

Advanced morphology and behaviour of extinct earwig-like cockroaches (Blattida: Fuziidae fam. nov.)

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Abstract: We describe the extinct cockroach family Fuziidae fam. nov., represented by *Fuzia dadao* gen. et sp. nov. from the ?Bathonian (168 Ma) Middle Jurassic sediments of Daohugou, Inner Mongolia, China. Males are characterized by unique, long and narrow bodies with a notch on forceps of earwig-like cerci, which attaches to the long external ovipositor during courtship. In a combination with the presence of male tergal glands, it appears the most advanced form of reproduction in the nearly 300 Myr history of long external ovipositor-bearing cockroaches. Its advanced morphology significantly supports attribution of living and fossil cockroaches within a single order Blattida.

Key words: Middle Jurassic, Bathonian, China, Inner Mongolia, Daohugou, Insecta, Blattida (=Blattaria =Blattodea), fossil cockroaches.

Introduction

Along with the stunning paleontological discoveries from the world-renowned fossil beds in western Liaoning Province of China, recent findings from the lacustrine deposits exposed at Daohugou village near Ningcheng (Fig. 1), Inner Mongolia, include superbly preserved insect, pterosaur, salamander and plant fossils (Gao & Shubin 2003; Rasnitsyn & Zhang 2004; Gao & Ren 2006).

Cockroaches, with an evolutionary history extending over 320 Myr, and with over 100,000 fossil specimens collected so far, form the most complete group of fossil insects. They appear to be a varied and diverse group, giving rise to social termites and predatory mantises. This plasticity includes enormous structural variation of male genitalia among the major clades (see Klass 1997) and can be contrasted with the conservation of general body structures and most

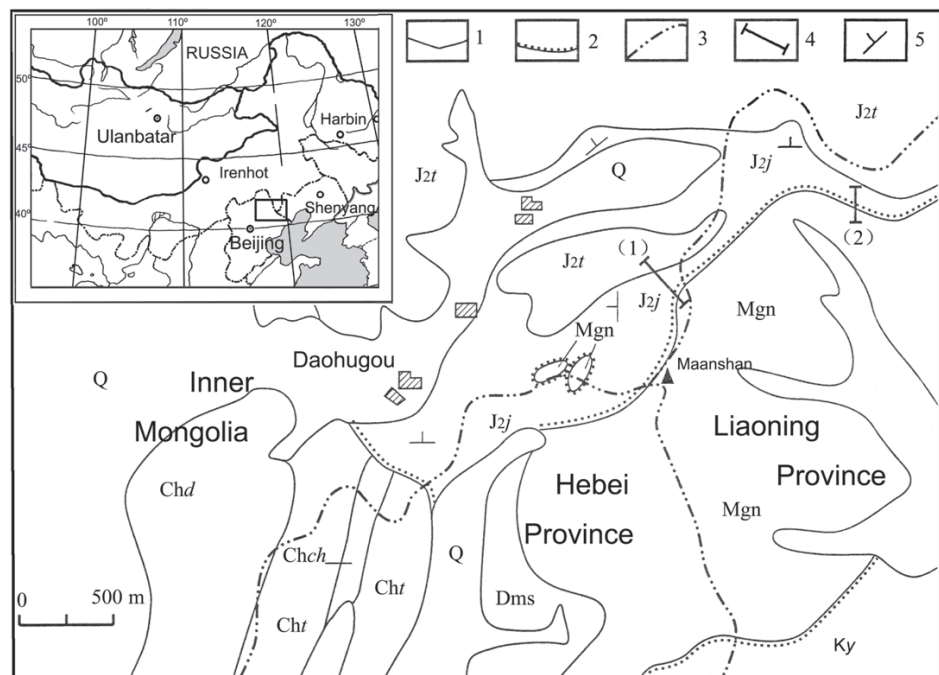


Fig. 1. Localization of Daohugou area at the juncture of three provinces of Liaoning, Hebei, and Inner Mongolia (E 119°14.318', N 41°18.979', height 607 m). Legend and abbreviations: 1 — stratigraphic boundary; 2 — unconformity; 3 — provincial boundary; 4 — location of geological section; 5 — strike and dip; Chc — Changchou Formation; Chch — Chuanlinggou Formation; Chd — Dahongyu Formation; Cht — Tuanshanzi Formation; Dms — Dalaiyingzi erosion surface; J2j — Jiulongshan Formation; J2t — Tiaojishan Formation; Ky — Yixian Formation; Q — Quaternary; Mgn — Maanshan gneiss. Modified after Ren et al. (2002).

characters during the phylogeny. At higher taxonomic levels, this body plan conservation results in 15 distinct extinct groups (corresponding to families all of which can be discriminated on the basis of both male and female terminalia). This paper describes a new species of fossil cockroach *Fuzia dadao* gen. et sp. nov., and attributes it to a separate family, Fuziidae fam. nov.

This species is important in several respects: it represents further evidence for decreasing variability of respective species over time (Vršanský 2000; Webster 2007) and also for occurrence of first mass animal deformations representing mutations (Vršanský 2004, 2005) — phenomena recently observed in the paleobotanical record as well (Krassilov 2003; Visscher et al. 2004; Foster & Afonin 2005).

The unique structures of this species are male copulatory forceps, which are commonly present in many other insect terminalia such as in Mantophasmatodea (Klass et al. 2003), Dermaptera, Japygidae, Odonata, and among Embioptera and Phasmatodea, but not previously reported in cockroaches. For a similar, although not homologous structure, see the *volsella* of male hymenopteras and scorpion-fly.

Material and methods

Nineteen complete males and sixteen females are described and were collected from the Middle Jurassic sediments of the Jiulongshan Formation (Ren et al. 2002; Shen et al. 2003; Liu et al. 2004; Rasnitsyn & Zhang 2004; Gao & Ren 2006), at the Daohugou locality in Inner Mongolia, China (Fig. 1). The Daohugou fossil beds consist of a set of intercalated, fine-grained lacustrine deposits and fine volcanic ash that unconformably overlay pre-Cambrian rocks (Ren et al. 2002; Liu & Jin 2002).

The accurate Ar-Ar and SHRIMP U-Pb dating shows that the age of intermediate-acid volcanic rocks overlying the Daohugou fossil-bearing beds is about 164–165 Ma, and that the age of these fossil-bearing beds is older than or equal to 165 Ma (Chen et al. 2004). Therefore the age of Daohugou biota is considered to be Middle Jurassic (Aalenian–Bathonian) (Ren et al. 1995; Gao & Ren 2006).

We studied the material using a Leica MZ12.5 dissecting microscope and illustrate them with attached drawing tube and photographs were made using Leica DC 300 photographic equipment.

The analysed specimens are listed in the table caption. The coefficient of variation (in percent) was computed as Standard deviation/Average.

The venial nomenclature follows the earliest studies of the senior author (Vršanský 1997).

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

Systematic paleontology

Order: **Blattida** Latreille, 1810
 Superfamily: **Caloblattinoidea** Vršanský & Ansoerge in Vršanský (2000)
 Family: **Fuziidae** fam. nov.

Type genus: *Fuzia* Vršanský, Liang et Ren, gen. nov. described below.

Composition: Type genus, some unidentified, but different genera from the Upper Triassic of the Madygen in Kirgizia, Middle Jurassic (?Bajocian) of Bakhar in Mongolia and Upper Jurassic (?Kimmeridgian) sediments of the Karatau in Kazakhstan.

Range: ?Upper Triassic–Middle–?Upper Jurassic.

Differential diagnosis: Fuziidae (Fig. 2b1) differ from all Paleozoic families except the Phylloblattidae Schneider, 1983 by the presence of intercalary branches (synapomorphy) [For character polarities see character analysis (list) below], and from the Phylloblattidae in having specialized and simplified venation, especially simple Sc and A branches (apomorphies).

The Fuziidae differ from all the known Mesozoic families (for comparison see below; for character polarities see character analysis) in the following characters: very small head covered by a very large pronotum (head less than a half of the pronotal width); forewing widest in the apical third, costal area very long (a third of wing) and wide (more than a third of wing). Wings except for hindwing (and possibly forewing) apex are without colouration. Forewing Sc strong, simple or with terminal branch; RS slightly differentiated in most individuals, even when there is an apparent trend of uniformization of R1 and RS in the present taxon (Fig. 7i — RS can be tracked only on the basis of more richly branched apical R1), distinctly expressed in all the Blattulidae.

Autapomorphies (see also character analysis) of the new family are: eyes significantly projected beyond the head outline; coloured labial palps; wide pronotum; shape of forewing, wide costal area, short clavus; curved ovipositor and forceps-like male cerci. Other significant shared apomorphies (perhaps synapomorphies) with the Blattulidae are simplified Sc and A, and bonded R1 with RS.

