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Paleocene origin of the cockroach families Blaberidae and Corydiidae: Evidence from Amur River region of Russia

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Abstract

Morphna paleo **sp. n.,** the earliest winged representative of any living cockroach genus and the earliest representative of the family Blaberidae, is described from the Danian Arkhara-Boguchan coal mine in the Amur River region (Russian Far East). The branched Sc and A suggest Ectobiidae (=Blattellidae) probably is not the ancestral family because Blaberidae were derived directly from the extinct family Mesoblattindae. The associated Danian locality Belaya Gora yielded *Ergaula stonebut* **sp. n.**, the earliest record of the family Corydiidae. Both species belong to genera codominant in the Messel locality, thus validating their dominance in early Cenozoic assemblages.

Key words: fossil insects, fossil cockroaches, Tertiary, Blaberidae, Corydiidae, *Morphna*, *Ergaula*

Introduction

The Paleocene epoch, with 177 known extinct insect species: 44 coleopterans, 28 dipterans, 28 hemipterans, 27 hymenopterans, 15 odonates, 10 orthopterans, 8 neuropterans, 6 trichopterans, 5 mecopterans, 2 dermapterans, and 1 lepidopteran (EDNA fossil insect database; http://edna.palass-hosting.org; active 2.5. 2012) is the least known Tertiary period in terms of insect diversity. No cockroaches, only two related termite species and a single mantodean *Arvernineura insignis* have been described from Menat (Piton 1940). In contrast, 6124 Eocene, 2663 Miocene and 2550 Oligocene species have been recorded. Pliocene and Pleistocene species are also numerous, but in EDNA underrepresented due to the presence of living species in these Epochs (EDNA catalogise only original designations of species).

Cockroaches originated in the Bashkirian Carboniferous, with the oldest record originating from the Quilianshan in China (Zhang *et al.* 2012, Guo *et al.* 2012). Typical Mesozoic families were derived from the Phyloblattidae near the P/T boundary and the stem of the living families (but also the stem for all mantodeans and termites) can be traced from the Mesozoic family Liberiblattinidae (Vršanský 2002, 2010, 2012). The earliest record of any living family is the ectobiid (blattellid) *Piniblattella vitimica* (Vishniakova, 1964) from the earliest Cretaceous (Vršanský 1997). Before this study, living cockroach genera, including highly advanced forms, were known starting from the early Eocene (Archibald & Mathewes 2000) and the modern fauna is considered to originate around the Paleocene-Eocene Thermal Maximum (PETM—Vršanský *et al.* 2011, 2012b). (The amber fossil *?Blattella lengleti*, is a nymph and may represent a separate genus.) The present study provides evidence for the occurrence of at least some extant genera before the Palaeocene side of the PETM, and in parallel provides earlier evidence for the two living families Corydiidae and Blaberidae.

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Material and methods

Two joined forewings were collected by Yu.L. Bolotsky in the stratotype section of the Tsagayan Formation (Belaya Gora locality). This specimen is deposited in the Amur Natural History Museum of the Institute of Geology and Nature Management, Far Eastern Branch Russian Academy of Sciences (ANHM IGNM FEB RAS), Blagoveshchensk, Russia. One isolated wing was collected by E.V. Bugdaeva in the upper plant-bearing bed in the Arkhara-Boguchan coal mine. This specimen is deposited in Paleontological Institute of Russian Academy of Sciences, Moscow, Russia. Comparative living material provided in the photograph originates from the collection of Vít Kubáň (Thailand, Mae Hong Son Province, Soppong, 7–12.V.1996) deposited in collection of the second author (ĽV) in the Institute of Zoology, SAS, Bratislava.

Geological background

The Zeya-Bureya Basin is located in the middle course of the Amur (Heilongjiang) River (Fig. 1B–D). Development of its sedimentary cover began in the Late Cretaceous with accumulation of the Kundur Formation (Santonian-Campanian). This stratigraphic unit is represented by sandstones, siltstones, and mudstones containing abundant freshwater fauna. These sediments in some structures are oil-and-gas bearing. Over them is the Tsagayan Formation, which is divided into three subformations. The lower Tsagayan Formation consists of conglomerates, mainly clays with sandstone interbeds; its geological age is the early-middle Maastrichtian (Bugdaeva 2001; Markevich 1994, 1995; Markevich *et al.* 2004, 2010, 2011). The late Maastrichtian part of the middle Tsagayan Formation includes conglomerates, sandstones siltstone, and lenses with plant remains. The Danian upper part of the Tsagayan Formation is represented by conglomerates, sandstones, clays and coal seams. The plant-bearing beds occur here. The fossil plants have been studied since the 19th century (Heer 1878; Kryshtofovich & Baikovskaya 1966; Krassilov 1976). This flora was named Tsagayan flora.

