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Two new species of *Lasiosyne* from the Lower Cretaceous Yixian Formation (Coleoptera, Lasiosynidae)

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ABSTRACT

Two new species, *Lasiosyne integera* sp. nov. and *Lasiosyne parva* sp. nov., are described from the Lower Cretaceous, Yixian Formation of Huangbanjigou Village, Liaoning Province, northeastern China. These two new fossil species can be assigned to the extinct Mesozoic beetle family Lasiosynidae, based on their elongate suboval body, filiform antenna, striate elytron with lateral edge emarginated at the middle, abdomen with five ventrites, and slightly narrow and simple 5-segmented tarsus. This Mesozoic family was placed in infraorder Elateriformia with a mixture of several characters among superfamilies of Dascilloidea, Elateroidea, Buprestoidea, and Byrrhoidea. These two new species enhance the diversity of the genus *Lasiosyne* during the mid-Mesozoic. In addition, they also provide additional information for future phylogenetic studies of Lasiosynidae evolution.

1. Introduction

Beetles (Coleoptera), with approximately 380,000 described species, occupy approximately 38% of all insect species among the 39 Orders of the Insecta (Zhang et al., 2018), and show significant taxonomic, morphological, and ecological diversity (Farrell, 1998; Toussaint et al., 2016). Up to date, the oldest beetle fossil was reported from the Permian (Kirejtshuk et al., 2014; Beutel et al., 2019a). Although many efforts have been made to explain this spectacular evolutionary radiation (Farrell, 1998; Hunt et al., 2007; Salem et al., 2020; Motyka et al., 2021), only a few attempts have been made to study the phylogeny of the entire Coleoptera (McKenna et al., 2015; Zhang et al., 2018; Beutel et al., 2019b; Cai et al., 2022).

Family Lasiosynidae was erected to include four genera: *Tarsomegamerus* Zhang, 2005, *Lasiosyne* Tan, Ren & Shih, 2007, *Anacapitis* Yan 2009, and *Bupredactyla* Kirejtshuk et al., 2010a, placed in Elateriformia (Tan and Ren, 2009; Kirejtshuk et al., 2010a). Elateriformia comprises four superfamilies of Dascilloidea, Buprestoidea, Byrrhoidea, and Elateroidea, based on morphological and molecular evidence (Bocakova et al., 2007; Hunt et al., 2007; Lawrence et al., 2011). When investigating the timing of diversification, the main issues and difficulties are caused by the lack of suitable fossil evidence. It was demonstrated that the family Lasiosynidae accounts for the third most common taxa in the late Mesozoic Asian region after Elateridae and Cerophytidae (Kirejtshuk et al., 2010a, 2010b) and represents an early stage of Elateriformia evolution (Yan et al., 2014a). This mysterious group should be placed in Elateriformia because they share typical characters such as characteristic elytral sculpture, contiguous metacoxae with raised femoral plate, trilobed aedeagus and abdomen with five ventrites. However, the placement of Lasiosynidae within Elateriformia has been disputed. And this family were believed to be the taxa in superfamily Byrrhoidea (Yan et al., 2013) and representing basal lineage (Yan et al., 2014a). Kirejtshuk and Azar suggested taxa in Lasiosynidae to be included in the family Eulichadidae as a subfamily Lasiosyninae with two genera *Lasiosyne* Tan, Ren & Shih, 2007 and *Bupredactyla* Kirejtshuk, Chang, Ren & Shih, 2010 (Kirejtshuk and Azar, 2013). However, this suggestion has not been accepted by Yan (2014), but advised Lasiosynidae to be treated as a separate family (Yan et al., 2014a, 2015).

It is of great significance to clarify the systematic position of Lasiosynidae as the basis to explore the evolution of beetles across the infraorder Elateriformia. In addition, the abundant Lasiosynidae fossil species with good preservation provide adequate evidence which contribute to the phylogenetic study of Elateriform beetles.

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0195-6671/

Since 2005, considerable progresses have been made in the redefinitions of the taxonomic positions of some genera (Zhang, 2005; Yan, 2009; Yan and Wang, 2010; Yan and Zhang, 2010; Li et al., 2021) in Lasiosynidae. The genus *Bupredactyla* Kirejtshuk, Chang, Ren & Shih, 2010 was synonymized with the genus *Lasiosyne* (Yan et al., 2014b) with normal "pentamerous" tarsi. The genus *Tarsomegamerus* Zhang, 2005, originally assigned to Chrysomelidae (Zhang, 2005), then, was included in the family Lasiosynidae, but now suggested as a member of Byrrhidae (Yan et al., 2013). Three beetle genera, *Artematopodites* Ponomarenko, 1990, *Dzeregia* Ponomarenko, 1985, and *Glaphyropteroides* Handlirsch, 1906 (preserved as separate elytra) were placed in Lasiosynidae and reclassified as Elateriformia *incertae sedis* (Kirejtshuk and Azar, 2013).

Lasiosynid beetles have been mainly distributed in China (Kirejtshuk et al., 2010a; Yan et al., 2013, 2014b), Russia (Handlirsh, 1906; Yan and Zhang, 2010; Yan, 2012; Yan et al., 2014a), Mongolia (Yan and Zhang, 2010; Yan, 2012; Yan et al., 2014a), and Kazakhstan (Yan, 2009), in the northern hemisphere. The largest genus *Lasiosyne* comprises 13 known species (Kirejtshuk et al., 2010a; Yan, 2012; Yan et al., 2014b; Li et al., 2021). Among these species, six species were described from the Middle Jurassic Jiulongshan Formation of the eastern Inner Mongolia, China; three species from the Upper Jurassic deposits of the Shar-Teg sequence of southwestern Mongolia; three species from Zaza Formation in Russia and Mongolia with unspecified Lower Cretaceous age; and one species reported from the Lower Cretaceous Shouchang Formation at Xiaqiao Village, Laozhu Town, Lishui City, Zhejiang Province, China (Li et al., 2021).

Herein, we describe and illustrate two new species *Lasiosyne integera* sp. nov. and *Lasiosyne parva* sp. nov. from the Lower Cretaceous of China. These two new species provide further evidence for the Cretaceous diversification of Lasiosynidae. The morphological trend of *Lasiosyne* during the Cretaceous and Jurassic Periods is discussed in details.

2. Material and methods

This study is based on two holotypes and several paratypes collected from Huangbanjigou, near Chaomidian Village, Beipiao City, Liaoning Province, China (N41° 18.979′, E119°14.318′); Lower Cretaceous; Yixian Formation (Fig. 1). All type specimens are deposited in the Key Lab of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, curator). The specimens were examined using LEICA MZ 12.5 dissecting microscope with an attached digital camera system and illustrated with the aid of a drawing tube attached to the microscope, and then readjusted on the photographs using image-editing software (CorelDraw 12.0 and Adobe Photoshop CS).

