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Enormously long, siphonate mouthparts of a new, oldest known spongillafly (Neuroptera, Sisyridae) from Burmese amber imply nectarivory or hematophagy

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Paradoxosisyra groehni gen. et sp. nov. (Neuroptera: Sisyridae) is described from Upper Cretaceous (lowest Cenomanian) Burmese amber as the oldest known sisyrid. The new genus is assigned to the new subfamily Paradoxosisyrinae, which is characterized by enormously long siphonate mouthparts, very long and slender hind legs, several setiferous calluses on the head and pronotum; deeply forked CuP and AA1 veins in the forewing; a complete inner gradate series of crossveins, and the RP vein with five branches in the hind wing. The greatly lengthened, laterally flattened galea and lacinia, and the labial ligula transformed into a long acute stylet are characteristic of only this species and do not occur in other insects. These siphonate mouthparts were likely used primarily to feed on flower nectar. The possibility remains, however, that the species was hematophagous (possibly facultative), feeding on the hemolymph of arthropods or the blood of such thin-skinned vertebrates as frogs.

1. Introduction

The order Neuroptera comprises 31 valid families, 16 of which are extinct (Makarkin et al., 2013; Peng et al., 2016). All families have (or are assumed to possess) specialized larvae with sucking mouthparts, and the vast majority of their adults bear generalized mandibulate biting/chewing mouthparts (New, 1989; Labandeira, 2010). Today, they are mostly predaceous, feeding on aphids, psyllids, mites, and other small arthropods on plants (e.g., Hemerobiidae, Chrysopidae, and Coniopterygidae), or catching various insects with raptorial forelegs on flowers (Mantispidae) and during flight (Ascalaphidae) (New, 1986; Tjeder, 1992; Canard, 2001). Many adults are omnivorous, feeding also on honeydew, pollen and fungi (e.g., Berothidae, Osmylidae: New, 1986; Monserrat, 2006; Dobosz and Górskí, 2008). Some Chrysopidae are thought to feed only on honeydew, pollen and nectar (Canard, 2001). The adults of all Nemopteridae are specialized pollen feeders, and most of them have elongated mouthparts (Tjeder, 1967).

All known species of spongillaflies (Sisyridae) have mandibulate mouthparts. Hitherto, this small family comprised two extinct genera (i.e., *Prosisyrina* Perkovsky & Makarkin, 2015 from the Upper Cretaceous of northern Siberia, and *Paleosisyra* Nel, Menier, Waller, Hodebert & de Ploëg, 2003 from the European Eocene), and four extant genera (i.e., *Sisyra* Burmeister, 1839, *Sisyrina* Banks, 1939, *Sisyborina* Monserrat, 1981, and *Climacia* McLachlan, 1869).

Here, I describe a new genus and species of the oldest known sisyrids, from lowermost Cenomanian Burmese amber, which I assign to a new subfamily. This taxon is remarkable for possessing amazing, enormously long siphonate mouthparts. Their structure implies that they were nectarivorous or hematophagous. Their labial ligula is transformed into a long acute stylet, a structure unknown in other Neuroptera, or, indeed, in other insects.

2. Material and methods

This study is based on one specimen (a female) of Sisyridae from Burmese amber. The amber piece was collected in the Hukawng Valley (in the state of Kachin in northern Myanmar). The precise mine from which this piece originated cannot be determined, as it was acquired from a fossil trader. The map of the Hukawng Valley is given by Grimaldi et al. (2002, fig. 1). The age of the volcaniclastic matrix of Burmese amber is estimated as 98.79 ± 0.62 Ma (earliest Cenomanian) based on U-Pb dating of zircons (Shi et al., 2012c), but the inclusions are considered to be slightly older, as late Albian (e.g., Ross, 2015).

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The specimen is embedded in a ca. 10 mm maximum long (as prepared) amber piece, without syninclusions. The photographs were taken by Carsten Grohn using a Zeiss stereomicroscope (modified with variable objectives: Nikon M Plan 5×, 10×, 20×, 40×; Luminar 18 mm, 25 mm, 40 mm) and an attached Canon EOS 450D digital camera. Line drawings were prepared using Adobe Photoshop CS3.

The venational terminology in general follows Kukalová-Peck and Lawrence (2004) as interpreted by Yang et al. (2012) and Yang et al. (2014a). Terminology of wing spaces and details of venation (e.g., spaces, veinlets) follows Oswald (1993). Crossveins are designated by the longitudinal veins with which they connect, and are numbered by gradate series to which they belong in sequence from the wing base, e.g., 2r-m, crossvein connecting the posterior-most branch of RP and MA in the second gradate series; 3ra-rp, crossvein between RA and RP in the third gradate series.

Abbreviations: AA1–AA3, first to third anterior anal vein; CuA, anterior cubitus; CuA1, proximal-most branch of CuA; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; RA, anterior radius; RP, posterior sector; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; ScA, subcosta anterior; ScP, subcosta posterior.

All taxonomic acts established in the present work have been registered in ZooBank LSID (see below), together with the electronic publication urn:lsid:zoobank.org:pub:11566C98-2E1E-4C29-892F-C143F3BB3AD.

3. Systematic palaeontology

Order: Neuroptera Linnaeus, 1758
Family: Sisyridae Banks, 1905
Subfamily: Paradoxosisyrinae subfam. nov.
urn:lsid:zoobank.org:act:6394D498-8611-411B-B7D5-21362F0AC919

Genus *Paradoxosisyra* gen. nov.
(urn:lsid:zoobank.org:act:A4D27209-024B-49E1-A85F-C7521A80CC5F)
Type and only species: *Paradoxosisyra groehni* sp. nov.

Derivation of name. From the Greek *paradoxos* [παράδοξος], paradoxical, strange, and *Sisyra*, a genus-group name of the family, referring to its mouthparts, which are unlike those of other sisyrids. Gender feminine.

Diagnosis. May be easily distinguished from all other known genera of Sisyridae by a combination of the following character states: enormously long siphonate mouthparts likely lacking mandibles [mandibulate mouthparts in other sisyrids]; several setiferous calluses on head, pronotum present [absent in other sisyrids]; very long, slender hind legs (hind tibia and tarsus together more than 2/3 of forewing length) [hind tibia and tarsus together ca. 1/2 of forewing length or shorter in other sisyrids]; deeply forked CuP, AA1 in forewing [these shallowly forked or simple in other sisyrids]; complete inner gradate series of crossveins in hind wing [incomplete in other sisyrids]; RP with five branches in hind wing [two-three branches in other sisyrids].

Remarks. The genus *Paradoxosisyra* gen. nov. is assigned to Sisyridae based on the characteristic shape and location of gonocoxites 9 of the female, which are very similar only to those of this family within the order. The size of specimen and its general habitus and venation do not contradict this attribution.

The new genus strongly differs from all known genera of the family by many character states, not only by those that are included in the diagnosis, but also, for example, the peculiar structure of the pedicellus. These character states allow the separation of *Paradoxosisyra* gen. nov. into the new subfamily Paradoxosisyrinae, with all other known genera constituting the subfamily Sisyrinae (although the monophyly of the latter is not yet established, pending a comprehensive phylogenetic analysis of the family). Many character states of Paradoxosisyrinae are clearly apomorphic (e.g., the strong reduction or loss of the mandibles; the strongly long, laterally flattened galea and lacinia; the transformation of the ligula into an acute stylet; the presence of setiferous calluses on the vertex and pronotum).

