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New cockroaches (Insecta, Blattaria, Fuziidae) from the Middle Jurassic Jiulongshan Formation in northeastern China

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Fuziidae is a significant cockroach family reported only from the Middle Jurassic Jiulongshan Formation of northeastern China. Male Fuziidae with forceps-like cerci are unique in the 320 Ma history of cockroaches. *Longifuzia pectinata* gen. et sp. nov. is described from the Jiulongshan Formation based on four male specimens. It can be distinguished from other fuziids by its larger body size, extremely long telescopic abdomen, numerous forewing veins, characteristic coloration on the forewing and unique male genitalia. Three of four type specimens have asymmetric venation in the wings. The narrow and elongate body shape is suggestive of alternative, non-standard diets because a wide (fat) body is necessary for nitrogen fixation in cockroaches. Nevertheless, well-developed male tergal glands provide evidence of nuptial female feeding on nitrogen provisions. This new taxon expands the known diversity and highlights the morphological disparity of this family at the Daohugou locality in northeastern China.

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FUZIIDAE, a small family documented only from the Middle Jurassic Jiulongshan Formation of northeastern China, was erected by Vršanský *et al.* (2009). To date, four genera with six species have been described: *Fuzia dadao* Vršanský *et al.*, 2009, *Parvifuzia marsa* Guo & Ren, 2011, *P. brava* Guo & Ren, 2011, *P. peregrina* Wei *et al.*, 2013, *Arcofuzia cana* Wei *et al.*, 2012b and *Colorifuzia agenora* Wei *et al.*, 2013 (Vršanský *et al.* 2009, Guo & Ren 2011, Wei *et al.* 2012a, 2012b, Wei *et al.* 2013).

The family representatives have unique characters (Vršanský *et al.* 2009), i.e., pronotum as wide as the width of the elongated body, very robust forewing with simple or branched Sc, wide costal area, short clavus and forceps-like male cerci. Owing to the high diversity of Fuziidae, it is the most significant (unique cerci shape and function in males) cockroach family at the site, and thus far has been found only in China. Other less prominent families that are also known from single localities include Olidae (Vršanský & Wang 2017, Li & Huang 2018a), Socialidae (Vršanský 2010),

Skokidae (Vršanský 2007), Alienopteridae (Bai *et al.* 2016, 2018, Kočárek 2018, Vršanský *et al.* 2018) =Aethiocarenidae (Poinar & Brown 2017) and possibly Manipulatoridae (Vršanský & Bechly 2015). Most of the other cockroaches described from amber shared broad habitats, even ranging between Laurasia and Gondwana (Vršanský 2003, Sendi & Azar 2017, Šmídová & Lei 2017, Mlynský *et al.* 2018, Podstrelená & Sendi 2018, Vršanský *et al.* 2019).

Material and methods

Four specimens were collected from the Middle Jurassic Jiulongshan Formation at Daohugou Village, Ningcheng County, Inner Mongolia, northeastern China (Ren *et al.* 2002, Gu *et al.* 2012, Wang *et al.* 2012, Meng *et al.* 2019).

The specimens were examined with an Olympus SZX7 dissecting microscope and illustrated with the aid of a drawing tube attached to the microscope. Line drawings were prepared using CorelDraw 12 graphic and Photoshop software. The photographs were taken using a Leica M205c microscope with an attached Leica DFC450c digital camera system, and detail

pictures of cerci were taking under alcohol. Material is deposited in the Capital Normal University, Beijing, China (CNUB, Curator: Dong Ren) and in the Tianjin Natural History Museum, China (TNP). Venation nomenclature follows Comstock & Needham (1898) and Li & Huang (2018b).

Abbreviations used: A— anal vein; Ant— antenna; Aro— arolium; C— cercus; Cl— claw; CuA— cubitus anterior; CuP— cubitus posterior; F. ant— antennal socket; G— gland; LFW— left forewing; M— media; Not— notch; Prn— pronotum; R— radius; Rs— radius sector; RFW— right forewing; Sc— subcosta; St— stylus; Tas— tarsus; T— tergites.

Institutional abbreviations: CNU— Capital Normal University, Beijing, China; TNP— Tianjin Natural History Museum, Tianjin, China.

Systematic palaeontology

Order BLATTARIA Latreille, 1810

Superfamily CALOBLATTINOIDEA Vršanský &

Ansorge in Vršanský, 2000

Family FUZIIDAE Vršanský *et al.*, 2009

Longifuzia gen. nov.