The stratotype section of Tsagayan Fm is outcropped in the mouth of the Darmakan River, along the northern and north-eastern slopes of Belaya Gora Mount. It is represented by conglomerates, sandstones, siltstones, and mudstones. We obtained from each bed abundant fossil spores and pollen that allowed us to define the Maastrichtian and Danian age of deposits and the position of the K-T boundary (Bugdaeva 2001). The clay with bedded plant remains lies 37 m above that boundary (Fig. 1C); the thickness of this bed is 3 m. The following fossil plants were collected: *Podocarpus tsagajanicus* Krassil., *Taxodium olrikii* (Heer) Brown, *Metasequoia disticha* (Heer) Miki, *Androvettia catenulata* Bell, *Potamageton* cf. *nordenskioldii* Heer, *Hydrocharis* sp., *Limnobiophyllum scutatum* (Dawson) Krassil., *Trochodendroides arctica* (Heer) Berry, *Carinalaspermum bureicum* Krassil. and *Nyssa bureica* Krassil. The burial is dominated by leaves of *Limnobiophyllum* and shoots and leaves of *Taxodium*. Other remains occur rarely. Remains of fossil insects have been found in this locality, including Buprestidae, Chironomidae, as well as caddisworm cases of *Folindusia* cf. *communita* Cockerell, 1925 and *Terrindusia minuta* Vialov et Sukacheva, 1976. The upper part of the upper Tsagayan Fm contains productive coal seams and several coal mines. One of the mines (Arkhara-Boguchan coal mine) is located near Arkhara settlement. It has three plant-bearing beds with abundant fossil plants; the cockroach wing was found in the upper plant-bearing bed (Figs. 1B–C).

The family name Ectobiidae is used instead of Blattellidae and Corydiidae is substituted for Polyphagidae, based on ICZN Ruling (see Beccaloni & Eggleton 2011; but with reservations of inclusion of termites within order of cockroches).

Systematic palaeoentomology

Blattaria Latreille, 1810 (= Blattodea Brunner von Wattenwyl, 1882)

Blaberidae Brunner von Wattenwyl, 1865

Epilamprinae Princis, 1960

Epilamprini Handlirsch, 1925

Morphna Shelford, 1910

= *Morphnina* Princis, 1958

Diagnosis (after Shelford 1910): Form rather dorsoventrally flattened. Vertex of head covered or almost covered by pronotum, which is trapezoidal, sub-cucullate and posteriorly produced obtusely. Tegmina and wings fully developed, exceeding the apex of the abdomen. Supra-anal lamina of typical Epilamprine shape. Cerci moderately long. Femora moderately armed with spines beneath. Posterior metatarsus equal in length to succeeding joints; all the joints entirely unarmed beneath, their pulvilli large, pulvillus of metatarsus apical but produced towards the base of the joint.

Type species. *Morphna maculata* (Brunner von Wattenwyl, 1865).

Composition (updated from Princis 1967, 1971).