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID for this publication: urn:lsid:zoobank.org:pub:DFE18331-8FF6-4873-9557-593E2096A561.

3. Locality and horizon

Huangbanjigou, near Chaomidian Village, Beipiao City, Liaoning Province, China (N41° 18.979′, E119°14.318′); Lower Cretaceous; Yixian Formation. The age of the Yixian Formation has been estimated at 125 Ma, ca. the Barremian–Aptian boundary (Swisher et al., 1999; Barrett, 2000; He et al., 2008; Chang et al., 2017), composed in tuffs, andesites, basalts, mudstones, tuffaceous shales, sandstones, conglomerates, and siltstones (Zhou et al., 2018). The stratum is representative of the Jehol Biota which is well-known for yielding fossils of plants, insects, diverse freshwater invertebrates, fish, dinosaurs, and birds (Pan et al., 2013; Shih et al., 2019).

4. Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Infraorder Elateriformia Leach, 1815
Family Lasiosynidae Kirejtshuk, Chang, Ren & Shih, 2010.

Genus *Lasiosyne* Tan, Ren & Shih, 2007.

Lasiosyne integera Guo, Shih & Ren sp. nov (Figs. 2–4)

Etymology. The specific epithet of this new species is of Latin word "integer" (complete), referring to this specimen with well-preserved body structures.
Type material. Holotype: male. No. CNU-COL-LB-20069861.
Paratypes: No. CNU-COL-LB-2021120, sex unknown, preserved only with head, pronotum, and part of elytron structure. No. CNU-COL-LB-2009488, probable male, with most of dorsal habitus and elytron, part of head and legs preserved.
LSID:urn:lsid:zoobank.org:act:74B670D8-4597-4DDD-A2A7-4074FE1683F6.

Diagnosis. Mandible large with distinct carinae; gula well-developed; antenna with slightly enlarged scape. Pronotum lateral edge depressed inward at posterior 1/3, widest at anterior 2/3. Metepisterna wide and about 2.5 times as long as wide. Mesocoxae large and nearly contiguous; tibia dilating apically.
Description of holotype. Body large (body 27.72 mm long and 9.92 mm wide); subparallel to subcylindrical (Fig. 2A–B); integument with varied and coarse sculptures, extremely densely punctate. Antenna and leg with dense fine hairs. Elytron large, with 11 subparallel striae formed by furrows, part of striae not clearly visible.
Head prognathous and slightly deflecting (head 2.67 mm long and 3.63 mm wide) (Fig. 3A). Eye relatively large, protuberant. Obvious high sclerotized orbital sclerite surrounding eye which is widest below the eye, with acute edge extending to mouthparts and narrowing gradually. Antenna 11-segmented, filiform, with very fine pubescence, relative length ratio of segments: 0.60:0.48:0.58:0.64:0.68:0.80:0.82: 0.83:0.76:0.68:0.85 (Fig. 3B). Scape moderately swollen, about 1.5 times as long as pedicel; pedicel subcylindrical and shortest; antennomeres 3–10 subequal; antennomere 11 longest. Clypeus subquadrate, frontoclypeal suture present (Fig. 3A). Labrum moderately large, labrum and clypeus separated by suture. Mandible strong, gradually curved and protruding forward with carinae. Maxillary palpomere well-developed. Occiput short, more or less retracted in pronotum, occipital suture not visible. Gula very large, narrowest at the middle; gular sutures widely separated (Fig. 2A).
Pronotum slightly transverse and quadrate (pronotum 3.96 mm long and 5.53 mm wide), about 0.67 times as long as wide, with dense pubescence. Anterior edge strongly produced and rounded, anterior angle blunt and rounded; lateral edge gradually curved at the middle and depressed inward at posterior 1/3; posterior angles sharp and produced behind. Prosternum anterior edge concave disposed behind anterior edge of pronotum.
Mesoventrite relatively small, longitudinal suture present at posterior and extending to mesocoxae. Mesepisterna subtriangular, mesepimera sub-rectangular. Mesocoxa large and elongate-oval, slightly oblique, and narrowly separated (Fig. 3C). Metaventrite sub-quadrate, about as long as wide; discrimen well-developed extending from posterior edge to anterior edge; transverse suture present and long; lateral sides parallel. Metanepisternum wide and