Type species. Longifuzia pectinata sp. nov. by monotypy.

Geographic range. Daohugou Village, Ningcheng County, Inner Mongolia, China.

Stratigraphic range. Jiulongshan Formation, late Middle Jurassic (Ren *et al.* 2002).

Derivation of name. The generic name is a combination of the Latin ‘*longis*’ referring to its long abdomen, and ‘*Fuzia*’, the type genus of Fuziidae.

Diagnosis. Body large. Extremely long telescopic abdomen; forewing with more branches than other representatives of the family; the characteristic striped coloration extensive on forewing excluding the costal area; forceps composed of three apical segments.

Differential diagnosis. The new genus differs from *Fuzia*, *Parvifuzia*, *Arcofuzia* and *Colorifuzia* in its larger body size; extremely long telescopic abdomen; forewing with more branches; Sc thick, simple or more branched; and characteristic striped coloration extensive on forewing (and partially on hind wing) excluding the costal area. Forceps in the new genus composed of three apical segments, which are different from forceps composed of two apical segments in the other three genera of Fuziidae, except for *Parvifuzia*.

Longifuzia pectinata sp. nov. (Figs 1–5)

Derivation of name. The specific name is from the Latin ‘*pectinatus*’ referring to the branches of R.

Holotype. CNU-B-NN-2006920 p/c (part and counterpart) (Figs 1 and 3A).

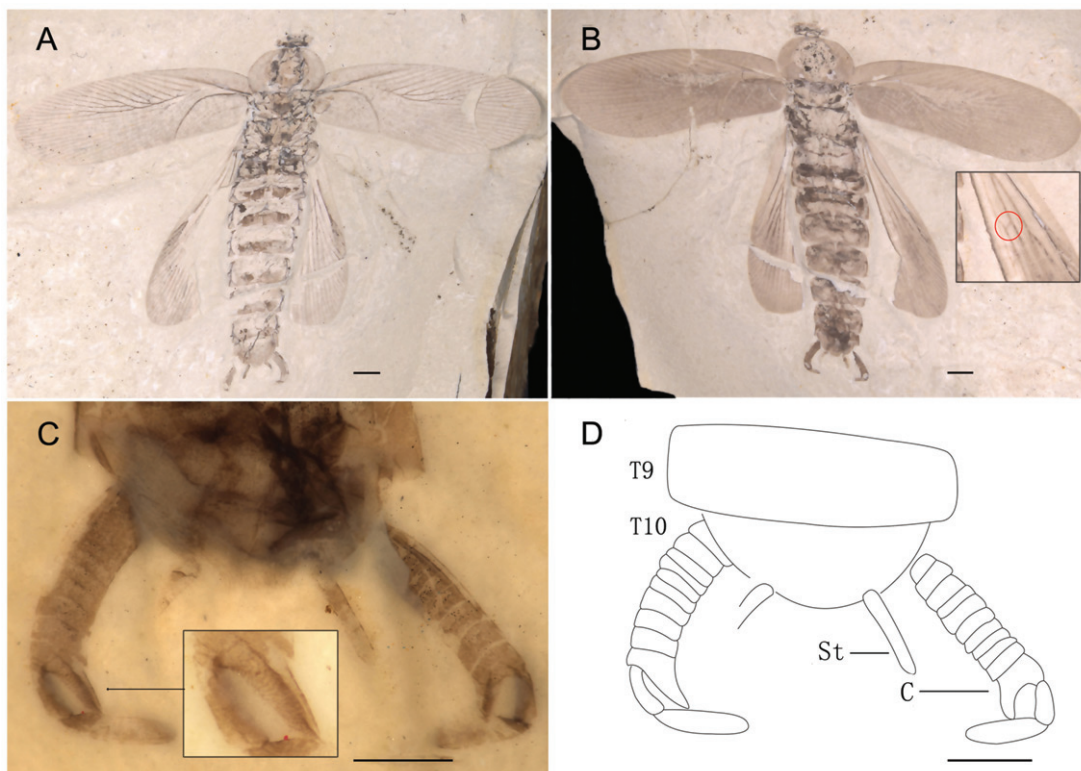


Fig. 1. *Longifuzia pectinata* Liang, Shih & Ren gen. et sp. nov. **A, B**, Part and counterpart of the holotype (CNU-B-NN-2006920), red circle in the window shows an extra cross-vein in the left hind wing; **C**, Detail of cerci, black box shows long sensilla chaetica on notch; **D**, Line drawing of cerci. Scale bars for A, B = 2 mm; for C, D = 1 mm.