The character of venation with numerous intercalaries and cross-veins forming comb are synapomorphic with the Caloblattinidae (i.e. unnamed relic caloblattinid from the Upper Jurassic of Shar-Teg in Mongolia — see Vršanský 2004, fig. 6.7–6.8 p. 464, which also share simplified A branches). The entire hindwing, differing from the ancestral state of the Caloblattinidae by having a reduced M and CuA and CuP branches limited to a simple vein, is homoplastic with the Liberiblattinidae. Fuziidae differ from the Liberiblattinidae having eyes which protrude beyond the outline of head (homoplastic with living cockroaches), the form of palps (palps of the Fuziidae resemble extant rather than Mesozoic cockroaches (except the Blattulidae), all of which have long palps), with apical segment partially cup-like; slightly curved forewing R, simple Sc; and richly branched hindwing CuA. It additionally differs from all other Polyphagoidea by having a narrow body with characteristic terminalia (autapomorphy) and in expanded venation, slender veins with very slender intercalaries and in wide costal field.

Additional families differ in possessing strong autapomorphies: Umenocoleidae Chen et Tian, 1973 differ in possessing hard elytra; Raphidiomimidae Vishniakova, 1973 are elongated with prognathous head; Latiblattidae Vishniakova, 1968 are extremely widened (all additionally with plesiomorphically

secondarily branched A and Sc) and Eadiidae Vršanský, 2009 have curved leg spurs and short pronotum.

Fuzia differs from the Mesozoic Blattoidea (Mesoblattinidae Handlirsch, 1906 and Blattellidae Karny, 1908) in having a short (25 % of wing length) and fluently curved CuP, wide costal field (autapomorphies) and by the presence of an external ovipositor with basal ridge serving for attachment of cerci, and double hook (plesiomorphies). The male terminal hook may be homologous to the hook *hla* (Klass 1997) including sclerite *L3* (see McKittrick 1964), but more probably to the terminal hooks of the right phallomere of some living Blattidae (McKittrick 1964; fig. 108) or terminal processes *paa + pda* of the left phallomere of some living Blattellidae (Klass 1997).

According to the basal position of the new family with respect to Mesozoic cockroaches, there is no need of (phylogenetic) comparison Fuziidae with the living families (which, for example all lack the external ovipositor). However, some superficial similarity is seen with the family Blattellidae (homoplastic simple forewing Sc and A; similar pleating) and also Polyphagidae (homoplastic or synapomorphic sharp but fluently curved CuP).

The area between CuA and CuP is irregular with the width of this area varying along the wing length, with free space for one CuA branch present. The clavus is very short (25 % of the wing length), with fluently curved CuP and a diagonal kink shifted posteriorly. Branches of A are simple, A1 occasionally has blind branches. Hindwing with facultative terminally dichotomized veins, differentiated R1 and RS, without pterostigma; and with secondary and tertiary branched CuA. Males with cerci forceps-like by notches on their distal mesal edges. Female with short (1/7 of total body length), rigid and curved external ovipositor with basal ridge on right side.

Description: As for the species.

Taxonomic position: *Character list* is provided in order to identify character states (polarities):

— *Shape of head:* eyes protruding beyond the outline of head: synapomorphic with the Blattulidae, Liberiblattinidae and living cockroaches (eyes does not protrude beyond the head outline in the stem family Caloblattinidae) (Even the head is well preserved, ocelli are invisible, in spite of their anticipated presence. All three ocelli of extinct cockroaches were plain and visible mostly in amber material (Vršanský 2008a; Anisyutkin & Gorochoy 2008);

— *Palps very short (shorter than length of the head):* synapomorphic with the Blattulidae (very long in ancestral Caloblattinidae, comparatively longer in the related Liberiblattinidae);

— *Apical segment of palps cup-like:* synapomorphic with advanced Caloblattinidae and its descendants (cup-like termination absent in early Caloblattinidae);

— *Large wide pronotum (as wide as the body):* autapomorphic (such a wide pronotum is present in some Paleozoic groups, but absent in the stem Caloblattinidae), homoplastic with the unrelated Latiblattidae;

— *Elongated body (4 times longer than wide):* autapomorphic (elongated body is present in some living cockroaches, but absent in Paleozoic and Mesozoic groups except homoplastic in Raphidiomimidae and some Umenocoleidae);

— *Tergal glands present:* plesiomorphic (according to phylogenetic position of *Fuzia*, which is not directly related to the

Liberiblattinidae, perhaps inherited from certain Caloblattinidae. Glands are plesiomorphically present in the Liberiblattinidae — stem for all living cockroaches, Skokidae, termites and mantises);

— *Cerci with reduced number of segments (under 15):* synapomorphic with the Blattulidae (the stem Caloblattinidae have numerous segments, Liberiblattinidae a little less numerous than the Caloblattinidae);

— *Cerci with forceps:* autapomorphic;

— *Styli very long (more than a half of cerci):* symplesiomorphic with the early Caloblattinidae (shorter in all advanced Caloblattinidae and also in the Blattulidae);

— *Curved external ovipositor with ridge:* autapomorphy;

— *Sledner carinated legs:* autapomorphy (in the stem group, the Caloblattinidae, the legs are strongly carinated; in some derived Liberiblattinidae homoplasically partially reduced; in Skokidae (as a jumping adaptation) and a new family (as a social adaptation) nearly reduced);

— *Forewing shape:* autapomorphic (the shape of wing with wide costal area, and the wing widest in the apical third is absent in Paleozoic and Mesozoic cockroaches, although homoplasically occurs in some advanced living groups);

— *Forewing costal area wide:* autapomorphy, homoplasically present in the Latiblattidae (Latiblattidae are not directly related, thus this character cannot be synapomorphic);

— *Forewing with more or less distinct intercalaries:* apomorphic with early Phylloblattidae, Caloblattinidae, Liberiblattinidae; present, but tend to reduce in the Blattulidae;

— *Forewing Sc simple:* synapomorphic with the Blattulidae (stem Caloblattinidae but also Liberiblattidae and all Mesozoic groups have Sc branched; Sc homoplasically reduce in the living Blattellidae);

— *Forewing RS indistinctly differentiated (see Figs. 7–8):* synapomorphic with the early Blattulidae (RS is not as distinct as in other Mesozoic families except for the Blattulidae: this partial reduction, completely expressed in the Blattulidae, is very unusual and sophisticated, and thus unlikely to represent a homoplasy);

— *Forewing venation rich:* symplesiomorphic with the Caloblattinidae (rich venation is generally a plesiomorphic state — venation tends to reduce in several independent lineages);

— *Forewing CuA expanded:* symplesiomorphic with the early Caloblattinidae (CuA is reduced even in the advanced Caloblattinidae and in all derived Mesozoic and living families);

— *Forewing clavus short (less than a third of wing):* autapomorphy;

— *Forewing branches of A simple:* synapomorphic with the Blattulidae (A are branched in the stem Caloblattinidae and all Mesozoic groups; A is homoplasically simplified in the living Blattellidae);

— *Hindwing terminal coloration:* symplesiomorphic with the advanced Caloblattinidae (present in some advanced Caloblattinidae, Liberiblattinidae, Blattulidae and Skokidae);

— *Hindwing R1 and RS with standard (not comb-like branches) dichotomisations:* symplesiomorphic with the Phylloblattidae (present also in the stem Caloblattinidae);

— *Hindwing M simplified:* synapomorphic with the Blattulidae (M is rich in the stem family Caloblattinidae, in the