The calluses on the vertex are somewhat similar to the two or three setiferous calluses found on the vertex in several neuropteran families (e.g., Dilaridae, Psychopsidae, Berothidae), which Tjeder (1960) called 'ocellar sclerites'. The vertex calluses of *Paradoxosisyra* gen. nov. are, however, much larger. Similar paired pronotal calluses are also present in some Dilaridae (e.g., *Dilar septentrionalis* Navás, 1912: pers. obs.). They most probably evolved independently in these families.

The venation of the new subfamily also differs strongly from that of the Sisyrinae. The most distinctive of these differences are mentioned in the diagnosis; however, there are many others, smaller ones by which their wings are distinctive, e.g., Paradoxosisyrinae possess the broad costal space with dense subcostal veinlets, the profusely branched MP, and the long branches of AA2 in the forewing; the very broad distal part of the costal space, and the very narrow subcostal space in the hind wing. Most of these are likely plesiomorphic.

Paradoxosisyra groehni sp. nov.
(urn:lsid:zoobank.org:act:B19B008C-AB6B-4156-9E10-D5DC948AE3BC)
Figs. 1–6A

Derivation of name. The specific epithet is formed from the surname of Carsten Gröhn, Glinde (Germany), in recognition of his efforts in collecting and promoting the study of Baltic amber inclusions.

Material. Holotype GPIH Typ. Kat. Nr. 4580 (collection of C. Gröhn, no. 11072), deposited in the Geological-Paleontological Institute and Museum of the University of Hamburg [Geologisch-Paläontologisches Institut und Museum der Universität Hamburg] (now Centrum of Natural History [Centrum für Naturkunde]). A nearly complete female specimen (the right mid-leg is missing). There are several large air bubbles near the specimen, which preclude observation of some details.

Locality and horizon. Burmese amber (Northern Myanmar: Kachin State: Myitkyina District: Tanai Township: Hukaung Valley). Upper Cretaceous: lowest Cenomanian.

Description. Head transverse, with large, oval eyes. Head capsule below (anteriad) eyes only very slightly extended. Vertex slightly raised, with rough surface, especially on paired large elongate dome-like calluses (vertex calluses; Fig. 2); setae numerous, long to very long. Frons with smooth surface, without long setae. Two rounded calluses located laterally to frons (near each eye) bear 4–5 long setae (Fig. 3D). Clypeus (or fused clypeus and labrum) short, with at least one long seta. Antenna long; scapus elongate, dorsally covered with long setae; pedicellus relatively large, medially dilated, with moderately long setae; flagellum consists of 61 flagellomeres; proximal flagellomeres short, transverse, with moderately long setae; distal flagellomeres slightly elongate (ca. 1.2–1.5 as long as wide), covered with quite dense, rather short setae; terminal flagellomere conical, ca. 3.0 as long as maximum width.
Mouthparts extremely long. Labrum not identified with confidence (lost or fused with clypeus). Mandibles not detected, lost or strongly

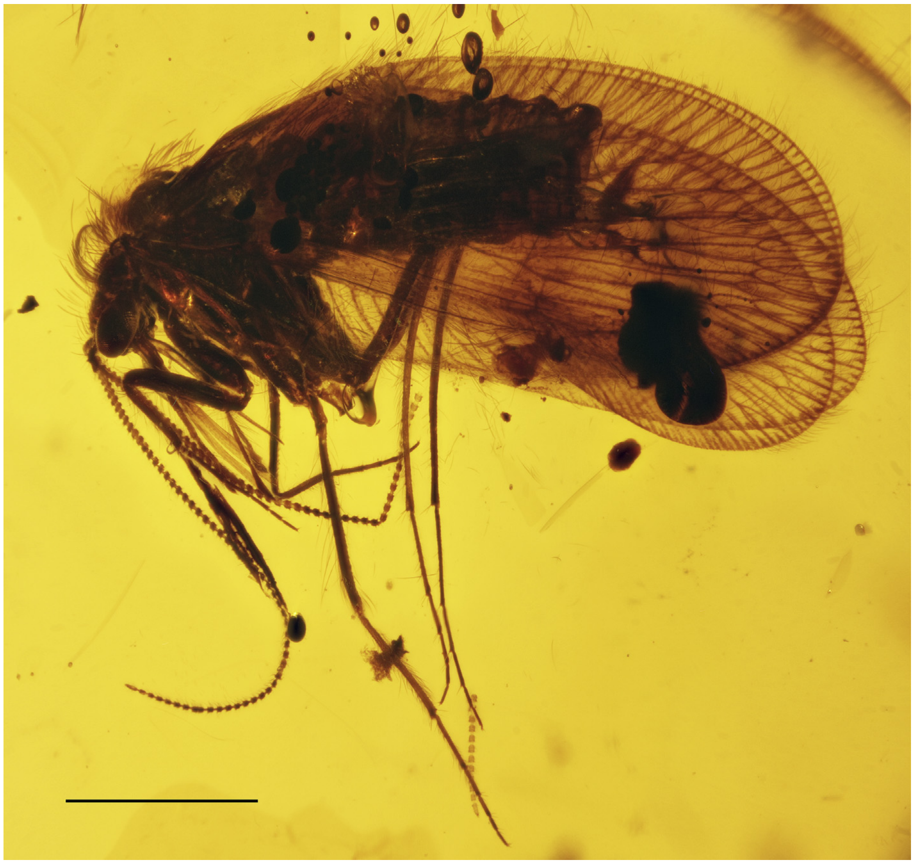

Fig. 1. *Paradoxosisyra groehni* sp. nov. Holotype GPIH Typ. Kat. Nr. 4580 as preserved (lateral left view). Scale bar represents 1 mm.

reduced. Maxillary cardo of usual size, probably without setae; stipes large, with long setae in anterior distal part. Galea, lacinia enormously long, similarly constructed: thin for entire length in frontal view (Fig. 3A), equally broad in lateral view with rounded apex (Fig. 3C, D). Galea (probably distigalea) rough on outer surface, covered by sparse, very short, decumbent setae; apical part paler, probably separated by suture (alternatively, this apical part represents digitus). Right lacinia not detected; left lacinia slightly shorter than galea, its apical part poorly visible; setae probably absent. Maxillary palpus very long, covered with very long setae (shorter on distal segment); three distal segments clearly identified (proximal-most portion of palpus poorly visible): presumable third segment longest; fourth, fifth shorter, nearly equal in length; distal segment markedly dilated medially (on right palpus in distal part). Labium large, elongate; its basal part (labelled fused mentum, submentum in Fig. 3) clearly separated by suture from elongate distal part interpreted here as prementum; few long setae posteriorly. Ligula long, slender, gradually narrowed apicad, with pointed apex, somewhat rough surface; setae not detected. Labial palpus long; its proximal two-thirds slender (segmentation not detected) covered by very long, dense setae; distal segment elongate, rather strongly dilated medially (on right palpus in distal part), covered by rather long setae, mainly posteriorly.

Pronotum short, transverse; two elongate calluses divergent anteriad with rough surface (pronotal calluses; Fig. 2); setae numerous, long. Anterior lateral cervical sclerite prominent, bearing numerous very long setae. Tigula large, prominent, bearing numerous very long setae. Mesonotum bearing dense, very long setae. Metanotum poorly visible.

Abdomen poorly visible (completely hidden by wings). Gonocoxites 9 typical for sisyrids; large, apically pointed (Fig. 4).

Foreleg markedly shorter than mid- and hind legs. Procoxa long, stout, with longish setae. Protrochanter rather long, curved. Profemur 0.69 long, nearly as long as procoxa, covered with long fine setae; left profemur rather stout, right profemur markedly more slender. Protibia markedly shorter than profemur, covered with long fine setae; left protibia slightly stouter than right protibia. Protarsus with all tarsomeres slender, elongated; probasitarsus covered with relatively short, dense fine setae; second to fourth tarsomeres lack visible setae except distal three-four quite strong, short setae forming apical collar; pretarsus with two very small claws. Relative length of left protarsomeres: 3.4–1.9–1.4–1–1.1.

