

Paraeuthyrrhapha groehni gen. et sp. nov., a new genus of the family Polyphagidae (Dictyoptera) from Baltic amber and its phylogenetical position

Leonid N. Anisyutkin¹

¹Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St.Petersburg 199034, Russia.
E-mail: dictyoptera@zin.ru, orthopt@zin.ru

ABSTRACT

Paraeuthyrrhapha groehni gen. & sp. nov. (Polyphagidae, Euthyrrhaphinae), is described from Baltic Amber (Eocene). Its morphology and that of the extant species *Euthyrrhapha pacifica* (Coquebert 1804) is studied. The hypothetical phylogeny of the subfamily Euthyrrhaphinae, including extant and all known fossil taxa, is suggested. The tribe Tiviini seems to be the sister group to all other representatives of the subfamily, except for the fossil genus *Erucoblatta* Gorochov & Anisyutkin 2007 in Gorochov 2007 which is of unclear systematic position. The fossil genus *Proholocompsa* Gorochov 2007 represents a sister group to [*Paraeuthyrrhapha* gen. n. + Holocompsini + Euthyrrhaphini]. The interrelationships between *Paraeuthyrrhapha* gen. n., Holocompsini and Euthyrrhaphini are less clear, but the new genus can be provisionally included in Holocompsini.

KEY WORDS: Dictyoptera. Euthyrrhaphinae. *Paraeuthyrrhapha*. Phylogeny. Baltic Amber.

INTRODUCTION

The subfamily Euthyrrhaphinae Handlirsch 1925 includes small cockroaches of very peculiar habitus. According to Princis (1960, 1963), the subfamily consists of three tribes: Euthyrrhaphini Handlirsch 1925, Tiviini J.W.H. Rehn 1951 and Holocompsini J.W.H. Rehn 1951. Princis considered them as a family and subfamilies respectively.

Several representatives of subfamily are known from fossil station. The *Proholocompsa fossilis* (Shelford 1910) was described from Baltic Amber (Eocene) (Weitschat & Wichard 1998) as a representative of the extant genus *Holocompsa* Burmeister 1838 and was subsequently raised to become the monotypic genus *Proholocompsa* Gorochov 2007. Several new taxa belonging to Euthyrrhaphinae were recently described from the Dominican Amber (Miocene) (Gorochov 2007). These are *Erucoblatta* Gorochov & Anisyutkin 2007 in Gorochov 2007 with its single species *E. semicaeca* Gorochov & Anisyutkin 2007 in Gorochov 2007, and 2 species of the extant genus *Holocompsa*: *H. nigra* Gorochov & Anisyutkin 2007 in Gorochov 2007 and *H. abbreviata* Gorochov & Anisyutkin 2007 in Gorochov 2007. In the present paper, a new genus and species belonging to Euthyrrhaphinae is described and its taxonomic position considered.

The suggested cladogram (Fig. 3) can only be considered as provisional due to the incomplete sample of taxa and morphological structures studied. Its main task is to clarify the taxonomic position of *Paraeuthyrrhapha* gen. n.

SYSTEMATIC PALAEOLOGY

Order: Dictyoptera Clairville 1798

Family: Polyphagidae Walker 1868

Subfamily: Euthyrrhaphinae Handlirsch 1925

GENUS: *Paraeuthyrrhapha* gen. n.

Type species: Paraeuthyrrhapha groehni sp. n.

Etymology. *Paraeuthyrrhapha* – something related to *Euthyrrhapha*.

Diagnosis. Sexual dimorphism not expressed; tegmina (fore wings) and hind-wings completely developed, entirely covering abdomen; tegmina and wings about the same length; tegmina divided obliquely into two portions (Figs 1, A, 2, A, 4, 6): sclerotized and opaque proximo-anterior part (including anal area) and membranous and more or less transparent distal-posterior part; tegmina with visible Sc, CuP and numerous branches of R, M and CuA in distal part; venation in anal area absent; wings with apical parts not sclerotized; pterostigma large, sclerotized, occupying most of the hind wing's anterior margin (Fig. 2, B), venation in pterostigmal area discernible; hind-wings with numerous and densely situated branches of R (behind pterostigma), M and CuA.

The weak sexual dimorphism (although only a single female of the type species is known) can be deduced from a rule usual for the cockroaches: the shortening of tegmina and wings due to sexual dimorphism is always more expressed in females. The opposite case (where males have shorter tegmina and wings than females) is still unknown. Inasmuch as the only known specimen of *Paraeuthyrrhapha* gen. n. is female and has completely developed tegmina and wings, it can be concluded that males are fully alate too.

