Alcheringa: An Australasian Journal of Palaeontology

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

The first Orthoptera (Insecta) from the Triassic of China

Chunpeng Xu, Yan Fang, Sam Heads, Qiang Zhang, Edmund A. Jarzembowski & BO Wang

To cite this article: Chunpeng Xu, Yan Fang, Sam Heads, Qiang Zhang, Edmund A. Jarzembowski & BO Wang (2020) The first Orthoptera (Insecta) from the Triassic of China, Alcheringa: An Australasian Journal of Palaeontology, 44:1, 93-98, DOI: 10.1080/03115518.2019.1662485

To link to this article: https://doi.org/10.1080/03115518.2019.1662485

Published online: 01 Dec 2019.

The first Orthoptera (Insecta) from the Triassic of China

CHUNPENG XU, YAN FANG, SAM HEADS, QIANG ZHANG, EDMUND A. JARZEMBOWSKI and BO WANG

Xu, C.P., Fang, Y., Heads, S., Zhang, Q., Jarzembowski, E.A. & Wang, B. 2 December. 2019. The first Orthoptera (Insecta) from the Triassic of China. *Alcheringa* 44, 93–98. ISSN 0311-5518.

The extinct family Locustavidae (Insecta: Orthoptera) is rare in the fossil record, and to date no representative has been reported from China. In this paper, *Hejiafanga tongchuanensis* gen. et sp. nov. is described based on a single forewing from the Middle Triassic Tongchuan Formation of Shaanxi Province, northwestern China. It is the first orthopteran to be reported from the Triassic of China and the oldest record of Caelifera from East Asia. The discovery expands the global distribution of Locustavidae (stem grasshoppers) and expands knowledge of this rare group during Middle–Late Triassic times.

Chunpeng Xu [cpxu@nigpas.ac.cn], State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, PR China; Yan Fang [yanfang@nigpas.ac.cn], State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, PR China; Sam Heads [sam.heads@gmail.com], Illinois Natural History Survey, University of Illinois at Urbana-Champaign, 1816 South Oak Street, Champaign, IL 61820-6960, USA; Qiang Zhang [cq@petrochina.com.cn], PetroChina Changqing Oilfield Changbei Operating Company, Xi'an, Shaanxi, 710016, PR China; Edmund A. Jarzembowski† [jarzembowski2@live.co.uk], State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, PR China; Bo Wang‡ [bowang@nigpas.ac.cn], State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, PR China. *Also affiliated with: University of Science and Technology of China, Hefei 230026, PR China. †Also affiliated with: Department of Earth Sciences, Natural History Museum, London SW7 5BD, UK. ‡Also affiliated with: Shandong Provincial Key Laboratory of Depositional Mineralization & Sedimentary Minerals, Shandong University of Science and Technology, Qingdao, Shandong 266590, PR China.* *Received 22.10.2019; revised 17.8.2019; accepted 28.8.2019.*

Key words: Triassic, Orthoptera, Caelifera, Locustavidae, Tongchuan, China.

ORTHOPTERA is traditionally divided into two suborders: Ensifera and Caelifera (Béthoux & Nel 2002, Rasnitsyn & Zherikhin 2002, Grimaldi & Engel 2005, Song *et al*. 2015). Ensifera incorporates crickets or katydids, whereas Caelifera includes the grasshoppers and their kin. Within Caelifera, there are 11 recognized superfamilies, eight of which are extant and three of which are extinct. Locustavidae is considered to be the oldest family of Caelifera (Sharov 1968, 1971, Storozhenko 1997) and was established by Sharov (1968) and divided into two subfamilies (Locustavinae and Praelocustopsinae) by Gorochov (2005). The fossil record of Locustavidae is extremely sparse, with only six genera reported to date (excluding the new genus): *Breviocustavus* Gorochov, 2005, *Locustavus* Sharov, 1968, *Mesacridites* Riek, 1954, *Miolocustavus* Gorochov, 2005, *Praelocustopsis* Gorochov, 2005 and *Triassolocusta* Tillyard, 1922 (Table 1). The family is exclusively Triassic, being reported from Kyrgyzstan, Russia and Australia (Sharov 1968, Béthoux & Ross 2005, Gorochov 2005). Here, we describe a new genus and species of Locustavidae from the Middle Triassic of China. The single specimen described here is not only the first Triassic orthopteran from China, but also the first locustavid from East Asia. The new find broadens our understanding of the palaeogeographic distribution of Locustavidae.