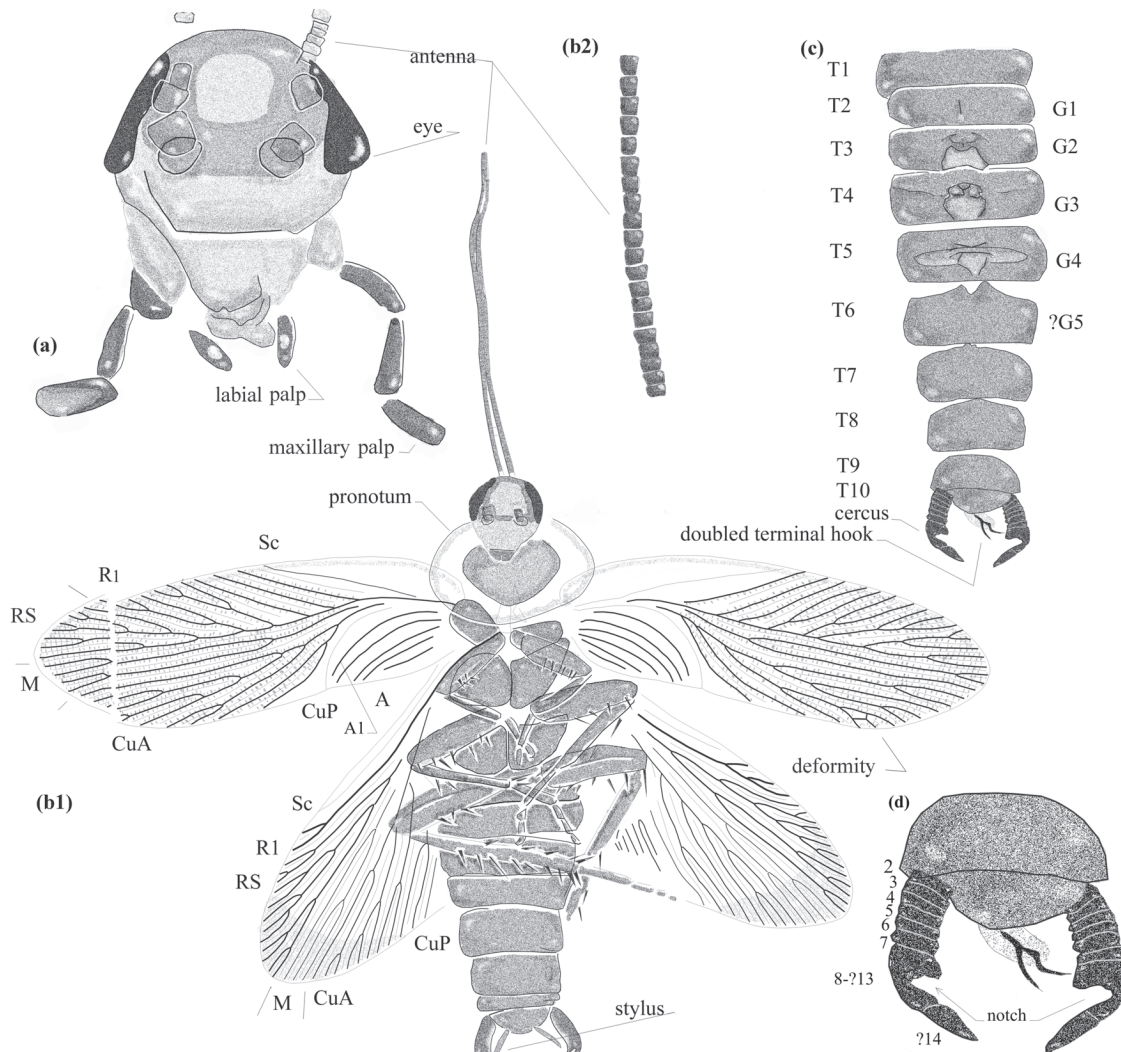


Fig. 2. Males of caloblattnoid *Fuzia dadao* sp. nov. **a** — Head (CNU-B-NN-2006-677); **b1-2** — Holotype CNU-B-NN-2006-666. A complete male; **c** — Dorsal view with tergal glands (CNU-B-NN-2006-357); **d** — Detail of cercus with numbered cercomeres and indicated notch (CNU-B-NN-2006-357). Notice the more sophisticated carving on the left cercus (arrow). Daohugou, Inner Mongolia, China. Middle Jurassic (?Bathonian). Abbreviations: **Sc** — subcosta, **R** — radius, **R1** — radius anterior, **RS** — radial sector, **M** — media, **CuA** — cubitus anterior, **CuP** — cubitus posterior, **A** — anal veins. **T** — tergites, **G** — glands. Right forewing length 13.7 mm.

Liberiblattnidae and Skokidae — thus homoplasy with the Blattulidae is unlikely; M is homoplasiically simplified in the Blattellidae);

— *Hindwing CuA multiply branched*: symplesiomorphic with the Caloblattnidae.

Genus *Fuzia* gen. nov.

Type species: *Fuzia dadao* sp. nov.; see below.

Description: As for the species.

Composition: Type species only.

Derivation of the name: *Fuzi* is Chinese for master.

Fuzia dadao sp. nov.

Figs. 2–8, Table 1

Holotype: CNU-B-NN-2006-666. A complete male. (Figs. 2b, 4A1–3).

Type locality: Daohugou, Inner Mongolia, China.

Type horizon: Jiulongshan Formation (designated by Ren et al. 2002). Middle Jurassic (?Bathonian).

Paratype: CNU-B-NN-2006-301. A complete female. (Figs. 3A, 6B1–2)

Additional material: CNU-B-NN-2006-031, 035=042, 038, 044, 322, 357, 669, 670, 671, 672, 673, 674, 675, 676, 677, 681, 682; TNP-42982 (complete males: Figs. 5, 7). CUN-B-NN-2006, 305, 306, 314F, 328, 341, 348, 371, 380, 381, 383, 1001, 1002, 1003, 1004, 1005 (complete females: Figs. 6, 8). The same locality as the type.

Derivation of the name: After *dadao* (Chinese for “perspicacious understanding of the path”; and also for sharp knife) — alluded also to the type locality, the Daohugou.

Description: Head small (ca. 1/8 of the total body length; pronotum width to head width ratio over 2:1), with palps shorter than head (Fig. 2a). Male head is almost globular (Fig. 2a), and slightly longer than wide (length/width 1.2–2/1.2–2 mm),

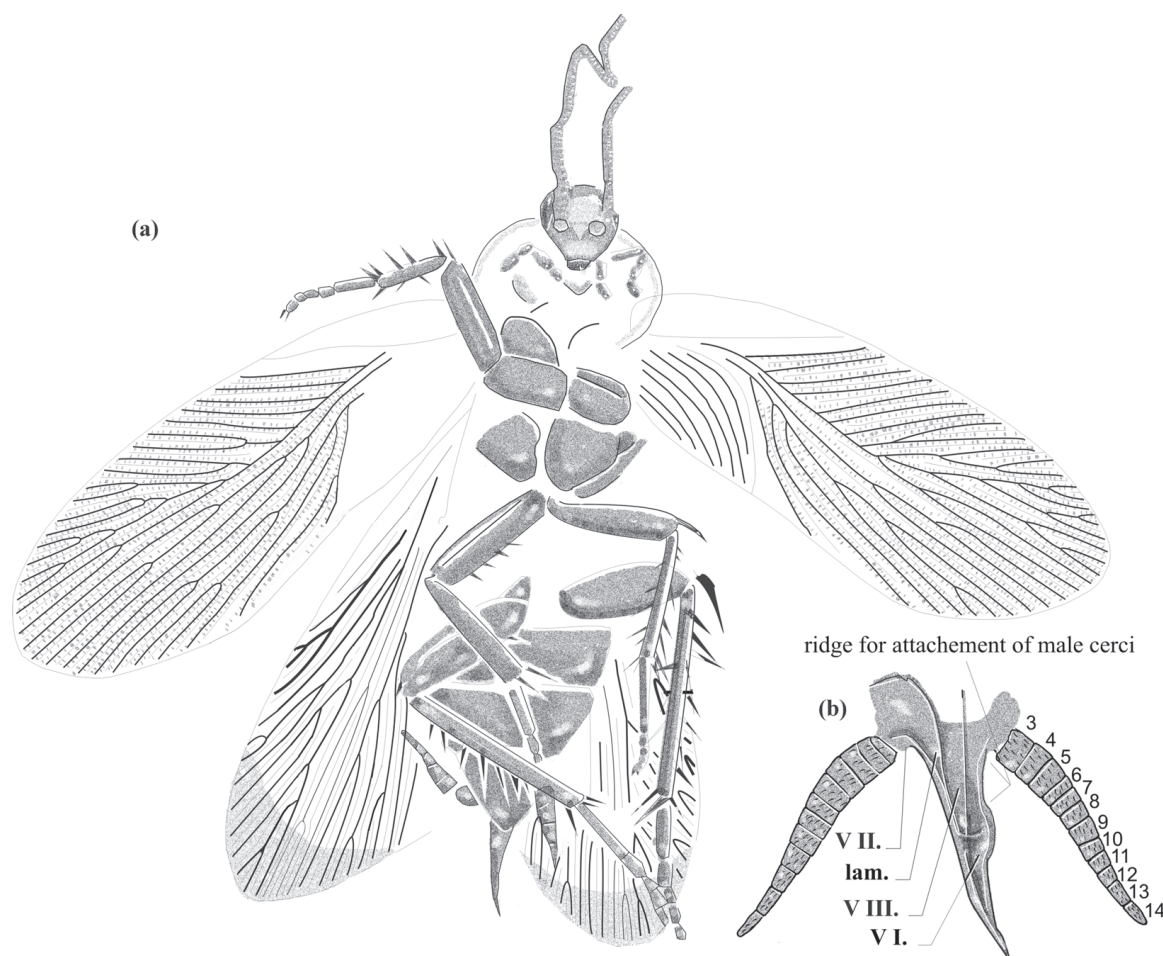


Fig. 3. Females of caloblattnoid *Fuzia dadao* sp. nov. **a** — Paratype (CNU-B-NN-2006-301); **b** — Dorsal view on the ovipositor and numbered cercomeri (CNU-B-NN-2006-383). Daohugou, Inner Mongolia, China. Middle Jurassic (?Bathonian). Abbreviations: **V I.** — Ventral valves I (gonapophyses 8 or 1st valves); **V II.** — Dorsal valves (gonapophyses 9 or 2nd valves); **V III.** — Outer valves III (gonoplacks or 3rd valves); **lam** — Ovipositor plates 1 and/or 2 (all homologized according to Vishniakova 1968). Alternatively (see Klass 1998), the median parts (**V I** and **V III**) represent the 1st valves (*ga* of Klass 1998), left and right, but not down to their bases. The lateral parts (**V II** and **lam**) represent the 2nd (*gp* of Klass 1998) and 3rd valves (*gl* of Klass 1998), together with coxite 9 (the anterolateral parts; lateral parts of *aa* of Klass 1998; = “lam 2” of Vishniakova 1968). In this part the origin of 2nd valves should be anteromesally (**lam**) and that of 3rd valves posterolaterally (**V II**), but the proportions do not really fit with this interpretation. Right forewing length 12.5 mm.

in females the head is significantly elongated (3/2.2 mm). The pronotum is very large, especially in females (2.5–3.1/4.2–4.5 mm) (2.2–2.6/3.2–3.8 mm in males), with very wide parantalia (Fig. 2b1) and two coloured central stripes. Forewing (Fig. 2b1) widest in apical third, with very wide costal area (nearly a third of the wing’s width), with intercalaries and numerous cross-veins forming comb-like structures. Length/width: 10–15.5/3.6–6.5 mm (in females 12.5–13/4.2–4.5 mm), with simple and very long (a third of a wing), strong partially coloured Sc (occasionally with 1 or two terminal dichotomies). The RS is differentiated in most individuals. R (15–25) is almost straight, the branches are simple or secondary branched, apical R1 vein (predeceasing RS) has multiple branches. M 3–10; CuA (4–13) expanded, and usually reaches the apical part of wing, this is expressed as narrowing towards apex. Clavus is very short (less than a third of the wing’s length), with simple branches of A running parallel to the anterior margin and to each other (A1 occasionally with

blind branches). A 4–7. The hindwing (Fig. 2b1) has facultative terminal branchelets, a simple Sc; R1 (3–4) and the RS (9–13) is differentiated, without pterostigma, but with a darkened R1. The M almost straight, but reduced to a few veins (2–6); CuA (6–11) are secondarily or tertiary branched, not reduced, and also with additional blind branches; and the CuP simple.

