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A new genus of the mantispid-like Paraberothinae (Neuroptera: Berothidae) from Burmese amber, with special consideration of its probasitarsus spine-like setation

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Abstract

Creagroparaberotha groehni **gen. et sp. nov.** (Neuroptera: Berothidae: Paraberothinae) is described from the earliest Cenomanian Burmese amber. The revised diagnosis of Paraberothinae is provided. The specialized probasitarsi in Paraberothinae, Rhachiberothinae (Berothidae) and Symphrasinae (Mantispidae) are considered as a homoiology (parallelism), i.e., convergent modifications of a homologous structure. The genus *Berothone* Khramov, 2015 is considered to belong to the subfamily Mesithoninae (Berothidae).

Key words: Paraberothinae, Rhachiberothinae, Symphrasinae, Burmese amber, Cretaceous

Introduction

The family Berothidae is relatively small comprising approximately 130 extant species (including Rhachiberothinae) (Oswald 2013). The fossil record is rich: fifty five fossil species in 35 genera (including Mesithoninae *in sensu* Makarkin *et al*. 2012) from the Middle Jurassic to late Eocene have been referred to Berothidae (Makarkin *et al.* 2011, 2012; Azar & Nel 2013; Khramov 2015; Makarkin 2015; Makarkin & Ohl 2015). This family dominates the neuropteran assemblage in the mid-Cretaceous Burmese amber, both in number of specimen and species, with 13 described species (Engel 2004; Engel & Grimaldi 2008; Makarkin 2015). There are also many undescribed specimens, predominantly in private collections.

Most of the Burmese berothids possess walking (cursorial) forelegs, a characteristic feature also observed in most extant berothids. Three genera and four species belong to Paraberothinae, a subfamily whose species possess raptorial forelegs: *Eorhachiberotha burmitica* Engel, 2004, *Eorhachiberotha* sp., *Scoloberotha necatrix* Engel et Grimaldi, 2008, *Micromantispa cristata* Shi *et al*., 2015a, each are represented by a single specimen. In this paper, a new genus and species of this subfamily (*Creagroparaberotha groehni* **gen. et sp. nov**.) is described from Burmese amber. At least eight other undescribed specimens of Paraberothinae are known from Burmese amber, deposited mainly in private collections (pers. obs.).

The subfamily Paraberothinae occurs only in the Cretaceous. This is one of three berothid subfamilies possessing raptorial forelegs. The others are Rhachiberothinae known from the late Eocene Baltic amber to Recent (Makarkin & Kupryjanowicz 2010), and Mesithoninae with several species known from the Middle Jurassic to Early Cretaceous of Asia (Panfilov 1980; Makarkin 1999; Makarkin *et al*. 2012; Jepson 2015). In Mesithoninae, raptorial forelegs are preserved in one undescribed specimen from the Middle Jurassic of the Chinese Daohugou locality (pers. obs.) and in the Late Jurassic genus *Berothone* Khramov, 2015 (**sit. nov.**) from Karatau (Kazakhstan). Up to date, the Paraberothinae include thirteen species from Cretaceous ambers found in the Northern Hemisphere, i.e., in France, Lebanon, Myanmar, U.S.A. (New Jersey) and Canada (Alberta) (Table 1) (Schlüter 1978; Whalley 1980; Grimaldi 2000; Engel 2004; Nel *et al*. 2005; Engel & Grimaldi 2008; McKellar & Engel 2009; Petrulevičius *et al*. 2010; Makarkin 2015).

The protarsus spine-like setation are greatly developed in *Creagroparaberotha* **gen. nov**. as compared with the

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vast majority of other genera. The basitarsus dorsal spine-like seta is considered in this paper as the possible first evolutionary stage of a condition occurring in Rhachiberothinae and Symphrasinae (Mantispidae).

TABLE 1. A checklist of Paraberothinae species.