https://doi.org/10.1080/03115518.2019.1662485

Geological setting

The specimen examined (an isolated forewing) was collected from the top of the lower part of the Tongchuan Formation in the Qishuihe outcrop, Hejiafang Village, near Jinsuoguan Town, Tongchuan City, in Shaanxi Province, China (Fig. 1A). It was recovered from a greenish grey shale of the Middle Triassic Tongchuan Formation (Fig. 1B). The Tongchuan Formation is overlain conformably by the Upper Triassic Yanchang Formation and overlies the Lower – Middle Triassic Ermaying Formation. The lower part of the Tongchuan Formation consists of greyish green or red sandstone, with the top interbedded with shale and mudstone. The upper part is composed of greyish green or red fine-grained sandstone and siltstone, interbedded with greyish green or black shale, with black oil shale at the top

Published online 01 Dec 2019

Table 1. Compilation of all known genera and species of Locustavidae.

Genus species	Formation, Age	Locality	Reference
Locustavus Sharov, 1968	Madygen Formation, Middle/Upper Triassic	Madygen, Kyrgyzstan	Sharov 1968,
Locustavus madygenicus Sharov, 1968	Madygen Formation, Middle/Upper Triassic		Gorochov 2005
Locustavus problematicus Gorochov, 2005	Madygen Formation, Middle/Upper Triassic		
Locustavus intermedius Gorochov, 2005	Madygen Formation, Middle/Upper Triassic		
Locustavus deformatus Gorochov, 2005	Madygen Formation, Middle/Upper Triassic		
Locustavus minutus Gorochov, 2005	Madygen Formation, Middle/Upper Triassic		
Miolocustavus Gorochov, 2005	Madygen Formation, Middle/Upper Triassic	Madygen, Kyrgyzstan	Gorochov 2005
Miolocustavus reductus Gorochov, 2005	Madygen Formation, Middle/Upper Triassic		
Brevilocustavus Gorochov, 2005	Madygen Formation, Middle/Upper Triassic	Madygen, Kyrgyzstan	Gorochov 2005
Brevilocustavus distinctus Gorochov, 2005	Madygen Formation, Middle/Upper Triassic		
Brevilocustavus microscopicus, 2005	Madygen Formation, Middle/Upper Triassic		
Brevilocustavus distinctus Gorochov, 2005	Madygen Formation, Middle/Upper Triassic		
Praelocustopsis Sharov, 1968	Bugarikta Formation, Lower Triassic	Krasnoyarsk, Russia	Sharov 1968,
Praelocustopsis mirabilis Sharov, 1968	Bugarikta Formation, Lower Triassic		Gorochov 2005
Mesacridites Riek, 1954	Hawkesbury Sandstone, Middle Triassic	Beacon Hill,	Riek 1954,
Mesacridites elongata Riek, 1954	Hawkesbury Sandstone, Middle Triassic	Brookvale, Australia	Bethoux 2005
Triassolocusta Tillyard, 1922	Blackstone Formation, Upper Triassic	Ipswich, Australia	Tillyard 1922,
Triassolocusta leptoptera Tillyard, 1922	Blackstone Formation, Upper Triassic		Gorochov 2005
Hejiafanga gen. nov.	Tongchuan Formation, Middle Triassic	Tongchaun, China	Herein
Hejiafanga tongchuanensis sp. nov.	Tongchuan Formation, Middle Triassic		

(Zheng *et al.* 2016; Fig. 1C). The Tongchuan Formation yields bivalves, spinicaudatans, ostracods, insects, tadpole shrimp, fish, reptiles, spores, pollen and plant macrofossils (Li *et al.* 2007, Sun & Hong 2011, Zheng *et al.* 2016), and has a total thickness of *ca* 596 m.