The (Fig. 2c) male body is significantly longer than the forewings, but body is very narrow (about as wide as pronotum) even in females, in contrast to all other cockroaches with external ovipositor, which have a wide body. Male body significantly elongate, very narrow, with cerci forming forceps (with notches). Tergal glands are present in at least three segments. The external ovipositor is very rigid (preserved 3D unlike rest of the fossils) curved, and of the long type.

All legs (Fig. 2b1) very short and comparatively slender and with slender carination. Fore femur length/width similar in males and females (2–2.22/0.67 mm — holotype and paratype

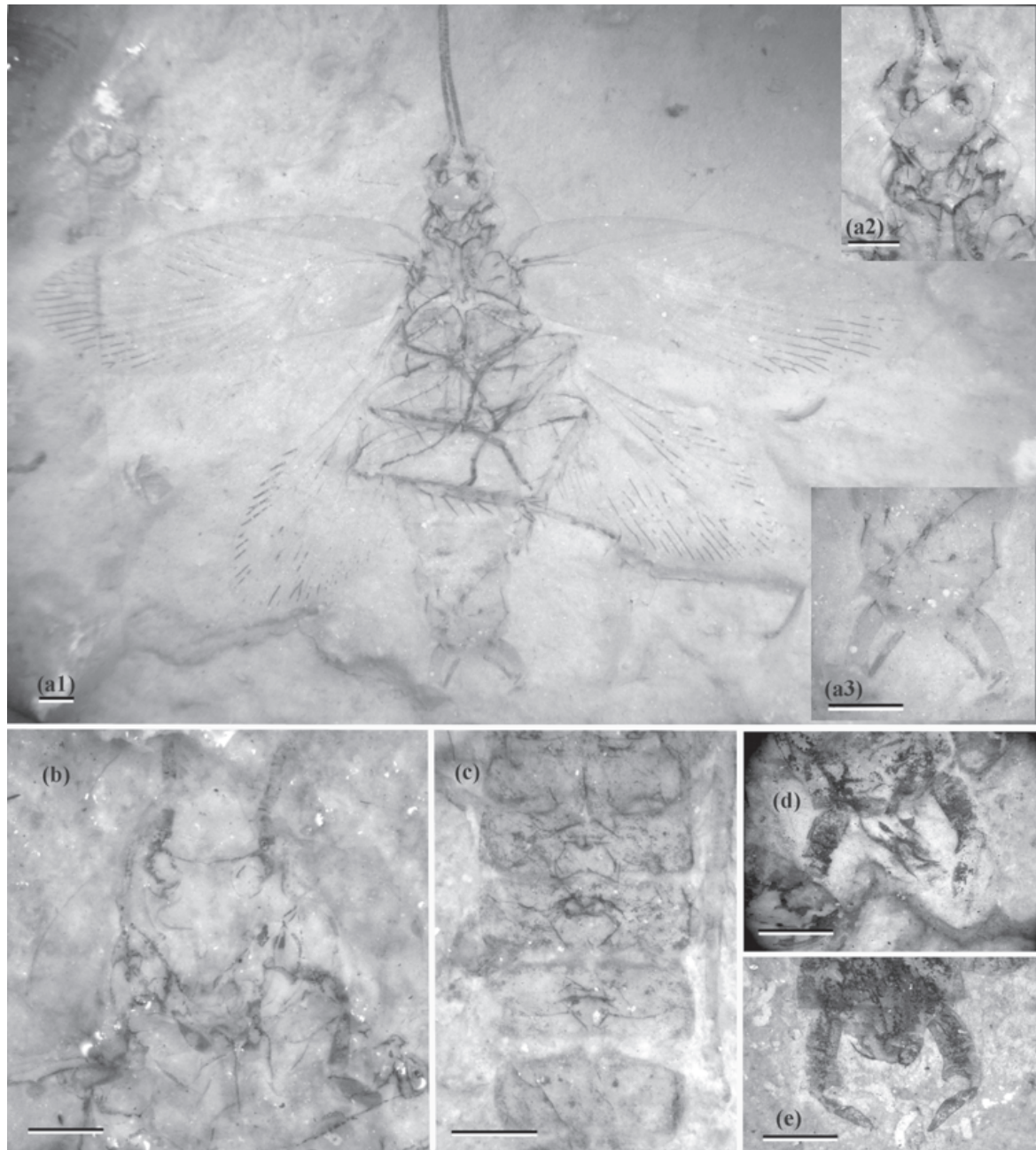


Fig. 4. Males of caloblattinoid *Fuzia dadao* sp. nov. **a1-3** — Holotype CNU-B-NN-2006-666. a1 — complete male (right forewing length 13.7 mm), a2 — head, a3 — terminalia with unsegmented styli. **b** — Detail of head (CNU-B-NN-2006-677); **c** — Tergal glands (CNU-B-NN-2006-357); **d** — Detail of terminalia with forceps-like cerci (CNU-B-NN-2006-675); **e** — The same (CNU-B-NN-2006-672). Daohugou, Inner Mongolia, China. Middle Jurassic (?Bathonian). Scales 1 mm.

considering their similar sizes of forewing about 12 mm); but fore tibia much shorter and stronger in females (1.56/0.33 mm compared with 1.89/0.22 mm of males). Mid femur identical in both sexes (2.78/0.89 mm), mid tibia more slender in males (2.67/0.33 mm compared with 2.44/0.56 mm of females). Hind femora and tibiae identical (3.11/1 mm: 4.44/0.56 mm). Both legs and pronotum are partially coloured.

The female terminalia (Fig. 3b) and curved ovipositor is comparatively short (less than 3 mm), and a long cerci has 14 (eventually 15) segments (the subapical segments are

fused). The male has 10–14 segments, segments 8–13 enlarged, fused with a narrow notch (Fig. 2d). In addition to the notch, cerci form a compact unit, as shown by shape of the segmental margins and uniform preservation. Male additionally possess a pair of unsegmented styli (Fig. 4a3). All cercal segments have numerous *sensilla chaetica*. Male tergal glands present at T3–5, possibly also in T2 and T6 (as in Figs. 2c, 4c). Male terminal hook (see family discussion for explanation of this structure) doubled (Fig. 4d — straight, Fig. 4e — hooked).

