Alcheringa: An Australasian Journal of Palaeontology

ISSN: 0311-5518 (Print) 1752-0754 (Online) Journal homepage: https://www.tandfonline.com/loi/talc20

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**To cite this article:** Alexander V. Khramov, Gi-Soo Nam & Dmitry V. Vasilenko (2020) First long-proboscid flies (Diptera: Zhangsolvidae) from the Lower Cretaceous of South Korea, Alcheringa: An Australasian Journal of Palaeontology, 44:1, 160-168, DOI: 10.1080/03115518.2019.1664634

**To link to this article:** https://doi.org/10.1080/03115518.2019.1664634

# First long-proboscid flies (Diptera: Zhangsolvidae) from the Lower Cretaceous of South Korea

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Khramov, A.V., Nam, G.-S. & Vasilenko, D.V. 13 December 2019. First long-proboscid flies (Diptera: Zhangsolvidae) from the Lower Cretaceous of South Korea. *Alcheringa* 44, 160–168. ISSN 0311-5518

*Buccinatormyia gangnami* sp. nov. (Zhangsolvidae) is the first record of Diptera from the Lower Cretaceous Jinju Formation of the Korean Peninsula. *B. gangnami* is described based on six specimens, the largest number of fossils known for a single species of Zhangsolvidae. Four specimens of *B. gangnami* preserve a long proboscis; mouthparts of this species show a twofold variation in relative length, which may be partially explained by sexual dimorphism. *B. gangnami* is the third known species of Zhangsolvidae with extremely elongate antennal flagella. The preserved abdominal colouration pattern in these fossils suggests that *B. gangnami* was probably a wasp mimic.

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Key words: Brachycera, Stratiomyomorpha, Zhangsolvidae, insect pollination, wasp mimicry, long-proboscid insects.

TOGETHER with scorpionflies (Mecoptera) and lacewings (Neuroptera), brachyceran flies constitute one of the three major lineages of Mesozoic insects that evolved a long proboscis suitable for nectarivory prior to the rise of angiosperms in the mid-Cretaceous (Ren *et al.* 2009, Labandeira *et al.* 2016, Khramov & Lukashevich 2019). It has been reasonably suggested that these early long-proboscid taxa could have fed on pollination drops and other sugary fluids produced by Mesozoic gymnosperms (Labandeira *et al.* 2007). Significantly, Brachycera remain one of the principal flower-visiting insects and pollinators (Wardhaugh 2015, Rader *et al.* 2016), whereas long-proboscid scorpionflies and lacewings of the Mesozoic are now extinct, probably owing to an inability to adapt to angiosperm-dominated ecosystems. New fossils of Brachycera with preserved mouthparts are key to understanding their past feeding habits, which in turn is essential to explain the long-term evolutionary success of this group.

At least 79 of the 159 extant dipteran families contain flower-visiting species (Wardhaugh 2015). However, the Mesozoic record of many principal anthophilous Brachycera is quite sparse; for example, the only known Mesozoic member of the Syrphidae, recorded from the Upper Cretaceous Taimyr amber, probably does not belong to this family at all (Popov 2015). The description of the earliest bee fly (Bombyliidae s.l.), *Palaeoplatypygus zaitzevi* Kalugina & Kovalev 1985 from the Middle Jurassic of Siberia is based on an isolated wing (Kalugina & Kovalev 1985), and few bombyliids described from the Upper Cretaceous Taimyr and Burmese ambers (Zaytsev 1987, Grimaldi *et al.* 2011, Grimaldi 2016, Ye *et al.* 2019) preserve the elongate proboscides typical for many extant bee flies. According to Nel (2008), bee flies become significantly more abundant in the Cenozoic, probably reflecting rapid diversification in response to the rise of flowering plants. However, the origins of other lineages of flower-visiting Brachycera can be traced well into pre-angiosperm times, which provides evidence that they may have initially evolved and diversified in association with the reproductive organs of gymnosperms.