The insect-bearing layer of the Tongchuan Formation is considered to be from the uppermost Ladinian stage (*ca* 238–237 Ma). The age for this deposit was determined by U–Pb geochronology (Zheng *et al.* 2018). The specimen we found is from the Tongchuan entomofauna, which is the most diverse Triassic entomofauna (an amalgam of local coeval insect-bearing assemblages), containing at least 28 insect families in 11 orders, including Blattodea, Coleoptera, Diptera, Grylloblattida, Glosselytrodea, Hemiptera, Mecoptera, Miomoptera, Odonatoptera, Orthoptera and Trichoptera (Zheng *et al.* 2018). Zheng *et al.* (2018) found more than 14 families of holometabolous insects in this entomofauna, and interpreted the depositional setting as lacustrine. The palaeolake was relatively small based on the limited lateral extent of the deposit.

Material and methods

The studied specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. The specimen was photographed using a Nikon D3S digital camera. Drops of ethanol were applied to the specimen to enhance the contrast and highlight the wing venation. Digital images were processed using Adobe Photoshop and imported into image-editing software (CorelDraw 13.0 and Photoshop CS) to create line drawings of the venation directly from the specimen images.

In this study, we use the following abbreviations for insect wing venation: ScA, Subcosta anterior; ScP, Subcosta posterior; RA, Radius anterior; RP, Radius posterior; M, Media; MA, Media anterior; MP, Media posterior; Cu, Cubius; CuA, Cubius anterior; CuP, Cubitus posterior; A, Analis, and 1A, first anal vein. We follow the wing venation scheme proposed by Béthoux & Nel (2001, 2002), although the works of Sharov (1968) and Gorochov (1995) were also consulted. For consistency with traditional nomenclatural procedure, we follow the classification of Orthoptera used by Sharov (1968).