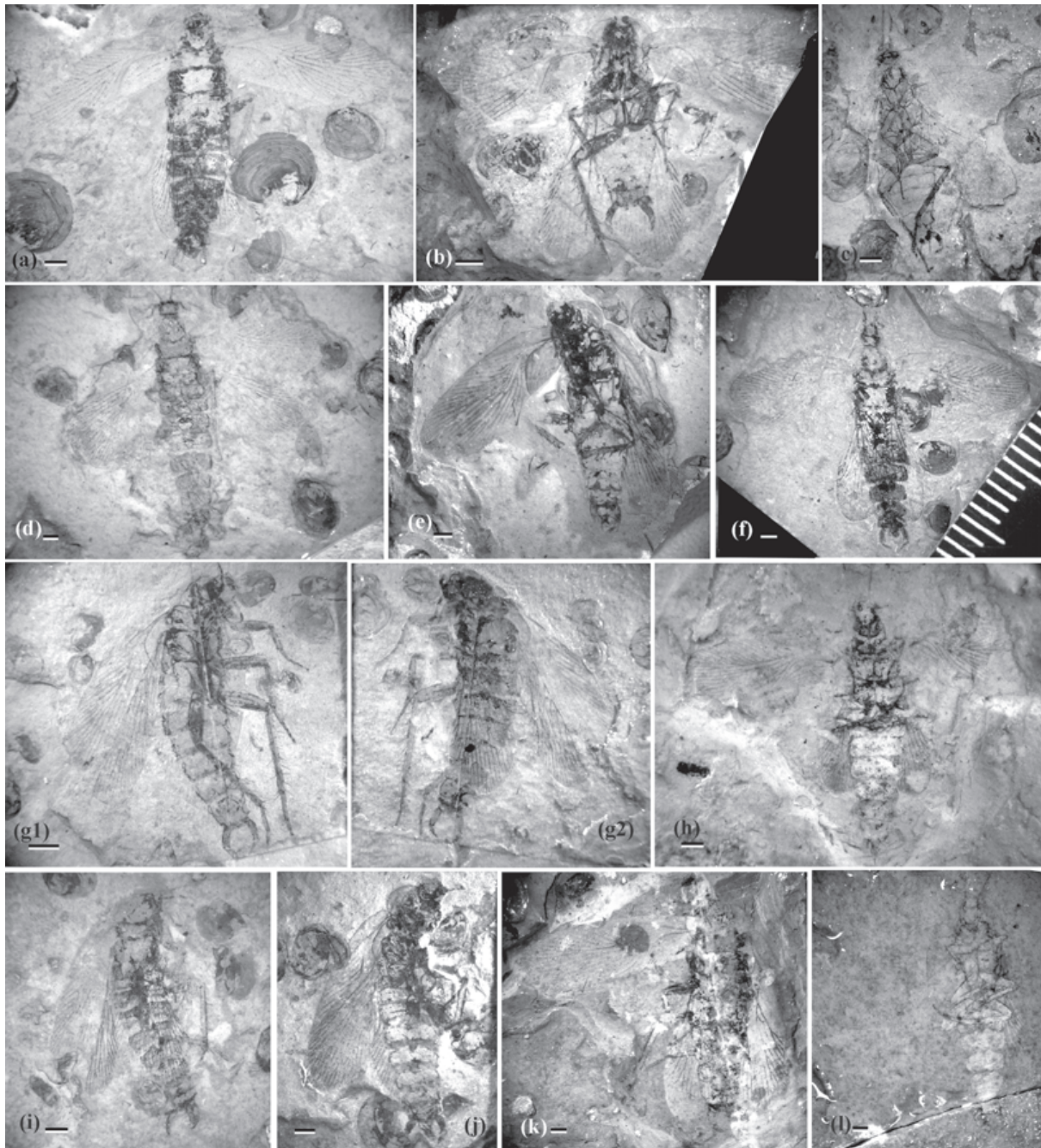


Fig. 5. Males of caloblattinoid *Fuzia dadao* sp. nov. **a** — CNU-B-NN-2006-322 (right forewing length 10 mm); **b** — TNP-42982; **c** — CNU-B-NN-2006-647; **d** — CNU-B-NN-2006-357 (right forewing length 10.6 mm); **e** — CNU-B-NN-2006-671 (right forewing length 15.5 mm); **f** — CNU-B-NN-2006-672 (right forewing length 10 mm); **g1** — CNU-B-NN-2006-042; **g2** — CNU-B-NN-2006-035; **h** — CNU-B-NN-2006-676 (right forewing length 14.5 mm); **i** — CNU-B-NN-2006-044; **j** — CNU-B-NN-2006-675; **k** — CNU-B-NN-2006-670; **l** — CNU-B-NN-2006-677 (right forewing length 14 mm). Daohugou, Inner Mongolia, China. Middle Jurassic (?Bathonian). Scales 1 mm.

Discussion

The conservative phylogeny of cockroaches was first identified as problematic at the beginning of the 20th Century (Handlirsch 1903). The most likely explanation how to sustain the evolutionary pressure without morphological changes appears to be the adoption of a generalist strategy; and a large genome (Bier & Müller 1969) may play some role in achieving this

phylogenetic conservatism. Some of the extinct cockroach families and genera existed for over 200 Myr and 100 Myr respectively, while evolutionary tempo of respective species was rather high — a single species is documented to persist for over ~200 kyr (Vršanský 1997, 2008b).

Attribution of fossil (long or short external ovipositor bearing — surpassing the hind margin of the subgenital plate), and living cockroaches (without external ovipositor) into two re-

spective orders has caused broad discussion. Vishniakova (1968) studied and described Mesozoic ovipositors in detail and homologized the outer ovipositor valves with the inner valves of living cockroaches, thus allowing the classification of extant and extinct cockroaches within a single order (Hennig 1981, with reservations). The most significant difference remained the presence of the ootheca (egg-case) in all living forms, except for some derived species (Roth & Willis 1958). Nevertheless, an unnamed living relic cockroach bears external ovipositor (L. Vidlička, P. Vršanský in preparation) and apparently *Melyroidea*, in spite of its alternative categorization as a terminal blattellid taxon also has a similar terminalia structure (Vršanský 2003).

Grimaldi (1997) divided the monophyletic Dictyoptera into living cockroaches without external ovipositor (Blattaria), termites and mantises; and extinct Blattodea — cockroaches with external ovipositor. However, the Liberiblattinidae — stem group of the living Dictyoptera, Skokidae, Mesoblattinidae (precursors of the Blattellidae, Blaberidae and Blattidae), and also some living cockroaches possess rudimentary external ovipositor (Vršanský 2002). Thus the loss of the external ovipositor is an evolutionary trend and the Blattaria *sensu* Grimaldi would appear polyphyletic. Inward et al. (2007) simply place termites within the order of cockroaches, but this opinion is not supported (see also Lo et al. 2007) as living cockroaches and termites (as well as mantises) evolved from Mesozoic cockroaches independently (Vršanský 2008b).

Thus, the taxon Blattida (=Blattaria) is of paraphyletic (non-cladistic) nature (see also Vršanský et al. 2002; Lo et al. 2007). The hypothesis of Béthoux & Wieland (2009) suggesting that the holophyly of mantises started from the non-blattarian Carboniferous ancestor cannot be followed for the reason of the well traced transition of the Mesozoic cockroaches Liberiblattinidae into the Baissomantidae mantises (Vršanský 2002).

Among fossil cockroaches, three families (Latiblattidae, Eadiidae; a new family) appear endemic and limited to a few specimens from the Upper Jurassic Lagerstätte of Karatau and from the Mesozoic Archingey amber, suggesting that indigenous families were not uncommon.

Complete, well preserved specimens of the new family Fuziidae, are only abundant at the present locality. However, some poorly preserved wings from the slightly older sediments from the Bakhar in Mongolia, some complete specimens from the ?Kimmeridgian Upper Jurassic of Karatau in Kazakhstan, and also some specimens from the Upper Triassic locality Madygen in Kirgizia, show identical venation pattern and elongated body. Thus, the family had perhaps originated during the Triassic, and persisted until the Upper Jurassic.

Evidence for behaviour in extinct insects from amber comprise a wide variety of patterns including mating, egg-laying, progeny care, food carriage, parasitism, mutualism and phoresy (Ariño 2007), and distinct morphology such as preservation of metapleural glands in primitive ants (Engel & Grimaldi 2005) indirectly indicates a competent behaviour. In the sedimentary record, evidence for distinct behaviour is also common, such as sound apparatus preserved in grasshoppers (Sharov 1968; Martins-Neto 1999), evidence for parasitism (Brauckmann et al. 2007), pollination (Krassilov & Rasnitsyn

1982; Rasnitsyn & Krassilov 1996a,b; Labandeira 2000), feeding on plants (see Labandeira 2002) and insects (Durdin 1988), and oviposition (Béthoux et al. 2004; Labandeira 2006). The presence of male tergal glands which are used for pre-copulation attraction of females in the extant cockroach species is unique, even the glands, indicated as plesiomorphic for living taxa, must have been present in most Mesozoic cockroaches (but also in termites and mantises — see below).

This character, supported here to be plesiomorphic for all Mesozoic-originating cockroaches is thus not an autapomorphy of living lineages of cockroaches and contributes to the attribution of Mesozoic and living families within a single order, the Blattida (typified ordinal name of Blattaria = Blattodea, paraphyletic in respect to Isoptera and Mantida), supported additionally by modern morphology as shown here.

All Mesozoic (except Subioblattidae, Poroblattinidae, Spiloblattinidae originating in the Paleozoic), Cenozoic and living cockroaches (together with mantises and termites) are monophyletic, originating from the Phyloblattidae-Caloblattinidae lineage — see Vršanský (2002) and Vršanský et al. (2002). The present taxon, the Fuziidae, may be categorized within Blattida (all Dictyoptera other than termites and mantises, that is, the Blattaria) on the basis of general habitus (Fig. 2b1), of a large pronotum with distinct paranotolia, multisegmented cerci (Fig. 2c) with numerous *sensilla chaetica*, and carinated legs. Synapomorphies with the Blattida are a hypognathous head directed backwards (Fig. 2a), and characteristic venation pattern of forewings (with pectinated regularly branched veins, and with distinct clavus) and hindwings (simple Sc; R1 somewhat comb-like, RS differentiated, simplified M and expanded CuA, simple CuP).

We now briefly designate ovipositor types of cockroaches. The external ovipositor of *Fuzia* is assigned to the “Mesozoic long type” (found in the Caloblattinidae, Umenocoleidae, Latiblattidae) based on the general robust shape with more or less parallel linear dorsal and ventral outer valves (V1 and V2) and the sharp apex, and with distinct external ovipositor plates (Lam 1, 2 according to Vishniakova 1968) and V3. This type can be contrasted with the two alternative types of ovipositor. The slender “short-type” external ovipositor of the Blattulidae characterized by a dominant U-shaped, sharply cut at apex parallel outer ventral and dorsal (V1, 2) valves, with internalized rudimentary valves V3. The “rudimentary-type” external ovipositor of the Skokidae, Raphidiomimidae and Mesoblattinidae, is characterized by short, triangular dorsal and ventral valves, with merged slender short ovipositor plates (Lam 1 according to Vishniakova 1968), terminated by small, but distinct and hardly sclerotised V3.

