GEOLOGICA CARPATHICA, AUGUST 2013, 64, 4, 291–304 doi: 10.2478/geoca-2013-0021

Completely preserved cockroaches of the family Mesoblattinidae from the Upper Jurassic-Lower Cretaceous Yixian Formation (Liaoning Province, NE China)

DANDAN WEI and DONG REN

College of Life Science, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing, 100048, P.R. China; rendong@mail.cnu.edu.cn

(Manuscript received January 1, 2013; accepted in revised form March 14, 2013)

Abstract: Although cockroaches were the dominant insects in various Paleozoic and Mesozoic insect assemblages, their general morphology was extremely conservative. One of the most common of them, the Jurassic-Cretaceous family Mesoblattinidae, is described here for the first time on the basis of completely preserved specimens. Ninety-two specimens of *Perlucipecta aurea* gen. et sp. n. reveal details of head, mandible, male tergal glands and terminal hook; cercal, leg and antennal sensilla. Its congener, *P. vrsanskyi* is described from the same sediments of the Yixian Formation (Upper Jurassic–Lower Cretaceous). The forewing venation variability of *P. aurea*, analysed for the first time in this family is nearly identical (CV = 6.23 %) with variability of two species of family Blattulidae that occur at the same locality (CV = 6.22 %; 5.72 %). The transitional nature of morphological characters represented by asymmetry between left and right wings (simple/branched forewing SC and hind wing M) in *P. aurea* documents the phylogenetic relation between the families Mesoblattinidae and Ectobiidae.

Key words: Jurassic, Cretaceous, Liaoning Province, fossil insects, Blattaria, Ectobiidae, Mesoblattinidae, new genus, new species.

Introduction

Blattaria (i.e., cockroaches), important as ecological decomposers, are one of the phylogenetically old insect groups. Fossil cockroaches occurred for the first time in the Late Carboniferous (Brongniart 1885; Zhang et al. 2012), and gave birth to two different orders Isoptera and Mantodea (Vršanský 2002, 2010). They adapted to multiple types of ecosystems and reached a high level of ecological and morphological diversity (disparity) over the course of their evolution, including aquatic (Shelford 1909), pollinating (Nagamitsu & Inoue 1997), jumping (Vršanský 2007; Bohn et al. 2010; Picker et al. 2012), light-mimicking (Zompro & Fritzsche 1999; Vršanský et al. 2012), translucent (Vidlička et al. 2003), predatory (Vishniakova 1973; Liang et al. 2009, 2012), beetle-like (Vršanský 2003a), and eusocial (Vršanský 2010) forms.

Cockroaches are composed of 27 families in their 320 Myr-long history. The oldest reproductively and sensory-advanced family of cockroaches, the Mesoblattinidae, evolved during the Early Jurassic (Vršanský 2000, 2003b; Vršanský & Ansorge 2007). Nevertheless, their diversity at the genus level is low, and only 12 genera are known in their history. The morphological differences among genera are mostly based on wings or on characters preserved in amber (*Mesoblattina* Geinitz, 1880, *Praeblattella* Vršanský, 2003b, *Archimesoblatta* Vršanský, 2003b, *Brachymesoblatta* Vršanský, 2003b, *Breviblattina* Vršanský, 2004a, *Mongolblatta* Vršanský, 2004a, *Turoniblatta* Vršanský, 2004b, *Gondwablatta* Vršanský, 2004b, *Nymphoblatta* Vršanský & Grimaldi, 2004, *Sivis* Vršanský, 2009, *Hispanoblatta* Martínez-Delclòs, 1993, *Artitocoblatta* Meunier, 1914) (Geinitz 1880; Meunier 1914; Martínez-Delclòs 1993; Vršanský 2003b, 2004a,b, 2009). A large numbers of taxa described and placed in this family in the past were transferred into Caloblattinidae (Vršanský 2000).

Well-preserved complete fossil specimens with ultrastructure details and colouration recovered from the Yixian Formation, belonging to *Perlucipecta* gen. n. and described in this study, are significant because they represent the first complete Mesozoic cockroach recovered from sediments with such details, and also correspond to the first members of the Mesoblattinidae preserved in the Yixian Formation. The aim of this paper is to describe the morphological structures of the specimens, and compare them with representatives of their descendants, the Cretaceous–Recent family Ectobiidae (= Blattellidae).

We test whether their morphology and microstructures are similar to the morphology of another family Ectobiidae, and compare coefficients of variation in the number of veins with other Jurassic cockroaches. The venation variability coefficients observed in these specimens, comparable to variability of species belonging to the family Blattulidae preserved at the same locality is surprising because variability trends are traceable in respective phylogenetic lineages and not in respective localities (and possibly in specific environments).

Material and methods

A total of ninety-two specimens of *P. aurea* and ten specimens of *P. vrsanskyi* are deposited in the fossil insect collection of the Key Laboratory of Insect Evolution & Environmental

Changes, Capital Normal University, Beijing, China. The specimens were examined with a Leica MZ 12.5 dissecting microscope and illustrated with the aid of a drawing tube attached to the microscope. Line drawings were made with Photoshop CS 8.0 graphic software. Photographs of the fossils were taken by a MZ12.5 dissecting microscope (Leica, Wetzlar, Germany), either dry or with alcohol applied to the surface (to reveal contrast and organic matter). The coefficient of variation was computed as the standard deviation in the number of veins divided by the average number of veins, on the basis of thirty-nine specimens with complete forewings, using SPSS 16.0 Statistical software. We refer to the total number of veins meeting the wing margin.

All specimens were found in a section exposing the Jianshangou Bed of the Yixian Formation at Chaomidian village, Beipiao City, western Liaoning Province, China. This area is situated in a volcanic sediment basin (Fig. 1). There are at least three thick fossil-bearing beds formed by tuffaceous shales within the Yixian Formation, including the Jianshangou Bed located in the lower part of Yixian Formation. Three sections that expose the Jianshangou Bed are represented by Libalanggou-Sihetun, Jianshangou, and Huangbanjigou (Chen et al. 2004). The material in this study came from several unidentified beds of the Huangbanjigou section that span dozens of meters. This section previously revealed a large number of well-preserved insects (Liu et al. 2007a,b; Tan et al. 2007; Gao & Ren 2008). The age of the Yixian Formation is still debated, with three opinions: the Late Jurassic (based on insects and primitive fossil birds — Ren et al. 1997), transitional Late Jurassic–Early Cretaceous (based on diverse insects, pterosaurs, ostracods and fish — Wang et al. 2004, 2005), and the Early Cretaceous (based on ostracods — Pang et al. 2002; Zhou et al. 2003). Here, we consider the age of the Yixian Formation to be Late Jurassic or Early Cretaceous. The climate and the approximate paleolatitude of the location during the depositon of the Jianshangou Bed was subtropical humid as indicated by the cockroaches considered here.

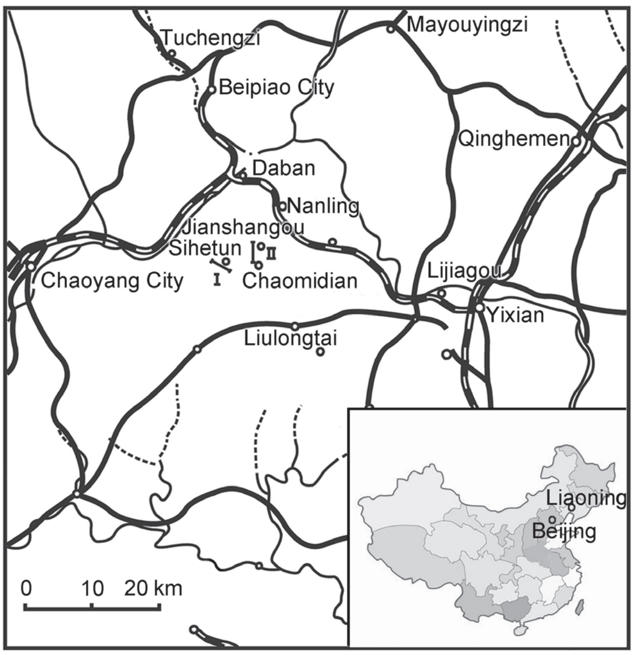

Fig. 1. Localities of the Yixian Formation in Jinzhou-Yixian area, western Liaoning (modified after Ren et al. 2010). Sihetun section (thickness: 264.95 m), Jianshangou section (thickness: 79.46 m).

The venation nomenclature used in this paper is based on the terminology of Comstock & Needham (1898). Abbreviations used: RFW — Right forewing, LFW — Left forewing, HW — Hind wing, Sc — Subcosta, R — Radius, Rs — Radius sector, M — Media, Cu — Cubitus (A — anterior, P — posterior), A — Anal vein.

Systematic paleontology

Order: **Blattaria** Latreille, 1810
Family: **Mesoblattinidae** Handlirsch, 1906

Genus: *Perlucipecta* Wei & Ren, gen. n.

Type species: *Perlucipecta aurea* sp. n.

Composition: Type species and *P. vrsanskyi* sp. n.