Mid-leg long, slender. Mesocoxa conical, rather short. Mesotrochanter elongate, more than twice as long as wide. Mesofemur long, rather slender, covered with dense, very long setae. Mesotibia moderately long (0.95 mm), slender, covered with long, dense setae, four (or more) distal stronger setae forming apical collar. Mesotarsus long, slender; basitarsus covered with dense, rather long fine setae, ca. four distal stronger setae forming apical collar; second to fourth tarsomeres lack visible setae except distal ca. four quite strong, short setae forming apical collar; pretarsus with two very small claws. Relative length of left mesotarsomeres: 3.9–2.0–1.5–1–1.3.

Hind leg very long, slender. Metacoxa conical. Metatrochanter poorly visible. Metafemur rather stout, long; setation poorly visible. Metatibia very long (ca. 1.4 mm), slender, slightly curved, covered with long fine setae, several (>5) ventral medial and ca. four distal stronger setae forming apical collar. Metatarsus very long (left

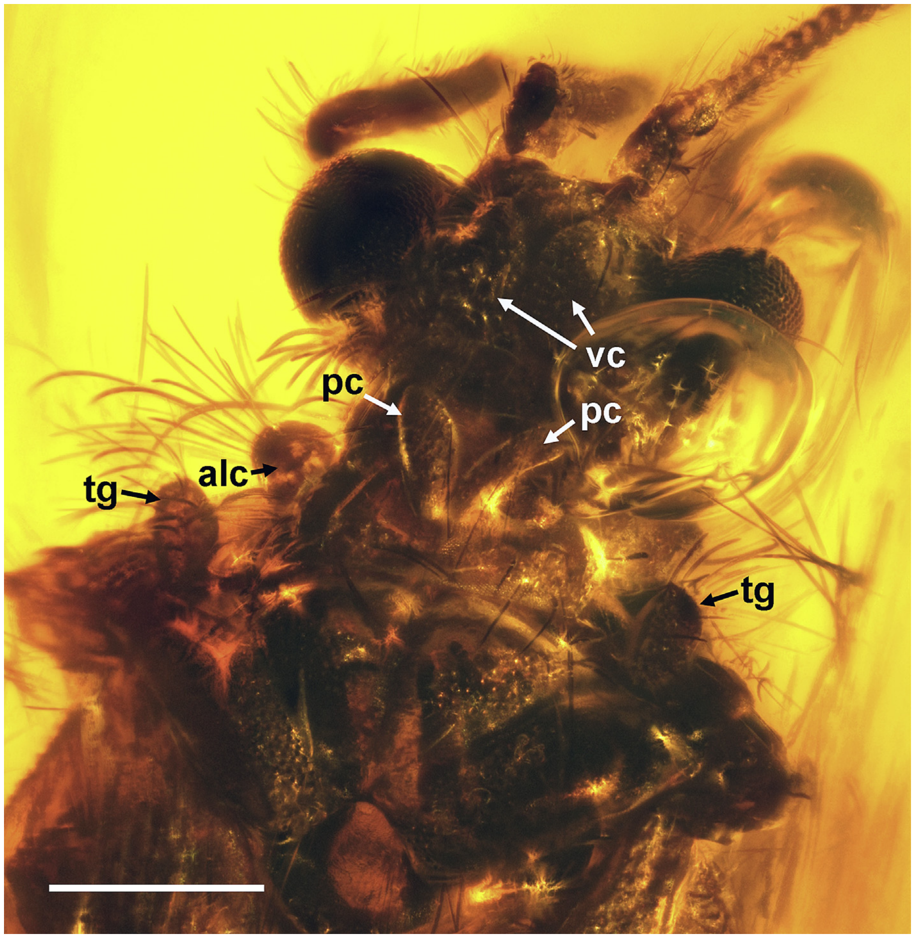

Fig. 2. *Paradoxosisyra groehni* sp. nov. Holotype GPIH Typ. Kat. Nr. 4580. Head, pronotum, and mesonotum (dorsal view). alc, anterior lateral cervical sclerite; pc, pronotal callus; tg, tigula; vc, vertex callus. Scale bar represents 0.25 mm.

metatarsus 1.18 mm long), slender; basitarsus (0.52 mm long) covered with rare short fine setae; several (ca. 4–5) ventral medial plus ca. four distal stronger setae forming apical collar; second to fourth tarsomeres lack visible setae except distal three-four (second tarsomeres) or two (third, fourth tarsomeres) quite strong, short setae forming apical collar; pretarsus with two very small claws. Relative length of right metatarsomeres: 4.4–2.1–1.6–1–1.

Forewing relatively broad, 3.68 mm, 1.56 wide. Costal space broad; markedly narrowed basally, only slightly narrowed apically. Subcostal veinlets simple, closely spaced; medial subcostal veinlets slightly curved, thickened. ScP thickened, terminating at RA (alternatively, terminating at C, connecting with RA by extremely stout crossvein). RA thickened. Presumed fusion of ScP, RA, and entire stem of ScP + RA strongly thickened, pale. ScP + RA entering margin far before wing apex, with six straight long branches. Subcostal space broad proximally (except basally), gradually narrowed distad; crossveins not detected. RA space nearly as broad as subcostal space; with two crossveins detected (one proximad fusion of ScP, RA, other distad this fusion). RP originated far from wing base, with four branches: three proximad 3ra-rp, one distad. Stem of RP, RP3, RP4 rather deeply once forked. RP1 with two pectinate distal branches in both wings. RP2 profusely, rather deeply branched, with five branches entering wing margin, but differently configured on left, right wings: in right wing, primary fork located just distad outer gradate series, with three pectinate branches (one branch forked); in left wing, primary fork located proximad outer gradate series (additional crossvein in this series present between two main branches), with dichotomous branching, one branch once forked, other twice. M not fused with R basally. Basal portions of M, Cu, AA1 cannot be traced with confidence. MA dichotomously branched: forked primarily at outer grate series of crossveins; two branches forked again far from wing margin. MP pectinately branched, with three branches (proximal branch twice forked, other branches simple). CuA pectinately branched, with four branches (three proximal branches simple, fourth branch once forked). CuP deeply forked. AA1 pectinately branched, with two branches. AA2 pectinately branched, with three branches: proximal branch once forked, other branches simple. AA3 poorly discernible (alternatively, proximal forked branch of AA2 represents AA3). Two complete gradate series of crossveins detected: third ('inner') series consists of five crossveins from RA to MP; fourth ('outer') series consists of seven crossveins from RA to CuA; one preserved crossvein (between CuA, CuP) represents second series. Trichosors prominent along entire margin, except indistinct proximally. Trichiation on veins, margin very long, especially along hind (cubital, anal) margin.