Systematic palaeontology

Superfamily LOCUSTOPSOIDEA Handlirsch, 1906
Family LOCUSTAVIDAE Sharov, 1968

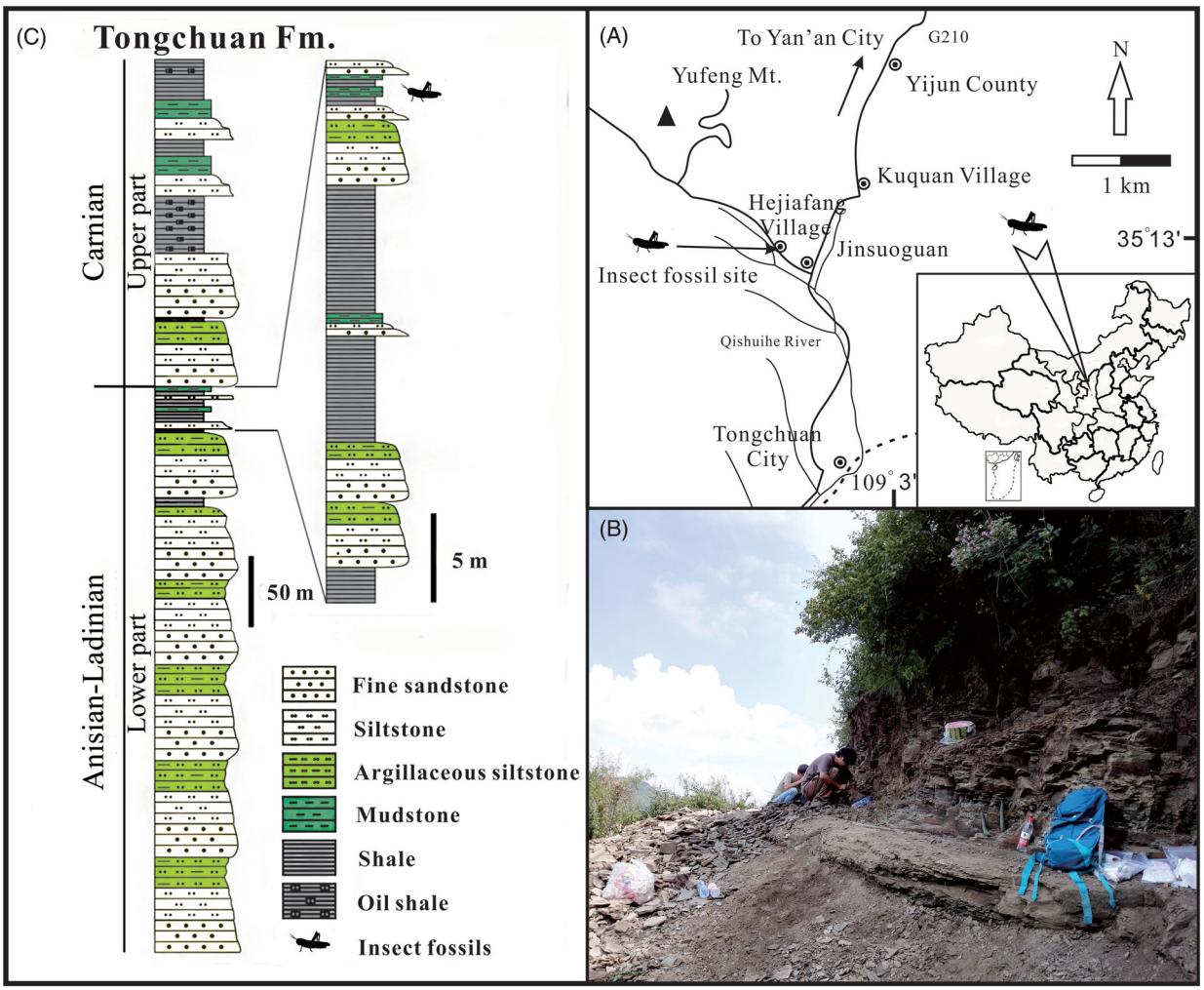

Fig. 1. Fossil locality in the Qishuihe outcrop of Jinsuoguan Town, Tongchuan City, Shaanxi Province, China. **A**, Geographical sketch map of Jinsuoguan Town; **B**, Photograph of the Qishuihe outcrop yielding the fossil insects; **C**, Stratigraphic column of the Tongchuan Formation (modified after Zheng *et al*. 2018).

Hejiafanga gen. nov.

Type species. Hejiafanga tongchuanensis sp. nov. by designation herein; monotypic.

Etymology. The generic name is from the village name 'Hejiafang' where the type species was discovered.

Diagnosis. Forewing: small, long and narrow; ScP with not less than 17 branches of which six end in stem ScA and the 6th−12th branches of ScP give off arched crossveins; M with three branches, first branch originating near base of forewing; RP diverging from R very proximal of 1A and ending in posterior margin; distance between the MA/MP and MA1/MA2 splits relatively long; CuA + CuPaα pectinately two-branched.

Hejiafanga tongchuanensis sp. nov. (Fig. 2)

Diagnosis. First simple branch of M originating quite near forewing base; stem RA and RP quite long and the branches of RA and RP close to the apical part of forewing.

Etymology. The specific epithet is derived from the type locality, Tongchuan City.

Holotype. NIGP170040, part and counterpart; isolated forewing with apex not preserved.

Type locality, unit and age. Hejiafang village, Suojinguan Town, Tongchuan City, Shaanxi Province, China; Tongchuan Formation; Middle Triassic.

Description. Forewing long and narrow, missing parts of the base and apex. Preserved length 16.20 mm, total length 20.0−26.0 mm; width 4.53 mm.