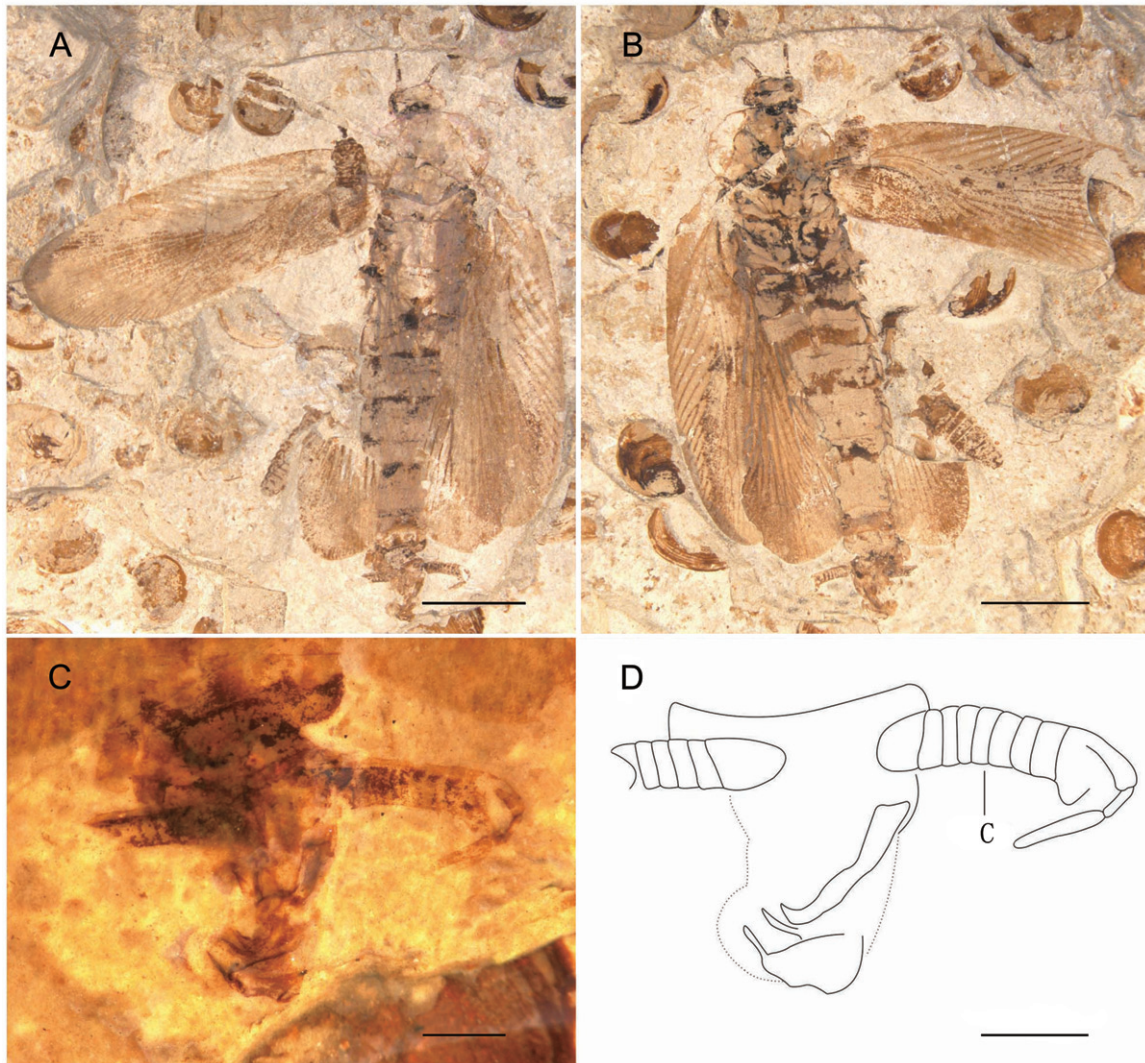


Fig. 2. *Longifuzia pectinata* Liang, Shih & Ren gen. et sp. nov. paratype TNP42409. **A, B**, Habitus, part and counterpart; **C**, Cerci; **D**, Line drawing of cerci. Scale bars for **A, B** = 5 mm; for **C, D** = 1 mm.