Hind wing broad distally, ca. 3.20 mm, 1.38 wide. Costal margin strongly convex. Costal space relatively broad (compared with extant taxa), narrowed medially, very broad distally. Subcostal veinlets simple, closely spaced; medial subcostal veinlets strongly oblique, thickened. ScP stout, nearly straight, terminating at RA (alternatively, terminating at C and connecting with RA by stout crossvein). ScP + RA (or RA) entering margin far before wing apex, with six straight long branches. Subcostal space very narrow; crossveins not detected (if ScP terminating at RA) or one stout distal (if ScP terminating at C). RA space dilated proximally,

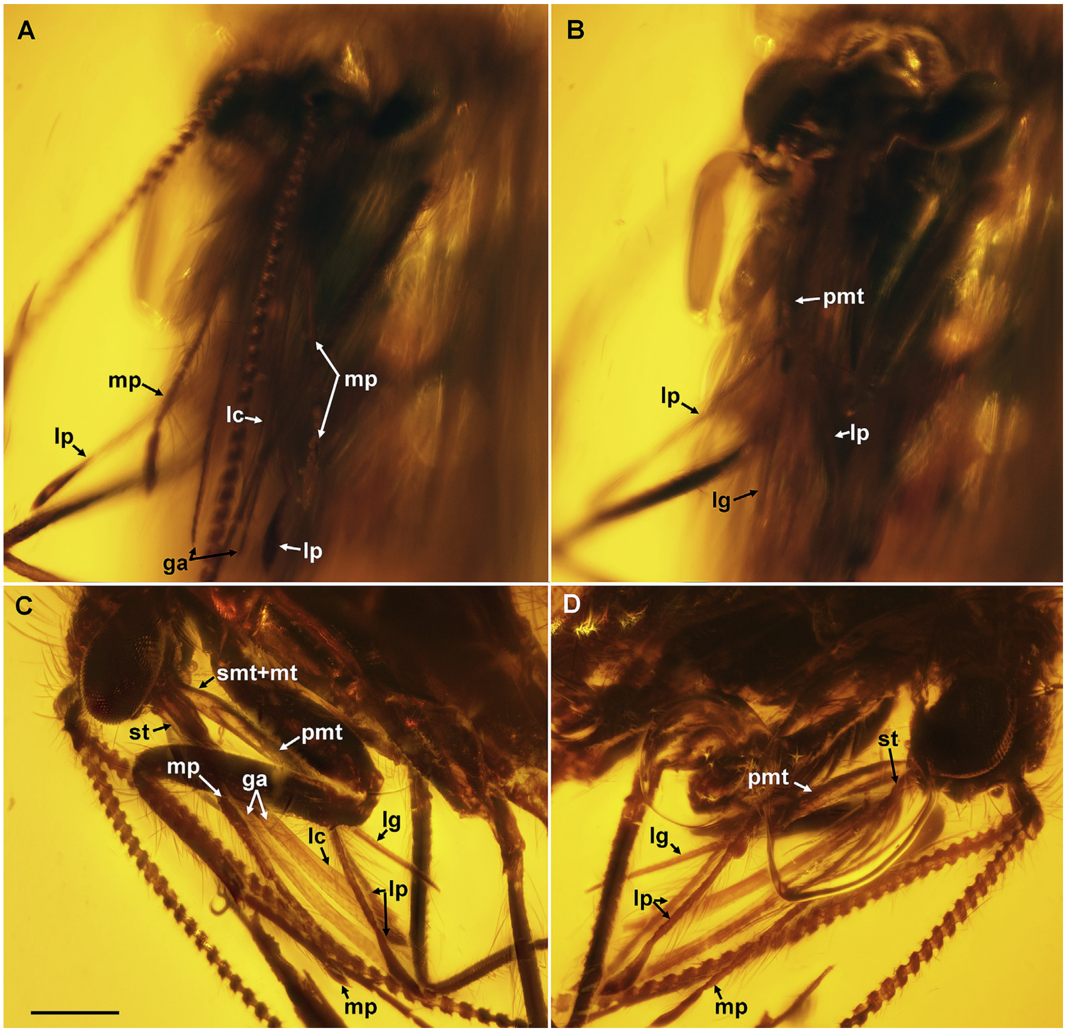

Fig. 3. Mouthparts of *Paradoxosisyra groehni* sp. nov. Holotype GPIH Typ. Kat. Nr. 4580. A. frontal view showing maxillae. B. frontal view showing labium. C. lateral left view. D. lateral right view. ga, galea; lc, lacinia; lg, ligula; lp, labial palpus; mt, mentum, mp, maxillary pulpus; pmt, prementun; smt, submentum; st, stipes. Scale bar represents 0.25 mm (all to scale).

strongly narrowed distad; one crossvein detected, belonging to second ('inner') gradate series of crossveins. RP originated far from wing base, with five branches: three proximad 2ra-rp, two distad. Stem of RP, RP2, RP5 once forked; RP1, RP3 rather deeply twice forked; RP4 simple. Proximal portions of M, Cu, anal veins cannot be traced with confidence. MA profusely (in general, dichotomously) branched, with seven branches entering wing margin. MP dichotomously branched, similar to branching of MA in forewing. CuA pectinate, poorly discernible, with three visible simple distal branches. Second ('inner') gradate series of crossveins complete, consisting of six crossveins from RA to MP. Crossveins of third ('outer') series poorly discernible; distal two crossveins detected (between RP1, MA, and MP, CuA). Trichosors prominent along entire margin, except indistinct proximally. Trichiation on veins, margin very long, especially along hind (cubital, anal) margin.

4. Discussion

4.1. Mouthparts of adult Neuroptera

Generalized mandibulate mouthparts are characteristic of the vast majority of adult extant Neuroptera (including Sisyridae). These are similarly constructed in most extant families, consisting of an unpaired labrum, paired mandibles and maxillae, and the labium (the fused second maxillae) (Figs. 6B–G). The mouthparts of most Nemopteridae are quite strongly derived, but consist of the same structures.

The labrum is usually a transverse plate, sometimes medially excavated (e.g., Chrysopidae: Tjeder, 1966, fig. 1088); elongated in most Nemopteridae (Tjeder, 1967, figs. 1898, 1905).

The mandibles are well-developed and strongly chitinized structures in the vast majority of extant species. These are often strongly asymmetrical (e.g., Osmylidae: Tjeder, 1957, figs. 165, 166), sometimes very large (Ithonidae: Riek, 1974, figs. 19, 23, 30) or elongate and slender (Nemopteridae: Tjeder, 1967, fig. 1910).

Each maxilla consists of cardo and stipes, and three distal appendages (i.e., galea, lacinia and maxillary palpus). The cardo is usually a small structure, constituting the basal part of maxilla divided into the basicardo and disticardo, and is rather similarly constructed in most neuropteran families. The stipes is a larger, usually elongated structure, with several setae on its outer side which are sometimes dense, numerous and long (e.g., in the Ascalaphidae: Tjeder, 1992, figs. 10, 14). The stipes sometimes bears a pair of long palpigera (e.g., Nemopteridae: Tjeder, 1967, figs. 1907, 1908).

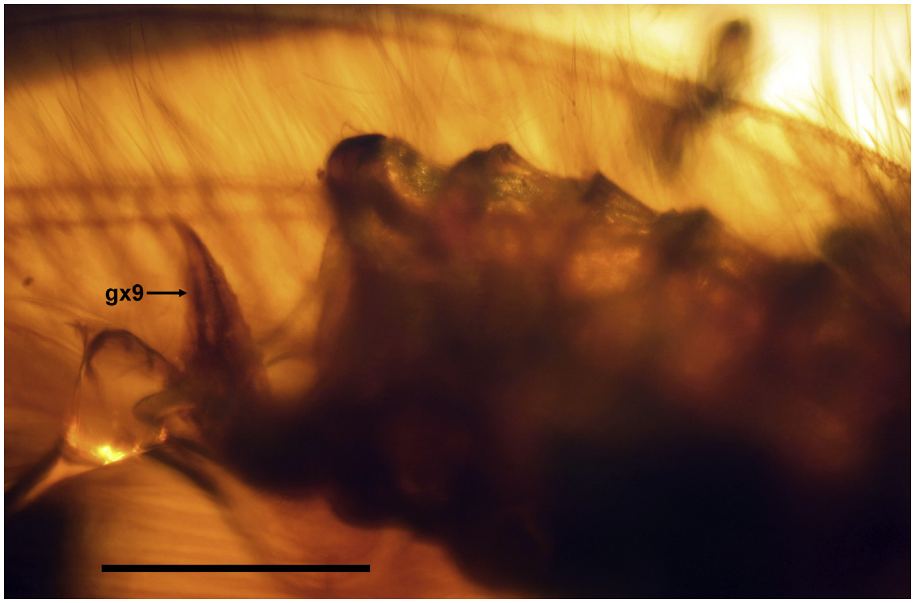

Fig. 4. Apex of abdomen of *Paradoxosisyra groehni* sp. nov. Holotype GPIH Typ. Kat. Nr. 4580. gx9, gonocoxites 9. Scale bar represents 0.5 mm.