Morphna amplipennis (Walker, 1868) (India)
  = *Epilampra amplipennis* Walker, 1868
Morphna auriculata (Brunner von Wattenwyl, 1865) (India)
  = *Epilampra auriculata* Brunner von Wattenwyl, 1865
Morphna badia (Brunner von Wattenwyl, 1865) (Thailand, Malaysia, Sumatra, Java, Borneo)
  = *Epilampra badia* Brunner von Wattenwyl, 1865
  = *Epilampra ramifera* Walker, 1869
Morphna clypeata Anisyutkin & Gorochov, 2001 (Vietnam)
Morphna decolyi (Bolívar, 1897) (India)
  = *Molytria decolyi* Bolívar, 1897
Morphna dotata (Walker, 1869) (Thailand, Malaysia, Borneo)
  = *Epilampra dotata* Walker, 1869
Morphna humeralis Bruijning, 1948 (Sumatra)
Morphna imperatoria (Stål, 1877) (Philippines)
  = *Epilampra imperatoria* Stål, 1877
Morphna maculata (Brunner von Wattenwyl, 1865) (Malaysia, Sumatra, Java, Borneo)
  = *Epilampra maculata* Brunner von Wattenwyl, 1865
  = *Epilampra polyspila* Walker, 1868
  = *Molytria shelfordi* Kirby, 1903
Morphna moloch (Rehn, 1904) (Thailand)
  = *Epilampra moloch* Rehn, 1904
Morphna plana (Brunner von Wattenwyl, 1865) (India, Sri Lanka)
  = *Epilampra plana* Brunner von Wattenwyl, 1865
  = *Homalopteryx biplagiata* Bolívar, 1897
  = *Epilampra punctifera* Walker, 1868
  = *Homalopteryx templetoni* Kirby, 1903
Morphna pustulata Hanitsch, 1930 (Sumatra)
Morphna sp. (Germany) extinct, Eocene (MES 10188)

Morphna paleo sp. n.
(Figs. 1A, 2C)

Holotype. PIN 5142/12. Right forewing fragment; type locality, Archara-Boguchan, Far East, Russia; type horizon, Tsagayan Formation, Danian Paleocene.

Diagnosis. Forewing with length about 23 mm, width 9 mm. Numerous cross-veins present in M and CuA. Anal intercalaries punctuated.