Comparison. The new genus is related to the recent genera *Euthyrrhapha* Burmeister and *Tivia* Walker. From the former it readily differs in its incompletely sclerotized tegmina (multiple veins are visible in its distal part – Figs 1, A, 2, A) and wings which do not exceed the tegmina in length (Fig. 1, A). *Paraeuthyrrhapha* gen. n. differs from the latter genus in having distinctly reduced venation in the tegmina, in the presence of a large pterostigma (Fig. 2, B) and a lack of not expressed sexual dimorphism: females of *Paraeuthyrrhapha* are completely alate, while ones of *Tivia* are completely wingless. Representatives of the recent genus *Hypercompsa* Saussure (= *Diaphana* Brunner von Wattenwyl) have a somewhat similarly structured tegmina and developed pterostigma, but readily differ from the new genus in the remarkably modified tegmina venation (Brunner von Wattenwyl 1865, Tab. X, Fig. 51, B, C). From the recent genus *Holocompsa* Burmeister the new genus differs in the presence of well developed venation of the wings and apical portion of the tegmina.

Included species. Type species only.

Paraeuthyrrhapha groehni sp. n.

(Figures 1, A, B, 2, A-D, 4-7)

Etymology. *Paraeuthyrrhapha groehni* – this species is named in honour of collector Dr. Carsten Gröhn (Hamburg, Germany).

Material. Holotype. Female, “GPIH 4501, collection Gröhn no. 2811”, with 1 specimen of very small Hymenoptera (Parasitica), below the cockroach.

Repository. The holotype of *Paraeuthyrrhapha groehni* gen. et sp. nov. is deposited in the collection of the amber working group at the Geological-Palaeontological Institute of Hamburg University.

This specimen is come from Jantarny location (Kaliningrad distr., Russia).

Occurrence. Baltic Amber, Eocene of Europe.

Diagnosis. As for the genus.

Description. (female). Holotype nearly complete; head, pronotum, underside of thorax, part tegmina and most parts of abdomen and legs covered with a “milk cover” (opaque whitish deposit – Shelford 1910); many cracks approaching the insect’s body in different planes along lateral sides, a few stellate hairs, one coprolite and some dispersed gas bubbles.

General colour reddish-brown; meso- and metathorax from above blackish; anal area of wings transparent; any visible elements of colour pattern absent. Surfaces smooth;

proximal sclerotized parts of tegmina with sparse punctation; pronotum and scutellum covered with recumbent bristles.

Vertex of head projecting beyond pronotum, eyes wide apart (Fig. 1, A). Antennae long, no less than one-half of total length of insect; length of scapus, pedicellum and 1st segment of flagellum as in Fig. 2, C, 1st segment of flagellum about equal in length and width, succeeding segments transverse, more elongated towards apex (Fig. 2, C). Apical segments of maxillary palpi as in Fig. 2, D; 4th segment (penultimate) cone-shaped, 5th (ultimate) more robust. Pronotum trapezoidal; anterior and lateral margins widely rounded; posterior margins weakly prominent; latero-caudal angles rounded (Fig. 1, A). Scutellum triangular, exposed (Fig. 1, A). Tegmina elongate ovoid, with prominent anterior and (to a lesser degree) posterior margins, apex rounded (Figs 1 A, 2, A); Sc simple and strong, R very weak, proximally indistinct, with about 10 subobsolete anterior branches; membranous posterior part of tegmina with about 30 weak and partly indistinct subparallel branches of R, M and CuA with indistinct proximal parts; CuP strong, distinctly angulate. Wings wide, with anterior margin distinctly bulging at middle of pterostigma, apical and posterior margins widely rounded (Figs 1, A, 2, B); pterostigma large; Sc reaches to about one-third of wing length, for most length fused with R; RA strong, nearly straight, without discernible branches, abruptly terminating in pterostigma; RS with at least 1 branch within pterostigma and about 14 apical branches (including intercalary veins); M originating from anterior part of arculus, with about 5 branches (including intercalary veins); CuA more or less pectinate, with about 7 complete and 2 incomplete, partly branched veins (without multiple intercalary veins); branched intercalary vein situated between CuA and CuP; CuP simple and strong; A1 with about 6 branches (without intercalary veins); A2 with numerous (more than 20, including intercalary veins) branches. Antero-ventral margin of front femur with row of piliform spinules and several longer ones at proximal part of femur; apical spines 2; tibiae with spines on outer side triseriately- and on inner side biseriately-arranged; anterior tibiae with at least 2 spines on outer side and about 5 spines at distal end; middle tibiae with about 9, 3 and 4-5 spines on outer, inner sides and at distal end respectively; hind tibiae with more than 10 spines on outer, about 4 on inner sides and about 4 at distal end respectively; hind metatarsus most likely longer than other tarsomeres combined, with about two (as it can be discern on inclusion) rows of spinules along lower margin; tarsal pulvilli very small and apical (if present at all– as it can be discern on include); tarsal claws symmetrical and simple; arolium medium-sized, about one half length of claw. Abdominal sternites without visible glandular specializations; 7th abdominal sternite (genital plate) large, valvular, with sharpened postero-lateral angles (Fig. 1, B). Anal plate (X, ultimate tergite) rounded, caudally protruded; cerci longer than anal plate, with segments bead-like (Fig. 1, B).