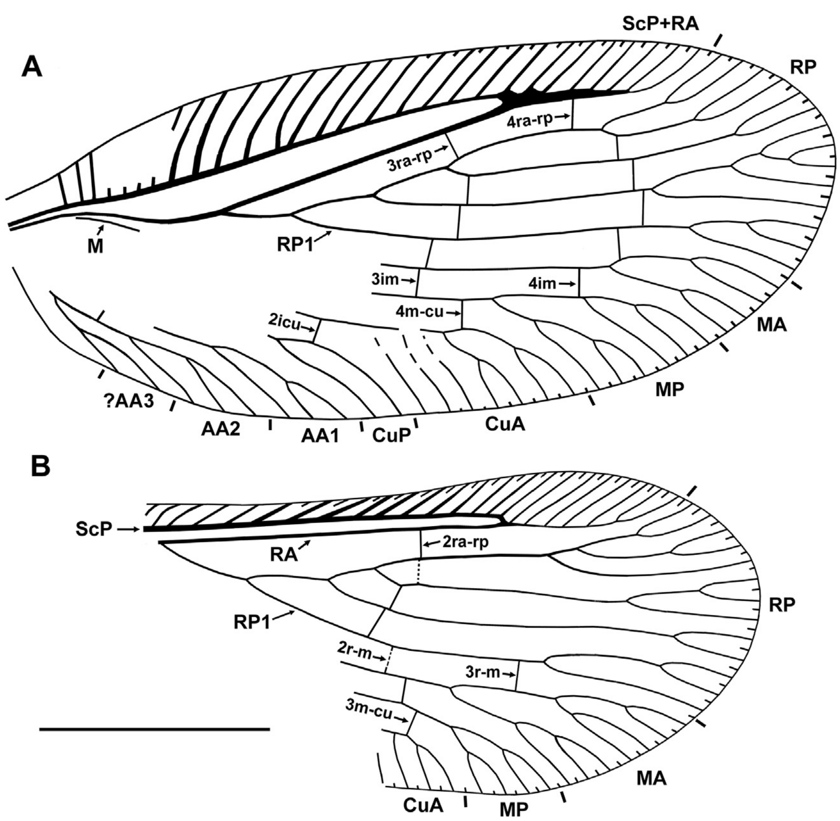

Fig. 5. Wing venation of *Paradoxosisyra groehni* sp. nov. Holotype GPIH Typ. Kat. Nr. 4580. A. right forewing. B. right hind wing. Scale bar represents 1 mm.

The galea is an elongate structure, especially in some Berothidae (e.g., MacLeod and Adams, 1968, fig. 4; Aspöck and Aspöck, 1988, figs. 4), and strongly elongate in most Nemopteridae. It is often divided into basigalea and distigalea (the former is lost in Sisyridae: Randolf et al., 2013); and usually bears the digitus, a sclerotized finger-like apical process ('knob' of authors; 'papilliform process' of Killington (1936); 'apical papilla' of Brooks and Barnard (1990)). The very long distigalea of Crocinae (Nemopteridae) is telescopically hidden into the tubular palpiger and stipes (see Tjeder, 1967, figs, 1907, 1908). The galea of *Sisyra* lacks the digitus, but possesses numerous apical *sensilla basiconica*, which are superficially similar to the digitus (Fig. 6G; Randolf et al., 2013, fig. 6).

The lacinia is usually elongate and brush-like with dense setae (e.g., Berothidae: Tjeder, 1959, figs. 227; Psychopsidae: Tjeder, 1960,

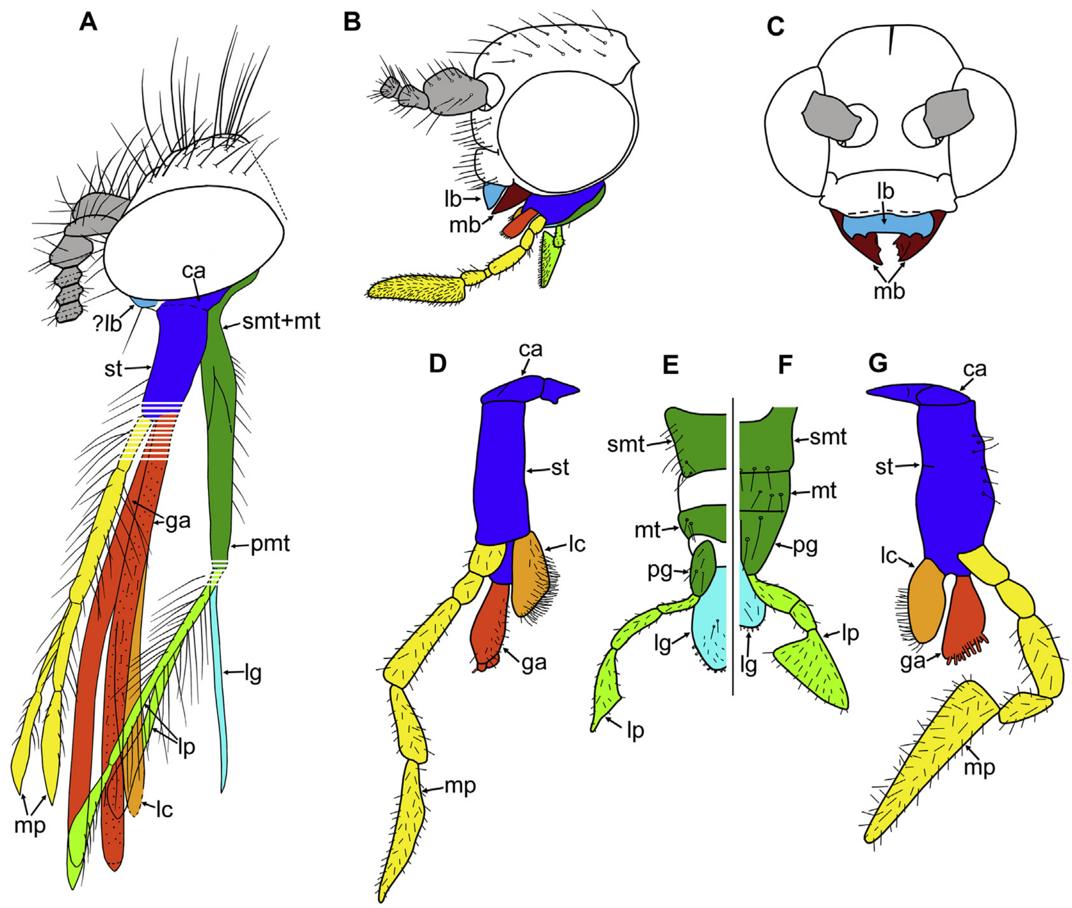

Fig. 6. Comparative mouthparts of *Paradoxosisyra groehni* sp. nov. (A) and extant species of Sisyridae (B–G). A. head of the holotype GPIH Typ. Kat. Nr. 4580, lateral view (lined areas are poorly discernible and slightly hypothesized). B. *Sisyra producta* Tjeder, 1957, head, lateral view. C. same, frontal view. D. *Climacia areolaris* (Hagen, 1861), maxilla. E. same, left half of labium (ventral view). F. *Sisyra vicaria* (Walker, 1853), right half of labium (ventral view). G. same, maxilla. ca, cardo; ga, galea; lb, labrum; lc, lacinia; lg, ligula; lp, labial palpus; mt, mentum; mb, mandible; mp, maxillary palpus; pg, palpiger of prementum; pmt, prementun; smt, submentum; st, stipes. Redrawn from Tjeder (1957) (B, C) and Parfin and Gurney (1956) (D–G), slightly simplified. All not to scale.

figs. 344, 406); elongate and slender in some Berothidae (MacLeod and Adams, 1968, fig. 4; Aspöck and Aspöck, 1988, fig. 4), and very long and slender in Crocinae (Nemopteridae) (Tjeder, 1967, figs, 1907, 1908).