Differential diagnosis: The present genus can be assigned to the family Mesoblattinidae based on the following features: branched forewing Sc; hindwing simple Sc, Rs differentiated, simplified M, CuA with secondarily branched veins and blind rami.

It differs from all the other representatives of the family by the following features: expanded venation with retained intercalaries and distinct cross-veins; large size; facultative simplification of hindwing M.

Description: Head inverted-triangular shape, extending beyond the pronotum.

Pronotum elliptical, transversal (width longer than length), transparent near edges and coloured in the center.

Abdomen broad, with dark coloured longitudinal stripes. Cerci gradually pointed to the end, 9 segments and with alternating dark and pale colouration.

Forewing long, with rich venation (more than 42 branches at margin), Sc bifurcated, R rich and stem straight, M with abundant branches, CuA sparse, reaching the posterior wing, CuP radian concave and then convex to the posterior wing, A rich, simple, costal space shorter and smaller than clavus.

Hind wing Sc simple, R and Rs rich and branched, M simple or simply branched, CuA with abundant dichotomized branches and blind rami.

Character list

- Head: inverted-triangular shape, extending beyond the pronotum slightly; eyes protruding beyond the outline of head: synapomorphic with living cockroaches;
- Antennal sockets conspicuous at sides; antenna slender, almost as long as the body; mouthparts hypognathous, mandible strong with sharp teeth: synapomorphic with living cockroaches;
- Sensilla throughout the antennal segment: unknown;
- Palps (maxillary and labial) long: homoplastic with Caloblattinidae;

• Pronotum: large, wide (as wide as the body), almost 3 times wider than the head; elliptical, parallel edge; transparent margin and with dark markings at center: symplesiomorphic at the level of Phyloblattoidea;

• Body wide (with markings at margin), slightly shorter than forewing: autapomorphic;

• Tergal glands present: synapomorphic at the level of Caloblattinidae or earlier;

• Cerci: with reduced number of segments (under 10) and alternating colouration: synapomorphic at the level of the family;

• Cercal sensilla small circle, present at the margin of each segment: synapomorphic at the level of the family;

• Legs: slender, with rich spines: symplesiomorphic at the level of Phyloblattoidea;

• Forewing with distinct markings only from the center to the posterior end: autapomorphic;

• Forewing with distinct intercalaries: symplesiomorphic at the level of advanced Phyloblattoidea;

• Forewing with distinct crossvein-like reticulations: symplesiomorphic at the level of advanced Phylloblattoidea;

• Forewing costal area narrow: synapomorphic with advanced Liberiblattinidae and Blattellidae, homoplastic with Blattulidae;

• Forewing Sc short and branched: symplesiomorphic (level of earliest cockroaches);

• Forewing Rs indistinctly differentiated: unknown;

• Forewing venation rich: symplesiomorphic (level of earliest cockroaches);

• Forewing medial area wide and expanded: symplesiomorphic (level of earliest cockroaches);

• Forewing cubital area narrow and reduced: autapomorphic;

• Forewing clavus long (longer than Sc) and wide: not diagnostic;

• Forewing A simple and rich: synapomorphic with Blattellidae, simplicity is homoplastic with Blattulidae;

• Hindwing Rs differentiated: symplesiomorphic at the level of Phyloblattoidea;

• Hindwing M facultatively simple: synapomorphic with Blattellidae;

• Hindwing CuA multiply branched: symplesiomorphic at the level of Liberiblattinidae.

Etymology: *Perlucipecta* is a combination of *perlucidus* (Latin for transparent) and *pectus* (Latin for thorax), referring to its specially transparent (in the edge) and coloured (in the middle) pronotum; gender feminine.

Perlucipecta aurea sp. n.
(Figs. 2–7, 10a,c,e,g,i,k; Table 1)

Holotype: CNU-B-NN-2011610pc (part and counterpart), a well-preserved complete specimen (Figs. 2a, 3b).

Type locality: Huangbanjigou, Chaomidian village, Beipiao City, Liaoning Province, North-east China.

Type horizon: Yixian Formation, Upper Jurassic or Lower Cretaceous.

Additional material: CNU-B-NN-2011600, 601, 603–606, 609, 611–613, 615, 617, 622, 627, 628, 631–635, 638, 640, 641, 643, 644, 646–649, 652, 657, 658, 660–666, 668–671, 673pc–674, 675, 677–680, 683–692, 694, 697–699, 701, 703, 706, 712, 715, 732, 733, 737, 739, 742–744pc, 747pc, 748, 749, 754, 757, 759, 774, 784–790, 795.

Etymology: The specific name is derived from the Latin word "*aureus*" — (meaning "golden"), for the colour of the Yixian Formation sediment.

Differential diagnosis: The species differs from its congener *P. vrsanskyi* by distinct markings under forewing R region; the shape of a more simple tergal gland (convex to the abdominal segment) (Fig. 2e), larger size and the shape of dark markings in pronotum.

Description: Middle-sized, with body length 8.9–13.2 mm (excluding pronotum), length of abdomen 9.0–12.5 mm, width of abdomen 3.5–6.0 mm. Head small, inverted-triangular shape, slightly longer than wide, slightly extending beyond the pronotum (length/width 1.9–2.2/2.4–2.8 mm) (Figs. 2h, 3a); antennal socket and compound eye obvious at sides, antenna length 12.4–13.5 mm, with 76–77 very short segments (Figs. 2b, 10k); antenna sensilla throughout the antenna segment (Figs. 2c, 3g); mandibles strong (Fig. 2i, Fig. 3d).

Pronotum breadthwise elliptical, broad (length/width 2.9–4.5/4.5–5.5 mm), transparent by the edge and with dark markings in the middle; abdomen broad, with 6–8 segments distinct, with dark markings at margin; gland length 0.4–0.7 mm, width 1.2–1.5 mm, convex to the abdominal segment (Figs. 2e, 10a,c,e,g,i); terminalia smooth, with cerci gradually to the end (9 segments) and alternating colouration (Fig. 2f), cercus sensilla preserved as small circles at the margin of each segment (Figs. 2g, 3e).

Forewing: Length 12.0–17.0 mm, width 4.0–5.6 mm; broad, with distinct markings only from the middle to posterior end (Figs. 2a, 3b, 4–7), with intercaleries and numerous crossveins; venation rich, with 43–54 veins at margin, forewing sensilla present in the veins (Fig. 2l); Sc short and

Table 1: *Perlucipecta aurea* sp. n. Variability of forewing venation. **CV** — coefficient of variability; **Sc** — subcosta; **R** — radius; **M** — media; **CuA** — cubitus anterior; **A** — anal veins; **SUM** — A excluded; **Total** — total number of veins.

	Sc	R	M	CuA	A	Sc+R	R+M	R+Cu	M+Cu	SUM	Total
Number	36	36	32	30	33	33	30	28	32	32	29
Minimum	1	18	7	3	6	20	26	23	14	35	43
Maximum	4	24	15	10	10	26	37	31	22	46	54
Median	2.00	20.00	11.00	5.00	7.00	23.00	32.00	26.00	17.00	39.50	47.00
Mode	2	20	11	5	7	22	31	26	17	39	46
Std. error of mean	0.13	0.29	0.37	0.27	0.20	0.31	0.49	0.44	0.37	0.47	0.55
Std. deviation	0.77	1.71	2.08	1.40	1.16	1.75	2.65	2.32	2.09	2.68	2.96
CV in %	31.68	8.28	18.48	28.21	15.88	7.53	8.3	8.72	12.13	6.23	6.67