Area between ScA and anterior margin narrow, with network of crossveins; ScA almost straight and oblique anteriorly, ending in anterior margin at 5.35 mm distal of wing base (Fig. 2). Crossveins between ScA and anterior margin strong and weakly reticulated. ScP very long, with no less than 17 distinct

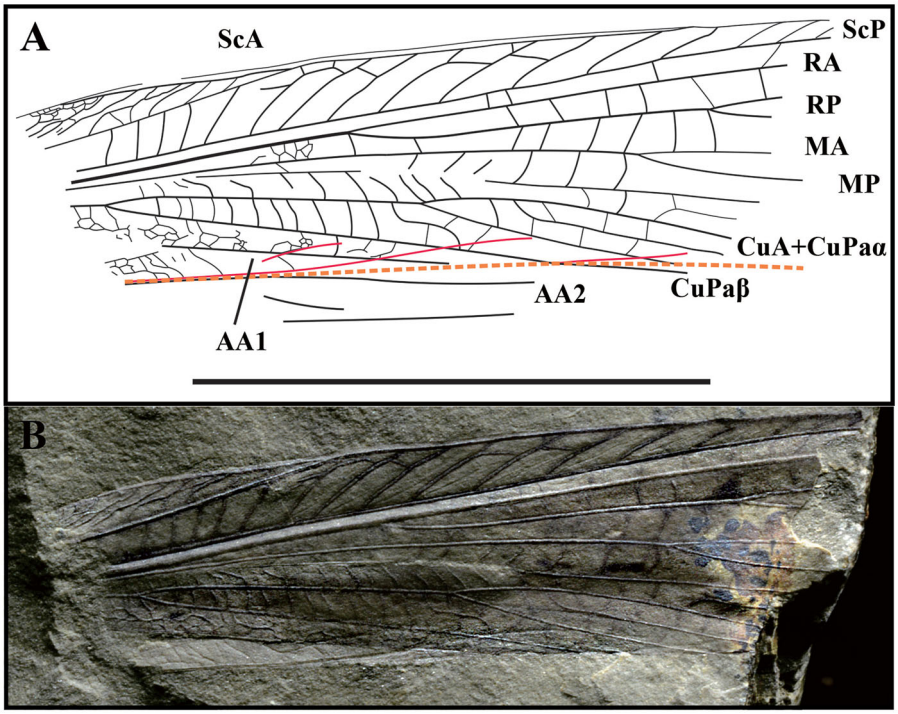

Fig. 2. Holotype NIGP162042, **A**, Drawing (the orange imaginary line is the axis of symmetry inflexion, and the red lines are the impressed veins); **B**, Photograph. Scale bar = 10 mm.

and oblique branches, of which six end in stem ScA; branches 6−12 of ScP with arched crossveins. R strongly marked and oblique anteriorly; RA and RP diverging at 6.6 mm distal of forewing base, area between R/RA and ScP narrow. First branch of RP originating at about 13.6 mm distal of forewing base, only two branches of RP preserved; area between RP and RA slightly broader than area between RA and ScP; first simple branch of M originating near forewing base (about 3.3 mm), much basal of origin of RP; second and third simple branches of M diverging at about 12.0 mm distal of forewing base; area between main branch of M and R narrow; area between main branches of M and RP narrow in its basal half, and progressively broadening in its middle part; MA forking into two branches. Distance between the MA/MP and MA1/MA2 splits relatively long (8.7 mm); MA1/MA2 split between RA/RP splits and the first forking of RP, and close to the first forking of RP, not RA/RP split; RA/RP split between MA/MP and MA1/MA2 split; CuPaβ diverging from CuA + CuPaα proximally, 1.1 mm distal of forewing base, and much basal of origin of first branch of M; CuA + CuPaα with two branches in total; provided that the material is probably a damaged wing, the visible vein is probably 1A overlapping CuPb, and 1A almost straight; 2A slightly curved. Crossveins between RA and RP, RP and M, branches of M, M and CuA + CuPaα all straight; crossveins between CuA + CuPa/1A(1A overlapping CuPb) and 2A irregular. Crossveins between CuA + CuPa/1A and 2A disjoined from each other to form a network.