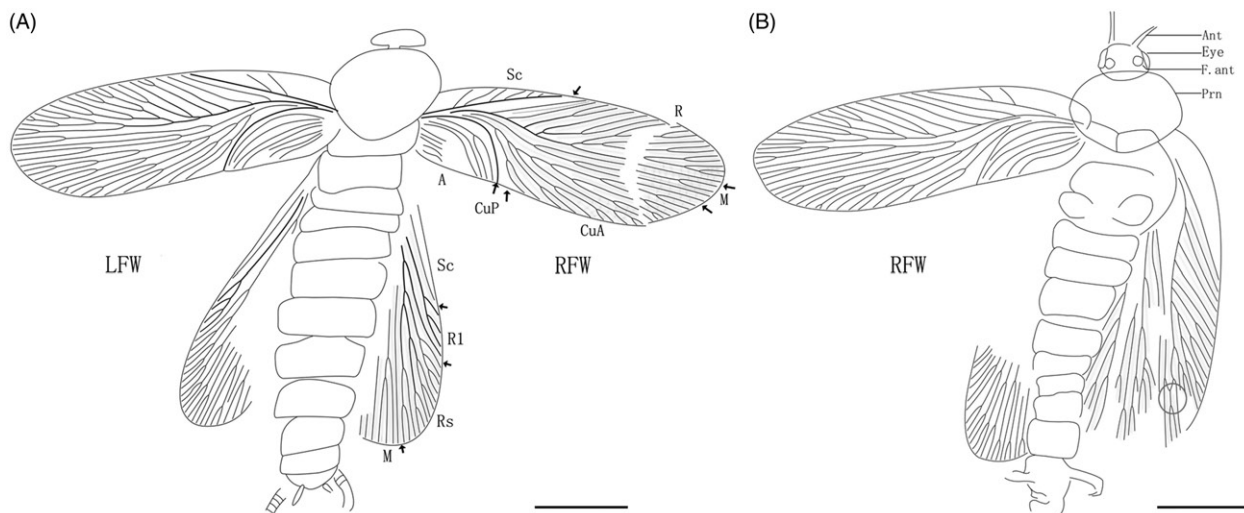


Fig. 3. Line drawings of *Longifuzia pectinata* Liang, Shih & Ren gen. et sp. nov. **A**, Holotype CNU-B-NN-2006920; **B**, Paratype TNP42409, red circle in right forewing indicates asymmetric veins. Scale bars = 5 mm.