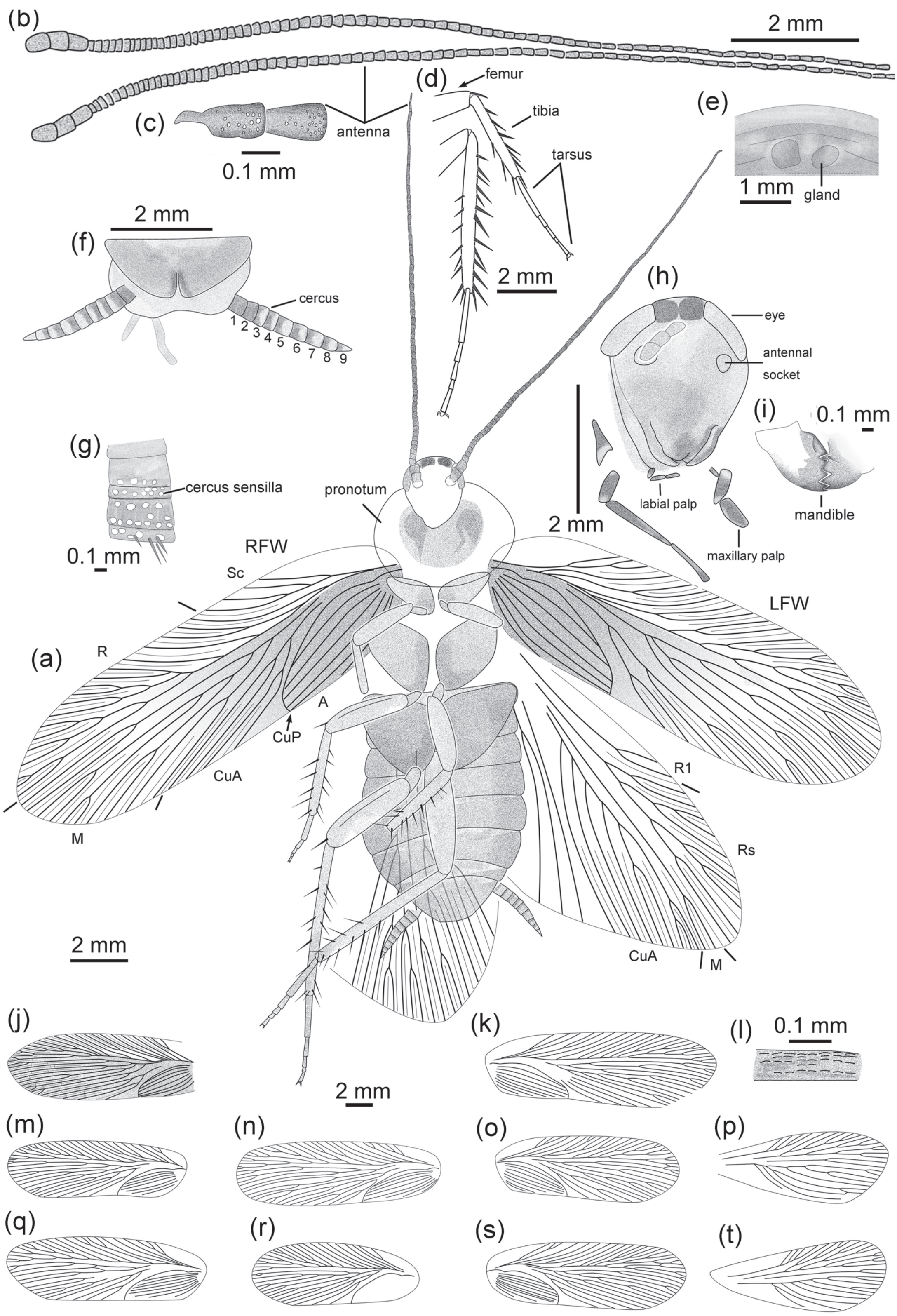

Fig. 2. Drawings of *Perlucipecta aurea* sp. n. (collection CNU-B-NN-2011). **a** — Holotype 610; **b** — Antenna (606); **c** — Detail of antenna sensilla (733); **d** — Legs (609); **e** — Ventral view with glands (600); **f** — Detail of terminalia with cerci (606); **g** — Detail of cerci sensilla (640); **h** — Head (603); **i** — Detail of head mandible (759); **j** — Left forewing (length 14.0 mm) (687); **k** — Right forewing (length 17.0 mm) (784); **l** — Detail of forewing sensilla (640); **m** — Left forewing (length 13.5 mm) (670); **n** — Right forewing (length 15.0 mm) (698); **o** — Right forewing (length 13.5 mm) (669); **p** - Right hind wing (length 13.0 mm) (789); **q** — Right forewing (length 13.9 mm) (699); **r** — Right forewing (length 12.5 mm) (670); **s** — Left forewing (length 15.0 mm) (684); **t** — Hind wing (length 13.9 mm) (668).

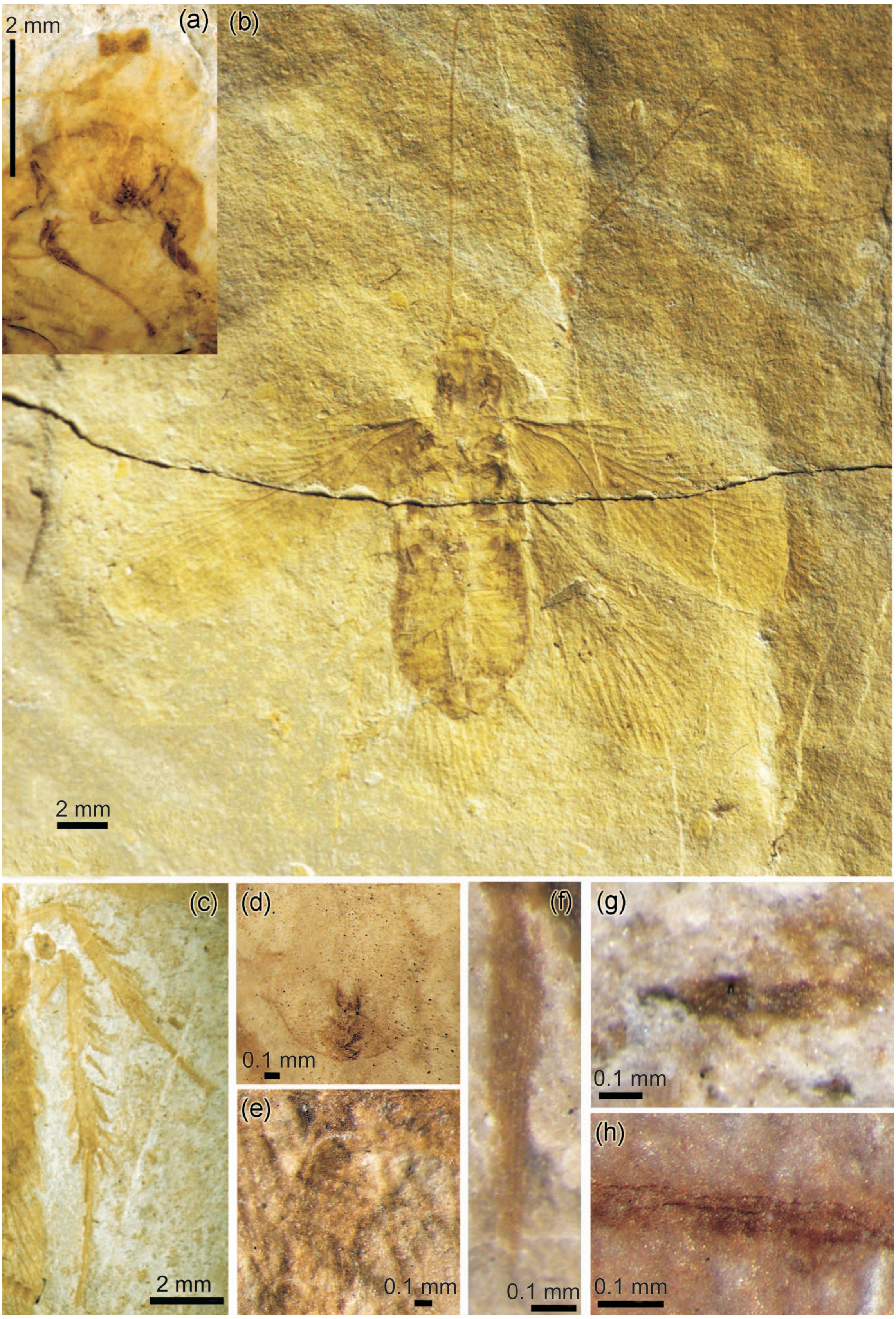

Fig. 3. Photographs of *Perlucipecta aurea* sp. n. (collection CNU-B-NN-2011). **a** — Head (603); **b** — Holotype 610; **c** — Legs (609); **d** — Detail of head mandible (759); **e** — Detail of cercal sensilla (640); **f** — Detail of spines (664); **g** — Detail of antennal sensilla (733); **h** — Detail of wing sensilla (640).