To date, six brachyceran lineages have been found with elongate siphonate mouthparts in the Mesozoic, a condition that can be viewed as a strong indication for nectar-sucking behaviour. Five of these lineages still exist today. Mesozoic Nemestrinidae, the most ancient family of anthophilous Brachycera, with the first records in the Lower Jurassic, contains five long-proboscid species placed within the genera *Protonemestrius* Rohdendorf, 1968, *Florinemestrius* Ren, 1998a and *Prosoeca* Schiner, 1867, recorded from the Upper Jurassic of Kazakhstan (Rohdendorf 1968, Mostovski 1998) and Lower Cretaceous of China and Spain (Ren

https://doi.org/10.1080/03115518.2019.1664634

*Table 1.* Species of Zhangsolvidae.

| Species | Proboscis length (mm) | Ratio of proboscis to body length | Locality | Age | References |
|---|---|---|---|---|---|
| *Zhangsolva cupressa* (Zhang *et al.*, 1993) | 5.2 | 0.38 | Laiyang Formation, China | Upper Barremian | Nagatomi & Yang (1998) |
| *Cratomyia macrorrhyncha* Mazzarolo & Amorim, 2000 | 7 | 0.29 | Santana Formation, Brazil | Aptian | Mazzarolo & Amorim (2000) |
| *C. cretacica* (Willkommen, 2007) | *ca* 1.3 | 0.14 | Santana Formation, Brazil | Aptian | Willkommen & Grimaldi (2007) |
| *Buccinatormyia magnifica* Arillo *et al.*, 2015 | 3.85 | 0.42 | Spanish amber (El Soplao), Spain | Upper Albian | Arillo *et al.* (2015) |
| *B. soplaensis* Arillo *et al.*, 2015 | >1 | *ca* 0.3 | Spanish amber (El Soplao), Spain | Upper Albian | Arillo *et al.* (2015) |
| *B. gangnami* sp. nov. | 2.9–5.2 | 0.19–0.4 | Jinju Formation, South Korea | Lower to middle Albian | Present paper |
| *Burmomyia rossi* Zhang *et al.*, 2019 | 0.66 | 0.2 | Burmese amber, Myanmar | Lowermost Cenomanian | Zhang *et al.* (2019) |
| *Cratomyia zhuoi* Zhang *et al.*, 2019 | 1.9 | 0.34 | Burmese amber, Myanmar | Lowermost Cenomanian | Zhang *et al.* (2019) |
| *C. mimetica* Grimaldi, 2016 | Proboscis long, only base preserved | – | Burmese amber, Myanmar | Lowermost Cenomanian | Grimaldi (2016) |
| *Linguatormyia teletacta* Arillo et al., 2015 | 4.37 | 0.46 | Burmese amber, Myanmar | Lowermost Cenomanian | Arillo *et al.* (2015) |

1998b, Mostovski & Martínez-Delclòs 2000), alongside the numerous species with short mouthparts recorded from these and other localities (e.g., Zhang *et al.* 2017, Liu & Huang 2019). Six species of long-proboscid Tabanomorpha, belonging to the genera *Atherhagiox* Grimaldi, 2016, *Eopangonius* Ren, 1998a, *Galloatherix* Nel *et al.*, 2014 and *Palaepangonius* Ren, 1998a, were described from the Lower Cretaceous of China and Upper Cretaceous Burmese amber (Ren 1998a, Grimaldi 2016). Some of these species probably used their mouthparts for nectar feeding like the extant Pangoniinae (Tabanidae) (Ren 1998b). Two other long-proboscid species—*Archocyrtus kovalevi* (Nartshuk, 1996) of the Acroceridae and *Cretahilarimorpha lebanensis* Myskowiak *et al.*, 2016 of the Hilarimorphidae—were found in the Upper Jurassic of Kazakhstan and Lower Cretaceous Lebanese amber, respectively (Myskowiak *et al.* 2016, Khramov & Lukashevich 2019). Finally, undescribed long-proboscid members of *Protapiocera* Ren, 1998a (Mydidae) were recorded from the Lower Cretaceous of Russia (Labandeira *et al.* 2007).

The Zhangsolvidae are the only extinct family of long-proboscid Brachycera known from the Mesozoic. This exclusively Cretaceous family belongs to the infraorder Stratiomyomorpha, which includes three extant families, the Stratiomyidae, Xylomyidae and Pantophthalmidae (Arillo *et al.* 2015). The extinct superfamily Archisargoidea, which includes families such as Archisargidae, Eremochaetidae and Tethepomyiidae, has sometimes been allied with this infraorder (Oberprieler & Yeates 2012, Arillo *et al.* 2015). The Zhangsolvidae are the only members of Stratiomyomorpha to have a long proboscis (Peñalver *et al.* 2015), with all but one of the nine hitherto described species preserving elongate mouthparts (Table 1). This makes the family the most diverse of the Mesozoic Brachycera in regard to long-proboscid taxa. In the present paper, we describe a new species of Zhangsolvidae with a long proboscis from the Lower Cretaceous of South Korea, thus expanding our knowledge of the distribution, diversity and morphology of this ecologically important group of Mesozoic nectar feeders and pollinators. The new species constitutes the first record of Diptera from the Lower Cretaceous of the Korean Peninsula, a region which still remains poorly studied with respect to fossil insects.