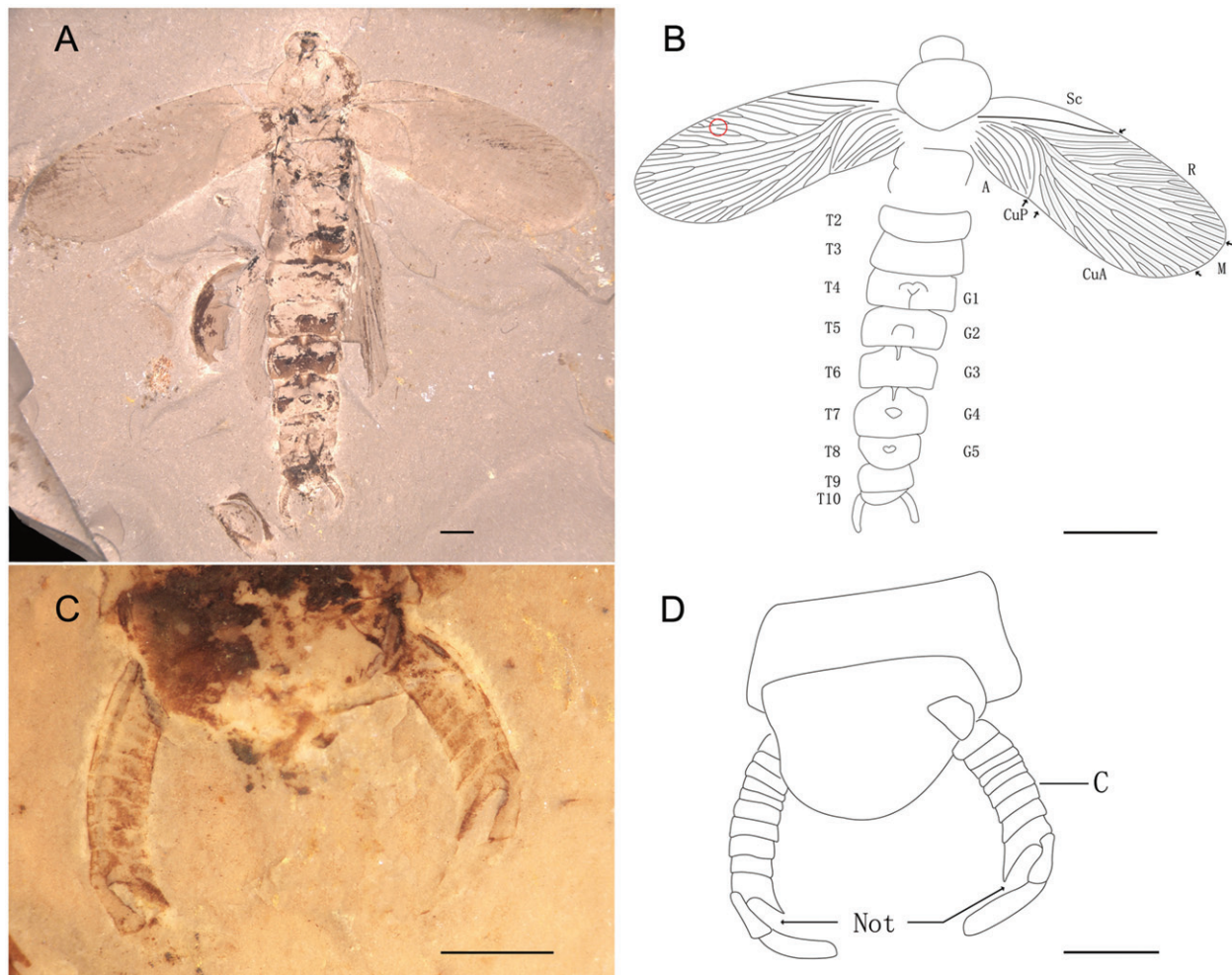


Fig. 4. *Longifuzia pectinata* Liang, Shih & Ren gen. et sp. nov. Paratpe CNU-B-NN2006950. **A**, Habitus; **B**, Line drawing, red circle in left forewing indicates asymmetric veins; **C**, Detail of cerci; **D**, Line drawing of cerci. Scale bars for A = 2 mm; for B = 5 mm; for C, D = 1 mm.

Type locality. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Type unit. Jiulongshan Formation, the Middle Jurassic.

Paratypes. TNP42409 p/c (part and counterpart) (Figs 2 and 3B), CNU-B-NN-2006950 (Fig. 4), and CNU-B-NN-2006951 (Fig. 5). From the same locality as the holotype.

Diagnosis. Forewing with 41–59 veins. Sc simple or branched; Rs differentiated; CuP strongly curved, clavus very short; R, M and CuA branches secondarily divided.

Description. Male large cockroach, with body length (excluding the head and cerci) 24.2–28.5 mm, width of abdomen 4.0–5.6 mm. Head slightly wider (length/width 2.0/2.7 mm; Fig. 3B); eyes protruding beyond the outline of head; antennal sockets circular; pronotum elliptical, length 4.0–6.0 mm, width 4.5–6.1 mm (measurements see Table 1).

Forewing with distinct intercalaries, and cross-veins present in R, M and CuA areas (visible on left

forewing of CNU-B-NN-2006920), length/width: 13.6–17.9 mm/5.5–6.0 mm, venation dense, with 41–59 veins at wing margin. Characteristic striped coloration extensive on forewing (and partially on hind wing) excluding costal area (Fig. 5A, B). Forewing areas 93.7 mm², 91.5 mm² in -920 LFW and RFW; 86.8 mm² in -42409 LFW; 80.6 mm² and 77.5 mm² in -950 LFW and RFW; 70.84 mm² in -951 LFW; Sc thick, simple or branched, with 1–7 somewhat obscure branches (1–7); Rs differentiated, branches secondarily divided; R 15–22; M 3–9; CuA 10–17; CuP strongly curved; A 6–9, clavus very short, less than one-third of the wing's length. Hind wing length about 16.5 mm, with distinct intercalaries; Sc simple; R1 and Rs differentiated, R1 thick, 3–4, and Rs 14–15; M 14, with secondary branches; CuA secondarily branched and with many branches (number of veins see Table 3).