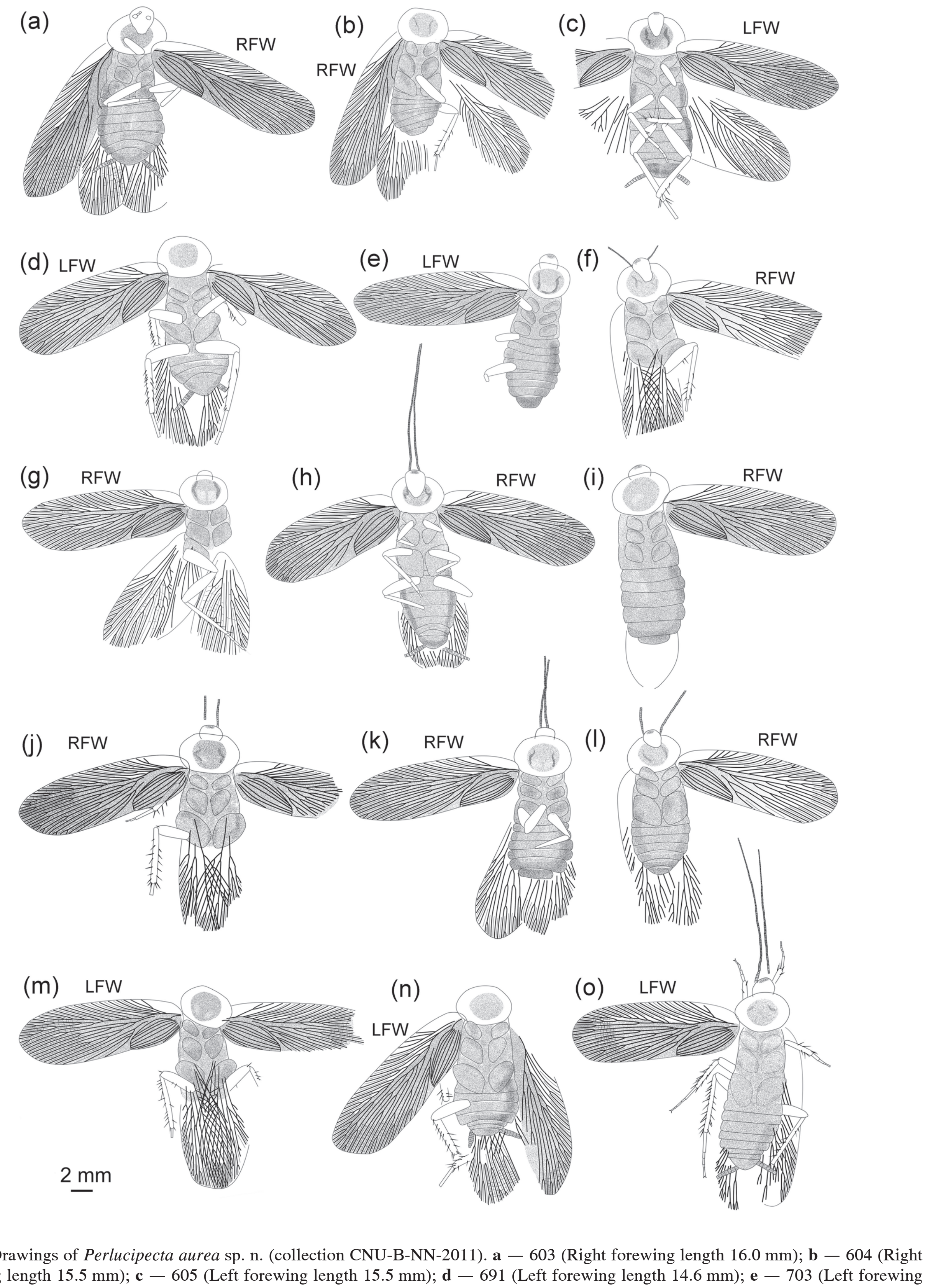

Fig. 4. Drawings of *Perlucipecta aurea* sp. n. (collection CNU-B-NN-2011). **a** — 603 (Right forewing length 16.0 mm); **b** — 604 (Right forewing length 15.5 mm); **c** — 605 (Left forewing length 15.5 mm); **d** — 691 (Left forewing length 14.6 mm); **e** — 703 (Left forewing length 15.0 mm); **f** — 685 (Right forewing length 15.0 mm); **g** — 601 (Right forewing length 15.0 mm); **h** — 606 (Right forewing length 14.5 mm); **i** — 694 (Right forewing length 15.0 mm); **j** — 662 (Right forewing length 16.0 mm); **k** — 675 (Right forewing length 15.0 mm); **l** — 689 (Right forewing length 15.0 mm); **m** — 663 (Left forewing length 16.0 mm); **n** — 664 (Left forewing length 16.5 mm); **o** — 609 (Left forewing length 15.0 mm). Scale bar = 2 mm.

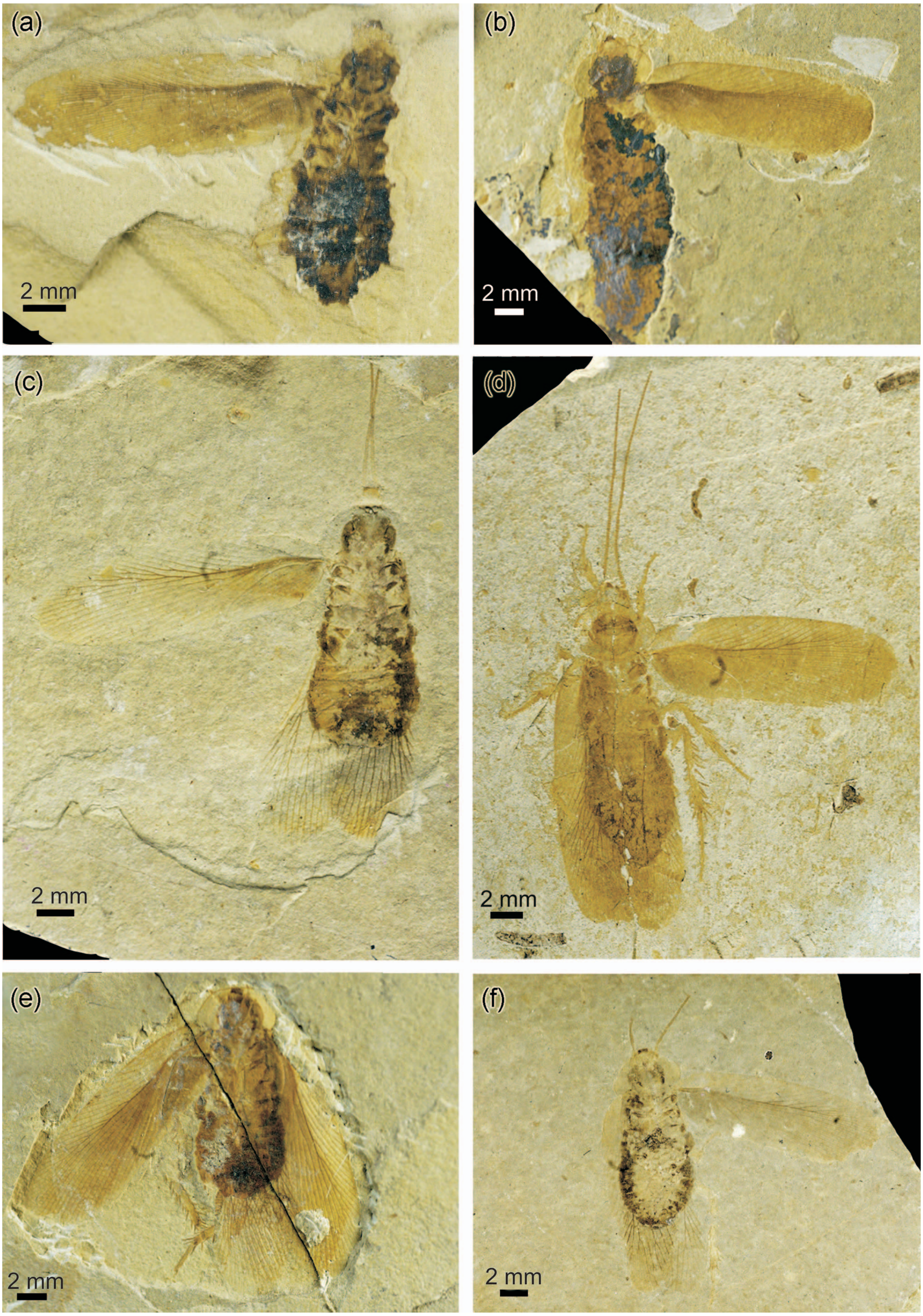

Fig. 5. Photographs of *Perlucipecta aurea* sp. n. (collection CNU-B-NN-2011). **a–f** — (703, 694, 675, 689, 664, 609).

branched, with 1–4 veins reaching anterior wing margin at narrow space, Sc area shorter than clavus; R stem straight reaching wing apex, with regular branching pattern reaching anterior wing margin, posteriorly pectinate with secondary forks, with 18–24 branches; main stem of M parallel to R; medial area wide, with 7–15 terminal branches; cubital area narrow and gently curved, with 3–10 branches reaching the posterior wing; CuP with radian convex to the posterior wing near 40 % of wing length, terminal almost with bending; clavus broad, more than 50 % of wing width; A gently curved, with 6–10 veins, some reaching CuP.

Hind wing: Length 11.0–13.9 mm; with intercalaries and without pterostigma; with about 22–29 veins of remigium; Sc simple; R1 (2–4) and the Rs (8–14) are differentiated; M simple or bifurcated near margin, almost straight to wing apex; CuA with about 9–11 branches.