The fore wings are widest in the apical third. This is frequently found in several extant Blattida families and should not normally be used to diagnose on family level. Nevertheless this character state was absent in all the Mesozoic cockroaches, and thus at that stage of the evolution of cockroaches was a significant character transformation.

The RS is indistinct and reduced also in the Blattulidae, but the presence of the long external ovipositor of caloblattinid type, the hindwing lacking pterostigma, and branched CuA (strong plesiomorphies) exclude direct ancestry of the Blattulidae.

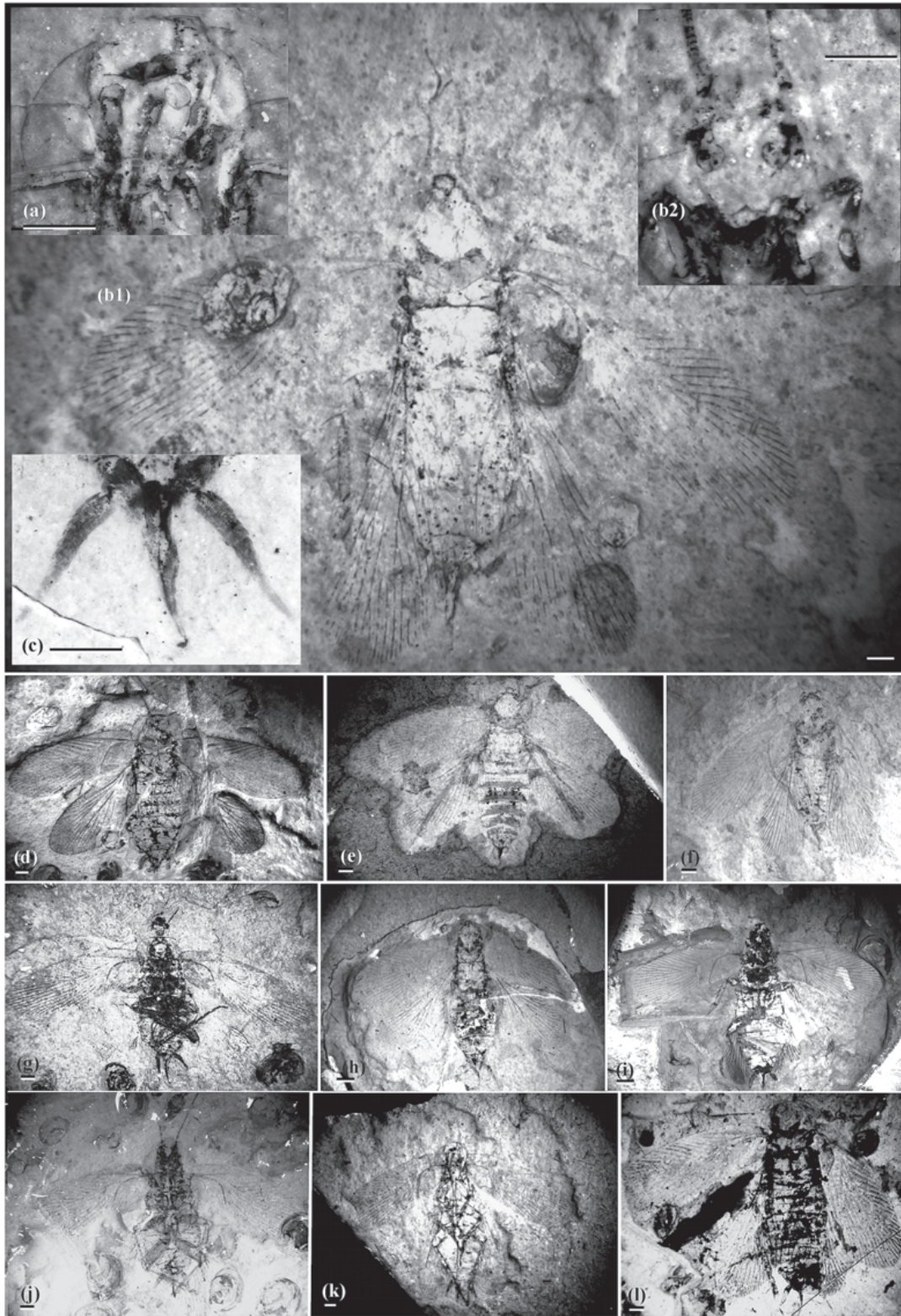


Fig. 6. Females of caloblattinoid *Fuzia dadao* sp. nov. **a** — Detail of head (CNU-B-NN-2006-371); **b1-2** — Paratype CNU-B-NN-2006-301, **b1** — general view, **b2** — head; **c** — Detail of female terminalia with curved ovipositor and 14-segmented cerci (CNU-B-NN-2006-383). Daohugou, Inner Mongolia, China. Middle Jurassic (?Bathonian). Complete females: **d** — CNU-B-NN-2006-306 (right forewing length 13 mm); **e** — CNU-B-NN-2006-380 (right forewing length 12.5 mm); **f** — CNU-B-NN-2006-1005 (right forewing length 12.5 mm); **g** — CNU-B-NN-2006-328 (right forewing length 13 mm); **h** — CNU-B-NN-2006-1001; **i** — CNU-B-NN-2006-341 (right forewing length 12.5 mm); **j** — CNU-B-NN-2006-314 (right forewing length 12 mm); **k** — CNU-B-NN-2006-371 (right forewing length 12 mm); **l** — CNU-B-NN-2006-348 (right forewing length 12 mm). Scales 1 mm.