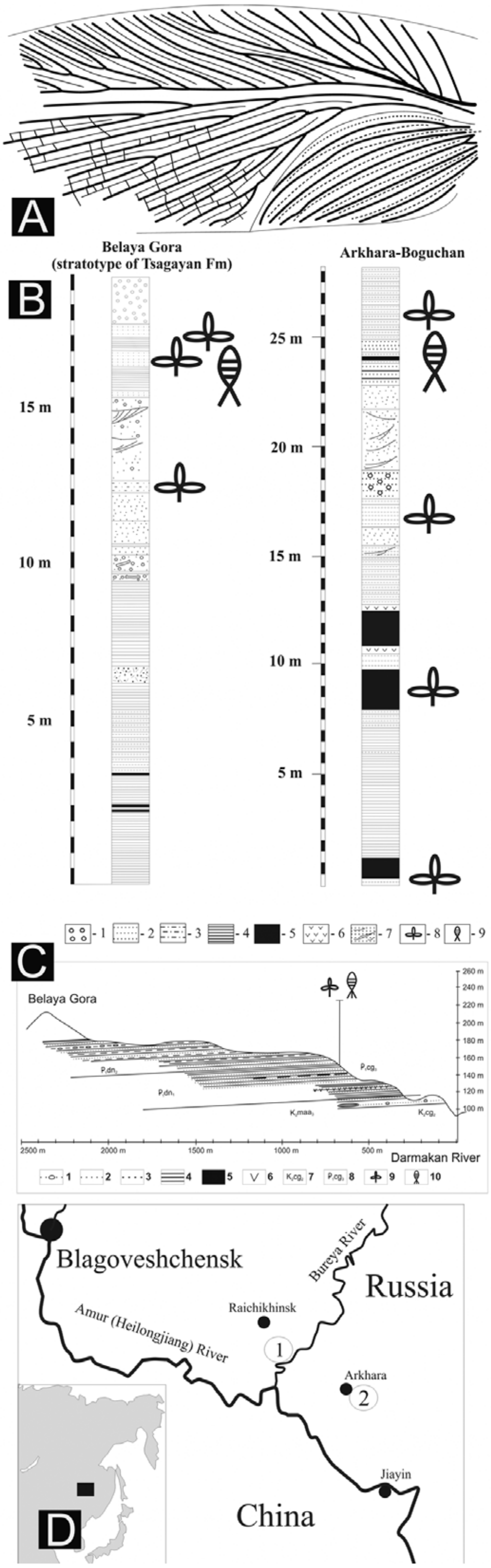

FIGURE 1. **A**) *Morphna palaeo* **sp. n.**, holotype PIN 5142/12; Danian sediments (or Paleocene sediments) of Archara-Bogučan in the Far East of Russia. Forewing length 23 mm; **B)** sections of Danian localities Belye Gory: Belaya Gora (**1**) and Arkhara-Boguchan (**2**) (1—conglomerate; 2—sandstone; 3—siltstone; 4—claystone; 5—coal; 6—acid tuff; 7—strata with cross-bedding; 8—locality of fossil flora; 10—locality of fossil insects); **C)** Profiles of Belaya Gora locality, the stratotype section of Tsagayan Formation (1—conglomerate; 2—sandstone; 3—siltstone; 4—claystone; 5—coal; 6—acid tuff; 7—deposits of the Maastrichtian middle Tsagayan Formation; 8—deposits of the Danian upper Tsagayan Formation; 9—locality of fossil flora; 10—locality of fossil insects; **D)** Localization (Japan to the Right).