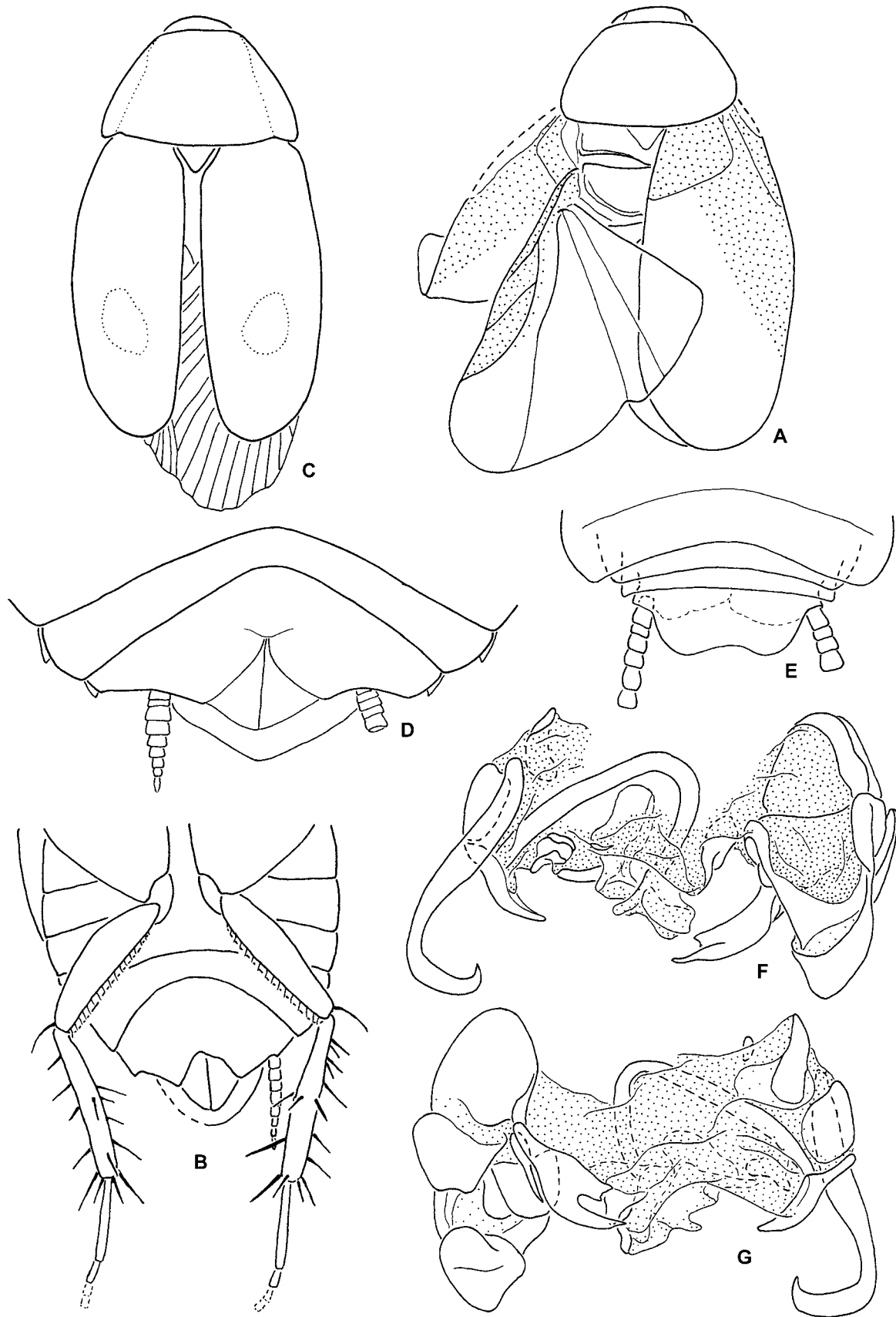


Figure 1. *Paraeuthyrrhapha groehni* sp. n. gen. n., holotype, GPIH 4501, collection Gröhn no. 2811, in Baltic Amber (A, B) and *Euthyrrhapha pacifica* (COQUEBERT), Madagascar (C-G): female (Fort Dauphin) (C, D), male (Amber Gebirge) (E-G), collection ZIN RAS. A. General dorsal view; B. Hind part of body from below; C. General dorsal view; D. Abdominal apex from below; E. Abdominal apex from above; F. Male genitalia from above; G. Male genitalia from below. Dotted area shows sclerotized (A) or membranous parts (F, G); dotted line shows yellow spots (C) or hidden parts of sclerites (E-G).

Male unknown.

Measurements (mm). Length: pronotum 1.4; tegmina 5; wings about 4.5. Width: head about 1.2; pronotum 2.5.

Comparison. As for the genus.

GENUS *Euthyrrhapha* Burmeister 1838

Type species: Blatta pacifica Coquebert, 1804.

Diagnosis. Sexual dimorphism not expressed, tegmina and wings in both sexes completely developed, entirely covering abdomen; tegmina strongly sclerotized, with reduced venation (Figs 1, C, 2, F); wings noticeably longer than tegmina, apical parts protruding in repose (Fig. 1, C); apical parts of wings (protruding from tegmina) and pterostigma sclerotized, other parts more or less subhyaline (Fig. 2, G); pterostigma distinct, occupying about one-third of anterior margin of wing, venation in pterostigmal area practically absent; wings with branches of R (beyond pterostigma), M and CuA not multiplicated, as compared with *Paraeuthyrrhapha* gen. n.

Included species. According to Princis (1963, 1971).

Euthyrrhapha pacifica (Coquebert 1804)

(Figures. 1, C-G, 2, E-H)

Material. Madagascar, "Amber Gebirge Nd. Madagascar H. Rolle, Berlin, SW. 11.", "Eutyrrhapha [sic! – L.A.] Burm. pacifica Coq.", 1 male; "Fort Dauphin Madagascar mer. Sicora 1899", *Euthyrrhapha* [sic! – L.A.] *pacifica*, Coq.", "R. Shelford det.", 1 female. Reunion Is., "Euthyrrhapha [sic! – L.A.] *pacifica* Coqueb. Ins. Reunion", "Brunner v. W. [Wattenwyl – L.A.] det.", 1 male. Brazil, "Euthyrrhapha *pacifica* Cq. S. Paul. Staudinger.", 1 male.

Repository. All these specimens are recent (pinned) and deposited in the collection of Zoological Institute RAS (St. Petersburg), Russia.

Occurrence. *E. pacifica* is a pantropical species that was distributed by man with African origin.