	Species	Age	Locality
1	*Chimerhachiberotha acrasarii* Nel *et al*., 2005a	Neocomian	Lebanese amber
2	*Paraberotha acra* Whalley, 1980	Neocomian	Lebanese amber
3	*Raptorapax terribilissima* Petrulevičius *et al*., 2010	Neocomian	Lebanese amber
4	*Spinoberotha mickaelacrai* Nel *et al*., 2005a	Neocomian	Lebanese amber
5	*Alboberotha petrulevicii* Nel *et al*., 2005a	late Albian	Charentese amber (France)
6	*Creagroparaberotha groehni* **gen. et sp. nov.**	earliest Cenomanian	Burmese amber
7	*Eorhachiberotha burmitica* Engel, 2004	earliest Cenomanian	Burmese amber
8	Paraberothinae sp.: Engel, 2004: Fig. 2	earliest Cenomanian	Burmese amber
9	*Micromantispa cristata* Shi *et al*., 2015a	earliest Cenomanian	Burmese amber
10	*Scoloberotha necatrix* Engel et Grimaldi, 2008	earliest Cenomanian	Burmese amber
11	*Retinoberotha stuermeri* Schlüter, 1978	early Cenomanian	French amber at Bezonnais
12	*Rhachibermissa phenax* Engel et Grimaldi, 2008	Turonian	Raritan (New Jersey) amber
13	*Rhachibermissa splendida* Grimaldi, 2000	Turonian	Raritan (New Jersey) amber
14	*Albertoberotha leuckorum* McKellar et Engel, 2009	Campanian	Canadian amber

Material and methods

This study is based on single specimen of Paraberothinae embedded in a 20 mm long piece of Burmese amber, with a small Dermaptera-like larva (~1.3 mm) as a sininclusion. The photographs were taken by Carsten Gröhn using a Zeiss stereomicroscope (modified with variable objectives: Nikon M Plan 5x, 10x, 20x, 40x; Luminar 18 mm, 25 mm, 40 mm) and an attached Canon EOS 450D digital camera. Line drawings were prepared by the author using Adobe Photoshop CS3.

The venational terminology in general follows Kukalová-Peck & Lawrence (2004) as interpreted by Yang *et al*. (2012, 2014). Terminology of wing spaces and details of venation (e.g., spaces, veinlets) follows Oswald (1993). Crossveins are designated after the longitudinal veins which they connect and are numbered in sequence from the wing base, e.g., 1scp-r, first (proximal-most) crossvein connecting ScP and R/RA; icu, crossvein between CuA and CuP.

Abbreviations: AA1–AA3, first to third anterior anal vein; CuA, anterior cubitus; CuA1, proximal-most branch of CuA; CuP, posterior cubitus; hv, humeral veinlet; hp, humeral plate; MA and MP, anterior and posterior branches of media; RA, anterior radius; RP, posterior sector; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; ScA, subcosta anterior; ScP, subcosta posterior.

Systematic paleontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Berothidae Handlirsch, 1906

Subfamily Paraberothinae Nel *et al*., 2005

Genus *Creagroparaberotha* gen. nov.

Type and only species. *Creagroparaberotha groehni* **sp. nov.**

Etymology. From the Greek *kreagris* [κρεαγρις], fork, and *Paraberotha*, a genus-group name of Berothidae, in reference to the majority of the forewing subcostal veinlets being forked. Gender feminine.

Diagnosis. May be distinguished from other similar genera, which bear spine-like curved seta on outer (dorsal) edge of two proximal protarsomeres, by a combination of the following character states: scapus long, ca. 5–6 times as long as wide [relatively short, maximum of ca. 2.5 times as long as maximum wide in *Scoloberotha* Engel et Grimaldi, 2008, *Micromantispa* Shi *et al*., 2015a]; protibia with numerous (>10) inner (ventral) spine-like setae for entire length [only three (*Scoloberotha*, *Micromantispa*) and four (*Rhachibermissa* Grimaldi, 2000) distal]; probasitarsus with six ventral spine-like setae [two in *Micromantispa*; one in *Rhachibermissa*]; forewing: dark maculation present [absent in *Scoloberotha*, *Micromantispa*]; costal space broad [moderately narrow in *Rhachibermissa*; *Scoloberotha*, *Albertoberotha*, *Micromantispa*]; most subcostal veinlets forked [all or most subcostal veinlets simple in *Rhachibermissa*; *Scoloberotha*, *Albertoberotha* McKellar et Engel, 2009]; CuP deeply forked [shallowly pectinate in *Albertoberotha*].