## Materials and methods

The specimens were collected from outcrops of the Jinju Formation near Jinju city, South Gyeongsang Province. The geology of this southeastern part of the Korean Peninsula consists of the Cretaceous Gyeongsang Supergroup, which is subdivided into the Sindong, Hayang and Yucheon groups in ascending order. The lower Sindong Group is in turn subdivided into three formations, of which the Jinju Formation is uppermost (Chang 1975).

The Jinju Formation consists of grey to black shale, intercalated by packets of sandstones, and is estimated as lower to middle Albian in age based on U–Pb zircon dating (Kang & Paik 2013). The Jinju Formation has yielded numerous fossils, including terrestrial arthropods, plants, fishes, crustaceans and trace fossils. Five insect orders have been recorded from this assemblage, including the Blattodea (Baek & Yang 2004), Coleoptera (Park *et al*. 2013), Dermaptera (Engel *et al*. 2002), Odonata (Nam & Kim 2016) and Raphidioptera (Engel *et al*. 2006). Various spiders have also been described (Selden *et al*. 2012, Park *et al*. 2019).

All specimens described in the present paper are housed at the Gongju National University of Education (Gongju city, South Korea). Photographs were taken using a Canon EOS 6 D DSLR camera attached to a Nikon SMZ 800 stereomicroscope. Line drawings were prepared from photographs using the image-editing software Adobe Photoshop CS6. Vein abbreviations follow Arillo *et al*. (2015).

## Systematic palaeontology

Order DIPTERA Linnaeus, 1758
Infraorder STRATIOMYOMORPHA Hennig, 1973
Family ZHANGSOLVIDAE Nagatomi & Yang, 1998
**Buccinatormyia** Arillo *et al*., 2015

urn:lsid:zoobank.org:act:D0CF9654-69D3-41A0-AEB7-157BAED4CDF6
**Buccinatormyia gangnami** Khramov & Nam, sp. nov. (Figs 1–3)

*Etymology*. Named after the hit song ‘Gangnam Style’ by the South Korean musician Psy.

*Material*. Holotype GNUE-219001, presumably female; paratype GNUE-219002, presumably male; paratypes GNUE-219003, 219005, 219004, 219010, sex unknown. Lower Cretaceous Jinju Formation, South Korea.

*Diagnosis*. Proboscis longer than head, antennal flagellum very elongate, abdominal tergites with paired light-coloured spots; wing with stem of Rs long, C ending slightly beyond $R_5$, cell $m_3$ long and narrow, cell d equal in length to cell $m_3$, veins $M_1$ and $M_2$ diverging directly from cell d or from very short common stem ($M_{1+2}$).

*Description*. Proboscis 2.9–5.2 mm long, 0.19–0.4 times body length (Table 2; Figs 1, 2); slightly widened at the apex, labellum small, about as wide as proboscis in distal part; maxillary palps 1.5–2.6 mm long, appears two segmented, shorter or slightly longer than head (Fig. 2A, B). Antennae 6.0–6.9 mm long, slender, longer than proboscis, with presumably third flagellomere extremely elongate, total number of flagellomeres unknown (Fig. 2). Second foretarsomere equal in length to combined third and fourth foretarsomeres (Fig. 2A, B); third metatarsomere longer than fourth and fifth metatarsomeres combined (Fig. 1C,D). Abdomen broader than thorax, consisting of 7–8 visible segments; second to fifth abdominal tergites with a pair of large light-coloured spots near ventral margin, with spots half as wide as tergites; sixth abdominal tergite uniformly dark or with a pair of small light-coloured spots; eighth tergite significantly narrowed in males, cerci widely separated in females (Fig. 1A, B).