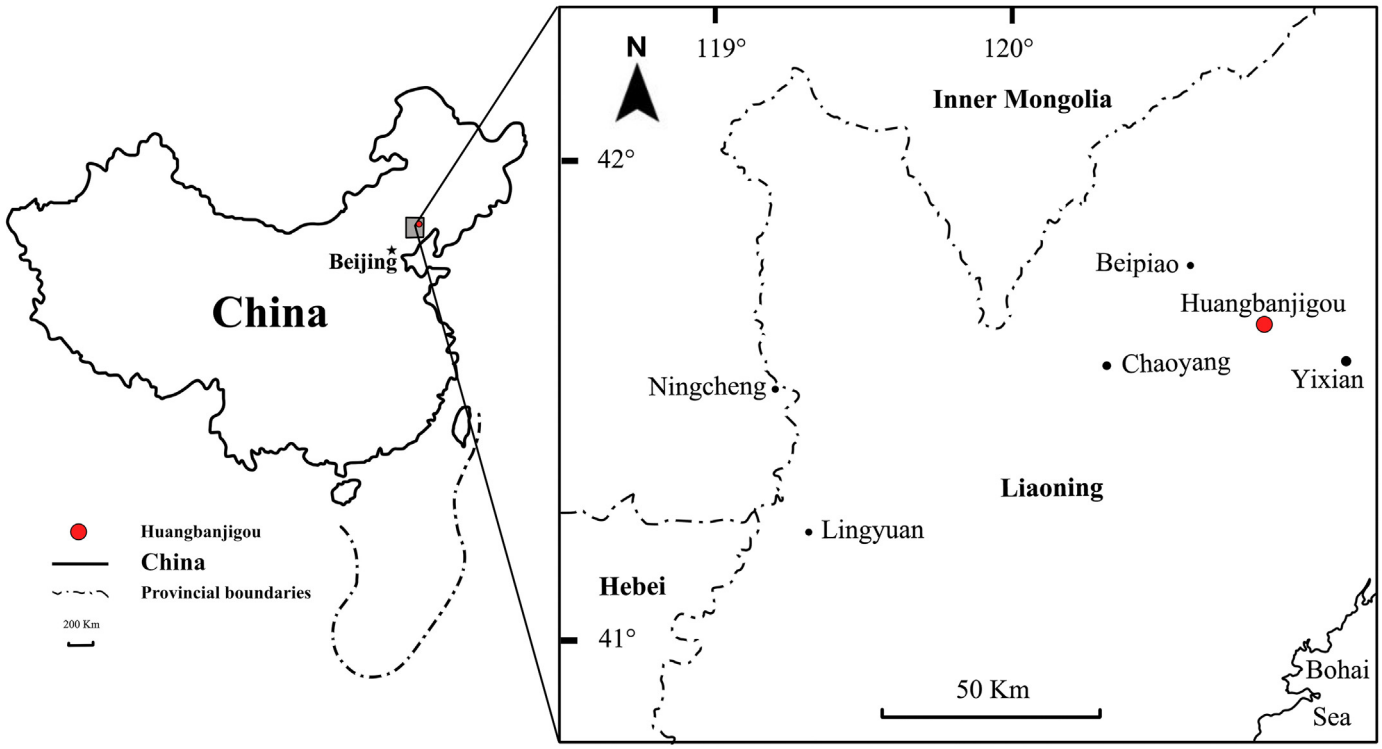


Fig. 1. Map showing the location of fossil localities of Yixian Formation (after Chen et al., 2014).

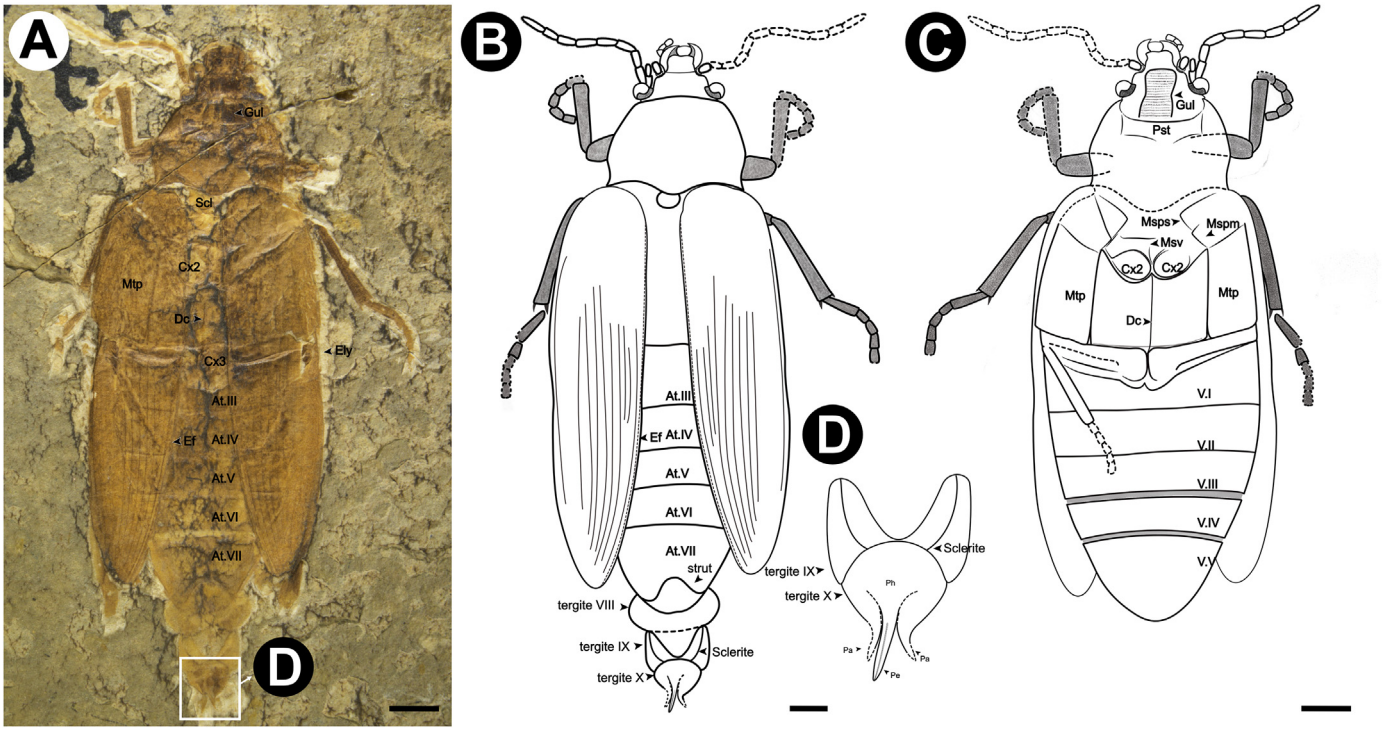


Fig. 2. *Lasiosyne integera* sp. nov., male, holotype CNU-COL-LB-2009861. (A) Dorsal side. (B) Line drawing of dorsal side. (C) Line drawing of ventral side. Note: The structures of the thorax and legs not visible on fossil. Dashed lines used to indicate the prothorax and mesothorax in the line drawing. (D) Line drawing of male aedeagus. Scale bars: 2 mm. Abbreviations: Cx2, Mesocoxa; Cx3, Metacoxa; Dc, Discrimen; Ef, Elytral flange; Ely, Elytron; Gul, Gular plate; Pa, Parameres = Lateral Lobes; Pe, Penis = Median Lobe; Ph, Phallobase = Basal Piece; Pst, Prosternum; Scl, Scutellum; Mtp, Metapleuron; Msps, mesepisternum; Mspm, mesepimeron; Msv, Mesoventrite; At.III–VII, Abdominal tergites segments III–VII.