The maxillary palpus is five-segmented (four-segmented in most Nemopteridae). Terminal segment is sometimes dilated (e.g., Coniopterygidae: Meinander, 1972, figs. 7E, G; some Sisyridae: Nel et al., 2003, fig. 7; Randolf et al., 2013, fig. 6).

The labium consists of submentum, mentum, prementum, ligula, and a pair of labial palpi.

The submentum is broad and elongated, usually much longer than the mentum (e.g., Hemerobiidae: Killington, 1936, fig. 6; Psychopsidae: Tjeder, 1960, fig. 345); these are sometimes nearly equal in length and short (e.g., Coniopterygidae (Meinander, 1972, fig. 7C). The prementum laterally has a pair of palpigera, which bear the labial palpi. The prementum is sometimes entirely divided into two lateral halves (e.g., in the Nemopteridae: Tjeder, 1967, fig, 1909; Ascalaphidae: Tjeder, 1992, figs. 11, 15).

A pair of glossae (sensu Matsuda, 1965) is fused to form a ligula, which is usually semi-oval or rounded, but elongate in some Berothidae (MacLeod and Adams, 1968, fig. 3; Aspöck and Aspöck, 1988, fig. 3), and covered with setae and bristles, sometimes very dense (e.g., Hemerobiidae: Killington, 1936, fig. 6; Chrysopidae: Tjeder, 1966, figs. 801, 849, 1090, 1137, 1181); sometimes apically bilobed (e.g., Osmylidae: Beutel et al., 2010, fig. 7), reduced to a short semi-oval membranous structure (e.g., Ithonidae: Tillyard, 1919, fig. 6, and Dilaridae: pers. obs.), or bears apical paired digitus and setose paraglossae (e.g., Nevrorthidae: Randolf et al., 2014, figs. 3C, 5).

The labial palpus is three-segmented (two-segmented in some Nemopteridae). The terminal segment is sometimes strongly dilated (e.g., Coniopterygidae: Meinander, 1972, fig. 7C; some Sisyridae: Nel et al., 2003, fig. 7; Randolf et al., 2013, fig. 6).

Such generalized mandibulate mouthparts are present (or implied, judging from their preserved parts) in many extinct families of Neuroptera, i.e., Permithonidae (e.g., Vilesov, 1995, figs. 1, 6), Parakseneuridae (e.g., Yang et al., 2012, fig. 28A), Grammolingiidae (e.g., Shi et al., 2012b, fig. 6B), Mesochrysopidae (e.g., Ren et al., 2010a, fig. 1), Palaeoleontidae (e.g., Menon and Makarkin, 2008, fig. 4a; Shi et al., 2012a, fig. 2A), Araripeneuridae (e.g., Martins-Neto and Vulcano, 1989, fig. 5G), and Dipteromantispidae (e.g., Grimaldi, 2000, fig. 13). Unfortunately, their detailed structure is largely unknown in these families.

The mouthparts of Nemopteridae are specialized to feed upon pollen and possibly nectar: all examined guts of many Nemopteridae (including Crocinae) contain only pollen grains (e.g., Grinfel'd, 1959; Tjeder, 1967; Makarkin, 1992; Popov, 2002). The mouthparts of these are considered mandibulate (Labandeira, 2010), although their mandibles are very weak, are only slightly or not at all movable (e.g., *Derhynchia vansoni* Tjeder, 1967, fig. 1883), and have probably lost their biting/chewing function (Tjeder, 1967; Krenn et al., 2008). Their heads are often modified (especially in Crocinae) to bear a long rostrum with elongated clypeus, labrum, mandibles, maxillae and labium (Tjeder, 1967, figs. 1891–1894, 1898–1902, 1905–1909; Krenn et al., 2008, figs. 3–8). The long rostrum of Crocinae and telescopic movements of their galea are thought to be "particular specializations for nectar feeding from long floral spurs" (Krenn et al., 2008, p. 276). However, the elongated lacinia and galea, which are inserted into a flower during feeding, are covered with dense setae (see e.g., Tjeder, 1967, figs, 1907, 1908), which are more suited for collecting pollen than obtaining nectar. If Crocinae (and generally Nemopteridae) feed on nectar, this is at least not their preferred food.

Therefore, the mouthparts of Nemopteridae (especially those of Crocinae) may be interpreted as morphologically and functionally intermediate between the siphonate and mandibulate types, as their mandibles appear not functional for chewing and biting, but on the other hand, their mouthparts are only slightly prominent beyond the labrum, not differing in this respect from mandibulate mouthparts.

The mouthparts of the Mesozoic family Kalligrammatidae are siphonate (Labandeira, 2010). These are very long (8–20 mm), and their distal prominent parts are thought to consist only of the proboscis and maxillary palpi (Labandeira et al., 2016). The proboscis is thought to consist of "conjoined maxillary galeae to form a tubular siphon that is anatomically similar to that of the lepidopteran Glossata" (Labandeira, 2010, p. 495), or simply of "maxillary elements" (Labandeira et al., 2016, p. 6). The mouthparts of many species of Kalligrammatidae were recently studied by Labandeira et al. (2016), and some of them appear to support this interpretation. Indeed, the segmentation of the proboscis of most kalligrammatids is not visible (Labandeira et al., 2016, figs. 1S*c,f,i,k.q*; VM., pers. obs.), and some consist of four non-segmented elements (Labandeira et al., 2016, figs. 1S*c,n,q*), implying that these are long galeae and laciniae. Consequently, in these kalligrammatids the labium and its palpi appear to be reduced or even lost. On the other hand, the comparison of the photo of the mouthparts of *Meioneurites spectabilis* Engel, 2005 from the Upper Jurassic locality of Karatau and the figure of these in Labandeira et al. (2016) shows that the interpretation of its strongly setose proboscis as consisting of maxillary and labial palpi appears more accurate (see Ponomarenko, 2002, fig. 249; Engel, 2005, figs. 1, 2) than that they are consisting of maxillary palpi and a poorly visible proboscis (Labandeira et al., 2016, fig. 1S*l*). It is clear that the proboscis of the siphonate Kalligrammatidae evolved within the family and its structure somewhat differs within its various subtaxa. The subfamily Sophogrammatinae (more precisely, only the genus *Sophogramma* Ren & Guo, 1996) has only mandibulate mouthparts (see Yang et al., 2014b); the well-preserved mouthparts of an undescribed specimen from the Yixian Formation (China) clearly indicates this (VM, pers. obs.).