Wings 7.2–10.1 mm long (Table 3), *ca* 4.5 mm wide; vein C ending between $R_5$ and $M_1$; Sc terminates beyond level of r-m crossvein; stem of Rs *ca* 5 times longer than r-m crossvein; $R_1$ terminates at level of origination of $M_1$ and $M_2$ from cell d; fork of $R_4$–$R_5$ considerably shorter than that of $M_1$–$M_2$; cell bm longer than cell br; $M_1$ and $M_2$ diverge directly from cell d or from a small stem of $M_{1+2}$ distad to cell d; cell d 1.4–1.9 mm long, 0.46–0.82 mm wide, close to rectangular in shape; veins $CuA_1$ and $M_3$ joined into short vein before meeting wing margin; cell $m_3$ narrow, 1.34–1.8 mm long, 0.27–0.52 mm wide; crossvein m-m running into distal half of cell $m_3$; veins $CuA_2$ and $A_1$ joined into rather long vein before meeting wing margin, vein $A_2$ not preserved.

## Discussion

We consider all specimens reported herein as conspecific on the grounds of similar wing venation and abdominal colouration. Spot patterns in *Buccinatormyia gangnami* are similar to that of some species of *Stratiomys* Geoffroy, 1762 (Stratiomyidae) and many other anthophilous wasp-mimic Brachycera. Taking into account that *Cratomyia mimetica* Grimaldi, 2016 from the Burmese amber displayed an abdominal pattern close to that of yellowjackets (Grimaldi 2016), it can be concluded that wasp mimicry was quite common in the Zhangsolvidae. This can be taken as an indication of the prominence of Vespidae during the Cretaceous, despite the fact that the record of pre-Cenozoic vespids is scarce (Perrard *et al.* 2017). However, the possibility that zhangsolvids mimicked some other Hymenoptera with aposematic colour patterns can not be ruled out.

The generic placement of the new species is rather uncertain. It clearly does not belong to either *Linguatormyia* Arillo *et al*., 2015 or *Burmomyia* Zhang *et al*., 2019, based on the presence of a long Rs stem (which is short in *Linguatormyia*) and basally