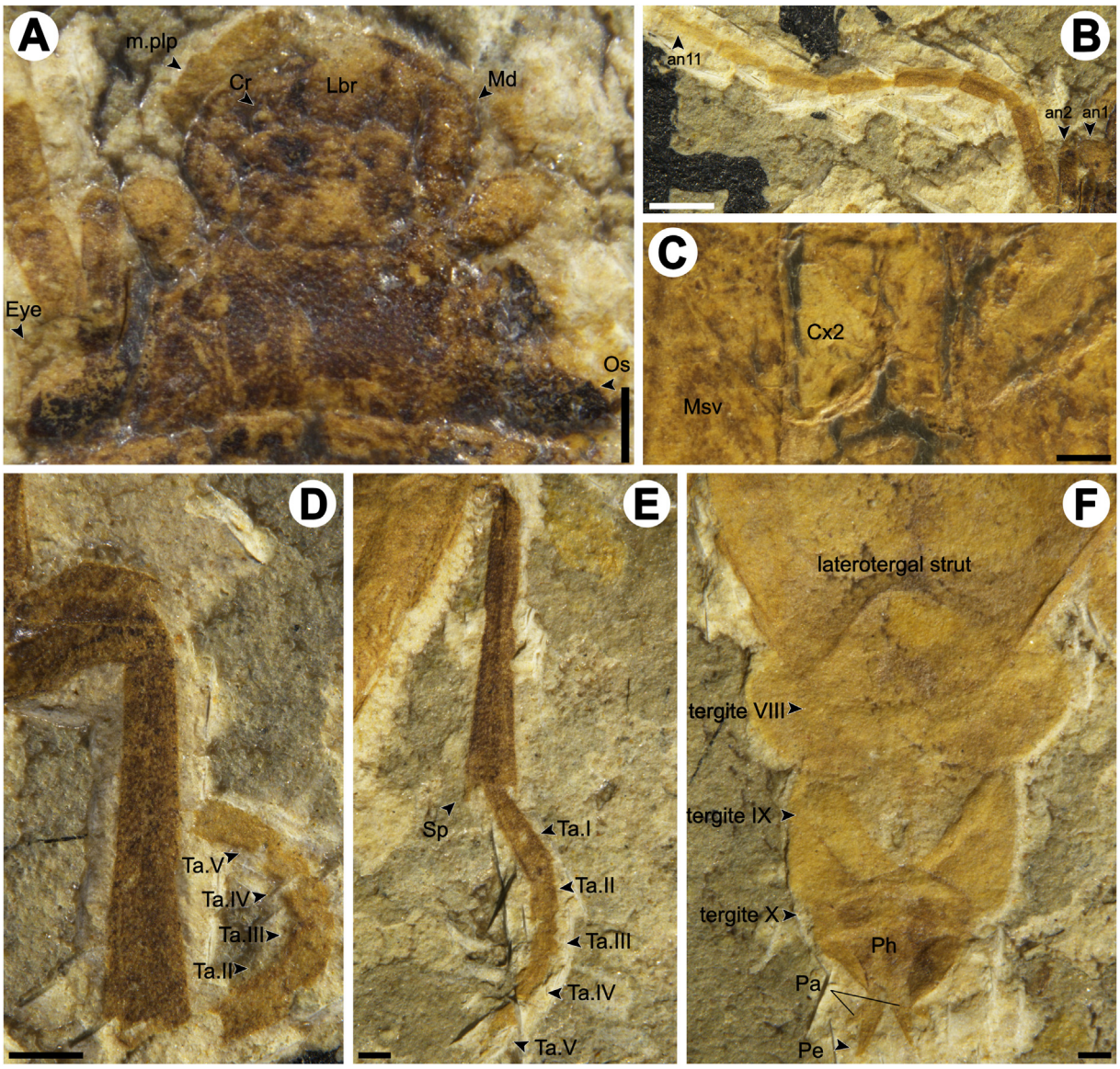


Fig. 3. *Lasiosyne integera* sp. nov., male, photographs of holotype CNU-COL-LB-2009861. (A) Head and mouthparts. (B) Antenna. (C) Mesocoxa and metasternal anterior process. (D) Fore-leg. (E) Meso-leg. (F) Male genitalia. Abbreviations: an1–11, antennal segment 1–11; Cr, Carinae of mandible; Cx2, Mesocoxa; Lbr, Labrum; Md, Mandible; m.plp, maxillary palpomere; Os, Orbital sclerite; Pa, Parameres = Lateral Lobes; Pe, Penis = Median Lobe; Ph, Phallobase = Basal Piece; Sp, Spur of tibiae; Msv, Mesoventrite; Ta.I–Ta.V, Tarsi segment I–V. Scale bars: 0.5 mm.

well-developed, lateral edges subparallel and about 2.4 times as long as wide. Metacoxae nearly contiguous; coxal plates moderately developed arcuately outlined in the median part.

Scutellum subcircular, rounded apically. Elytra (elytra 16.20 mm long and 7.92 mm wide) about 2 times as long as wide, with sides slightly constricted at middle; elytra width about 1.42 times of pronotum width. Each elytron with 11 deep longitudinal striae, the 2nd and 3rd hardly extend to basal half, remaining striae reaching elytral apices. Leg relatively slender, with dense and fine pubescence. Femur slightly raised; tibiae gradually widened toward apex; tarsomere I longest, subequal to succeeding two segments combined; tarsomeres II–IV nearly equal in lengths (Fig. 3D). Claw simple and curved.

Abdomen with five ventrites; terminal ventrite subtriangular; basal three segments connate, apical two segments free; narrowing from the third segment; length ratio of ventrites I–V: 1.92:1.73:1.51:1.59:3.65. Tergite VIII exposed with lateral edge slightly curved; Tergite X short. Aedeagus well-visible, typical trilobate type, and highly sclerotized. Genital ring present and distinct. Phallobase well-developed with gradually curved lateral edge; median lobe and parameres moderately developed, the median lobe seems longer than parameres.

Description of paratype (No. CNU-COL-LB-2021120). Antenna filiform. Head width much shorter than pronotum width, pronotum width 0.71 times of elytra width. Pronotum anterior edge slightly emarginate at middle, anterior angle not pointed; lateral edge slightly depressed inward at posterior (Fig. 4A, 4B).

This paratype specimen differs from holotype in its slightly emarginate anterior edge of pronotum.

Description of paratype (No. CNU-COL-LB-2009488). Body elongate (21.62 mm long and 6.60 mm wide), covered with dense sculpture (Fig. 4C).

Antenna filiform. Head much narrower than pronotum; pronotum width 0.71 times of elytron width. Pronotum anterior edge straight, anterior angles pointed; lateral edge curved. Mesoventrite small,