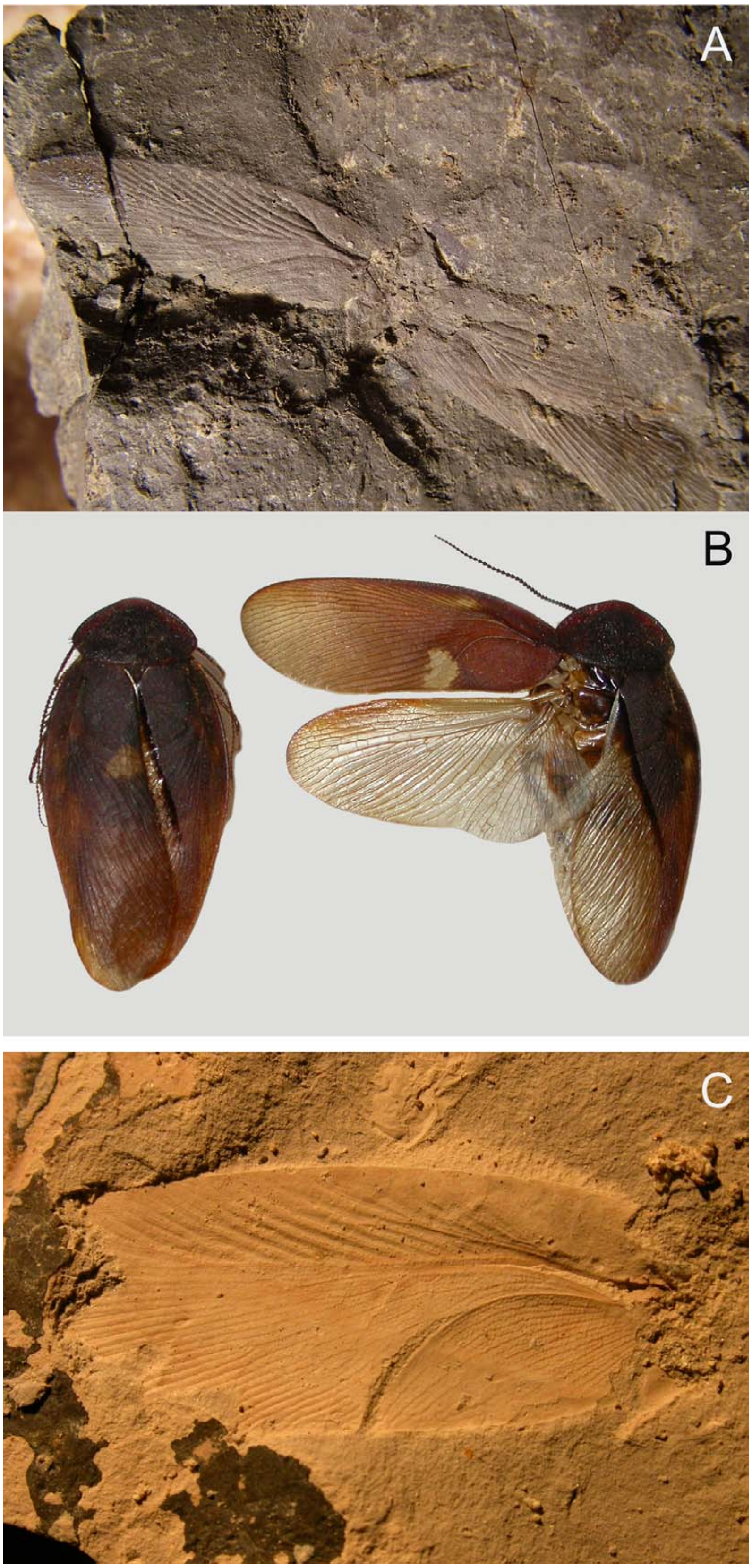

FIGURE 2. A) *Ergaula stonebut* **sp. n.** Holotype ANHM 4/7; Danian sediments (or Paleocene sediments) of Belaya Gora, Far East, Russia. Left forewing 31mm long. **B**) Males of *Ergaula capucina*, Thailand (Mae Hong Son prov., Soppong, 7.–12.V.1996, Vít Kubáň leg., coll. Ľ. Vidlička, ZIN SAS). Note significant folding line on right forewingand strong fold along Sc, apparent also in fossil. **C)** *Morphna palaeo* **sp. n.** Holotype PIN 5142/12; Danian sediments (or Paleocene sediments) of Archara-Bogučan in the Far East of Russia. Forewing length 23 mm.

Description. Forewing without coloration. Venation distinct with apparent intercalaries and rich cross-veins in M and CuA. Subcostal area wide, with Sc richly branched (secondarily). R regular, parallel; M (5) slightly curved, running close to R (apomorphy), fusing to CuA. CuA rich (8). Anal veins simple with punctuated intercalaries.

Remarks. The combination of parallel forewing margins, wide and branched Sc, fusion of M with CuA running close to R, basalmost branches of CuA running parallel to CuP and simple A place this taxon in *Morphna*.

Morphna has been considered to be a comparatively terminal taxon of Epilamprinae (Rehn 1951). Nevertheless, the new species points to a very initial stage of the evolution of Blaberidae, since compared with Ectobiidae (=Blattellidae) fusion of M with CuA running close to R and wide, branched Sc are apomorphies. In the living fauna, *Morphna* is restricted to southeast Asia (India, Sri Lanka, Malaysia, Sumatra, Java, Borneo, Philippines and Thailand). The genus is quite diverse in species and some seem to have little in common (e.g., *M. pustulata* is elongated, with curved forewing posterior margin). On the other hand, the most closely related living species, *M. plana* (Brunner von Wattenwyll, 1865) from Sri Lanka, differs only in possessing numerous cross-veins (plesiomorphy) and in size. All the living representatives of the genus are considerably larger than *M. paleo* **sp. n.** (apomorphy), with forewing lengths of 41–50 mm.

Two basal branches of R have teratological fusion of veins (see Vršanský 2005: this particular parallel fusion of two ascending R branches is unknown in fossils), but this character is without systematic value. Irregularity between R and M is interpreted as an apomorphy based on the absence of this character in Cretaceous cockroaches.

Etymology. From Greek *palaios*: ancient or primitive.

Corydiidae Saussure, 1864 (= Polyphagidae Walker, 1868)

Corydiinae Saussure, 1864 (= Polyphaginae Walker, 1868)
Corydiini *sensu* Rehn, 1951

Diagnosis (after Rehn 1951). Both sexes with at least tegmina present, wings usually present, but sometimes considerably reduced. Tegmina varying from normal to somewhat reduced, obovate and densely coriaceous (mostly in females). Humeral area more developed than in Polyphagini, if coriaceous then broadly expanded. Sc rami regular, not crowded. R without posterior branches, most branches terminating anteriorly, some apically, instead of curving posteriorly. M with free base, its branching regular and direct. Cu not curving distinctly away from plical furrow, CuP not joining cubitus.

Diagnosis (after Walker 1868). Female: Body short-elliptical, convex, dull, very thickly and minutely punctured. Head shining, impressed between the eyes, with a transverse furrow near the mouth. Eyes not far apart. Second joint of the palpi subclavate; third slightly securiform, very much longer than the second. Antennae setaceous, submoniliform, not more than half the length of the body; first, second and third joints short; following joints very short. Prothorax extending somewhat beyond the head and over the basal part of the fore wings when they are expanded, rounded in front and on each side, slightly furrowed along each side; its breadth along the hind border more than twice its length; hind border hardly rounded; hind angles slightly falcate; a lyre-shaped mark in the disk. Mesothorax, metathorax, pectus and abdomen shining, mostly smooth. Abdomen with the segments above and beneath near the tip retracted in the middle towards the disk; sides fringed, with bristles; subanal lamina small, bilobed. Cerci lanceolate, submoniliform, setose. Legs stout; tibiae armed with some strong spines; first joint of the tarsi twice the length of the fifth, which is very much longer than the second. Fore wings coriaceous, membranous towards the border; costa much rounded; tips conical; principal veins distinct in the coriaceous part; transverse sectors numerous, irregular. Hind wings membranous, strongly and thickly reticulated; transverse sectors numerous, irregular.