The elongated mouthparts of the Mesozoic family Aetheogrammatidae are very similar to those of closely related Kalligrammatidae, and are also siphonate, judging from the photograph of an undescribed species (Zhang, 2007, fig. on p. 104), which shows four long, slender, slightly divergent structures that may reasonably be interpreted as maxillary and labial palpi.

Labandeira (2010, fig. 3) believes that '*Tshekardithonopsis ? oblivius*' Vilesov, 1995 (Permithonidae) from the Permian locality of Chekarda (Russian Urals) has siphonate mouthparts; however this specimen is poorly preserved and this character appears indistinct, judging from the photographs provided. The holotype specimen of *T. oblivius* shows distinctly normal, mandibulate mouthparts (see Vilesov, 1995, fig. 6). It is possible that the apparent siphonate mouthparts of this specimen are an artefact of preservation.

The mouthparts are largely or entirely unknown in the extinct neuropteran families Archeosmylidae, Prohemerobiidae, Osmylopsychopidae, Panfiloviidae, Saucrosmylidae, Ascalochrysidae, and Babinskaiidae.

4.2. Food of extant adult Sisyridae

There are few data on the diet of adult Sisyridae. Tjeder (1944) observed a male of *Sisyra nigra* (Retzius, 1783) feeding on eggs of the alder fly *Sialis lutaria* (Linnaeus, 1758). Brown (1952) found that "the fecal droppings of captured adults [*Climacia areolaris* (Hagen, 1861)] may be largely composed of pollen grains" (p. 153). Tjeder (1957) found very small unidentifiable pieces of chitin in the guts of two South African *Sisyra* species. Kokubu and Duelli (1983) examined the crop and gut content of 34 specimens of *Sisyra terminalis* Curtis, 1854 from Switzerland, and found that it consisted of pollen grains, algae, fungi, aphids, and mites. Based on these data, they concluded that aphids appear to constitute the major portion of the diet of adults; the mites are an important part of their food, upon which the adults actively prey; and that the adults frequently feed on honeydew. Pupedis (1987) observed two North American species (*Sisyra vicaria* (Walker, 1853) and *C. areolaris*) feeding upon aphids. He examined the gut content of 44 specimens of these species, and found it to be similar to that of *S. terminalis*. He found distinct differences in the diet between these species in that the gut of many specimens of *S. vicaria* contained mites, whereas that of *Climacia areolaris* did not, and the gut of four specimens of *C. areolaris* contained only pollen grains. Therefore, at least some species of Sisyridae may be pollen feeders.

4.3. Comparative morphology of the *Paradoxosisyra* mouthparts

The structure of the mouthparts of *Paradoxosisyra groehni* sp. nov. is unique in Neuroptera, and in insects in general. These strongly differ from those of all other Neuroptera, both of the mandibulate and siphonate types (see above). Its labial ligula is transformed into a long, acute stylet lacking visible setae, and the paired elongated galeae and laciniae may act as a sucking food-canal (if these are conjoined), forming the proboscis. Therefore, the Sisyridae is the third known family within Neuroptera (in addition to Kalligrammatidae and Aetheogrammatidae), in which siphonate mouthparts are documented. It should be noted that all of these were restricted to the Mesozoic, and that their mouthparts do not appear to have been modified to form a true siphon (as in Lepidoptera), except possibly in some kalligrammatids.

In general, the structure of the maxilla and labium of *P. groehni* sp. nov. is most similar to that of the extant Crocinae (Nemopteridae) in having an elongated submentum, prementum, ligula, stipes, galea and lacinia. However, the ligula, galea and lacinia of *P. groehni* sp. nov. are further transformed. The strongly lengthened, laterally flattened galea and lacinia are characteristic of only this species, and does not occur in other insects. The mouthparts of *P. groehni* sp. nov. are also similar to those of some Kalligrammatidae, if the hypothesis that their proboscis consists of long galeae and laciniae is true (see above). However, the labium and its palpi in these taxa are hypothesised to be strongly reduced or lost.

The transformation of the ligula in *P. groehni* sp. nov. into a stylet is especially interesting. Outside of the Neuroptera, it is most similar – at least superficially – to that of some long-tongued bees (Hymenoptera: Apoidea) in that their prementum, palpi and ligula are elongate (see Winston, 1979, fig. 1). However, the apoid ligula possesses numerous transverse rows of dense short setae, giving it a rigged appearance; it is not acute at the end (expanded into the flabellum), and not used in piercing: used in pollen and nectar feeding in these bees. In general, the overall mouthparts of bees appear superficially similar to those of *P. groehni* sp. nov.

The stylet of such blood-sucking insects as Culicidae (Diptera), Reduviidae and Cimicidae (Homoptera s.l.) is formed by the paired mandibles and laciniae of the maxillae (Krenn and Aspöck, 2012). In these insects, the labium is also long, but its central groove is used to enclose the stylet and not for piercing. The labrum and the epipharyngeal blades pierce the prey in the Empidoidea, while the spear-like hypopharynx alone is used in piercing the prey in Asilidae (Bletchly, 1954; Sinclair and Cumming, 2006). The stylet of the Burmese amber *Parapolycentropus burmiticus* Ren et al., 2009 (Mecoptera: Pseudopolycentropodidae) is formed by the thickened labrum (Ren et al., 2009) or (in another interpretation) by the hypopharynx (Grimaldi and Johnston, 2014). This is the only known species of aneuretopsychine Mecoptera which bears stylate mouthparts.

Anatomically, the mouthparts of *Paradoxosisyra groehni* sp. nov. is most similar to that of Lepidoptera in that their proboscis is formed by a pair of long galeae, and the mandibles are reduced (Krenn, 2010). Similar long-proboscid siphonate mouthparts are present in the Mesozoic Mecoptera Aneuretopsychina, i.e., Pseudopolycentropodidae, Mesopsychidae, and Aneuretopsychidae (Rasnitsyn and Kozlov, 1990; Ren et al., 2010b, 2011; Shi et al., 2011). Their proboscis is thought to consist of paired labial elements “that are conjoined to anatomically form the siphon for the imbibition of fluids” (Lin et al., 2016, p. 19). However, Grimaldi and Johnston (2014) believe that the proboscis of at least the Burmese amber *Parapolycentropus burmiticus* Grimaldi & Rasnitsyn in Grimaldi et al. (2005) (Pseudopolycentropodidae) is formed by galeae. Superficially, the proboscis of glossatan Lepidoptera and aneuretopsychine Mecoptera look very similarly, their mandibles are strongly or entirely reduced, and their palpi are relatively short, but these mouthparts do not resemble those of *Paradoxosisyra groehni* sp. nov. in many details.

The proboscis of the nectarivorous *Nemognatha* Illiger, 1807 (Coleoptera: Meloidae) is also formed by conjoined galeae, and is sometimes very long (Labandeira, 2010, fig. 10B; Wilhelmi and Krenn, 2012). However, their mouthparts do not resemble those of *P. groehni* sp. nov., as their mandibles are well developed and the ligula is very short and hairy (see Wilhelmi and Krenn, 2012, fig. 2).