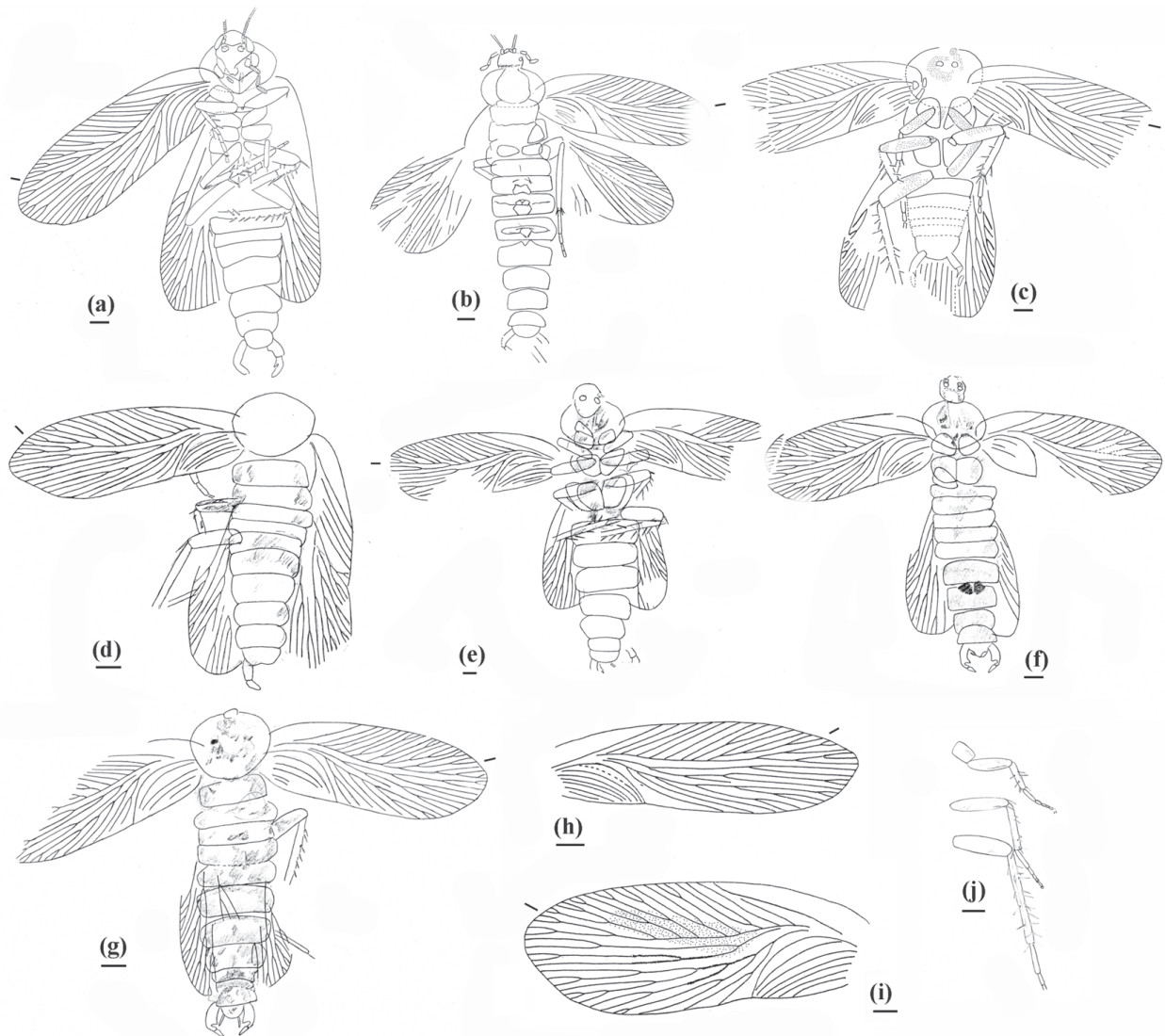


Fig. 7. Explanatory drawings of males of caloblattinoid *Fuzia dadao* sp. nov. **a** — CNU-B-NN-2006-677 (R)(right forewing length 14 mm); **b** — CNU-B-NN-2006-357 (right forewing length 10.6 mm); **c** — TNP42982; **d** — CNU-B-NN-2006-670; **e** — CNU-B-NN-2006-676 (R)(right forewing length 14.5 mm); **f** — CNU-B-NN-2006-672 (right forewing length 10 mm); **g** — CNU-B-NN-2006-322 (right forewing length 10 mm); **h** — CNU-B-NN-2006-669 (right forewing length 13 mm); **i** — CNU-B-NN-2006-671 (R)(right forewing length 15.5 mm); **j** — CNU-B-NN-2006-042. Daohugou, Inner Mongolia, China. Middle Jurassic (?Bathonian). **R** — reverse to actual position. Short line indicates position of R1 and RS. Scales 1 mm.

The hindwing (Fig. 2b1) is similar to the Liberiblattinidae Vršanský (2002), but the ancestry of Liberiblattinidae in respect to Fuziidae might be excluded on the basis of the apomorphically curved R in the forewing and the advanced external ovipositor of the “rudimentary-type”.

A globular head with short, as long as the head, maxillary palps, a fluently curved CuP, and simple A branches running parallel to the anterior margin are autapomorphic, whilst R reaching the apex is plesiomorphic. This combination of features prevents *Fuzia* being classified within the known Caloblattinidae. Instead, the Fuziidae+Blattulidae lineage probably diverged from the ancestors of Caloblattinidae or an earlier, yet undescribed representative of that family.

Enlargement of the pronotum combined with the large forewing costal area, especially in females, is a protective adaptation indicating a cryptic way of life. A coefficient of varia-

tion (CV) of 6.3 (for the total number of veins meeting margin) characterizes advanced modern taxa rather than Mesozoic cockroaches, which typically have a CV of 10–13. This CV might be caused by the conservative pattern of A, which varies in males, and more seriously by conservative female size.

Forewings are not symmetrical, but radial veins had a very low CV (14.44), which support comparatively good flight. The high total CV 8.51 for the total number of veins of both sexes indicates that the species, may have been the most specialized taxon of its age. Deformities (vein fusions) in the wing appear relatively common and distinct with seven vein fusions in 54 wings of 36 specimens suggesting that the species was undergoing rapid evolution.

The lack of coloration in both sexes may support the cryptic way of life (Jarzembowski 1994) of this large species, but it may indicate at least locally open environments (see below).

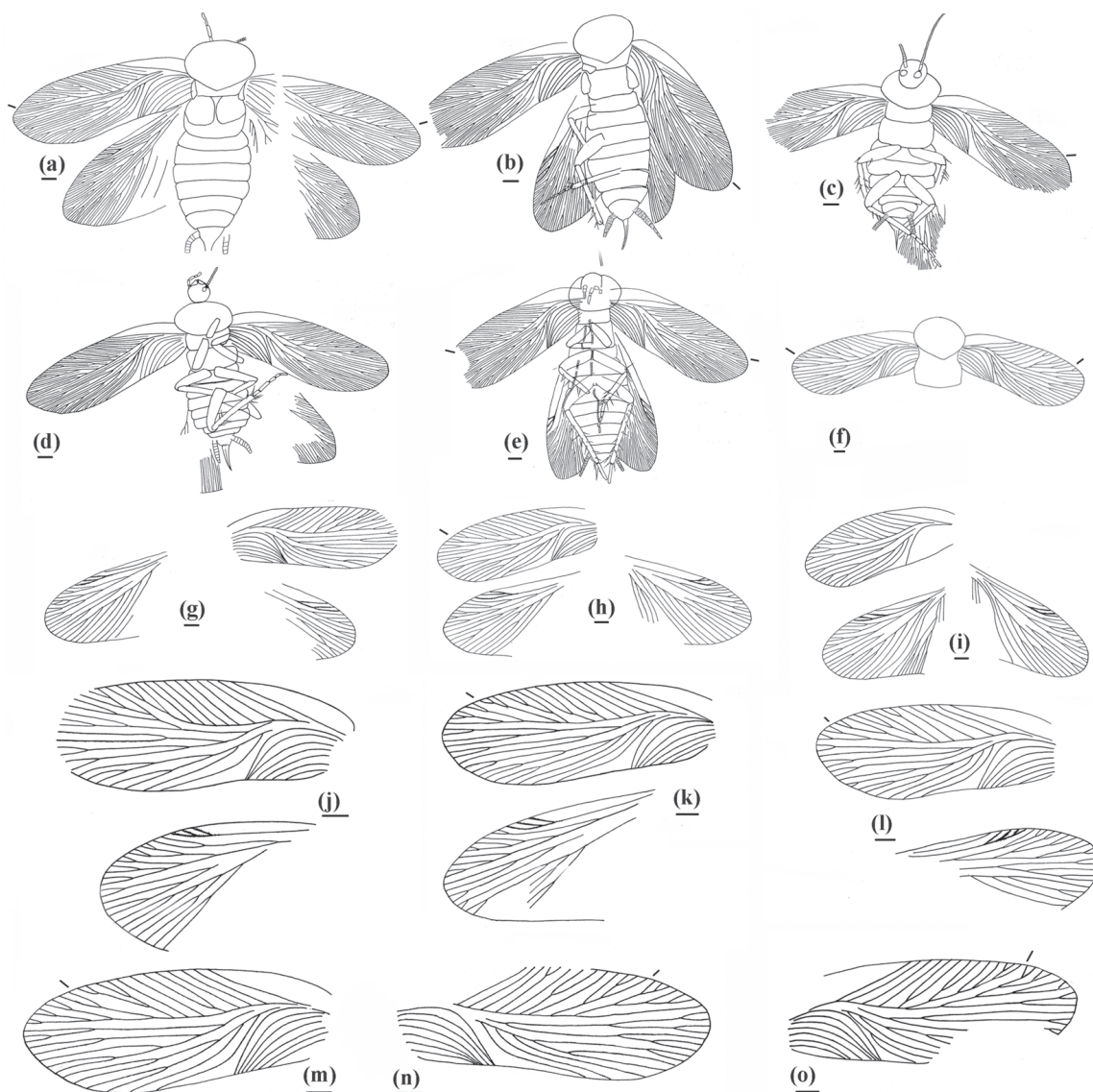


Fig. 8. Explanatory drawings of females of caloblattinoid of *Fuzia dadao* sp. nov. **a** — CNU-B-NN-2006-306 (R)(right forewing length 13 mm); **b** — CNU-B-NN-2006-348 (R)(right forewing length 12 mm); **c** — CNU-B-NN-2006-314 (right forewing length 12 mm); **d** — CNU-B-NN-2006-328 (right forewing length 13 mm); **e** — CNU-B-NN-2006-371 (right forewing length 12 mm); **f** — CNU-B-NN-2006-341 (right forewing length 12.5 mm); **g** — CNU-B-NN-2006-383 (right forewing length 13 mm); **h** — CNU-B-NN-2006-380 (R)(right forewing length 12.5 mm); **i** — CNU-B-NN-2006-1001(R)(right forewing width 4.2 mm); **j** — CNU-B-NN-2006-1005 (R)(right forewing length 12.5 mm); **k** — CNU-B-NN-2006-381 (R); **l** — CNU-B-NN-2006-1003 (R)(right forewing length 13 mm); **m** — CNU-B-NN-2006-1002 (R)(right forewing length 12 mm); **n** — CNU-B-NN-2006-1002 (R); **o** — CNU-B-NN-2006-305 (right forewing length 13 mm). Daohugou, Inner Mongolia, China. Middle Jurassic (?Bathonian). **R** — reverse to actual position. Short line indicates position of R1 and RS. Scales 1 mm.

The relative rarity of the species (ca. 3 % of all cockroaches) suggests that these “open-patch” environments were rare. It is notable that unlike in extant cockroaches (Vidlička 2001), the large Middle Jurassic cockroaches did not make themselves conspicuous.

The only coloured part of the present species is the hindwing apex (and possibly the forewing apex), which serves as terminalia-protection, as in fossil cockroaches apex hindwings are not covered by forewings. The presence of apex coloration also excludes unpreserved coloration of other body parts.

The non-segmented styli reaching the length of cerci is not recorded in any extinct cockroach families. The extruded pres-

ervation of male copulatory organs, including the hook, is unique and indicates that the terminalia were significantly protruded from the body at least during copulation.

Paleoethology and paleoecology of *Fuzia dadao* sp. nov.