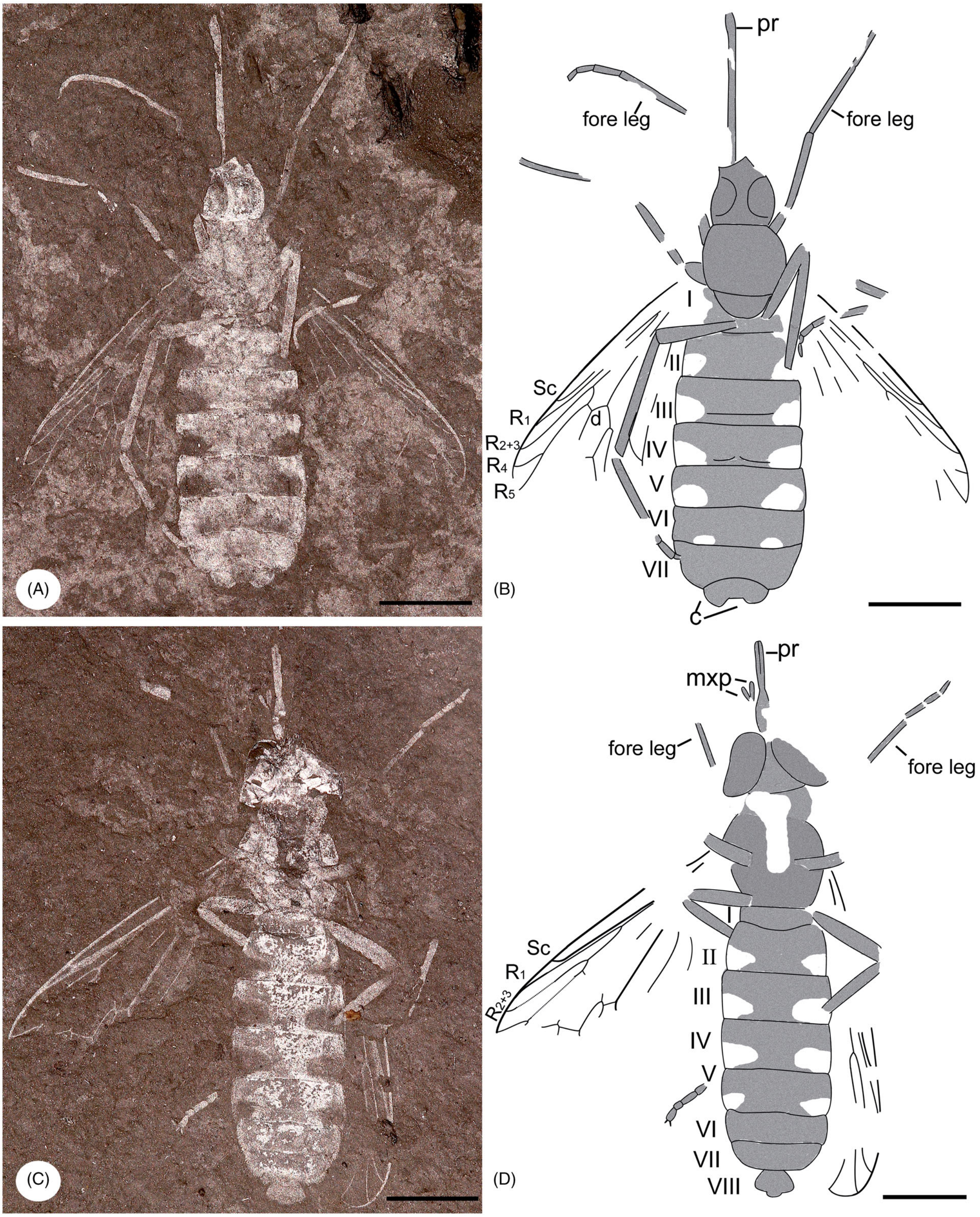

*Fig. 1.* Buccinatormyia gangnami sp. nov. (Zhangsolvidae): **A**, **B**, holotype GNUE-219001, presumably female; **C**, **D**, paratype GNUE-219002, presumably male. Abbreviations: c = cerci; mxp = maxillary palps; pr = proboscis. Roman numerals indicate abdominal segments. Scale bars 3 mm.

conjoined $M_1$ and $M_2$ (which diverge independently from cell d in *Burmomyia*). However, the new species is to some extent similar in wing venation to the three other zhangsolvid genera. The presence of a stem-vein $M_{1+2}$ in paratype GNUE-219010 (Fig. 3A,C) is reminiscent of *Cratomyia* Mazzarolo & Amorim, 2000, although in GNUE-219004 veins $M_1$ and $M_2$ instead diverge directly from cell d (Fig. 3B,D). As this latter specimen does not differ from GNUE-219010 in other respects, including abdomen colouration, it would be