Abdomen with 10 visible segments and tergal glands at T4–8 (Fig. 4B), and located in the centre of respective abdominal segments. Cerci with 11–12 segments with long sensilla chaetica (Fig. 1C), the

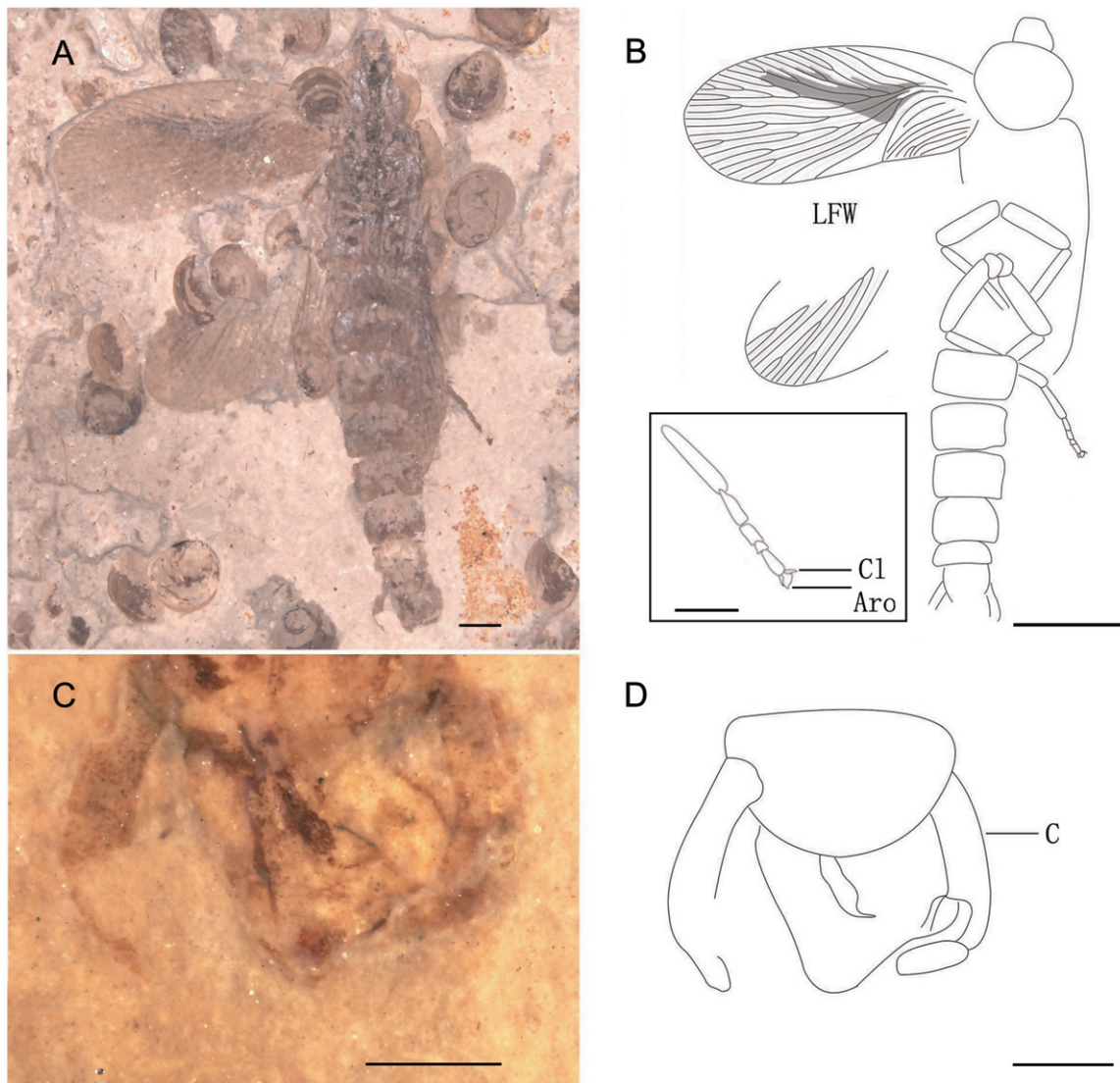


Fig. 5. *Longifuzia pectinata* Liang, Shih & Ren gen. et sp. nov. Paratype CNU-B-NN2006951. **A**, Habitus; **B**, Line drawing, black box shows the detail of tarsus of hind leg; **C**, Detail of cerci; **D**, Line drawing of cerci. Scale bars for A=2 mm; for B=5 mm; for C, D=1 mm.

Table 1. Measurements of body, pronotum and left and right forewing for four specimens.