Legs: Slender (Figs. 2d, 3c); length of fore femora 1.16–1.49 mm and tibiae 1.16–1.22 mm, length of mid femora

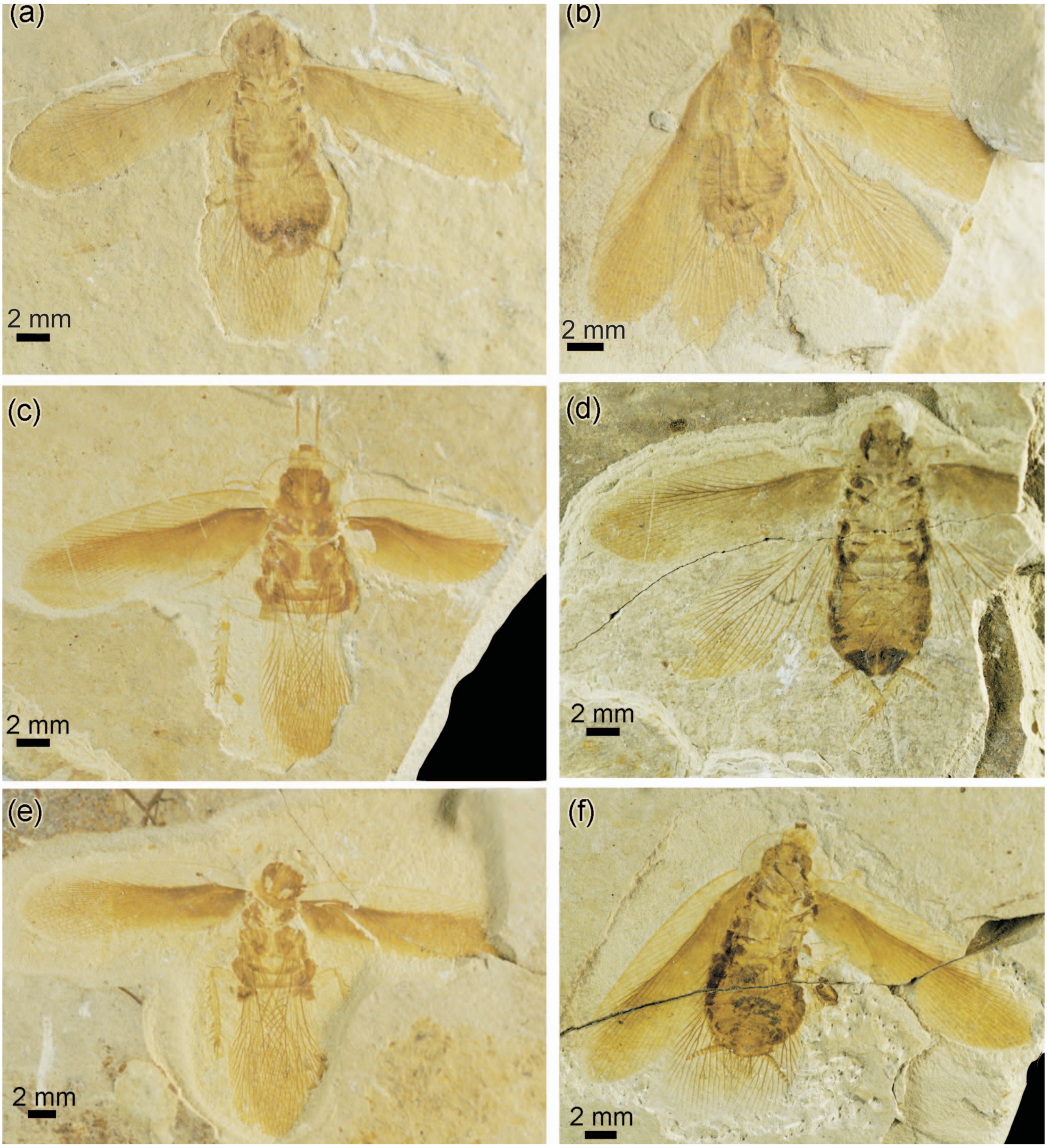

Fig. 6. Photographs of *Perlucipecta aurea* sp. n. (collection CNU-B-NN-2011) **a–f** — (691, 604, 662, 605, 663, 603).

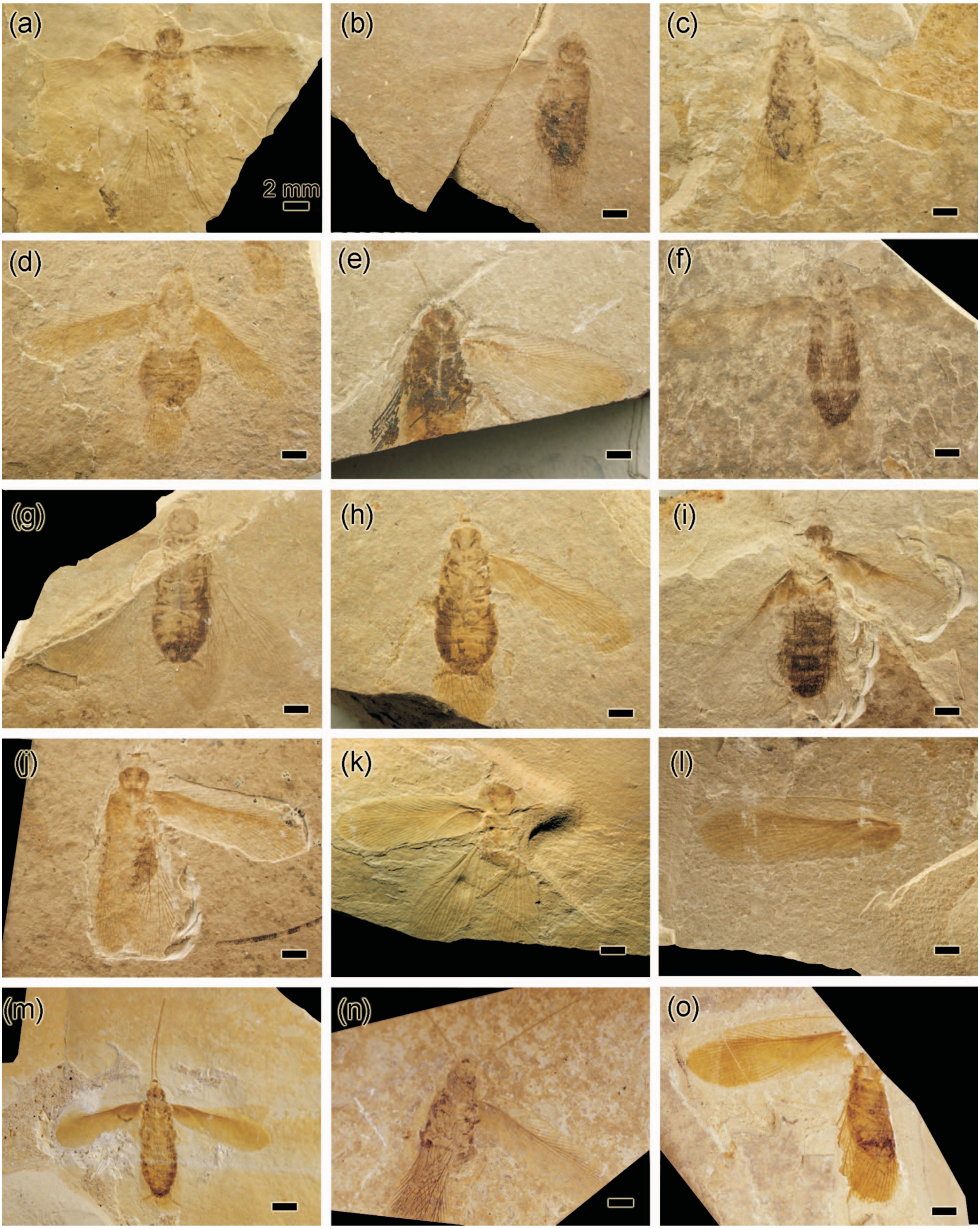

Fig. 7. Photographs of *Perlucipecta aurea* sp. n. (collection CNU-B-NN-2011). **a–f** — (789, 669, 759, 670, 784, 683, 668, 669, 715, 684, 601, 698, 606, 685, 687). Scale bar = 2 mm.

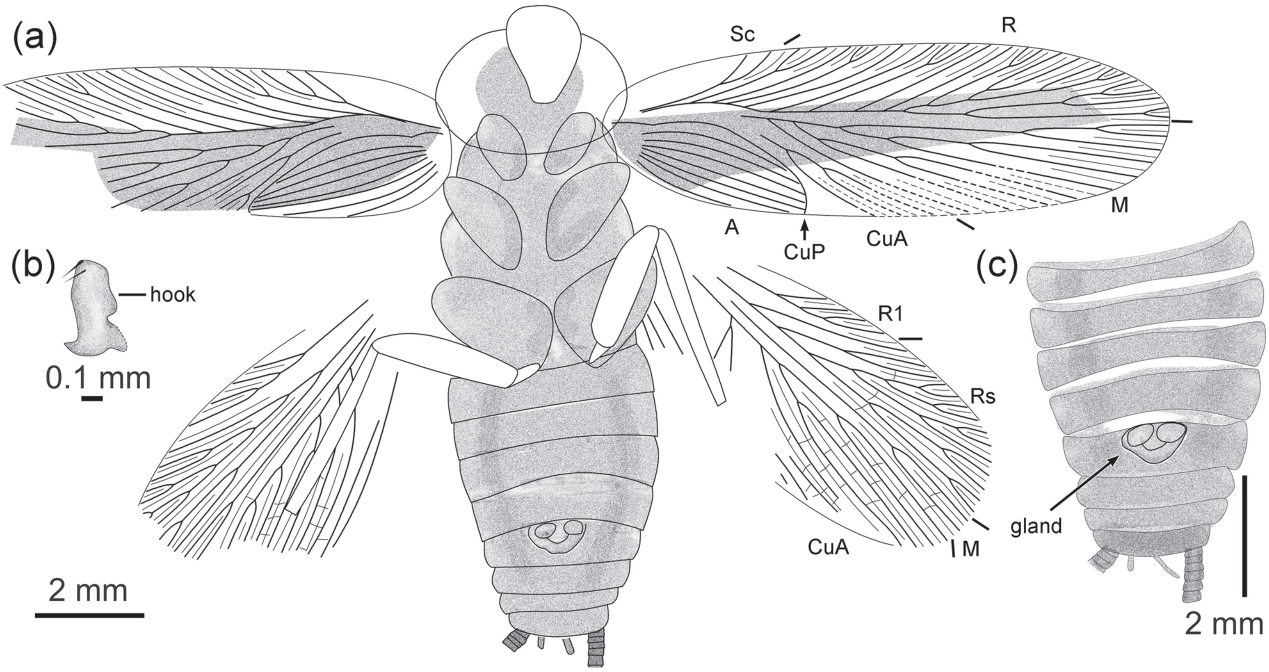

Fig. 8. Drawings of *Perlucipecta vrsanskyi* sp. n. (collection CNU-B-NN-2011). **a** — Holotype 704; **b** — Detail of terminalia with hook (794); **c** — Ventral view with glands (704).