Description. Male. General colour blackish-brown; lateral parts of pronotum and spots on tegmina yellow (Fig. 1, C). Surfaces dull, except more or less smooth head, pronotum and proximal parts of tegmina with fine punctation; pronotum, scutellum and tegmina covered with recumbent bristles.

Head rounded, convex, slightly wider than high; eyes comparatively small, interval between eyes about 1.2 times eye length; ocelli small; interval between antennal sockets about 3.5 times the length of scapus. Antennae about one half body length, with segments in proximal part (except for scapus) wider than high, more elongated towards apex. Pronotum more or less crescent-like (Fig. 1, C), with latero-caudal angles distinctly prominent and posterior margin weakly prominent. Scutellum subtrigonal, exposed (Fig. 1, C). Tegmina elongate ovoid, with prominent anterior and (to a lesser degree) posterior margins (Figs 1, C, 2, F); Sc with flange-like flap on ventral side, visible only on underside of tegmen. Wings elongate (Fig. 2, G); Sc simple and weak (not visible in specimen depicted, see Rehn

1951, Fig. 86); RA simple, reaching about one-third wing length, stalked on pterostigma along with RS and M; arcus present or not (intraspecific variation, see Rehn 1951, Fig. 86); R+M with 7-8 apical branches (without intercalary veins); CuA pectinate, with 7-8 complete veins; 1-2 simple intercalary veins situated between CuA and CuP; CuP strong, with remnants of crossveins, apically forked; A1 simple, thickened proximally, with 1-3 (including intercalary veins) independent veins posteriorly; A2 with 6-7 branches (without intercalary veins) and 2-3 simple veins posteriorly. Antero-ventral margin of front femur with row of piliform spinules and several longer spinules at proximal part of femur; apical spines 2; hind metatarsus slightly longer than other tarsomeres combined; metatarsus and 2nd tarsomere with 2 rows of spinules along lower margin; pulvilli absent; tarsal claws symmetrical and simple; arolium medium-sized, about one half length of claw. Abdominal tergites and sternites without visible specializations. Anal plate sub-rectangular (Fig. 1, E), with postero-lateral angles widely rounded, caudal margin widely emarginated; cerci elongated, with segments bead-like; paraprocts subrectangular, nearly symmetrical, without armament. Hypandrium slightly asymmetrical (Fig. 2, H), caudal margin widely concave, with bristles. Male genitalia (Fig. 1, F, G) in general outline similar to general type of Polyphaginae (Grandcolas 1994, Klass 1997).