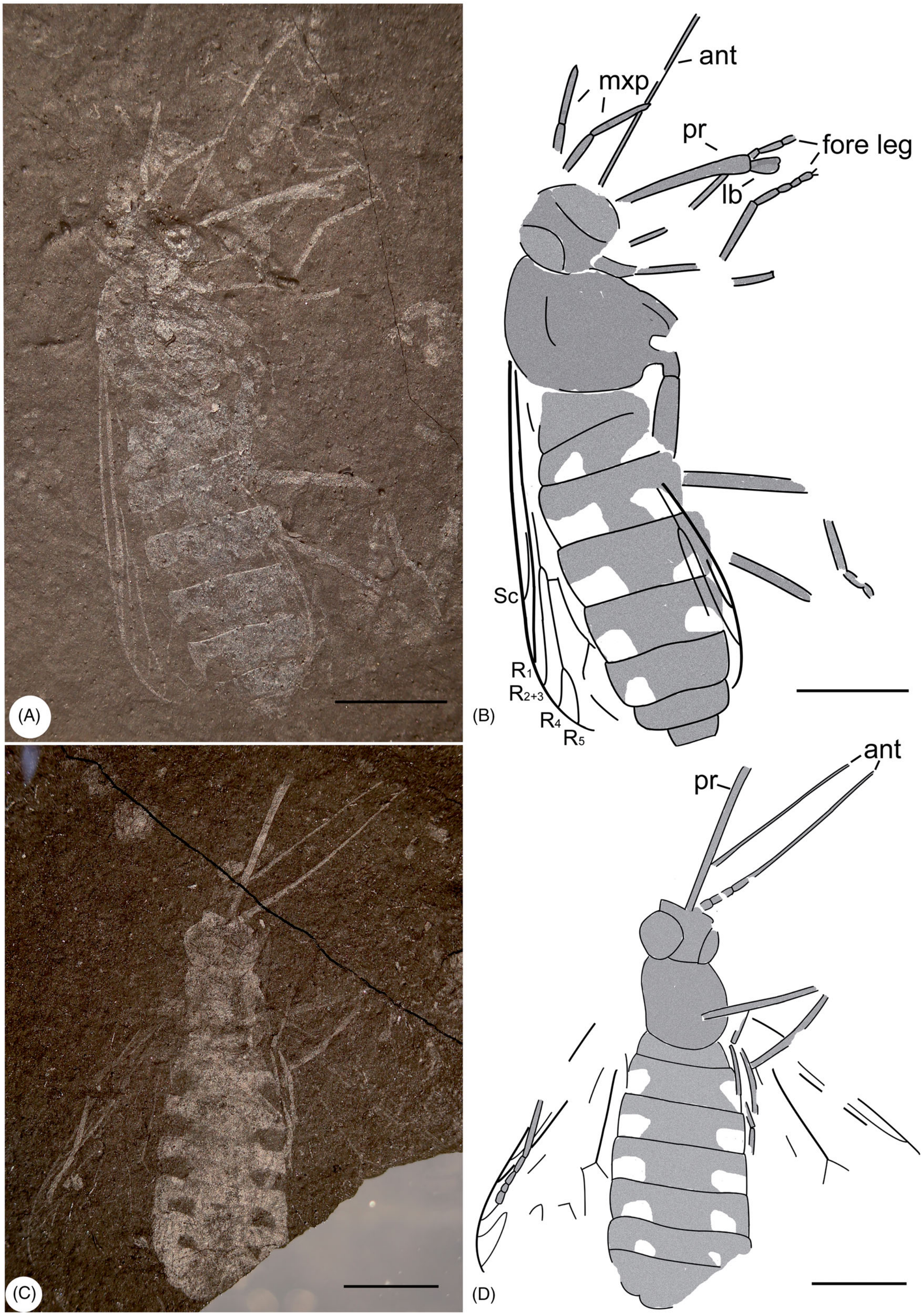

*Fig. 2.* Buccinatormyia gangnami sp. nov. (Zhangsolvidae): **A**, **B**, paratype GNUE-219003, sex unknown; **C**, **D**, paratype GNUE-219005, sex unknown. Abbreviations: ant = antenna; lb = labellum; mxp = maxillary palps; pr = proboscis. Scale bars: 3 mm.

unreasonable to assign it to a different taxon based on such a minor morphological difference. Moreover, the stem-vein $M_{1+2}$ is quite short and poorly discernible in GNUE-219010, whereas it is well developed in other members of *Cratomyia* (except *C. zhuoi* Zhang *et al.*, 2019). Based entirely on the wing venation, there are no obstacles to placing the new species within the genera *Zhangsolva* Nagatomi & Yang, 1998 or