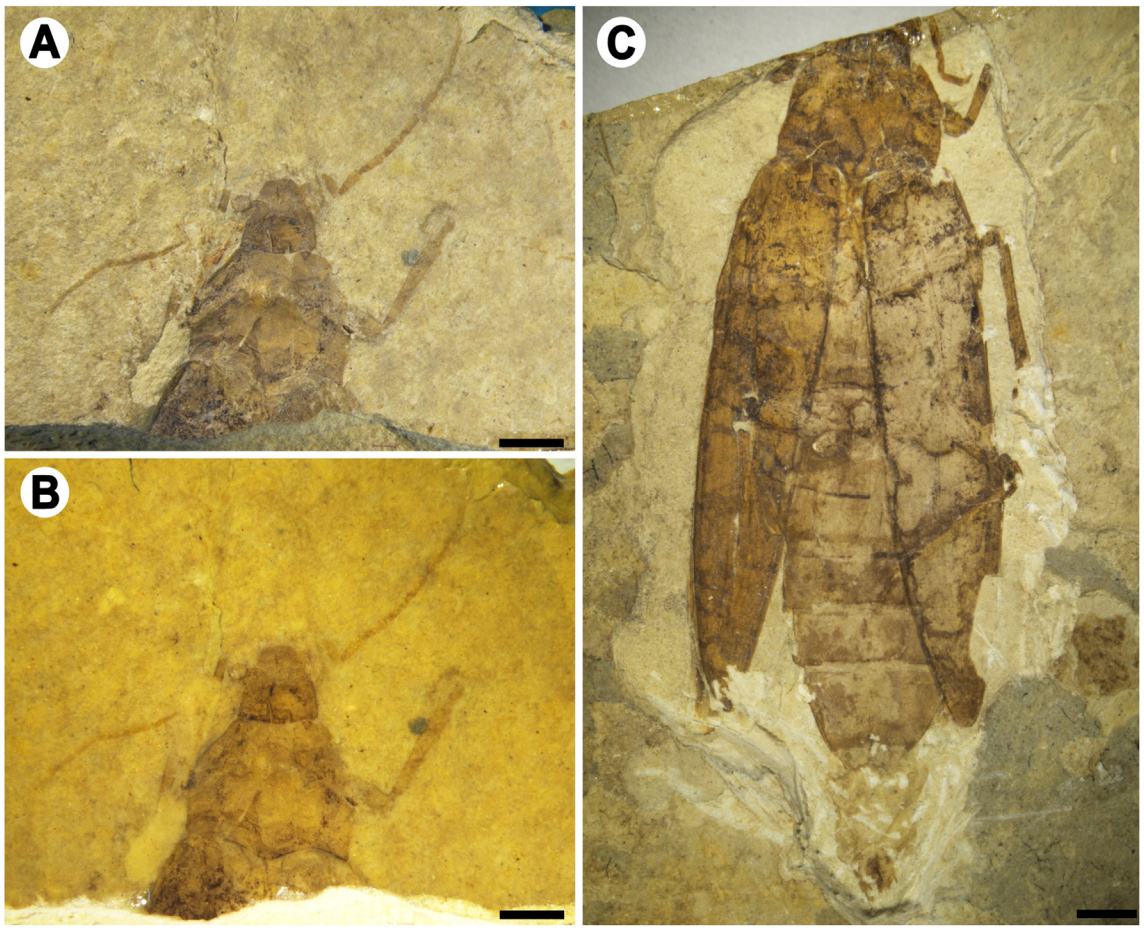


Fig. 4. *Lasiosyne integera* sp. nov., Photographs of paratype CNU-COL-LB-2021120, sex unknown, and paratype CNU-COL-LB-2009488, male. (A) Photograph of CNU-COL-LB-2021120. (B) Photograph of CNU-COL-LB-2021120 (under alcohol). (C) Photograph of CNU-COL-LB-2009488. Scale bars: 2 mm.

mesocoxae narrowly separated. Metaventrite about as long as wide; discrimen long and extending from posterior edge to nearly anterior edge. Metacoxal plates large and nearly contiguous, trochanter exposed.

Elytron slender, with 11 longitudinal striae, the 2nd and 3rd extending to basal half, remaining striae reach elytral apices. Abdomen with five ventrites; terminal ventrite longest with subcircular apex.

This paratype specimen differs from holotype in its more pointed anterior angle of pronotum and slightly sharp apex of abdomen.

Remarks. Lasiosyne integera sp. nov. is placed within the genus *Lasiosyne* in having a slender body; mandible large and with acute apex; width of pronotum much narrower than elytral base, elytron with 11 striae, and the 2nd and 3rd grooves shortened. The new species is differentiated from all other species of the genus in its large body size, very large mandible with distinct carinae, pedicel much narrower and pronotum lateral edge depressed inward at posterior 1/3.

Lasiosyne parva Guo, Shih & Ren sp. nov (Fig. 5)

Etymology. The Latin word "parva" meaning small or little, and this word was named for its small body size.

Type material. Holotype: probably female. No. CNU-COL-LB-2021080.

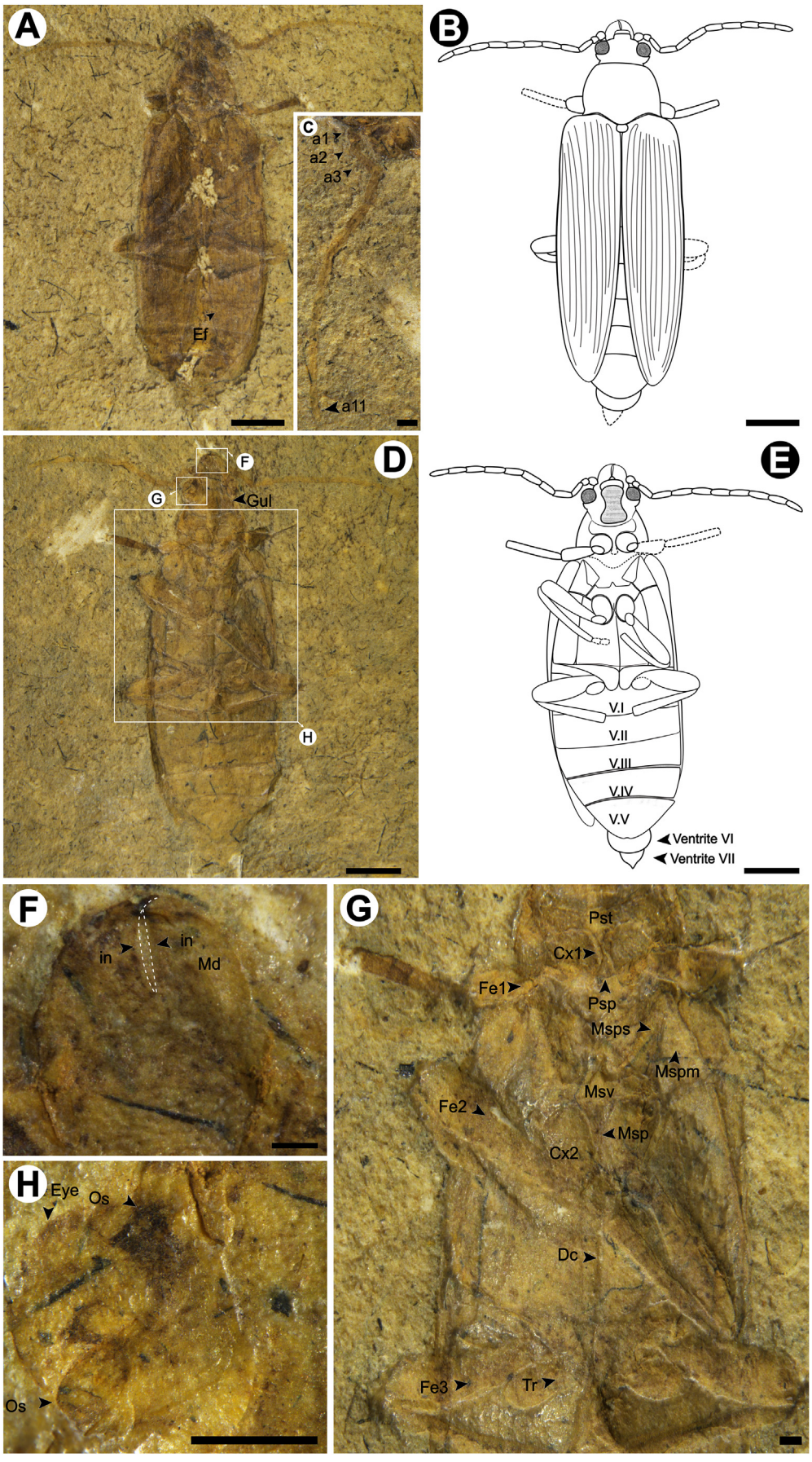
LSID:urn:lsid:zoobank.org:act:E4AEBC56-1939-4702-80DE-62C0130EFAE0.