Type species. *Ergaula carunculigera* (Gerstaecker, 1861)

Composition (updated from Princis 1963).

Ergaula Walker, 1868
= *Dyscologamia* Saussure, 1893 (type is *cesticulata* = *pilosa*)
= *Parapolyphaga* Chopard, 1929 (type is *erectipilis* = *pilosa*)
?= *Netherea* Vršanský et Anisyutkin, 2004 (type is *haatica*)

Ergaula capensis (Saussure, 1893) (Nigeria, Cameroon, Democratic Republic of the Congo, Congo, Uganda, Kenya, Tanzania, Zambia, Zimbabwe, Angola)
=*Dyscologamia capensis* Saussure, 1893
=*Dyscologamia wollastoni* Kirby, 1909
Ergaula capucina (Brunner von Wattenwyl, 1893) (Myanmar)
=*Homoeogamia capucina* Brunner von Wattenwyl, 1893
Ergaula carunculigera (Gerstaecker, 1861) (Philippines (Luzon))
=*Corydia carunculigera* Gerstaecker, 1861
=*Ergaula scaraboides* Walker, 1868
Ergaula funebris (Hanitsch, 1933) (Borneo)
=*Dyscologamia funebris* Hanitsch, 1933
Ergaula nepalensis (Saussure, 1893) (Nepal, Myanmar)
=*Dyscologamia nepalensis* Saussure, 1893
Ergaula pilosa (Walker, 1868) (Sumatra, Malaysia, Java, Borneo)
=*Zetobora pilosa* Walker, 1868
=*Dyscologamia cesticulata* Saussure, 1893
=*Dyscologamia chopardi* Hanitsch, 1923
=*Parapolyphaga erectipilis* Chopard, 1929
=*Polyphaga sumatrensis* Shelford, 1908
Ergaula silphoides (Walker, 1868) (Cambodia)
=*Polyphaga silphoides* Walker, 1868
Ergaula atica Vršanský et Anisyutkin, 2008 (Israel) extinct, ?Eocene (based on male)
?= *Netherea haatica* Vršanský et Anisyutkin, 2008 (Israel) extinct, ?Eocene (based on female)
Ergaula spp. (Germany) extinct, Eocene (common in Messel, based on both sexes)

Ergaula stonebut sp. n.

Holotype. IGNM FEB RAS ANHM 4/7. Both forewings; type locality, Archara-Boguchan, Belaya Gora locality, stratotype of the Tsagayan Formation, Far East, Russia; type horizon, Tsagayan Formation, Danian.

Diagnosis. Forewing narrow, length/width: 31/11 mm, its venation reduced to approximately 50 veins at margin. Sc branched broadly. Intercalaries distinct, coloration indistinct.

Description. Forewing fore margin slightly arcuate. Sc with both anterior (3 on left forewing, 1 on right forewing) and posterior (4, 4) branches. R more or less regularly branched, with venation more dense towards apex; veins secondarily branched (19, 16). M with secondary branches, curved posteriorly (11, 12). CuA largely simplified, reduced to 3 branches at most. Anal veins sparse (6, 7).

Remarks. *E. stonebut* **sp. n.** differs from *Therea* Bilberg, 1820 (India) (the same tribe) in having costal space comparatively narrow and Sc less expanded and with branches running more longitudinally, M and R reduced to some extent and fused. *Eucorydia* Hebard, 1929 (SE Asia) and *Miroblatta* Shelford, 1906 (Borneo) have exclusively straight stem of R (without any posterior branches), the latter comprises deviant forms with extremely wide forewings, sometimes reduced to some extent. *Homoeogamia* Burmeiser, 1838 is limited to America (Mexico and South America) today.

Ergaula stonebut **sp. n.** can be placed within *Ergaula* by simple exclusion and differs from its congeners only in minor characters. It is generally very similar to *E. atica* from the sediments of Israel (presumably Eocene in age), including the narrowness of forewings with distinct intercalaries and wide space between respective Sc branches (3 symplesiomorphies). *E. atica* also is very large, (forewing length 35 mm). The single preserved individual is distinctly coloured and posses numerous deformations. Undescribed specimens from the Messel, Germany are also very similar (H. Schmied, in preparation).