Female. Similar to male, but slightly larger and more robust; tegmina and wings seems relatively shorter. Eyes smaller; interval between eyes about 1.5 times eye length (Fig. 2, E); interval between antennal sockets about 4.9 times the length of the scapus. Front femora with 2-3 apical spines. Anal plate caudally protruded; cerci shorter, as compared with male, with segments more consolidated (Fig. 1, D). Ultimate sternite valvular (Fig. 1, D).

Measurements (mm). Length: head, male 1.3, female 1.5; pronotum, male 1.8-2, female 2.2; tegmina, male 5.6-5.7, female 5.6; wings, male 7.1-7.5, female ~ 7 (apex broken off). Width: head, male 1.5, female 1.7; pronotum, male 3-3.4, female 3.6.

Remark. Independent veins posterior of A1 (Fig. 2, G) are most likely branches of A1, with reduced proximal parts.

Euthyrrhapha sp.

Material. Madagascar, "Madagascar mer. Sikora 1899", "Euthyrrhapha [sic! – L.A.] *pacifica* Coq. var. minor. R. Shelford det.", 1 female.

Repository. The specimen is recent (pinned) and deposited in the collection of Zoological Institute RAS (St. Petersburg), Russia.

Description. Female. Differs from above described *E. pacifica* in smaller size, uniformly coloured pronotum and relatively larger yellow spots on tegmina.

Male unknown.

Measurements (mm). Length: head 1.1; pronotum 1.4; tegmina 3.2; wings 3.7. Width: head 1.1; pronotum 2.2.

Remark. It is most likely that this specimen represents a new species of the genus *Euthyrrhapha*.