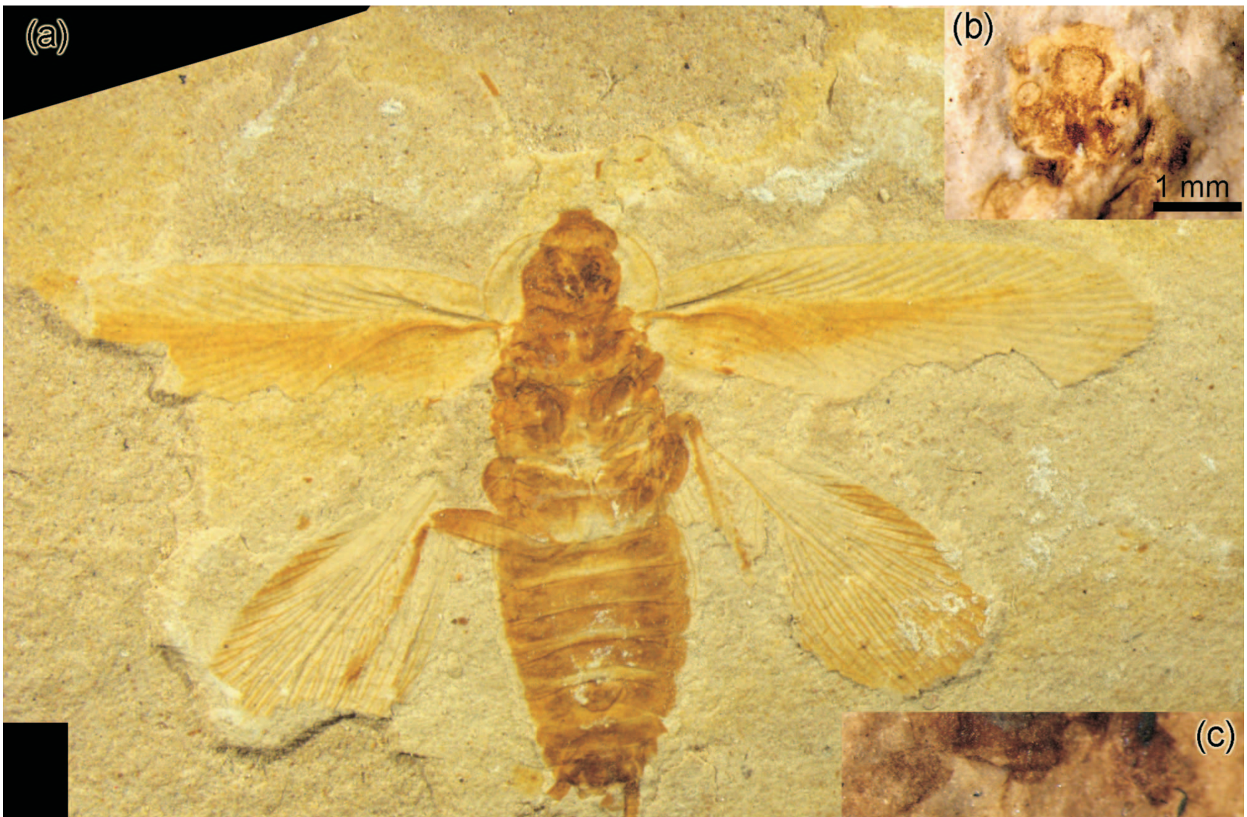

Fig. 9. Photographs of *Perlucipecta vrsanskyi* sp. n. (collection CNU-B-NN-2011). **a** — Holotype 704; **b** — Head (727); **c** — Detail of terminalia with hook (794).

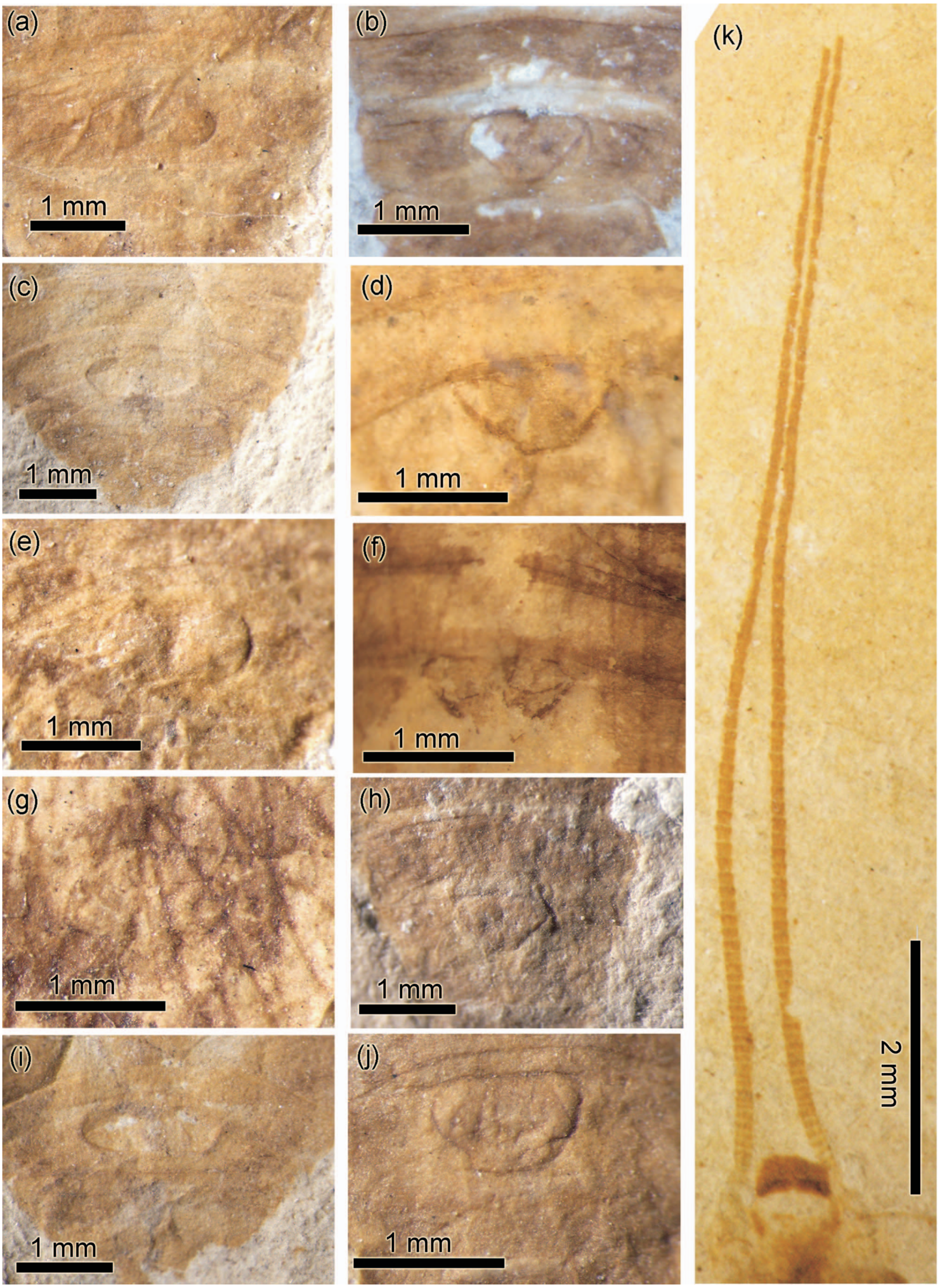

Fig. 10. Photographs of glands and antenna (collection CNU-B-NN-2011). **a** — Detail of *P. aurea* gland (600); **b** — Detail of *P. vrsanskyi* gland (704); **c** — Detail of *P. aurea* gland (661); **d** — Detail of *P. vrsanskyi* gland (626); **e** — Detail of *P. aurea* gland (627); **f** - Detail of *P. vrsanskyi* gland (654); **g** — Detail of *P. aurea* gland (706); **h** — Detail of *P. vrsanskyi* gland (770); **i** — Detail of *P. aurea* gland (671); **j** — Detail of *P. vrsanskyi* gland (791); **k** — Detail of a complete antenna (606).