Comments. *Creagroparaberotha* **gen. nov.** belongs to Paraberothinae with certainty as it shares all paraberothine diagnostic characters with other genera (see below), including one synapomorphy of the subfamily (i.e., the presence of spine-like setae on the inner edge of the protibia). Its venation is in general similar to that of the other genera including those known from Burmese amber (i.e., *Eorhachiberotha* Engel, 2004, *Scoloberotha* and *Micromantispa*). However, in the new genus, almost all the distal subcostal veinlets in the forewing costal space are forked, whereas they are mainly or entirely simple in all the other genera.

The foreleg of the new genus is similar to that of all the Burmese genera, *Rhachibermissa*, and *Albertoberotha*, in that their two basal tarsomeres each bear one curved spine-like seta on the outer (dorsal) edge. It is noteworthy that the foreleg structure of *Creagroparaberotha* **gen. nov.** is almost identical to that of the Canadian amber *Albertoberotha*, i.e., in the shape of the femur and similar setation of the femur, tibia, and tarsus. However, these two genera strongly differ in the venation: *Albertoberotha* has a narrow forewing and costal space, all the subcostal veinlets are simple, and CuP is pectinately branched; these features in the new genus are fundamentally different.

Scoloberotha and *Micromantispa* appear to be the most similar to each other, compared to the other genera, although the former genus is incompletely described. These genera share the following character states: the protibia with three distal spine-like setae on inner edge; the scapus is relatively short; the forewing lacks dark spots; and RP has four branches. However, they differ in the shape and setation of the profemur (cf. Engel & Grimaldi 2008: Fig. 46 and Shi *et al*. 2015a: Figs 3, 5B).

The genus *Micromantispa* was initially assigned to Mantispidae (Shi *et al*. 2015a). However, Makarkin (2015) argued that all available character states indicate a paraberothine affinity. This point was rebutted by Shi *et al*. (2015b); although the authors did not provide additional evidence of the mantispid affinity of the genus, they assumed that "further fossil findings might result in a different interpretation" (p. 426). *Creagroparaberotha* **gen. nov.** is such a "further fossil finding". The similarity of *Micromantispa* with other Burmese representatives of Paraberothinae and dissimilarity with any mantispids is so great that there is no doubt on its paraberothine affinity.

The morphology of the *Eorhachiberotha* species is incompletely described. In particular, the seeming absence of spine-like setae in the protibia and the protarsus in this genus is most probably an artefact.

***Creagroparaberotha groehni* sp. nov.**
Figs 1–6

Type material. Holotype GPIH Typ. Kat. Nr. 4568 (collection of C. Gröhn, no. 11071), deposited in the Geological-Paleontological Institute and Museum of the University of Hamburg [Geologisch-Paläontologisches Institut und Museum der Universität Hamburg]. A complete specimen.

Type locality and horizon. Burmese amber (Northern Myanmar: Kachin State: Myitkyina District: Tanai Township: Hukaung Valley). Late Cretaceous: earliest Cenomanian (the age according to Shi *et al*. 2012).

Etymology. After the surname of Carsten Gröhn, recognizing his help in the examination of the holotype.

FIGURE 1. *Creagroparaberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4568. Specimen as preserved. A, latero-dorsal view. B, latero-ventral view. Scale bar = 1 mm (A, B to scale).

FIGURE 2. *Creagroparaberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4568. A, anterior part of body (lateral view). B, left foreleg (lateral view). Scale bars = 0.5 mm (A), 0.3 mm (B).

Description. Body length 3.6 mm as preserved. Head with large eyes; postocular lobe not inflated. Frons and vertex with long scarce setae. Antennae: scapus long (ca. 5–6 times as long as maximum wide), slightly dilated towards apex; pedicellus elongate (approximately 3 times as long as maximum width), markedly dilated towards apex; flagellum with 32 segments, of these terminal eleven markedly darker than more proximal. Terminal segment of labial palpi narrow, acute.