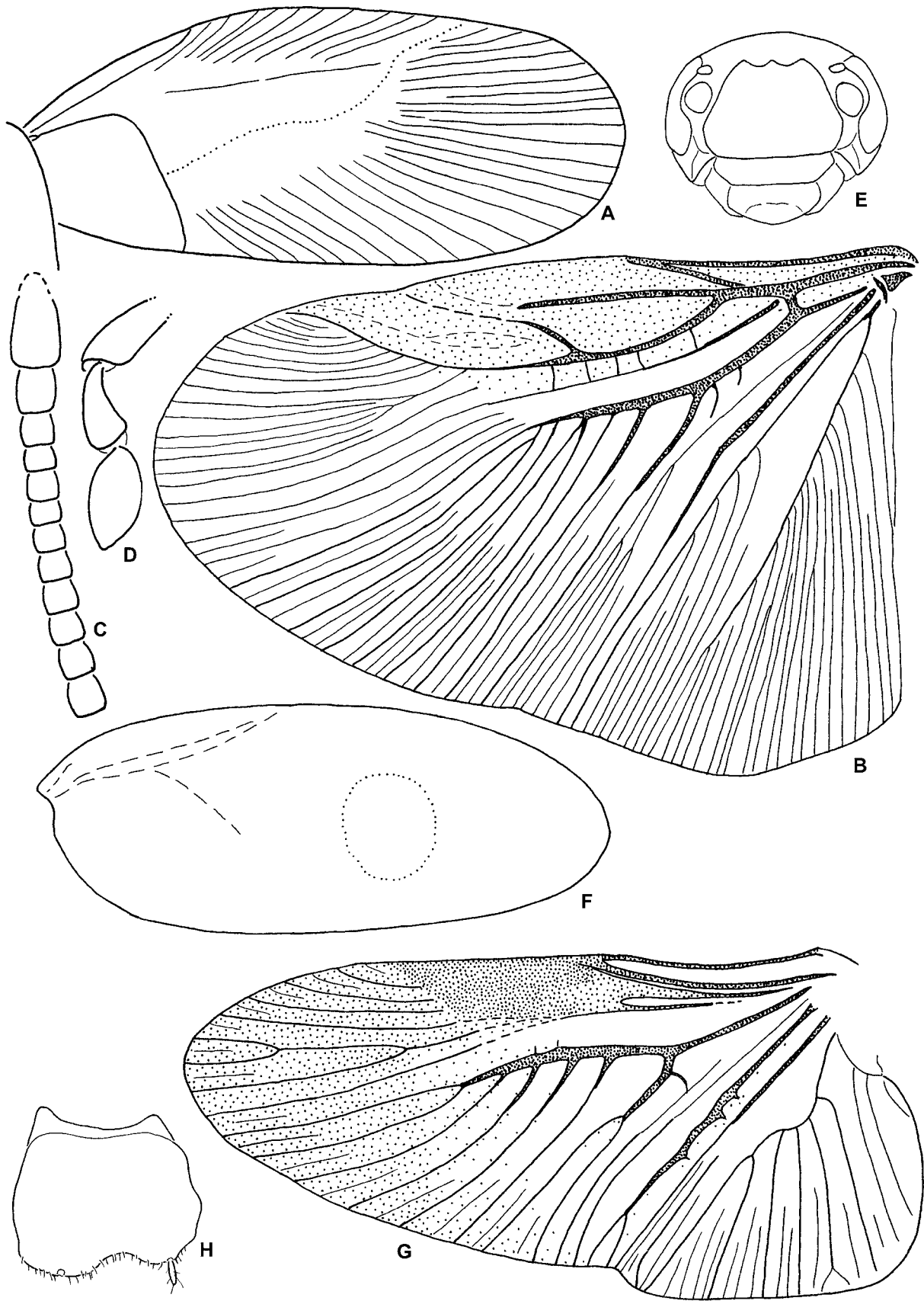


Figure 2. *Paraeuthyrrhapha groehni* sp. n. gen. n., holotype, GPIH 4501, collection Gröhn no. 2811, in Baltic Amber (A-D) and *Euthyrrhapha pacifica* (COQUEBERT), Madagascar (E-H): female (Fort Dauphin) (E), males (Amber Gebirge) (F, G) and Reunion Is. (H), collection ZIN RAS. A. Tegmen from above; B. Wing from above; C. Proximal part of antenna; D. Distal part of maxillary palpus; E. Head; F. Tegmen from above; G. Wing from above; H. Hypandrium from below. Dotted area shows sclerotized parts (B, G); dotted line shows margin of sclerotized part (A), remnants of venation and yellow spot (F) on tegmina.

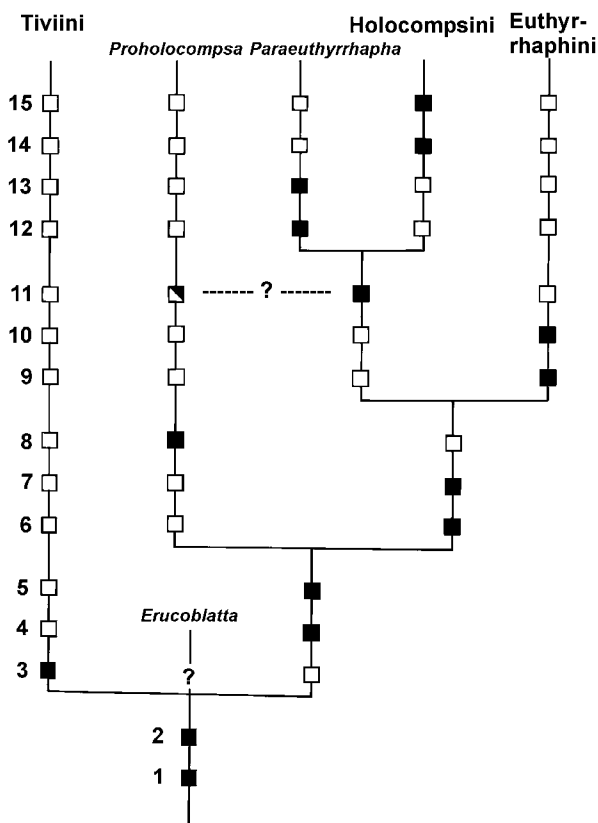


Figure 3. Cladogram of the subfamily Euthyrrhaphinae. Black squares show apomorphies, white ones show plesiomorphies. For details, see text.

RESULTS

Cladogram

(Figure 3)

Character checklist. This checklist is compiled from original and literary data. It includes all tribes and all fossil genera of the subfamily. Black squares indicate apomorphies, while white ones indicate plesiomorphies.