Diagnosis. Head with heavily sclerotized orbital sclerite frame forming behind eyes, scape slightly inflated, pedicel expanding at the middle. Mandible with blunt outer angle and pointed at apex, inner edge relatively straight; gula very large anteriorly extending towards eyes and clinging to the head posterior edge. The hind-femur distinctly enlarged, trochanter large and exposed.

Description. Body elongate (15.26 mm long and 5.08 mm wide), heavily sclerotized, covered with pubescence and clothed with relatively deep dense punctures (Fig. 5A, 5D).

Head transverse (1.70 mm long and 2.19 mm wide), strongly declined. Eye hemisphere, protuberant, the distance between eyes about 2.45 times of the diameter. A heavily sclerotized orbital sclerite frame behind eye, extending towards outer edge (Fig. 5G). Antenna filiform with 11-antennomeres (Fig. 5C); scape moderately stout; pedicel expanding at the middle and shorter than other antennomeres; antennomere 3 apex slightly expanded; antennomeres 4–10 subequal in lengths; antennomeres 11 longest; length ratio of antennomeres 1–11: 0.37: 0.34: 0.49: 0.67:0.66: 0.70: 0.69: 0.70: 0.56: 0.56: 1.04. Clypeus subquadrate and transverse, middle emarginated. Labrum more or less concealed. Mandible strong with blunt curved outer edge and inner edge slightly straight. Gula extremely developed, large; gular sutures separated, gula occupying 1/2 of interocular space, with curved anterior and slightly straight posterior edge (Fig. 5D). Occipital area short, cervical sclerites absent.

Pronotum slightly wider than long (2.49 mm long, 2.77 mm wide), with deep and dense puncture; pronotum width 1.27 times of head width and 0.54 times of elytron width; anterior margin slightly produced at the middle, anterior angles obtuse; posterior margin tri-sinuated and abruptly curved behind, posterior angles abrupt;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Ventrite VI
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Psp
Msps
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lateral margins not straight and produced. Prosternum moderately developed, with extremely deep and dense punctures, anterior margin strongly curved behind. Hypomeron developed and anterior angles strongly produced forward. Prosternal process well-developed, elongate, rounded apically; reaching procoxae and separating procoxae to 1/6 diameter. Procoxae large and slightly transverse, separated by intercoxal process (Fig. 5H).

Mesoventrite transverse, moderately large; mesosternal cavity elongate oblong and moderately separated; mesepisterna and mesepimera well-developed, subtriangular, mesepimera about 2 times as long as mesepisterna. Mesoventral process moderately large, separate mesocoxa to 1/6 diameter, without longitudinal suture. Mesocoxae suboval and narrowly separated. Metaventrite slightly transverse, about 1.3 times as long as wide; discrimen not extending to anterior; metepisternum broad and elongate, lateral sides sub-parallel. Meta-coxal plate well-developed. Hind wing invisible.

Scutellum subcircular and small. Elytra (elytra 10.27 mm long and 5.18 mm wide) about 2 times as long as wide, covered densely setiferous punctate. Each elytron with 11 deep various puncture rows; the 1st and 2nd striae conjoining at base forming an arcuate loop (Fig. 5A); the 2nd and 3rd not complete, only surpassing the elytral midlength, the rest striae nearly reaching elytral apex; lateral sides more or less parallel and emarginated at the middle. Epipleura well-developed, gradually narrowing at the middle posteriorly. Elytron sutural flange distinct and complete.

Leg slender. Trochanter exposed; femora well-developed, gradually widened toward apex in hind-leg (Fig. 5H); tibia slender; meso-tarsi I–II subequal in length, pro- and meta-tarsi not preserved.

Abdomen with five visible ventrites, length ratio of ventrites I–V: 1.49: 1.18: 1.12: 1.10: 1.65; basal three segments connate with distinct sutures; last two ventrites separated by a wide membranous suture. Pregenital segments and genitalia not preserved.

Remarks. The type specimen of *Lasiosyne parva* sp. nov. is relatively shallowly preserved, which may be due to the special burial conditions. *Lasiosyne parva* sp. nov. can be placed in Lasiosynidae based on the following morphological characters as preserved: head prognathous; elytron striate, lateral edge emarginated in basal 1/3 with 11 subparallel striae, pair of elytra striae forming arcuate loop at base. *Lasiosyne parva* sp. nov. can be placed in the genus *Lasiosyne* based on pronotum width much narrower than elytron width, and the 2nd and 3rd elytron puncture rows not complete. This new species shows several morphological characters similar to *Lasiosyne daohugouensis*, e.g., large eyes, and pronotum shape (excised anterior edge of prosternum). But it differs from all congeners of *Lasiosyne* in straight inner edge of mandible; protruding eye; large gula; developed and slightly expanding prosternal process; and enlarged femora.

