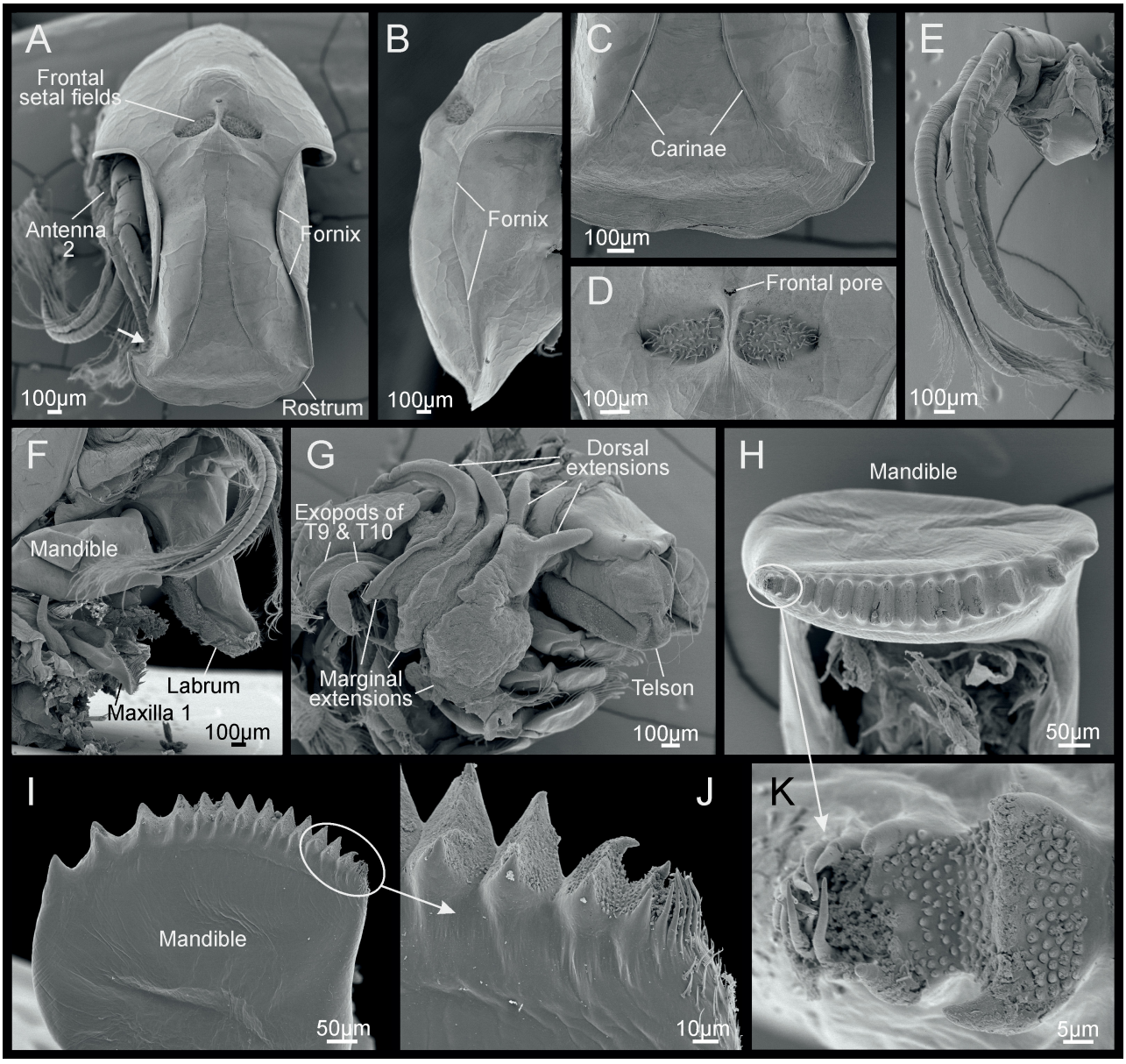

Fig. 8. *Lynceus amplopedia* sp. nov., female, scanning electron microscopy (paratype NHMD-615845). A) head, anterior view, (left antenna removed); B, head, left lateral view; C, rostral apex (magnification of A); D, frontal setal fields; E, left second antenna; F, mouthparts, right side: labrum, mandible, maxilla I; G, telson and left side posterior thoracopods with lamina abdominalis consisting of 4 dorsal and 3 marginal extensions; H, left mandible, apical view; I, left mandible, lateral view; J, mandible, magnification of I; K, mandible, magnification of H. Arrow = edge of rostrum broken. Abbreviations: T9–T10 = thoracopods IX–X.