Specimen	Body		Pronotum		LFW		RFW	
	Length	Width	Length	Width	Length	Width	Length	Width
-920	24.2	5.3	4.5	5.9	17.9	6.0	17.3	6.3
-950	27.0	5.6	4.8	5.7	15.3	5.5	15.0	6.0
-951	28.5	4.5	4.0	4.5	13.6	6.0		
-42409	24.9	4.0	4.6	6.0			17.9	5.8

terminal three segments are specially structured to form a pair of forceps with notches (for length/width of all segments of cerci see Table 2); titillator present, basally wide and become more slender and curved apically; styli unsegmented (Fig. 1C, D), the length/width of styli in specimen -920 (right) is 1.14/0.20.

Femur with short spines in hind leg, 7.8 mm long; tibia 4.9 mm long, with two long spines; tarsus five-segmented, the fourth segment the shortest (length of tarsomeres: 1st: 1.55 mm; 2nd: 0.70 mm; 3rd: 0.41 mm;

4th: 0.24 mm; 5th: 0.54 mm); pretarsus with a pair of claws and arolium (Fig. 5B). Female unknown.

Discussion and conclusion

The new genus can be assigned to Fuziidae based on the following diagnostic characters: large and wide pronotum, elongated body, cerci with forceps and the broad costal area of the forewing (Vršanský *et al.* 2009). *Longifuzia* is similar to *Colorifuzia* in its large

Table 2. Measurements of all segments of cerci (in millimetres) for three specimens.

Left cercus	Segment	Length	Width	Right cercus	Segment	Length	Width
-920	1	0.14	0.65	-920	1	0.16	0.33
	2	0.14	0.65		2	0.22	0.50
	3	0.11	0.65		3	0.20	0.52
	4	0.11	0.65		4	0.11	0.52
	5	0.15	0.65		5	0.17	0.52
	6	0.15	0.61		6	0.17	0.57
	7	0.15	0.61		7	0.22	0.52
	8	0.20	0.60		8	0.27	0.52
	9	0.79	0.55		9	0.67	0.54
	10	0.63	0.18		10	0.50	0.22
	11	1.16	0.27		11	1.07	0.27
-950	1	0.23	0.41	-950	1	0.27	0.42
	2	0.14	0.43		2	0.19	0.42
	3	0.15	0.47		3	0.13	0.42
	4	0.13	0.47		4	0.08	0.42
	5	0.19	0.47		5	0.06	0.42
	6	0.18	0.49		6	0.09	0.42
	7	0.22	0.52		7	0.13	0.42
	8	0.22	0.49		8	0.14	0.42
	9	0.19	0.46		9	0.15	0.47
	10	0.40	0.52		10	0.31	0.61
	11	0.58	0.23		11	0.46	0.18
	12	0.81	0.20		12	0.86	0.20
-42409	1	0.39	0.54				
	2	0.23	0.52				
	3	0.14	0.54				
	4	0.23	0.52				
	5	0.21	0.51				
	6	0.22	0.51				
	7	0.19	0.51				
	8	0.24	0.54				
	9	0.81	0.70				
	10	0.40	0.08				
	11	0.90	0.16				

Table 3. Number of veins for four specimens.

Specimen	Sc	R	M	CuA	CuP	A	Total
-920LFW	3	22	5	16	1	8+	55+
RFW	7	20	5	17	1	9+	59+
-950LFW	1	18	7	12	1	6	45
RFW	5	17	6	13	1	7	49
-951LFW	1	18	3	10	1	8	41
-42409RFW	1	15	9	15	1	7	48

body and large number of vein branches. However, the new genus has a longer body than *Colorifuzia*, and the color is distributed partly on R, and the basal parts of M and CuA, which differs from the scheme in *Colorifuzia* (color distributed partly on R and basal of M, but reaching to the forewing margin). The new genus also resembles *Arcofuzia* in its large body and more numerous veins, but differs in having a proportionately longer body, no diagonal kink in the anal field, and different coloration pattern and distribution. *Fuzia* and *Parvifuzia* have small body sizes, simple veins and no coloration characters that distinguish them from the new genus.

The new genus has unique, dark coloration concentrated in the middle of the forewing. However, specimen -950 has only partially preserved coloration. Owing to

other body and vein characters, we interpret it belong to *L. pectinata*. The same intraspecific variation in coloration occurs in *Solemnia alexandri* Vršanský, 2008.