Discussion

The new material is a wing that is damaged around the margin and partly creased. The axis of symmetry inflexion is in orange dashed line, the impressed veins are in red lines (Fig. 2).

Hejiafanga can be placed definitively in Locustavidae based on the following characters: ScA nearly straight, area between ScP and ScA widest near ScA, ending in anterior margin; distance between the MA/MP and MA1/MA2 splits relatively long; CuA + CuPaα pectinately two-branched; Cu branched near forewing base; and CuPb slightly longer than stem CuA + CuPa. Members of Locustavidae were known previously only from the Triassic of Kyrgyzstan, Russia and Australia (Tillyard 1922, Béthoux & Ross 2005, Gorochov 2005). To date, three genera (with nine species) have been reported from the Madygen Formation: *Locustavus*, *Brevilocustavus* and *Miolocustavus*. *Locustavus* and *Brevilocustavus* were attributed to the subfamily Locustavinae; and the genera *Praelocustopsis* and possibly *Triassolocusta* were considered to be members of Praelocustopsinae (Gorochov 2005). *Triassolocusta* with only one species, *T. leptoptera* Tillyard, 1922, is known from the Blackstone Formation of Queensland, Australia (Tillyard 1922). *Triassolocusta leptoptera* is a small species with CuP having only two simple branches, thereby differing from all other locustavids. *Mesacridites* is known from the Hawkesbury Sandstone (Middle Triassic) at Beacon Hill, Australia (Béthoux & Ross 2005). The new genus, *Hejiafanga*, is more or

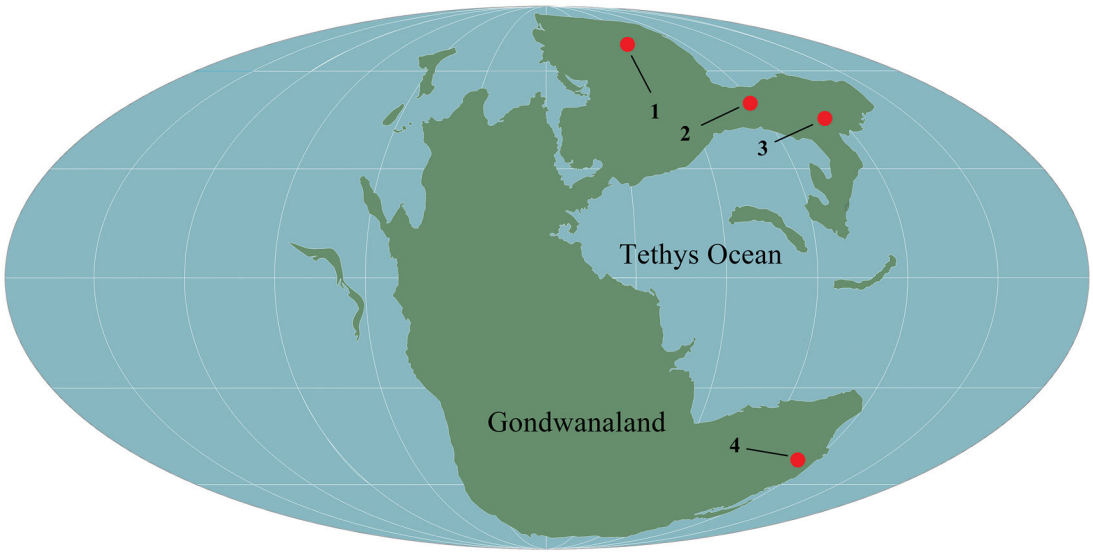

Fig. 3. Palaeogeographical map (modified after Scotese 2014) showing the Triassic global distribution of Locustavidae. 1: Tunguska Basin, Siberia, Russian Federation; 2: Madygen, Kyrghyzstan; 3: Tongchuan, Shaanxi, China; 4: Beacon Hill, Brookvale, New South Wales, Australia.