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dorsal to posterior thoracopods, bearing four dorsal and three marginal extensions. Anterior dorsal extension longest, arcuate and hamulate, tapering towards apex and directed anteriorly. Medial two dorsal extensions similar to anterior dorsal extension, about 2/3 and half as long, respectively. Posterior dorsal extension broadly triangular, directed posteriorly. Anterior marginal extension digitiform, straight, apex round. Medial and posterior marginal extensions lamellar, triangular, medial extension broader than posterior. All marginal extensions directed anteriorly.

Telson as in male.

Ecology and habitat

The type locality (easternYunnan Province, China) is in a karst region. The pool fills with both rain water and ground water from an adjacent cave. The water temperature was 22°C during sampling and the anostracan, *Streptocephalus sirindhornae* Sanomuang et al., 2000, and the spinicaudatan, *Leptestheria kunmingensis* Shu et al., 2015 were found co-occurring.

IUCN status

Lynceus amplopedia sp. nov. meets the IUCN criteria as a Critically Endangered (CR) species, with its occupancy area less than 10 km^2 (IUCN criteria B2). The species is known only from the type locality, and was collected during a survey in Qiubei County. This site is the only known location for *Lynceus* in Yunnan Province despite many years of survey (IUCN criteria B2a). In addition, the type locality is near farmland. Pollution and pesticide from local agriculture, and the fluctuation of subterranean water may decrease the quality of the habitat (IUCN criteria B2 b and c).

DISCUSSION

Differential Diagnosis

Lynceus amplopedia sp. nov. holds multiple unique morphological characters that distinguish it from all other described Laevicaudata. It is separated from all congeners by the greatly asymmetrically modified thoracopods (III–VI) and its distinctive sinuate head morphology in lateral view, with the compound eyes elevated on an ocular tubercle (as in some Spinicaudata), leaving the frontal setal fields in a deep concavity. The rostral carina in *L. amplopedia* sp. nov. is bifurcated, dividing just distad of the setal fields, something known from several other species of *Lynceus* including *L. spinimanus* from Thailand (only female) (Rogers et al. 2016), several African species (Daday 1927; Barnard 1924 1929; Gauthier 1936), and likely *L. mandsuricus* from northeastern China and Japan even though in the original description (Daday 1927) it is depicted with a carina bifurcating further distad to the setal fields. Furthermore, *L. amplopedia* sp. nov. can be separated from most Asian species by the smooth distal margin of the female rostrum, which is serrated in the *L. planifascius*, *L. spinimanus*, *L. biformis*, and *L. denticulatus* species complex (Rogers and Padhye 2015; Rogers et al. 2016; Yoon and Kim 2000).

Among other Asian *Lynceus* species, *L. amplopedia* sp. nov. is most similar to *L. spinimanus* (Rogers et al. 2016), especially in some female characters, as they both have double rostral medial carinae and the female of *L. spinimanus* has symmetrically modified thoracopods posterior to thoracopods II (see below). However, there are also several differences between these two species, as they are separated by (1) only one medial carina present in male *L. spinimanus* versus two in *L. amplopedia* sp. nov.; (2) clasper setae of *L. spinimanus* are simple, only two types present on endite III "gripping area", versus five types in *L. amplopedia* sp. nov.; (3) the female rostrum distal margin is serrate and with lateral corners in *L. spinimanus* versus round and smooth in *L. amplopedia* sp. nov.; (4) last three pairs of thoracopods are chitinised in female *L. spinimanus* but normal in *L. amplopedia.*