1. Sc of tegmina simple, without anterior branches (1) (Fig. 2, A); Sc with anterior branches (0).

The station of character (1) was treated as diagnostic for Euthyrrhaphinae by Princis (1960), but is present in some other cockroach taxa.

2. Clypeus (so-called postclypeal shield) large, occupying most of facial part of the head, reaching or surpassing dorsal border of the antennal sockets (1) (Fig. 2, E); clypeus smaller, never reaching dorsal border of the antennal sockets (0).

The station of character (1) seems to be unique for Euthyrrhaphinae within the cockroaches.

3. Sexual dimorphism strongly expressed: males completely winged, while females completely wingless (1); sexual dimorphism weak, the both sexes completely alate (0).

Strongly expressed sexual dimorphism is not a rare state for cockroaches.

4. Pterostigma present (1) (Figs 1, A, 2, B, G); pterostigma absent (0).

Only one known representative of genus *Proholocompsa*, *P. fossilis* (Shelford 1910), has a pterostigma: “Wings with a prominent stigma [=pterostigma – L.A.] on the anterior margin, formed by the incrassated rami of the mediastinal vein [=Sc – according to Rehn 1951] and by the fusion of some of the costal veins [R, RS – according to Rehn 1951].” (Shelford 1910, p. 352). The presence of developed pterostigma, character state (1), seems to be unique amongst the cockroaches for the group [Holocompsini + Euthyrrhaphini].

5. Tegmina partially sclerotized, divided obliquely into two portions: sclerotized and opaque proximo-anterior part and membranous distal-posterior part (1) (Figs 1, A, 2, A); tegmina more or less uniformly sclerotized, if its proximal part is more sclerotized, the tegmina are not obliquely divided into two portions (0).

This station of character (1) seems to be unique for the group [Holocompsini + Euthyrrhaphini] amongst the cockroaches.

6. Anal area of tegmina with obsolete venation (1) (Figs 2, A, F); venation in anal area of tegmina present (0).

This station of character (1) is present in some other cockroach taxa.

7. Venation in preanal area of tegmina irregular, subobsolete or obsolete (1) (Figs 2, A, F); venation in preanal area of tegmina somewhat weakened, but regular (0).

This character (1) occurs in some other cockroach taxa.

8. Wings with M completely absent (1); wings with M always visible (0).

This station of character (1) seems to be unique for the genus *Proholocompsa*, at least amongst the Polyphagidae.

9. Tegmina completely elytrized, venation obsolete (1) (Figs 1, C, 2, F); tegmina not completely elytrized, venation at least partially visible (0).

Strongly elytrized tegmina can be found in taxa of cockroaches belonging to other families (for example, *Diploptera* Saussure from Blaberidae, some *Plectoptera* Saussure from Blattellidae).

10. Pterostigma without any traces of venation (1) (Fig. 2, G); pterostigma with more or less visible venation (0) (Fig. 2, B).

This station of character (1) seems to be unique amongst the cockroaches for the genus *Euthyrrhapha*.

11. Wings with a rounded field in the pterostigma between RA and RS (1) (Fig. 2, B); wings without such field between RA and RS (0).

The station of character (1) is presents in the group [Holocompsini + *Paraeuthyrrhapha* gen. n.] and is not found in other cockroaches. The detailed structure of the pterostigma is unknown for *Proholocompsa*.



Figure 4. *Paraeuthyrrhapha groehni* sp. n. gen. n., holotype, GPIH 4501, collection Gröhn no. 2811, in Baltic Amber. General habitus in dorsal view.

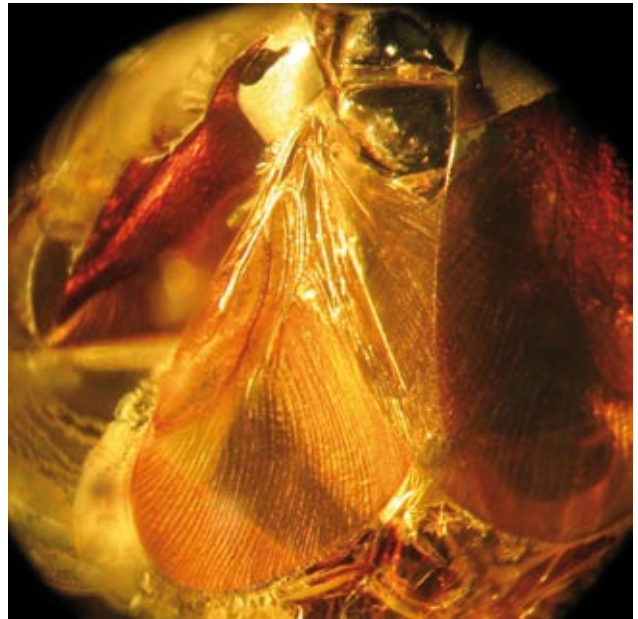


Figure 5. *Paraeuthyrrhapha groehni* sp. n. gen. n., holotype, GPIH 4501, collection Gröhn no. 2811, in Baltic Amber. Wing from above.