1.89–1.93 mm and tibiae 1.47–1.56 mm, length of hind femora 2.12–2.19 mm and tibiae 2.59–3.45 mm; legs gradually get longer from the front to the hind legs; mid and hind leg with spines on the tibiae, and spines strong and hard, with helical ridges (Fig. 3f).

Perlucipecta vrsanskyi sp. n.
(Figs. 8–9, 10b,d,f,h,j)

Holotype: CNU-B-NN-2011704, male, nearly complete specimen (Figs. 8, 9).

Type locality: Huangbanjigou, Chaomidian village, Beipiao City, Liaoning Province, North-east China.

Type horizon: Yixian Formation, Upper Jurassic or Lower Cretaceous.

Additional material: CNU-B-NN-2011626, 630, 654, 656, 716, 727, 770, 791, 794.

Etymology: The species name *vrsanskyi* is after Peter Vršanský, for the help he has given me for years.

Differential diagnosis: Differing from *P. aurea* in small size; pronotum colouration; shorter forewing; with markings only in the centre (Fig. 8a); hind wing with pterostigma; the shape of the gland (trapezoidal, parallel to the abdominal segment) as shown in Fig. 8c.

Description: Small-sized, with body length 8.7–10.0 mm (excluding pronotum), width of abdomen 3.1–3.8 mm. Head small, inverted-triangular shape (length/width = 1.5 mm/ 1.3 mm) (Fig. 9b), extending beyond the pronotum slightly; pronotum length 1.9–3.0 mm, width 2.9–3.5 mm, with dark markings at center; abdomen with 7–8 segments preserved, wide in the middle of segments; gland length 0.6–0.7 mm, width 0.9–1.0 mm, trapezoidal, parallel to the abdominal segment (Figs. 8c, 10b,d,f,h,j); terminalia with cerci alternating coloration.

Forewing: Length 9.0–11.0 mm, width 2.9–3.0 mm, with distinct markings in the center; with intercaleries and venation rich, with 46 veins at margin; Sc short and with 2 branches, Sc area shorter than clavus; R stem parallel reaching wing apex, with regular branching pattern reaching anterior wing margin, with 23 branches; main stem of M parallel to R; medial area wide, with 10 terminal branches; cubital area narrow and gently curved, with 3 branches reaching the posterior wing; CuP with radian convex; clavus broad, more than 50 % of wing width; A gently curved, with 7 veins, some reaching CuP.

Hind wing: Length 8.1 mm (as preserved); with intercalaries and with pterostigma; with about 26 veins of remigium; Sc simple; R1 (4) and the Rs (22) are differentiated; M bifurcated near margin.

Discussion

With the exception of the Mesoblattinidae, the Blattulidae, Liberiblattinidae and Caloblattinidae (Wang & Ren 2013) families, each represented by a few genera and species, occur in the deposits of the Yixian Formation (only the below-mentioned Blattulidae were described). Mesoblattinidae with ca. 200 specimens and 7 species (the two most common species are described here) numerically dominate in the cockroach assemblage from the Yixian Formation. Such dominance represents a standard pattern in all the Jurassic assemblages worldwide (Vršanský 2004a, 2008). The proportion of the representative species *P. aurea* relative to all cockroaches approaches 10 % — a similar proportion as in the Tithonian of the Shar-Teg locality in Mongolia and Chernovskie Kopi in Russia (Barna in print).

The Jurassic specimens of this family were predominantly represented by tegmina. The specimens described here are complete and thus reveal many details about the morphology of the Mesoblattidae. The presence of two sister species differing mostly in the male tergal gland can imply that they occupied different source habitats. A similar set of sister species is known in the Blattulidae (Vršanský 2003b), but nowhere else in cockroaches. Cockroaches with sophisticatedly coloured parts imply that the habitats of the Yixian Formation inhabited by these cockroaches were humid (Ding et al. 2003). Dry habitats are rather characterized by monochromatic and pale cockroach individuals.

Morphology (including microstructures, sexual glands and terminalia) is extremely similar to *Piniblattella vitimica* Vishniakova, 1964 of the family Ectobiidae (= Blattellidae), which were descendants of the Mesoblattinidae (see Vršanský 1997). Mesoblattinidae differ only in the following plesiomorphies: rich venation with local irregularities and with richly branched forewing Sc, specialized hind wing R1, branched hind wing M and in primitive reproduction with primitive ootheca.

The total number of forewing veins in *Perlucipecta* differs between the left and right wings in the same specimens. For example, it varies between 50 (right forewing) and 47 (left forewing) in the specimen CNU-B-NN-2011606 and between 43 (right forewing) and 44 (left forewing) in the specimen CNU-B-NN-2011610. These patterns show that cockroaches are often asymmetrical in their venation, as observed also in living individuals (Roth 1991), amber specimens (Vršanský et al. 2011) as well as in other fossil specimens preserved in sediments (Liang et al. 2012).

Intraspecific variability in wings (*P. aurea*) is revealed for the first time in this family (*Hispanoblatta* as a representative of the Blattellidae is not relevant). The coefficient of variation (CV) in the total number of veins (per wing) of *P. aurea* is relatively low (6.23 %). This can be associated with the higher age of the group at that time (since it originated in the earliest Jurassic), and fits well with the trend of the decreasing variability of insect species over time (Vršanský 2000). For comparison, this value is relatively similar to the CV of similar *Piniblattella vitimica* from the Valanginian of Siberia of the Ectobiidae (4.11 %). In contrast, the CV of species from the Early Jurassic is 11.24 % (Vršanský & Ansorge 2007). These coefficients of variation are also highly similar to those of species belonging to a different cockroach family, the Blattulidae, at the same locality (*Elisama extenuata* CV_{sum} = 6.22 %; *Habroblattula drepanoides* CV_{sum} = 5.72 %) (Wang et al. 2007a,b).

To summarize, these exceptionally well preserved representatives of the ecologically significant family Mesoblattinidae extend the appearance of the advanced cockroach characters such as details of reproductive tract and microstructures. These specimens document the transitional character of the species between the two well-defined cockroach families Mesoblattinidae and Ectobiidae (which had originated in or near the J/K boundary). Notably, this between-family transition did not influence the taxonomic diversity and/or ecological dominance of both groups during the Late Jurassic–Early Cretaceous.

Acknowledgments: We sincerely thank Dr. Ľubomír Vidlička and Dr. Peter Vršanský for revision of the manuscript, and are grateful to Yingying Cui, Dr. Yunzhi Yao, Dr. Junjie Gu, Qiang Yang, Taiping Gao, Chaofan Shi and other students of our laboratory for help. This research is supported by the National Basic Research Program of China (973 Program) (2012CB821906), the National Natural Science Foundation of China (No. 41272006, 31230065), the Project of Great Wall Scholar and Key Program (KZ201310028033), and China Geological Survey (1212011120115).

References

Barna P. in print: Low diversity cockroach assemblage from Chernovskie Kopi in Russia confirm wing deformities of insects at J/K boundary. *Biologia, Bratislava* (in print).

Bohn H., Picker M. & Klass K.D. 2010: A jumping cockroach from South Africa, *Saltoblattella montistabularis*, gen. nov., sp. nov. (Blattodea: Blattellidae). *Arthropod Systematic & Phylogeny* 68, 1, 53–69.

Brongniart C. 1885: Les insectes fossiles des terrains primaires. Coup d'oeil rapide sur la faune entomologique des terrains paléozoïques. *Bull. Soc. Amis Sci. Nat. Rouen* 1885, 50–68.

Comstock J.H. & Needham J.G. 1898: The wings of insects. *Amer. Naturalist* 32, 376, 231–257.

Chen P.J., Wang Q.F., Zhang H.C., Cao M.Z., Li W.B., Wu S.Q. & Shen Y.B. 2004: Disussion on the stratotype of Jianshangou of Yixian Formation. *Sci. China Ser. D, Earth Sci.* 34, 883–895 (in Chinese).

Ding Q.H., Zhang L.D., Guo S.Z., Zhang C.J., Peng Y.D., Jia B., Chen S.W. & Xian D.H. 2003: Paleoclimatic and palaeoenvironmental proxies of the Yixian Formation in the Beipiao area, western Liaoning. *Geol. Bull. China* 22, 3, 186–191.

Gao T.P. & Ren D. 2008: Description of a new fossil *Anthoxyela* species (Hymenoptera, Xyelidae) from Yixian Formation of Northeast China. *Zootaxa* 1842, 56–62.

Geinitz F.E. 1880: Der Jura in Mecklenburg und seine Versteinerungen. *Z. Dtsch. Geol. Gesell.* 22, 510–535.

Handlirsch A. 1906: Die Fossilen Insekten und die Phylogenie der rezenten Formen: Ein Handbuch für Paläontologen und Zoologen. *Engelmann*, Leipzig, 1–640, 36 plates.