The *E. stonebut* **sp. n.** forewing is without deformities; it is narrower than in any living species. The type species *E. carunculigera* differs in having a considerably smaller forewing (21–27 / 13.5 mm) (Gerstaecker 1861). *Ergaula*. *capucina* differs in having all Sc venation dense; *E. pilosa* has dense Sc venation in the anterior region only (Rehn 1951). Males of *E. capensis* are much larger (55–57 mm in total body length) (Hanitsch 1938).

The much smaller forewing of *E. funebris* (forewing length 22 mm: (Hanitsch 1933)) is monochromatic a character likely shared by *E. stonebut* **sp. n.** However, the wing of *E. funebris* is much wider. *Ergaula nepalensis* is unique in having discoidal veins straight and longitudinal (Saussure 1893), and *E. silphoides*, like most living species, has a rounded fore-margin of the forewing (Walker 1868).

Some distinct characters revealed in the course of study of living *E. capucina* are seen in forewing of the present fossil. The most distinct among them are asymmetrical sclerotisation (due to folding of wings over each other) and invagination in the base of R, which represents the huge ventral ridge serving for folding of the hind wing. Visible are also reticulations caused by sclerotisation in the costal area.

Etymology. *stonebut* is derived from some Slavic languages (means something).

Discussion

Based on study of terminal Mesozoic as well as Eocene cockroaches, it follows that most living cockroach genera originated directly at or around PETM (Vršanský *et al.* 2011, 2012b). Warming not only expanded the geographical range and the thermic optimum in more northern latitudes, but also produced conditions different from those present in the original source area. Changes on land resulted in a higher evolutionary tempo as evidenced by cockroaches (Vršanský 2011, 2012ab). Nevertheless, the present observations are direct evidence for the pre-PETM origin of some of cockroach genera, which was unexpected. It is notable that both of the species described herein belong to genera present (as codominants) in the Eocene Messel (47Ma) assemblage of Germany (Schmied 2009, unpublished observation), suggesting the characteristic Eurasian assemblage was already formed before the Paleocene side of the PETM.

Ergaula occurs also in the presumably Eocene or Oligocene mangals of Israel (Anisyutkin *et al.* 2008) and a leathery wing described as *Netherea haatica* Vršanský & Anisyutkin, 2008 seems to represent the smaller female of living *Ergaula*—a common sexual dimorphism of this genus. This associations are likely very similar unless identical in respect to generic content and support the Eocene stage for obscure (originally presumed to be Mesozoic) locality in Israel.

Different were some Eocene North American localities, where predominantly smaller species were preserved (Vršanský *et al.* 2011a, 2012).

Very little can be learned from the geography of the two specimens. *Ergaula* currently is widely distributed in Africa and Asia, but apparently was also present also in Europe in PETM, but absent in the Americas during the Eocene. *Morphna* has a similar wide pattern in Asia (absent in Africa), with occurrence in Europe during PETM.
The important aspect of deformed wings is ambiguous in this respect. While no wing deformation (developmental change modifying wing geometry, most often fusion of veins or irregularity), is reported in hundreds of Eocene individuals from the Green River in Colorado, very few are present in Early Miocene localities. Deformations are common and abundant in more recent fossils and in living cockroaches. The single specimen of *Morphna* from the Paleocene possesses at least one such deformity, which may be stochastic.

Morphna is peculiar also in another respect in that it is not only the earliest occurrence of any living genus, but also the first occurrence of the family Blaberidae. It is possible that the original blaberid genera, representing the most advanced cockroaches of the time, survived with minor modifications to the present. In any case, the traces of plesiomorphies are valuable: branched A, branched Sc and punctuated intercalaries are all characteristics of Mesoblattinidae, and were lost in the initial stage of the evolution of the family Ectobiidae (=Blattellidae). Therefore, it seems likely that Blaberidae originated directly from the extinct Mesoblattinidae, and not from Blattellidae as has been generally accepted (see Djernaes *et al.* 2012). These results do not contradict with living material-based analyses, as Blattellidae are direct descendants of the Mesoblattinidae.

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