The forewing areas in *L. pectinata* ($n=6$) range from 70.84 mm² to 93.7 mm² (mean 83.49 mm²), vein numbers ranged from 41 to 59+ (mean 49.5) and revealed a standard deviation of 6.6 and CV 13.3%. The area of the forewing is larger than *Fuzia dadao*, *Perlucipect aurea*, *Divocina noci* and *Ectobius sylvestris* Poda, 1761 (Oružinský & Vršanský 2017). The high CV indicates that the new species was not active, i.e., not a proficient and permanent flyer.

Forceps in the cerci of the new genus consist of three apical segments, thus differing from the forceps composed of two apical segments in other species of Fuziidae, except for *Parvifuzia peregrina*. The length of the 10th segment of the cerci (the 1st of the forceps) in specimen -950 is very short, only half the length of those in other specimens. Setae on the third terminal segment are denser than those at other cercomeres or at the abdomen (Fig. 1C). The cerci of *Longifuzia pectinata* have 9–12 segments. The terminal three segments are enlarged, deformed and fused with a narrow notch, which served for attaching to females during copulation (Vršanský *et al.* 2009).

The new taxon is erected based on males only; female individuals have not been identified. *Fuzia dadao* and *Colorifuzia agenora* are known from both males and females, and they can be excluded as representing females of the new taxon. *Parvifuzia marsa*, *P. brava*, *P. peregrina* and *Arcofuzia cana* were described based only on male specimens. Currently, no female specimens have been considered suitable candidates to be ascribed to *L. pectinata*.

Male tergal glands, located on T4–8 of *L. pectinata*, T3–5 of *Fuzia dadao* and T7 of *Perlucipecta vrsankyi* Wei & Ren, 2013 (Wei & Ren 2013), were used for attracting females before copulation (Vršanský *et al.* 2009). The shape of abdominal segment 6 and 7 of the new species is the same as that in the abdominal segment 6 of *Fuzia dadao*, which may also have glands as suggested by Vršanský *et al.* (2009). The narrow and elongate body shape is suggestive of alternative, non-standard diets as a wide body is necessary for nitrogen fixation in cockroaches (see Bell *et al.* 2007). Exceptions are found only in extremely specialized cockroaches and Nocticolidae, excluding *Blattabacterium* (Vidlička *et al.* 2017) associated with various alternative diets. Nevertheless, well-developed male tergal glands in *L. pectinata* provide evidence of nuptial female feeding on nitrogen provisions. However, some Nocticolidae also have these glands developed, although the amount of provisions and their function is ambiguous (Vidlička *et al.* 2017).

Longifuzia pectinata possesses a 1- to 7-branched Sc, which is a plesiomorphic character occurring in Palaeozoic cockroach families (Schneider 1983) and in basal Caloblattinidae (Vršanský 2000). Seven branches of Sc is a rare character state among Middle Jurassic cockroaches, 1–4 branches being typical. Therefore, *Longifuzia* appears to be a relatively basal genus among Fuziidae. More than six branches occur in the Palaeozoic families and in some derived modern taxa. A many-branched Sc occurs in the Middle Jurassic *Graciliblatta bella* Liang, Huang & Ren, 2012a (eight branches)—a very basal Chinese taxon among the Raphidiomimidae (Liang *et al.* 2012a). The condition of a more prolifically branched Sc (four branches) also occurs in *Perlucipecta aurea* Wei & Ren 2013 from the Lower Cretaceous Yixian Formation (Wei *et al.* 2013).

Asymmetric (possibly polymorphic) venation occurs in all four specimens of *L. pectinata*. Incomplete veins of R and Sc are present in specimens -921 and -950, respectively. In the left hind wing of -920, there is a cross-vein between Rs and M (Fig. 1B). In the right forewing of -42409, the branches of R and M reconnect and then fork again (Figs 2A and 3B). Wing deformities are rather common in cockroaches in the Jiulongshan Formation at Daohugou, e.g., in *Fortiblatta cuspicolor* Liang *et al.*, 2009 (Liang *et al.* 2009), *Divocina noci* Liang, Vršanský & Ren, 2012 (Liang

et al. 2012b), *Falcatusiblatta gracilis* Liang *et al.*, 2018 (Liang *et al.* 2018), *Fuzia dadao*, *Entropia initialis* Vršanský *et al.*, 2012 and *Colorifuzia agenora*, which suggests wing polymorphisms are potentially heritable characters (Vršanský 2005, Vršanský *et al.* 2012, Vršanský *et al.* 2017).

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