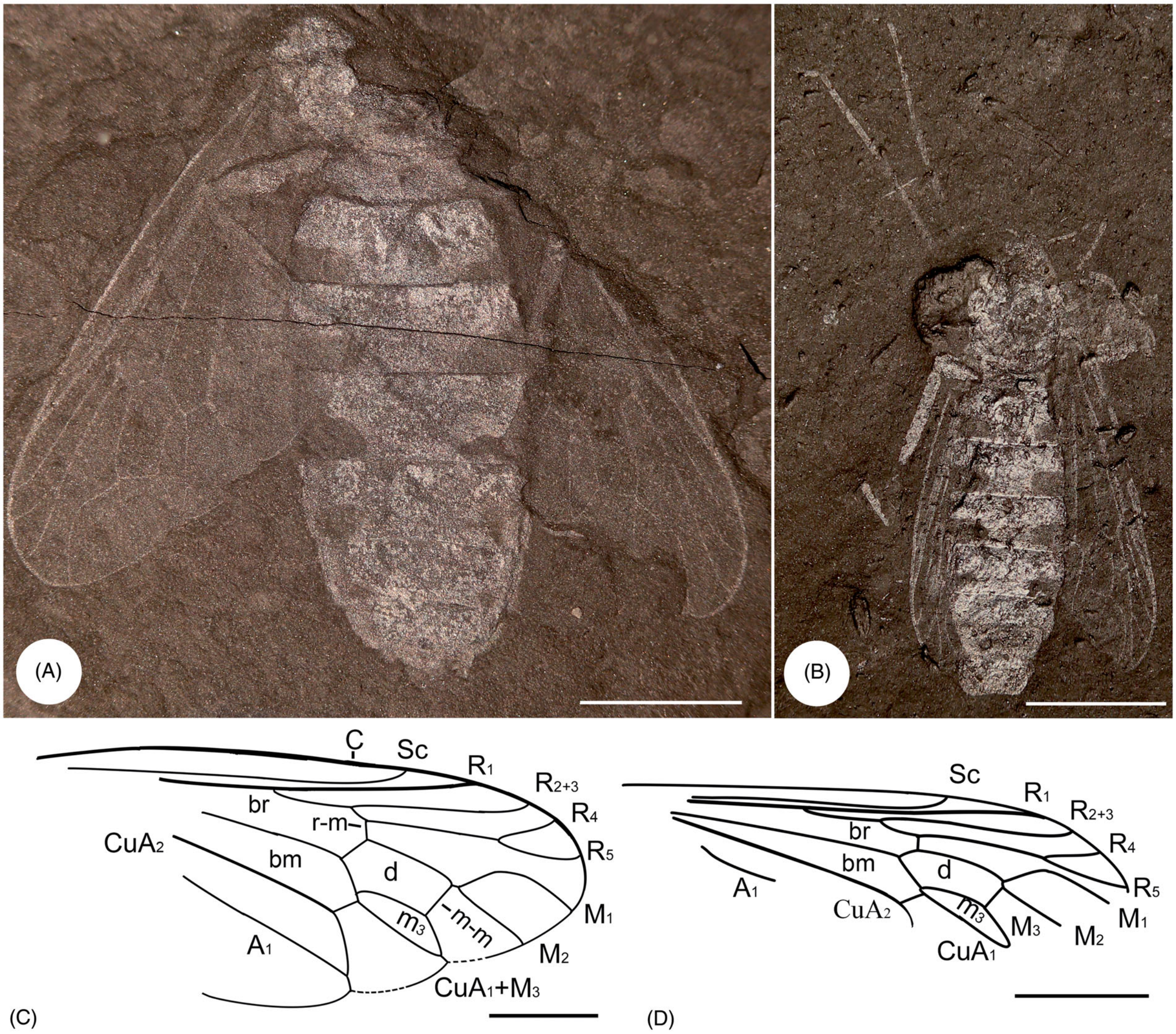

*Fig. 3.* Buccinatormyia gangnami sp. nov. (Zhangsolvidae): **A**, **C**, paratype GNUE-219010, sex unknown; **B**, **D**, paratype GNUE-219004, sex unknown. Scale bars 3 mm (A, B) and 2 mm (C, D).

*Table 2.* Body measurements of *Buccinatormyia gangnami* sp. nov. (Zhangsolvidae) from the Lower Cretaceous of South Korea.

| Specimen number | Head length (without proboscis, mm) | Antenna length (mm) | Proboscis length (mm) | Maxillary palp length (mm) | Body length (without head, mm) | Ratio of proboscis to body length |
|---|---|---|---|---|---|---|
| GNUE-219001 | 2.7 | – | 4.6 | – | 11.2 | 0.33 |
| GNUE-219002 | 2.0 | – | 2.9 | 1.5 | 13.0 | 0.19 |
| GNUE-219003 | *ca* 2 | *ca* 6 | 4.1 | 2.6 | 12.9 | 0.27 |
| GNUE-219004 | – | – | – | – | *ca* 9 | – |
| GNUE-219005 | *ca* 2 | 6.9 | 5.2 | – | 10.8 | 0.40 |
| GNUE-219010 | – | – | – | – | *ca* 12.3 | – |

*Buccinatormyia* Arillo *et al.*, 2015. However, the only known species of *Zhangsolva*, *Z. cupressa* (Zhang *et al.*, 1993), has antennae of moderate length [the number of flagellomeres of *Z. cupressa* is 12 according to the original description (Nagatomi & Yang 1998) or no more than 8 as Grimaldi et al. (2011) suggest] in contrast to the extremely elongated flagellum seen in the antennae of the new species. Since *Buccinatorymyia soplaensis* Arillo *et al.*, 2015 possesses antennae of similar morphology to the Korean zhangsolvids, we tentatively assign the new species to *Buccinatormyia*.