4.4. *Feeding habit of* Paradoxosisyra

The structure of the mouthparts of *Paradoxosisyra groehni* sp. nov. implies that these sisyrids could consume only liquid food, i.e., nectar of flowers of angiosperms, pollination droplets of reproductive organs of gymnosperms (i.e., their ovulate secretions), hemolymph of arthropods or blood of vertebrates. The strong reduction, or even absence of mandibles indicates that they were unable to consume solid food. Given these structures and the feeding habits of extant taxa, nectarivory was the most probable feeding habit of *P. groehni* sp. nov., as some extant Neuroptera feed on the pollen of flowers (e.g., in the Nemopteridae, Chrysopidae, Berothidae, and Sisyridae). This is implied mainly from the morphology of its galea and lacinia. The presence of the long palpi characteristic of *P. groehni* sp. nov. and such nectarivorous insects as bees and culicid males also indicates that this new species was primarily nectarivorous. If so, the function of the labial stylet is unclear. Nevertheless, its presence implies possible hematophagy (i.e., feeding on blood or hemolymph). If the ligula was actually used for piercing arthropods, vertebrates or plants to suck internal fluids by the maxillary proboscis, then this would be unique among insects. The short (ca. 0.4 mm) stylet of *P. groehni* sp. nov. appears to have been suitable only to pierce some arthropods, the soft parts of plants, or the skin of only such thin-skinned vertebrates as frogs. The distal placement of the labial palpi would not allow the use of the entire labium during piercing. Therefore, the possibility remains that the ligula (and entire labium in general) served in an accessory function during feeding on nectar, not for piercing.

Nectar-feeding insects with long mouthparts occur in different insect orders, e.g., Hymenoptera (e.g., Apoidea), Diptera (especially Brachycera), Lepidoptera (Glossata), and Coleoptera (e.g., Meloidae). In particular, of Diptera with long mouthparts (e.g., Culicidae; Empidoidea, some Asilidae, Tabanidae (especially Pangoniinae), Bombyliidae, Nemestrinidae), only Asilidae are obligate predators (Szucsich and Krenn, 2000; Sinclair and Cumming, 2006; Karolyi et al., 2012; Carno, 2014). Others (at least some of their taxa) may be nectarivorous. Bombyliidae feed exclusively on flowers, mainly on nectar, but some feed on pollen in plants that produce none (Deyrup, 1988; Szucsich and Krenn, 2002). In the latter, pollen appears to be mixed with a liquid when it is transported through the proboscis (Deyrup, 1988).

Nectarivory, however, is often combined with hematophagy within a species or a family in Diptera (Kniepert, 1980; Grimaldi and Johnston, 2014). The females of Culicidae are hematophagous, and the males of many species are nectarivorous. The structure of their mouthparts differs in many details, e.g., the maxillae and mandibles of males are much shorter than the proboscis, while in the females these are nearly equal (Wahid et al., 2003). What is relevant here is that in many culicid species, the maxillary palpi of nectarivorous males are much longer than those of blood-feeding females (Snodgrass, 1959; Wahid et al., 2003; Bohbot et al., 2014). It is interesting to note that in a culicid species from Burmese amber, the maxillary palpi are much longer than the proboscis (Borkent and Grimaldi, 2004, figs. 7, 8). This species could be nectarivorous, although the authors that it was a vertebrate blood feeder. Many extant females of the Pangoniinae (Tabanidae) possessing extremely long proboscides specialized for nectar-feeding retain the ability to feed on blood (Morita, 2008). Most empidid genera are primarily predaceous, feeding on various insects. Others, however, who have long proboscides (especially *Empis* Linnaeus, 1758), are primarily nectar-feeding. Even in these genera, females receive prey from males during mating and copulation (Chvála, 1994). Moreover, a blood-feeding habit occurs even in adults of the glossatan Lepidoptera, e.g. in the vampire moth genus *Calyptra* Ochsenheimer, 1816 (Erebidae: Calpinae). In these moths, the proboscis is apically pointed and bears a piecing armature, i.e., strong tearing hooks and erectible barbs, allowing them to pierce the skin and suck blood from large mammals, including humans (Bänziger, 2007, figs. 10, 11; Krenn, 2010, fig. 5e; Zaspel et al., 2011, figs. 3e,f).

Many Middle Jurassic to mid-Cretaceous insects with a long proboscis are assumed to be associated with extinct gymnosperms, feeding mostly on secretions of their reproductive organs (Ren et al., 2009; Labandeira, 2010). These include Diptera (e.g., Zhangsolvidae), Mecoptera (families of Aneuretopsychina), and Neuroptera (Kalligrammatidae, probably Aetheogrammatidae) (Ren et al., 2009; Labandeira, 2010; Grimaldi and Johnston, 2014; Arillo et al., 2015; Peñalver et al., 2015; Lin et al., 2016). In particular, abundant gymnosperm pollen grains were found on the body of one specimen of the long-proboscid *Buccinatormyia magnifica* Arillo et al., 2015 (Zhangsolvidae) from Burmese amber (Peñalver et al., 2015). Also, pollen grains of the extinct conifer family Cheirolepidiaceae (i.e., *Classopollis* cf. *annulatus*) are found in matrix adjacent the maxillary palp base of the kalligrammatid *Meioneurites spectabilis* (Labandeira et al., 2016). These authors assume that the gymnosperm seed family Williamsoniaceae (Bennettitales) “most likely formed a close pollinator mutualism with the Kalligrammatidae” (p. 7). But Burmese amber bears the last record of these insect groups, in a time when angiosperms were becoming diverse and beginning their dominance in terrestrial ecosystems (Heimhofer et al., 2005). Several flowers of various taxonomic affinities are known from this amber (see Grimaldi et al., 2002; Poinar and Chambers, 2005; Santiago-Blay et al., 2006; Poinar et al., 2007, 2008; Chambers et al., 2010; Poinar et al., 2013). The relatively short proboscis of *Paradoxosisyra groehni* sp. nov. (ca. 1 mm) is most similar in length to that of minute species of the Jurassic Pseudopolycentropodidae (Mecoptera) (1.5–1.9 mm). The single species of the family (and more generally of the Aneuretopsychina) known from Burmese amber (see above) had the shortest proboscis in the family (1.3 mm), but stylate mouthparts of this species were probably used to feed on the hemolymph of small insects (Grimaldi and Johnston, 2014). Other long-proboscid species of Mesozoic Diptera and Mecoptera associated with gymnosperms have a longer proboscis, e.g., 3.9–4.4 mm in Zhangsolvidae; 4.7–6.8 mm in Aneuretopsychidae, and 8.8–10.1 mm in Mesopsychidae (Shi et al., 2011; Arillo et al., 2015). The proboscis of Kalligrammatidae was still longer, up to 20 mm (Labandeira et al., 2016).

The known flowers from Burmese amber are mostly small to very small with a shallow calyx, often less than 1 mm, both in length and diameter (see e.g., Grimaldi et al., 2002, fig. 13; Poinar et al., 2007, fig. 2), and so the proboscis of *P. groehni* sp. nov. would have been suitable to feed on nectar from these.

The origin of angiosperms and their diversification during the Cretaceous strongly changed the structure of terrestrial ecosystems. The large-scale processes of the transition from gymnosperm-dominated to angiosperm-dominated ecosystems took place most intensively in the Aptian to Turonian (Labandeira, 2014). The emergence of flowers as a food source for insects is a vitally important part of this change. In particular, the change from hematophagy to nectarivory in Chironomidae (Diptera) during the Cretaceous is assumed to be linked to the diversification of the angiosperms in that time (Choufani et al., 2013). The subfamily Paradoxosisyrinae might have become extinct later in the Cretaceous as its mouthparts were perhaps too specialized, rendering them incapable of competing with other, more successful flower visitors, e.g., bees, which diversified later.

5. Conclusion

The mouthparts of this new, oldest known, amazing sisyrid from Burmese amber *Paradoxosisyra groehni* sp. nov. are the most specialized within the order. Their structure is unknown in other groups of Neuroptera, or in insects of any other order. I argue that its siphonate mouthparts were likely used to feed on nectar of the flowers, but if so, the function of the stylate labium is unclear. Alternatively, the possibility remains that these sisyrids were hematophagous (possibly facultative), feeding on the hemolymph of arthropods or blood of thin-skinned vertebrates like frogs.

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