Liang J.H., Vršanský P. & Ren D. 2012: Variability and symmetry of a Jurassic nocturnal predatory cockroach (Blattida: Raphidiomimidae). *Rev. Mexicana Ciencias Geol.* 29, 2, 411–421.

Liang J.H., Vršanský P., Ren D. & Shih C.K. 2009: A new Jurassic carnivorous cockroach (Insecta, Blattaria, Raphidiomimidae) from the Inner Mongolia in China. *Zootaxa* 1974, 17–30.

Liu M., Lu W.H. & Ren D. 2007a: A new fossil mordellid (Coleoptera: Tenebrionoidea: Mordellidae) from the Yixian Formation of Western Liaoning Province, China. *Zootaxa* 1415, 49–56.

Liu Y.S., Sinitshenkova N.D. & Ren D. 2007b: A new genus and species of stonefly (Insecta: Plecoptera) from the Yixian Formation, Liaoning Province, China. *Cretaceous Research* 28, 322–326.

Martínez-Delclòs X. 1993: Blátidos (Insecta, Blattodea) del Cretácico Inferior de España. Familias Mesoblattinidae, Blattulidae y Poliphagidae. *Bol. Geol. Minero* 104, 5, 52–74.

Meunier F. 1914: Un blátido y una larva de odonato del Kimeridgense de la Sierra del Montsech (Lérida). *Mem. Real Acad. Ciencias y Artes de Barcelona* 11, 9, 121–124.

Nagamitsu T. & Inoue T. 1997: Cockroach pollination and breeding system of *Uvaria elmeri* (Annonaceae) in a lowland mixed-dipterocarp forest in Sarawak. *Amer. J. Botany* 84, 208–213.

Pang Q.Q., Li P.X., Tian S.G. & Liu Y.Q. 2002: Discovery of ostracods in the Dabeigou and Dadianzi Formations at Zhangjiagou, Luanping County, northern Hebei Province of China and new progress in the biostratigraphic boundary study. *Geol. Bull. China* 21, 6, 329–336.

Picker M., Colville J.F. & Burrows M. 2012: A cockroach that jumps. *Biol. Lett.* 8, 3, 390–392.

Ren D., Shih C.K., Gao T.P., Yao Y.Z. & Zhao Y.Y. 2010: Silent stories — insect fossil treasures from dinosaur era of the Northeastern China. *Sci. Press*, Beijing, 1–17.

Ren D., Guo Z.G., Lu L.W., Ji S.A., Tang F., Jin Y.G., Fang X.S. & Ji Q. 1997: A further contribution to the knowledge of the Upper Jurassic Yixian Formation in western Liaoning. *Geol. Rev.* 43, 5, 449–460 (in Chinese with English abstract).

Roth L.M. 1991: New combinations, synonymies, redescriptions and new species of cockroaches, mostly Indo-Australian Blattellidae. *Invertebrates Taxon* 5, 953–1021.

Shelford R. 1909: Note on some amphibious cockroaches. *Record Indian Mus.* 3, 125–127.

Tan J.J., Ren D. & Shih C.K. 2007: New ommatids of Ommatinae (Coleoptera: Archostemata: Ommatidae) from the Yixian Formation of western Liaoning, China. *Progress Nat. Sci.* 17, 7, 803–811.

Vidlička L., Vršanský P. & Shcherbakov D.E. 2003: Two new troglobitic cockroach species of the genus Speleoblatta (Blattaria: Nocticollidae) from North Thailand. *J. Nat. Hist.* 37, 107–114.

Vishniakova V.N. 1964: Additional characters of wing venation in forewings of a new Upper Jurassic cockroach. *Paleontol. Zh.* 1, 82–87 (in Russian).

Vishniakova V.N. 1973: New cockroaches (Insecta: Blattodea) from the Upper Jurassic sediments of Karatau. In: Narchuk E.P. (Ed.): Problems of the insect palaeontology (in Russian): Lectures on the XXIV Annual Readings in Memory of N.A. Kholodkovsky (1–2 April, 1971) [Voprosy paleontologii nasekomykh. Doklady na 24-m Ezhegodnom chtenii pamyati N.A.Kholodkovskogo, 1971.] *Nauka*, Leningrad, 64–77 (in Russian).

Vršanský P. 1997: *Piniblattella* gen. nov. — the most ancient genus of the family Blattellidae (Blattodae) from the Lower Cretaceous of Siberia. *Entomol. Probl.* 28, 1, 67–79.

Vršanský P. 2000: Decreasing variability — from the Carboniferous to the present! (Validated on independent lineages of Blattaria). *Paleont. J.* 34, 3, 374–379.

Vršanský P. 2002: Origin and the early evolution of mantises. *AMBA Projekty* 6, 1, 1–16.

Vršanský P. 2003a: Umenocoleoidea — an amazing lineage of aberrant insects (Insecta, Blattaria). *AMBA Projekty* 7, 1–32.

Vršanský P. 2003b: Unique assemblage of Dictyoptera (Insecta-Blattaria, Mantodea, Isoptera, Mantodea) from the Lower Cretaceous of Bon Tsagaan Nuur in Mongolia. *Entomol. Probl.* 33, 1–2, 119–151.

Vršanský P. 2004a: Transitional Jurassic/Cretaceous cockroach assemblage (Insecta, Blattaria) from the Shar-Teg in Mongolia. *Geol. Carpathica* 55, 6, 457–468.

Vršanský P. 2004b: Cretaceous Gondwanian Cockroaches (Insecta: Blattaria). *Entomol. Probl.* 34, 49–54.

Vršanský P. 2007: Jumping cockroaches (Blattaria, Skokidae fam.n.)

from the late Jurassic of Karatau in Kazakhstan. *Biologia, Bratislava* 62, 5, 588–592.

Vršanský P. 2008: New blattarians and a review of dictyopteran assemblages from the Lower Cretaceous of Mongolia. *Acta Palaeont. Pol.* 53, 1, 129–136.

Vršanský P. 2009: Albian cockroaches (Insecta, Blattida) from French amber of Archingeay. *Geodiversitas* 31, 1, 73–98.

Vršanský P. 2010: Cockroach as the earliest eusocial animal. *Acta Geol. Sin. Engl. Ed.* 84, 793–808.

Vršanský P. & Ansorge J. 2007: Lower Jurassic cockroaches (Insecta: Blattaria) from Germany and England. *African Invertebrates* 48, 103–126.

Vršanský P., Cifuentes-Ruiz P., Vidlička L., Čiampor F.J.R. & Vega F.J. 2011: Afro-Asian cockroach from Chiapas amber and the lost Tertiary American entomofauna. *Geol. Carpathica* 62, 5, 463–475.

Vršanský P., Chorvát D., Fritzsche I., Hain M. & Ševčík R. 2012: Light-mimicking cockroaches indicate Tertiary origin of recent terrestrial luminescence. *Naturwissenschaften* 99, 9, 739–749.

Wang C.D. & Ren D. 2013: *Nuurcala obesa* sp. n. (Blattida, Caloblattinidae) from the Lower Cretaceous Yixian Formation in Liaoning Province, China. *ZooKeys* 318, 35–46.

Wang T.T., Liang J.H. & Ren D. 2007a: Variability of *Habroblattula drepanoides* gen. et sp. nov. (Insecta: Blattaria: Blattulidae) from the Yixian Formation in Liaoning, China. *Zootaxa* 1443, 17–27.

Wang T.T., Ren D., Liang J.H. & Shih C.K. 2007b: New Mesozoic cockroaches (Blattaria: Blattulidae) from Jehol biota of western Liaoning in China. *Ann. Zoologici* 57, 3, 483–495.

Wang W.L., Zhang L.J., Zheng S.L., Ren D., Zheng Y.J., Ding Q.H., Zhang H., Li Z.T. & Yang F.L. 2005: The age of the Yixian stage and the boundary of Jurassic-Cretaceous — the establishment and study of stratotypes of the Yixian stages. *Geol. Rev.* 51, 3, 234–242.

Wang W.L., Zhang L.J., Zheng S.L, Zheng Y.J., Zhang H., Li Z.T. & Yang F.L. 2004: A new study on the stratotype and biostratigraphy of the Yixian stage in Yixian-Beipiao region, Liaoning — establishment and study of stratotypes of the Yixian stage. *Acta Geol. Sin.* 78, 4, 433–447.

Zhang Z.J., Schneider J.W. & Hong Y.Q. 2012: The most ancient roach (Blattida): A new genus and species from the earliest Late Carboniferous (Namurian) of China, with discussion on the phylomorphogeny of early blattids. *J. Systematic Palaeont.* 11, 27–40.

Zhou Z.H., Barrett P.M. & Hilton J. 2003: An exceptionally preserved lower Cretaceous ecosystem. *Nature* 421, 807–814.

Zompro O. & Fritzsche I. 1999: *Lucihormetica* n. gen. n. sp., the first record of luminescence in an orthopteroid insect (Dictyoptera: Blaberidae: Blaberinae: Brachycolini). *Amazoniana* 15, 211–219.