Modified thoracopods

The thoracopods posterior to the claspers are often very similar along the anterior/posterior body axis across the Laevicaudata, except for some size variation of various limb parts (Olesen et al. 2016; Sigvardt et al. 2019). Traditionally, thoracopod descriptions of laevicaudatans have been simple and generalised, and thoracopod characters are unreported in most species. However, Ferrari and Grygier (2012) examined the variability of thoracopod limbs along the anterior/posterior body axis of *Lynceus biformis* and found many minor exceptions to the assumed pattern of serial similarity. Most notable within Laevicaudata is the modified male thoracopod II in *Paralimnetis* (Americas), *Lynceiopsis* (Africa), and in *Lynceus aequatorialis* (South America), where these limbs are strongly modified, but not in the same way (Martin and Belk 1988). *Lynceus simiaefacies* (Yemen) has some weak modifications in the male thoracopod II (Harding 1941); the male of *L. mucronatus* (Packard, 1875) has its last thoracopod pair with a strong, sclerotized, hamulate projection (Martin and Belk 1988), and female *L. spinimanus* (Thailand) has the last three thoracopod pairs chitinised, with thoracopod XI with a hamulate

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exopodal process (Rogers et al. 2016).

In this paper we report the first record of a laevicaudatan in which males have significant modifications of the thoracopods posterior to thoracopod II. The modifications are bilaterally asymmetrical in the sense that the appendages are not modified the same way in left and right side. Furthermore, the morphological modifications are not confined to the same side in all specimens. In most specimens (19 of 22) the left side thoracopods III–V have notably broader bases and thoracopods III and IV have characteristically explanate endites 4, 5 and endopod; this side has therefore been termed the 'explanate modified side' (more modifications mentioned in RESULTS). In the same specimens the right side thoracopod V has a broad base, endite 3 of thoracopod VI is elongate similar to endites 4–5, and endites 4 of thoracopod V and endites 4 and 5 of thoracopod VI have robust spines; this side has therefore been termed the 'spinose modified side'. In the remaining specimens the same types of thoracopodal modifications were present, but left and right sides were reversed.

The function of these thoracopodal modifications in *L. amplopedia* nov. sp. are unknown but may be involved in mating, for example in sperm transfer, which in *Lynceus brachyurus* most likely occurs during phases of characteristic rapid brushing movements by the non-modified thoracopods (Sigvardt and Olesen 2014). However, the function of the male modified non-clasper thoracopods in *L. amplopedia* nov. sp., and those of *Paralimnetis*, *Lynceiopsis*, and *L. aequatorialis* are in need of detailed studies of live, mating specimens, preferably involving high resolution video recordings. No left-right side preference was observed when male *Lynceus brachyurus* amplexed the female carapace margin (Sigvardt and Olesen 2014). If indeed the asymmetrical thoracopod modifications found in *L. amplopedia* are involved in mating, then this may be reflected in a preference for amplexing to one side of the female during mating. Another possible function of the modified thoracopods in *L. amplopedia* sp. nov. is that the increased surface area increases respiration (Boxshall and Jaume 2009). However, this does not explain the asymmetry of the appendages.

Rogers and Olesen (2016) regarded the elongate and digitiform thoracopod endites 4, 5 and endopod of most thoracopods as a unique feature in Laevicaudata, and suggested it to be diagnostic for the order. However, in *L. amplopedia* sp. nov., these structures are often broadly ovate, and significantly different from other species with detailed limb descriptions (*e.g.*, Martin et al. 1986; Ferrari and Grygier 2012; Olesen et al. 2016; Sigvardt et al. 2019). Furthermore, in *L. amplopedia* sp. nov., where these endites are not distinctly different from the more basal endites, they may appear as more plesiomorphic, but this requires evaluation in a broader phylogenetic context. General thoracopod morphology has unfortunately been neglected in many previous laevicaudatan taxonomic treatments (Rogers and Olesen 2016).

Chinese *Lynceus* diversity

There are few reports on clam shrimp diversity in China and Southeast Asia from the last century, but research has increased recently (Rogers et al. 2012 2016; Shu et al. 2015). Daday (1913 1927) described *L. mandsuricus* from Shenyang City, China based on male specimens, and Uéno (1940) later gave a short description of the female. Subsequent Chinese workers followed Uéno's figures (Dai 1982; Hu 1988). Unfortunately, none of these treatments of *L. mandsuricus* are very detailed, especially for the female (Rogers et al. 2016).