Figure 6. *Paraeuthyrrhapha groehni* sp. n. gen. n., holotype, GPIH 4501, collection Gröhn no. 2811, in Baltic Amber. Tegmen from above.



Figure 7. *Paraeuthyrrhapha groehni* sp. n. gen. n., holotype, GPIH 4501, collection Gröhn no. 2811, in Baltic Amber. Abdominal apex from below.

12. Wings with multiplied venation (1) (Fig. 2, B); wings venation not multiplied (0) (Fig. 2 G).

This station of character (1) seems to be unique amongst the Euthyrrhaphidae for *Paraeuthyrrhapha* gen. n.

13. Pterostigma comparatively large, occupying most of wing fore margin (1) (Fig. 2, B); pterostigma smaller, occupying less than one half of wing fore margin or absent (0).

This station of character (1) seems to be unique for *Paraeuthyrrhapha* gen. n. at least amongst Euthyrrhaphinae.

14. Apical part of tegmina membranous, with venation obsolete (1); apical part of tegmina not membranous, with venation present (for except *Euthyrrhapha*) (0).

This station of character (1) seems to be unique for the Holocompsini amongst Euthyrrhaphinae. In *Euthyrrhapha* the lack of tegminal venation is of fundamentally another nature: due to sclerotization instead of membranization as seen in the Holocompsini.

15. Wings considerably membranous, with venation obsolete (1); wings not membranous, venation distinct (0).

This station of character (1) seems to be unique amongst cockroaches for the Holocompsini.

DISCUSSION

The holophyly of the subfamily Euthyrrhaphinae (Fig. 3) is supported by two characters [1, 2], with one of them (the shape of clypeus – station of character (1) apparently unique for the cockroaches.

It is difficult to discuss the taxonomic position of genus *Erucoblatta* Gorochov & Anisyutkin, because the only known specimen of this taxon is a young larva (Gorochov 2007): however the presence of a large clypeal shield confirms that it belongs to the Euthyrrhaphinae.

The tribe Tiviini seems to be a sister-group to all other known representatives of the Euthyrrhaphinae. It is characterized by strongly expressed sexual dimorphism [character 3] and the comparatively unspecialized structure of the tegmina and wings.

Group [*Proholocompsa* + *Paraeuthyrrhapha* gen. n. + Holocompsini + Euthyrrhaphini] is well supported by two unique apomorphies [characters 4, 5]. The genus *Proholocompsa* represents a basal branch of this group and stands apart from the other representatives due to one unusual character – the complete reduction of M in the wings [character 8]. This feature excludes *Proholocompsa* from hypothetical ancestors of the group.

The group [*Paraeuthyrrhapha* gen. n. + Holocompsini + Euthyrrhaphini] is supported by specializations in tegmen and wing structure [characters 6, 7]. A possible synapomorphy of the group [*Paraeuthyrrhapha* gen. n. + Holocompsini] is the peculiar structure of the pterostigma [character 11], namely the presence of the rounded field between RA and RS (1) (Fig. 2, B). However, the detailed

structure of *Proholocompsa*'s pterostigma is not clear (see above the description of character 4). If the structure of the pterostigma in *Proholocompsa* is similar to *Paraeuthyrrhapha* gen. n. and the Holocompsini, then this character is really a plesiomorphy and the trichotomy [*Paraeuthyrrhapha* gen. n. + Holocompsini + Euthyrrhaphini] is still unresolved. The genus *Paraeuthyrrhapha* gen. n. is habitually similar to representatives of Holocompsini, but the new genus is characterized by the very peculiar structure of the hind-wings [characters 12, 13]. The tribes Holocompsini and Euthyrrhaphini are characterized by sets of unique apomorphies [characters 14, 15 and 9, 10 respectively]. None of these groups (*Paraeuthyrrhapha* gen. n., Holocompsini, Euthyrrhaphini) cannot be considered as potential ancestors of the others.

According to the cladogram suggested (Fig. 3), the genus *Paraeuthyrrhapha* gen. n. can be provisionally placed within the tribe Holocompsini. As regards the reconstruction of Euthyrrhaphinae phylogeny, it would be prudent to wait until additional data, including additional important example taxa, are included in order to better test some of these relationships within the subfamily.

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