Our samples allow some data on the paleoecological preferences of *Fuzia dadao* sp. nov. to be inferred. The most distinct structure of the present species is the forceps of males, and the ovipositor of the females. The forceps are formed by asymmet-

rical cerci, with narrow notches in strong, fused and widened cercal segments 8–13. The female ovipositor is comparatively short, extremely rigid (in contrast to other, also comparatively hard body structures, was preserved in 3D) and curved. The male notches fit to the ridge formed by the base and the strong tubercle of narrowed lateral margins of the female ovipositor outer valves — suggesting that the forceps served primarily for attaching to females during courtship and copulation.

Such a strong adaptation suggests fusion during copulation and, perhaps protection against extra mate copulation, however, such a protection is extraordinarily rare among extant insects. The presence of a long external ovipositor, suggest that the only possible position during courtship was with heads opposed, as observed in living cockroaches lacking external ovipositor (face-to-face position appear unrealistic because of the eventual reverse angle of male terminalia with respect to the body in such a pose).

The presence of male tergal glands also indicates an elaborated reproductive behaviour. Such glands are used for pre-copulation attraction of females in the living cockroach species. The female is posed over males first, attracted by male pheromones and feeding on its secretions (male with outstretched wings — Vidlička 2001). Prior to this study, the tergal gland was not recorded in any of thousands of fossil specimens of external ovipositor-bearing cockroaches, and thus it was thought the secret-feeding phase of courtship was absent. Nevertheless, the presence of these glands in such an old lineage is a direct indication of the plesiomorphy of glands and also this kind of behaviour.

The position of glands and their development vary among living cockroaches, and have different position (T2–T6) and

number (5 in *Fuzia*). According to the frequent action of homeotic genes it can be concluded the origin of the tergal glands is single, and this character plesiomorphic at the level of Mesozoic-originating Dictyoptera.

This hypothesis is additionally supported by a recent discovery of similar sexual pheromones in mantises (Hurd et al. 2004) and male accessory glands are found also in the lower termites (Weesner 1969).

Some additional inferences can be drawn from the available fossil record. The morphology of female ovipositor suggests that it served for oviposition into hard substrate, such as roots, straws or, less likely — because of the lack of wing coloration — into decaying wood (wood is rare in open environments). Hard wood as an oviposition substrate can be excluded because newborn cockroaches would be unable to emerge from the wood.

Transfer of nutritional packets from the female may have played a more prominent role in the ancestors of current cockroaches (R. Brossut personal communication to Nalepa 1994).

The longest observed fusion of cockroaches during copulation lasted 180 minutes (in the German cockroach — but usually 72–115 minutes in this species).

Long-lasting attachment of sexes during courtship is a common adaptation of insects, as with the Southern green stink bug *Nezara viridula* (Linnaeus 1758) may be attached for up to 80 days (P. Štys, personal communication 2008).

An alternative to grasping directly on the ovipositor would be merely to use it for grasping onto the abdomen itself, as often occurs in tettigoniids where males grasp the tegumentary foldings at the abdomen tip with their specialized cerci. Nevertheless, the specialized ridge, absent in all other external ovipositors strongly suggests attachment directly to the ovipositor. The tubercle defining the ridge is quite apart from the base excluding its ovipositor-strengthening function. A considerable gap left between the male and female genital orifices would make copulation problematic, but male terminalia are preserved quite far from abdomen, suggesting they were capable of protrusion.

In addition, the strongly sclerotized forceps at the end of an elongated plastic body may have served as a protective device against common predatory cockroaches and/or other carnivores, as in some living beetles such as the Staphilinidae mimicking wasp behaviour (their abdomen apex bears no threat to predators) and, to a lesser extent it may have been used in male combat. Notwithstanding, most living insects protect themselves by body movements, or through the mimicking of stinging insects, which did not become abundant until the Cretaceous (Rasnitsyn 2002) — therefore the origin of this form of protection in the present species remains obscure, also contradicted by the fact that females lack them. Anyway, once evolved, a structure may be secondarily used in this derived purpose.

The preferred habitat of *Fuzia dadao* sp. nov. is probably a more open shrub and/or woody habitat rather than forest landscape, because large species, such as those studied from the canopy forests in Laos, Borneo and Ecuador, are rarely uncoloured in rainforests (L. Vidlička, P. Vršanský, in preparation). Open habitat is also supported by the improved flight abilities of the both sexes — the roughly similar ratio of both sexes and low CV of female forewing venation indicate fe-

Table 1: *Fuzia dadao* sp. nov. Variability of forewing venation. **n** — number of wings (one individual occasionally reveal data for both wings (LR)); **min** — minimum; **max** — maximum; **dev** — standard deviation; **ave** — average; **CV** — coefficient of variation; **Sc** — subcosta; **R** — radius 1+radius sector (when differentiated); **M** — media; **CuA** — cubitus anterior; **CuP** — cubitus posterior; **A** — anal veins; **L** — left, **R** — right. **Total** — total number of veins (all veins, and CV, are measured when meeting margin). Length and width in mm. Analysed males: 042, TNP42982LR, CNU-B-NN-2006-322LR, 357L, 666LR, 669R, 671R, 672LR, 676LR, 677L; analysed females: CNU-B-NN-2006-305R, 306LR, 314LR, 328LR, 341LR, 348LR, 371LR, 380R, 381R, 383R, 1001R, 1002LR, 1003R, 1005R.

	length	width	Sc	R	M	CuA	CuP	A	total
<i>males/n</i>	12	12	15	15	15	15	15	14	14
max	15.5	6.5	1	25	10	13	1	7	51
min	10	3.6	1	15	3	4	1	4	37
dev	2.07	0.77	0	2.58	1.99	2.16	0	1.06	4.46
ave	12.15	4.33	1	18.4	6.46	8.93	1	5.85	40.93
CV	17.07	17.73	0	13.75	30.33	24.24	0	18.25	10.90
<i>females/n</i>	12	13	21	20	20	21	21	19	19
max	13	4.5	1	23	15	10	1	7	45
min	12.5	4.2	1	11	4	4	1	6	36
dev	0.45	0.15	0	2.50	2.32	1.63	0	0.37	2.55
ave	12.54	4.38	1	17.65	6.85	7.43	1	6.16	40.44
CV	3.59	3.47	0	14.15	33.92	21.94	0	6.08	6.30
<i>all/n</i>	28	25	36	34	35	36	36	31	32
max	15.5	3.6	1	25	12	13	1	7	51
min	10	4.7	1	11	3	4	1	5	36
dev	1.466	0.53	0	2.50	2.15	1.96	0	0.74	3.46
ave	12.35	4.36	1	17.33	6.69	8.06	1	6.03	40.66
CV	11.87	12.17	0	14.44	32.18	24.27	0	12.27	8.51

males were active in flight. Conversely, the large pronotum, a highly protective structure suggests cryptic habits and the presence of litter (Mesozoic cockroaches with such a large pronotum are extremely rare, even when many living cockroaches have pronota much more pronounced.). An entirely open landscape of the Daohugou source area might also be excluded based on the presence of an abundant flora.

Another phylogenetic trend is also apparent — the reduction of leg carination, indicating the stress in the protection was progressively changed from a passive, morphological, to an active, behavioural defence. It should have been connected with the radiation of effective predators such as beetles, but also the carnivorous cockroaches during the Early and Middle Jurassic.

It can be argued that in living cockroaches reduction of leg carination relates more to the kind of substratum the cockroaches live in (bark, leaf litter, plants leaves, etc.), but in all Mesozoic cockroaches carination is extensive. It is reduced only in actively moving jumping cockroaches (Vršanský 2007), in the blattulid *Tarakanula shcherbakovi* Vršanský, 2003, adapted to rapid running, and in extinct eusocial cockroaches (P. Vršanský, submitted).

Nevertheless, cryptic habits (in leaf litter for instance) cannot be definitely excluded for *Fuzia*, because its short legs are not a good defence against an agile predator.

The dietary specialization of *Fuzia dadao* sp. nov. can, to some extent, be inferred from the mouthpart morphology. Short palps, and long and wide mandibles exclude the palynivory [a single known palynivorous extinct cockroach *Skok svaba* Vršanský, 2007 has long, cup-like palps and small mandibles (Vršanský 2007)] as well as carnivory [carnivorous cockroaches have elongated mandibles with sharp teeth (Vishniakova 1973; Liang et al. 2009); early carnivorous mantises have wide but short and robust mandibles (Vršanský 2002)]. This suggests saprophagous diet analogical to those of most cockroaches, particularly to Blattulidae, that also have short palps.

Conclusions

— *Fuzia dadao* gen. et sp. nov. from the Bathonian Middle Jurassic of the Daohugou in Inner Mongolia, China, represents a new family Fuziidae. It was a species with cryptic habits in shrub source-area, with females active in flight. The presence of male forceps attaching to the notch in the female external rigid ovipositor is unique. Male and female body size is similar, but a peculiarity is the variability range of females, falling within the variability range of males;

— According to the basal position of the present species with respect to Mesozoic cockroaches, the presence of male tergal glands is a plesiomorphic character for most Mesozoic and all living cockroaches (excluding the very basal Phylloblattidae and Caloblattinidae);

— Mesozoic cockroaches had a modern morphology, superficially similar to living cockroaches.

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