Lynceus taianensis Han, Shu et Liu, 1995 was described from Shandong Province, China (Han et al. 1995), but the description (and the figures) is poor and not useful: "Male with one growth line in carapace, thoracopods 10 pairs, first pair modified as claspers, unequal left and right side. Female with one growth line in carapace, thoracopods 12 pairs, thoracopods IX and X carry eggs, lamina abdominalis present near telson." The characters in this too brief description are common to the genus, and a growth line in *Lynceus* is highly doubtful, even though Linder (1945) reported a similar finding from Siberian specimens. Furthermore, no type specimens, type locality, or museum material was designated, and no differential diagnosis was provided. Therefore, we regard *L. taianensis* as a nomen nudum, according to article 13.1 of the ICZN.

Lynceus biformis has been reported in China, Japan, Korea and Taiwan (Olesen et al. 2016; Rogers et al. 2016; Rogers and Olesen 2016), and is apparently widely distributed in East Asia. Thus, *L. amplopedia* sp. nov. is the third valid species of Laevicaudata reported from China.

Knowledge about *Lynceus* diversity in China is limited, and the diversity is most likely larger than the literature indicates. *Lynceus brachyurus* is distributed widely in the Holarctic, ranging from the USA to Europe and Russia (Martin and Belk 1988; Rogers and Olesen 2016), and there is a doubtful record from northernmost India (Rogers and Padhye 2015). Due to this wide distribution of *L. brachyurus* it is not unlikely that it may also occur in northwest China. *Lynceus indicus* is only reported from the Indian side of the Himalayas, which is near the Chinese Tibetan plateau (Rogers and Padhye 2015), so it is likely that this

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species also occurs in China. Thus, Chinese *Lynceus* diversity needs further exploration, especially in the western and northern regions, which are close to India and Russia (Rogers and Padhye 2015; Vekhov 1993).

Key to Chinese male and female *Lynceus*

A key to Chinese *Lynceus* (males and females) is presented below. However, similar to the key to all Eurasian species provided by Rogers et al. (2016), caution is needed when attempting to identify lynceids from the northern and northeastern parts of China, because the morphology of *L. mandsuricus* females is unclear, and additional species reported from nearby may also occur in the region.

1. First thoracopod pair modified as claspers (males) 2
– First thoracopod pair not modified as claspers (females) 4
2. Rostrum bifurcating basally; clasper endite 4 ("small palp") digitiform 3
– Rostrum medial carina bifurcating distally; clasper endite 4 bulbous (Taiwan) ..... *Lynceus biformis* (Ishikawa, 1895)
3. Double carina bifurcating right below setal fields; clasper endopod ("movable finger") only reaching to middle of endite III; clasper limb with one broadly transverse projection laterally between clasper "palm" and exopod (Yunnan) .... *Lynceus amplopedia* sp. nov.
– Double carina bifurcating distally to setal fields; clasper endopod reaching nearly to or slightly beyond endite III; clasper limb with two distinct projections laterally between clasper "palm" and exopod, distal one lobiform, proximal one broadly transverse (Liaoning) ..... *Lynceus mandsuricus* Daday, 1927
4. Rostrum with single medial carina, distal margin denticulate (Taiwan) ..... *Lynceus biformis* (Ishikawa, 1895)
– Rostrum bicarinate (double carina), distal margin smooth (Yunnan) ..... *Lynceus amplopedia* sp. nov.

CONCLUSIONS

We collected specimens of smooth clam shrimps from Yunnan, China and described them as a new species, *Lynceus amplopedia* sp. nov. The morphological characteristics of this species differ distinctly from other congeners in the following rostrum sinuate in both sexes, compound eyes protruding, male claspers with endopod constricted and endite 3 with two scale patches, and the significantly asymmetrically modified thoracopods III–VI. The characters of non-clasper thoracopods will be beneficial for taxonomic research in *Lynceus*. The new species is only known from a single karstic temporally pond and meets the IUCN criteria as a Critically Endangered (CR) species. Three species of *Lynceus* are herein recognised from China, with *L. taianensis* regarded as a nomen nudum according to article 13.1 of the ICZN.

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Availability of data and materials: All materials in this paper were deposited in the museums listed above.

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Ethics approval consent to participate: Not applicable.

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