Specimens of *B. gangnami* differ significantly from each other in the morphology of the last abdominal segments (Fig. 1) and are therefore considered individuals of different sexes. It is worth noting that GNUE-219002, putatively interpreted herein as a male, has a proboscis proportionally much shorter than GNUE-219001, interpreted to be of the opposite sex. Therefore, it is possible that there is sexual dimorphism

*Table 3.* Wing measurements of *Buccinatormyia gangnami* sp. nov. (Zhangsolvidae) from the Lower Cretaceous of South Korea.

| Specimen number | Wing length (mm) | Wing width (mm) | Cell m3 length (mm) | Cell m3 width (mm) | Cell d length (mm) | Cell d width (mm) |
|---|---|---|---|---|---|---|
| GNUE-219001 | *ca* 9.5 | – | – | 0.30 | – | 0.65 |
| GNUE-219002 | *ca* 10 | – | – | – | – | – |
| GNUE-219003 | *ca* 9.2 | – | – | – | – | – |
| GNUE-219004 | *ca* 7.2 | – | 1.34 | 0.27 | 1.4 | 0.46 |
| GNUE-219005 | *ca* 10 | – | – | – | – | – |
| GNUE-219010 | *ca* 10.1 | *ca* 4.5 | 1.80 | 0.52 | 1.9 | 0.82 |

in the proboscis length of this species, a feature also observed in the tabanomorph fly *Galloatherix completus* Grimaldi, 2016 from the Burmese amber (Grimaldi 2016) and some extant brachycerans. At the same time, this difference might simply be an example of individual variation, which is not unexpected as great variation is also seen in the proboscis lengths of some extant conspecific Brachycera (e.g., Anderson *et al*. 2005).

*Buccinatormyia gangnami* is the third known species of Zhangsolvidae with extremely elongate antennae (Fig. 2), joining the aforementioned *B. soplaensis* from the Spanish amber and *Linguatormyia teletacta* Grimaldi, 2015 from the Burmese amber (Arillo *et al*. 2015). This feature of zhangsolvid antenna morphology, unique within both extant and extinct Brachycera, can be viewed as an extreme case of antennal evolution towards the spatial separation of olfactory sensing and mechanoreception, as observed in many brachycerans, where the former becomes localized in the flagellar base and the latter is localized to the apical flagellomeres (Stuckenberg 1999). The thin, elongate antennal flagella of *B. gangnami* and other zhangsolvids clearly had a tactile function. Arillo *et al*. (2015) hypothesize that elongate zhangsolvid antennae may have been used for guidance during feeding, but it is equally possible that they may also have been involved in courtship behaviour or in selecting a place for oviposition.

Pollen grains of the form-genus *Exesipollenites* Balme, 1957, attributable to Bennettitales, were found attached to the abdomen of *Buccinatormyia magnifica* Arillo *et al*., 2015 from Spanish amber (Peñalver *et al*. 2015). This result was taken as evidence that Zhangsolvidae and other long-proboscid Mesozoic insects were gymnosperm pollinators. However, Zhangsolvidae could also have visited the first flowers, as the radiation of angiosperms started in the Valanginian and was well under way by the early Aptian (Heimhofer *et al*. 2005, Doyle 2012). The fact that the genus *Buccinatormyia*, previously known only from the Spanish amber, is now found in nearly contemporaneous deposits in South Korea, together with geographically distant records of *Cratomyia* species in the Cretaceous of Brazil and Myanmar, indicates that zhangsolvid genera were broadly distributed. This could reflect ecological flexibility in the flies' diets or, conversely, wide distribution of their host plants owing to the equable climatic conditions of the Mesozoic era.

It has been suggested that Zhangsolvidae became extinct due to the demise of Mesozoic gymnosperms, which served as the main food source for their imagoes (Zhang & Wang 2017). However, this explanation does not seem sufficient, given the fact that other ancient lineages of long-proboscid Brachycera, like Acroceridae and Nemestrinidae, were also initially gymnosperm associated and nevertheless managed to survive the floral turnover linked to the rise of the angiosperms in the mid-Cretaceous (Khramov & Lukashevich 2019). So, rather than be too quickly satisfied with easy answers, we should admit that the evolutionary success or failure of different insect groups depends on many factors, including aspects of larval biology of which we know nothing for fossil taxa.

## Acknowledgements

We are thankful to the editors and two anonymous reviewers for valuable comments and suggestions.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

The research was supported by Russian Foundation for Basic Research [Grant No. 18-04-00322].

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