less similar to *Mesacridites* in that the area between ScP and ScA/anterior margin has numerous branches, rather than the condition in Locustavinae and Praelocustopsinae in which genera, such as *Locustavus*, *Miolocustavus* and *Brevilocustavus*, have few branches (between two and four branches) ending at the anterior margin. By contrast, *Hejiafanga* and *Mesacridites* possess ten or 11 branches, seven branches close to ScA, and have distinct crossveins between them. Another obvious difference between *Hejiafanga* and all other locustavid genera is the origin of MP close to the forewing base, much closer to the origin of CuPb (rather than close to the bifurcation point of CuPa). In addition, the new genus differs from *Mesacridites* in the cubital area with four branches (six in *Mesacridites*), and narrower anal area with fewer anal veins.

Prior to the discovery of *H. tongchuanensis*, only three Caelifera were described from the Mesozoic of China: *Pseudoacrida costata* Lin, 1982 (Lower Cretaceous, Liupanshan Group of Gansu Province and Laiyang Formation of Shandong Province), *Mesolocustopsis sinica* Hong, 1990 (Lower Cretaceous, Laiyang Formation of Shandong Province) and *Locustopsis rhytofemoralis* Gu *et al.*, 2016 (Lower Cretaceous, Jehol biota of Liaoning Province). These three species were attributed to Locustopsidae. To date, no Orthoptera have been described from the Triassic of China. The specimen described here is not only the first Triassic locustavid from China, but also the oldest caeliferan described from East Asia.

Locustavid fossils are rare and restricted to the Middle – Late Triassic of Kyrgyzstan, Australia, Russia and China (Fig. 3). We note that this family had a high-latitude distribution during the Middle – Late Triassic, which does not fit the distribution of most Orthoptera (most Orthoptera are cosmopolitan except for permanently ice-covered areas). There are two explanations for this phenomenon. The first is that Locustavidae was definitively distributed in middle and high latitudes, which is similar to *Bohemanella*—a genus of Orthoptera found only in middle and high latitudes (e.g., France, Italy, Greece and Canada: Defaut 1999, Skareas & Hsiung 1999, Willemse & Willemse 2008, Massa *et al.* 2012). The other explanation is that Locustavidae had a cosmopolitan distribution, but owing to the incomplete fossil record, its recorded geographic range is still limited. Locustavidae was probably distributed in middle–low latitudes. Fossils from additional sites are needed to resolve this issue.

Acknowledgements

We thank two anonymous reviewers for providing some constructive suggestions and the editor for editorial assistance. Thanks also go to D.R. Zheng and X.D. Zhao for helpful dicussion.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This research was supported by the Strategic Priority Research Program (B) of the Chinese Academy of Sciences [XDB26000000], the National Natural Science Foundation of China [41572010, 41622201, 41688103], and the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) [No. 183101]. This is a Leverhulme Emeritus Fellowship contribution for EAJ.

References

Béthoux, O. & Nel, A., 2001. Venation pattern of Orthoptera. *Journal of Orthoptera Research 10*, 195–198.]

Béthoux, O. & Nel, A., 2002. Venation pattern and revision of Orthoptera *sensu n*. and sister group. Phylogeny of Palaeozoic and Mesozoic Orthoptera *sensu. n*. *Zootaxa 96*, 1–88.

Béthoux, O. & Ross, A.J., 2005. *Mesacridites* Riek, 1954 (Middle Triassic; Australia) transferred from Protorthoptera to Orthoptera: Locustavidae. *Journal of Paleontology 79*, 607–610.

Carde, R., 2009. *Encyclopedia of Insects*. Elsevier/Academic Press, Burlington, MA, 209 pp.

Defaut, B., 1999. *La Détermination Des Orthoptères de France*. Edition à Compte D'auteur, Bédeilhac, France, 83 pp.