Key to species of Genus Lasiosyne

1. Antennae moniliform……2
Antennae filiform or sub-filiform……3
2. Antennae moniliform in all segments, short and equal to at most 1/3 of body length. Antennomeres 5 and 6 are elongate oval, apical one equal to antennomeres 5 and 6 together……*Lasiosyne insculpta* Yan, 2012.
Antennae not moniliform completely, antennomeres 3–5 sub-trapezoidal, antennomeres 6–11 sub-oval……*Lasiosyne laxa* Yan, Wang & Zhang, 2014
3. Scutellum length more than 1/3 of the width of elytron base……*Lasiosyne punctata* Yan, 2012.
Scutellum length less than 1/3 of the width of elytron base……4
4. Mesocoxae completely separated; metaventrite anterior process separate mesocoxae to not less than half of mesocoxae width……*Lasiosyne longitarsa* Yan, 2012.
Mesocoxae not completely separated; metaventrite anterior process separate mesocoxae to less than half of mesocoxae width……5
5. Elytral groove 2 reaching middle of elytron, longer by 1/3 than groove 3; groove 5 and 6 confluent at elytral apex……*Lasiosyne shartegiensis* Yan, 2012.
Elytral grooves 2 and 3 are approximately in equal length, not reaching the apex of elytron, the rest striae converging and complete……6
6. Frontogenal sutures absent……7
Frontogenal sutures present, stretched from the anterior margin of the frons to the middle of the internal margins of the eyes……*Lasiosyne decora* Yan, 2012.
7. Punctures on frons and pronotum very dense; the distance between two punctures no more than puncture diameter……8
Punctures on frons and pronotum deep sparse; the distance between punctures longer than 2 times of puncture diameter……*Lasiosyne cataphracta* Yan, 2012.
8. Anterior edge and lateral edges of pronotum almost straight; anterior angles with clear top……*Lasiosyne quadricollis* Kirejtshuk, Chang, Ren & Shih, 2010
Anterior edge and lateral edges of pronotum more or less curved; anterior angles not pointed……9
9. Mesoventrite longitudinal suture cross the whole length……*Lasiosyne fedorenkoi* Kirejtshuk, Chang, Ren & Shih, 2010
Mesoventrite longitudinal suture not complete……10
10. Metepisterna 2.0–2.5 times as long as wide……11
Metepisterna length more than 2.5 times as width……12
11. Frontoclypeal suture invisible; pro- and meso-tibiae elongate and with dense pubescence, protarsomeres 1–4 moderately lobed……*Lasiosyne euglyphea* Kirejtshuk, Chang, Ren & Shih, 2010
Frontoclypeal suture visible; pro- and meso-tibiae expanding towards apex, protarsomeres 1–4 simple lobed……***Lasiosyne integera* sp. nov.**
12. Metaventrite discrimen cross whole length……13
Metaventrite discrimen not reaching anterior edge……*Lasiosyne gratiosa* Kirejtshuk, Chang, Ren & Shih, 2010
13. Elytron length 4 times as long as pronotum……14
Elytron length less than 4 times as long as pronotum……*Lasiosyne multituberata* Kirejtshuk Chang, Ren & Shih, 2010
14. Prosternal process well-developed, surpassing procoxae and separating procoxae to 1/6 diameter rounded in apically; meta-femora well-developed, strongly widened toward apex……***Lasiosyne parva* sp. nov.**
Prosternal process weakly developed; meta-femora not or slightly widened toward apex……*Lasiosyne daohugouensis* Kirejtshuk Chang, Ren & Shih, 2010.

Fig. 5. *Lasiosyne parva* sp. nov., probable female. Photographs of holotype CNU-COL-LB-2009080. (A) Part as preserved (dorsal side). (B) Line drawing of part. (C) Antenna. (D) Counterpart as preserved (ventral side). (E) Line drawing of counterpart. (F) Mandible. (G) Eye. (H) Thorax and legs. Abbreviations: a1–a11, antennal segment 1–11; Cx1/2, Pro-/Mesocoxa; Dc, Discrimen; Ef, Elytral flange; Epi, Epipleura; Fe1/Fe2/Fe3, Pro-/Meso-/Metafemur; Gul, Gular plate; in, inner edge; Md, Mandible; Msp, Mesesternal process; Msps, mesepisternum; Mspm, mesepimeron; Msv, Mesoventrite; Os, Orbital sclerite; Pst, Prosternum; Psp, Prosternal process; Tr, Trochanter; V.I–V.VII, abdomen ventrite I–VII. Scale bars: (A–B, D–E), 2 mm; (C, F–G), 0.5 mm.

Note: This key is based on fossil records and previous key to *Lasiosyne* as proposed by Yan (2012). We reconsidered the characters important and applicable to this genus and updated the key to *Lasiosyne*.

5. Discussion

With several morphological differences among the Jurassic and the Cretaceous species, we propose the probable morphological trend of *Lasiosyne*. The Cretaceous lasiosynids, documented in China, have distinct heavily-sclerotized orbital sclerite frame forming behind eyes (Fig. 3A, Fig. 5D), but the Jurassic lasiosynids have constricted temples and large eyes without obvious orbital sclerite. Besides, the Cretaceous lasiosynids have tibiae developed and strongly enlarged (Fig. 6E–H), this state of tibiae becomes more obvious in *Lasiosyne parva* sp. nov. (more prominent in hind–leg) (Fig. 5H). Lasiosynid beetles have been well-documented as being the most important and highly conservative aedeagal type character. The Jurassic species placed in *Lasiosyne* are all characterized by dense pubescence and elongated tibiae on all legs with slightly enlarging apices (Fig. 6A–D), and protarsus 5-segmented with tarsomeres 1–4 moderately lobed. However, these characters are not obvious in the Cretaceous *Lasiosyne* beetles with tibiae not so elongated as shown in the Jurassic lasiosynids, and *Lasiosyne integera* sp. nov. having significant expanding pro/meso-tibiae (Fig. 3D–E) with simple tarsi lobed (Fig. 6F). Mesoventrite with long longitudinal suture extending to anterior margin on the Middle Jurassic specimen *L. daohugouensis* Kirejtshuk, Chang, Ren and Shih, 2010 and more obvious in *L. fedorenkoi* Kirejtshuk, Chang, Ren and Shih, 2010 (specimen CNU-COL-NN-2006015) with posterior wing open; but mesoventrite longitudinal suture in *Lasiosyne parva* sp. nov. short and present only in posterior area extending to mesoventrite process only (Fig. 5E). Besides, the *Lasiosyne* species have metaventrite discrimen coinciding with posterior margin of metaventrite (Yan et al., 2014a), this seems to be an important character in morphological evolution. *Lasiosyne parva* sp. nov. has metaventrite discrimen long and extending to anterior process of metaventrite (Fig. 5E).

Yan et al. (2013) put forward two evolutionary trends in Lasiosynidae: one trend is represented by genera *Lasiosyne* and *Cretasyne* with elongated body and rectangular metaventrite(Kirejtshuk et al., 2010a; Yan et al., 2014a). Genus *Cretasyne* was characterized

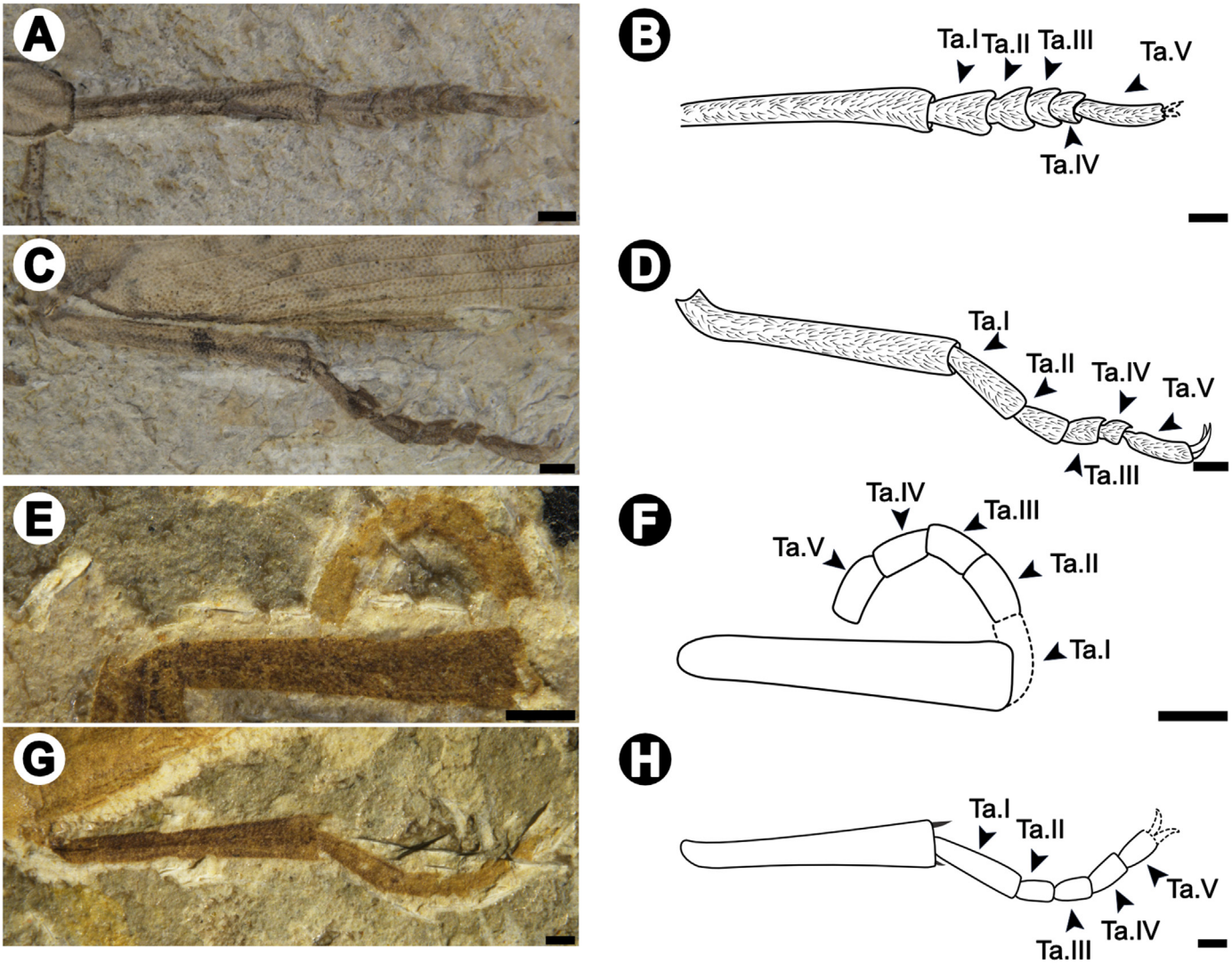

Fig. 6. The details in different species of Lasiosynidae: (A, B) Pro-leg of *Lasiosyne euglyphea* Kirejtshuk, Chang, Ren & Shih, 2010, holotype CNU-COL-NN-2006013. (C, D) Meso-leg of *L. euglyphea* Kirejtshuk, Chang, Ren & Shih, 2010, paratype CNU-COL-NN-2009126. (E, F) Proleg of *Lasiosyne integera* sp. nov. (G, H) Meso-leg of *Lasiosyne integera* sp. nov. Abbreviation: Ta.I–V, Tarsi segment I–V. Scale bars: A–H, 0.5 mm.

by slender prosternal process entirely separating procoxae and anterior angles of metaventrite strongly protruding anteriorly. However, the metathoracic discrimen disappeared in the Cretaceous genus *Cretasyne*, well-developed in new species of *Lasiosyne integera* sp. nov. and *Lasiosyne parva* sp. nov. with discrimen nearly coincides with both anterior and posterior margin. Some specimens of lasiosynid beetles have metaventrite with a comparatively or distinctly transverse suture (katepisternal), this feature was pronounced in the Jurassic fossil specimens. Considering the abovementioned, morphological evolution of *Lasiosyne* during the Jurassic and Cretaceous Periods may show in gradually developing prosternal process; shorter mesoventrite longitudinal suture; stronger and widened femora, and simpler tarsomeres without lobes. These two new species we described also proved that *Lasiosyne* continued to exist as parallel to *Cretasyne*, the phenomenon seems to support Yan (2014) and this trend from *Lasiosyne integera* sp. nov. and evolved into the emergence of *Cretasyne* which might have a wider body.

The Cretaceous Period, with significant evolution of angiosperms and beetles (Wang et al., 2013; Cai et al., 2022) are usually regarded as a time of major reorganization and modernization of ecosystems (Lloyd et al., 2008). The two new species with complete preservation of body habitus allow us to analyze the evolution trends of *Lasiosyne*.

6. Conclusion

Based on fossil specimens from the Lower Cretaceous Yixian Formation, we described two new lasiosynid species, *Lasiosyne integera* sp. nov. and *Lasiosyne parva* sp. nov. (Coleoptera, Lasiosynidae). Comparing to other species attributed to *Lasiosyne*, the new lasiosynids described here show morphological modifications of mesoventrite longitudinal suture, metaventrite katepisternal suture and tarsi. As we discussed above, these changes document a probable morphological evolution of *Lasiosyne* during the Jurassic and Cretaceous Periods. These findings broaden the diversity of Lasiosynidae in the Cretaceous, also enhance our understanding of the early evolution of *Lasiosyne*.

Data availability

No data was used for the research described in the article.

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