Gorochov, A.V., 1995. System and evolution of the suborder Ensifera (Orthoptera) (in 2 parts). *Proceedings of the Zoological Institute, Russian Academy of Science 260*, 1–224. (Russian)

Gorochov, A.V., 2005. Review of Triassic Orthoptera with descriptions of new and little known taxa: Part 2. *Paleontological Journal 39*, 272–279.

Grimaldi, D. & Engel, M., 2005. *Evolution of the Insects*. Cambridge University Press, New York, 755 pp.

Gu, J.J., Yue, Y.L., Shi, F.M., Tian, H & Ren, D., 2016. First Jurassic grasshopper (Insecta, Caelifera) from China. *Zootaxa 4169*, 377–380.

Li, Z., Hong, Y.C. & Yang, D., 2007. A new Middle Triassic genus and species of Mylacridae (Blattodea) from China. *Zootaxa 7*, 53–59.

Massa, B., Fontana, P., Buzzetti, F. M., Kleukers, R & Odé, B., 2012. *Fauna d'Italia—XLVIII—Orthoptera*. Calderini, Bologna, 563 pp.

Rasnitsyn, A.P. & Zherikhin, V.V., 2002. *History of Insects*. Springer, Netherlands, 437–444 pp.

Riek, E.F., 1954. Further Triassic insects from Brookvale, N.S.W. (orders Orthoptera Saltatoria, Protorthoptera, Perlaria). *Records of the Australian Museum 23*, 161–168.

Scotese, C.R., 2014. *Atlas of Middle & Late Permian and Triassic Paleogeographic Maps, Maps 46 from Volume 3 of the Paleomap Atlas for ArcGIS (Jurassic and Triassic) Mollweide Projection*. PALEOMAP, Evanston.

Sharov, A.G., 1968. Phylogeny of orthopteroid insects. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR 118*, 1–217. (Russian)

Sharov, A.G., 1971. *Phylogeny of the Orthopteroidea*. Academy of Science of the USSR. Transactions of the Institute of Paleontology, Volume 118. Translated from Russian by Salkind, J. Keter Press, Jerusalem, vi + 249 pp. 53 figs, 12 pls.

Skareas, S. D. & Hsiung, C.C., 1999. Male genitalia of selected genera of the subfamily Melanoplinae. *Journal of Orthoptera Research 8*, 125–145.

Song, H.J., Amédégnato, C., Cigliano, M.M., Desutter-Grandcolas, L., Heads, S.W., Huang, Y., Otte, D & Whiting, M.F., 2015. 300 Million years of diversification: elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics 31*, 621–651.

Storozhenko, S.Y., 1997. *Bionomics of Grasshoppers, Katydids and Their Kin, Fossil History and Phylogeny of Orthopteroid Insects*. CAB International, Wallingford, UK, 59–82 pp.

Sun, X.L. & Hong, Y.C., 2011. Mid-Triassic species of Mesopanorpodidae (Insecta, Mecoptera) from Shaanxi, China. *Acta Zootaxonomica Sinica 36*, 26–28.

Tillyard, R.J., 1922. Mesozoic insects of Queensland. 9. Orthoptera, and additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. *Proceedings of the Linnean Society of New South Wales 47*, 447–469.

Willemse, F.M.H. & Willemse, L.P.M., 2008. An annotated checklist of the Orthoptera-Saltatoria from Greece including an updated bibliography. *Articulata Beiheft 13*, 50.

Zheng, D.R., Nel, A., Wang, B., Jarzembowski, E.A., Chang, S.C. & Zhang, H.C., 2016. The first Triassic 'Protodonatan' (Zygophlebiidae) from China: stratigraphical implications. *Geological Magazine 10*, 1–6.

Zheng, D.R., Chang, S.C., Wang, H., Fang, Y., Wang, J., Feng, C.Q., Xie, G.W., Jarzembowski, E.A., Zhang, H.C & Wang, B., 2018. Middle–Late Triassic insect radiation revealed by diverse fossils and isotopic ages from China. *Science Advances 4*, eaat1380.