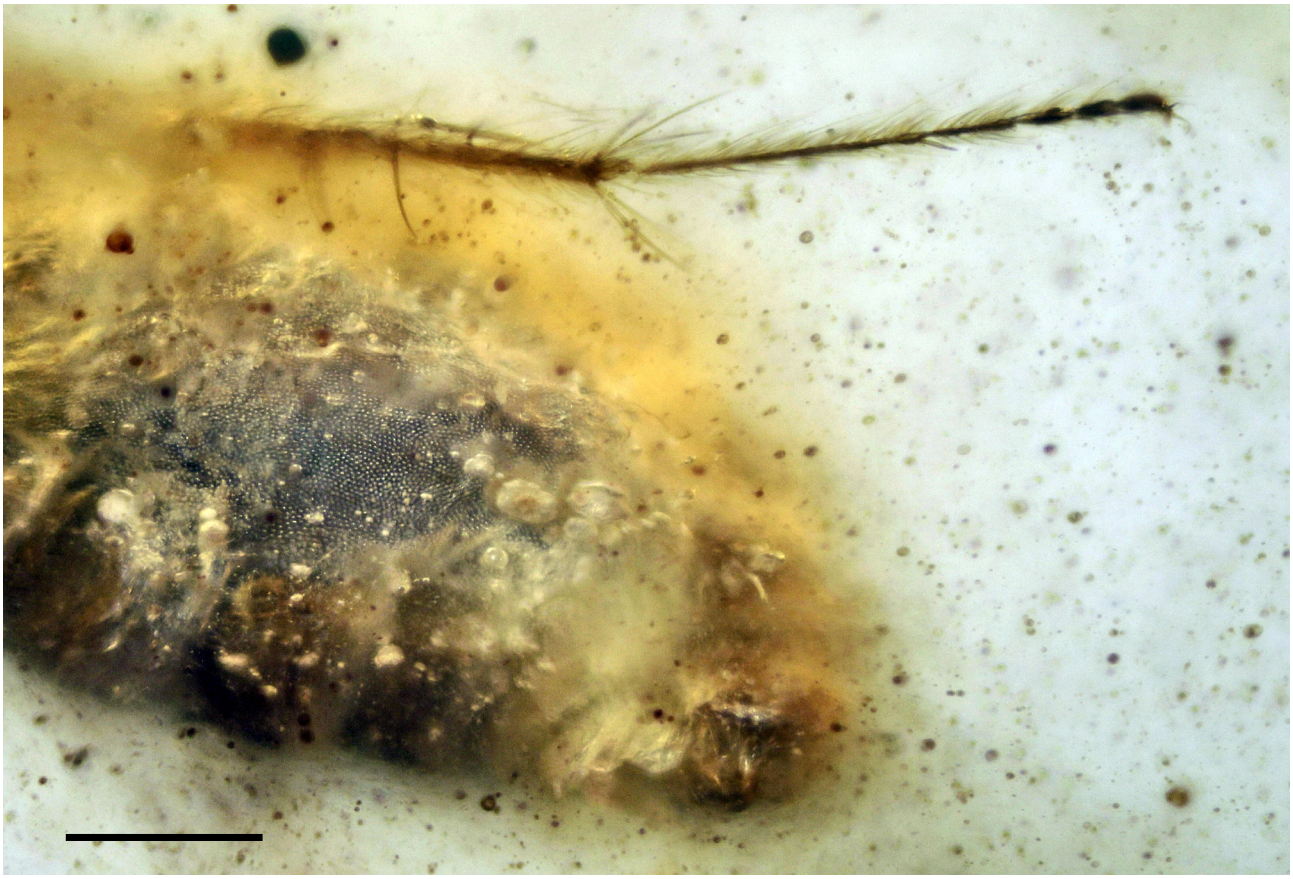

FIGURE 3. *Creagroparaberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4568. Distal portions of abdomen (latero-ventral view) and left hind leg. Scale bar = 0.25 mm.

Pronotum elongate, narrow; only slightly wider than width of head between eyes; covered with long setae. Structure of mesothorax, metathorax unclear.

Foreleg. Procoxa very long (ca. 0.8 mm), narrowed distally. Protrochanter elongate (nearly three times as long as wide), slightly curved. Profemur long (ca. 0.9 mm), markedly narrowed towards apex; covered with dense fine setae which becoming slightly longer and stronger towards apex on outer (dorsal) and lateral edges, and with several long spines and numerous shorter spine-like setae on inner (ventral) edge, only slightly bent towards apex or standing at right angles. Protibia long, slender; covered with fine long setae on outer and lateral edges, and with at least 12 long strong spine-like pale setae bent towards apex on inner edge. Protarsus: probasitarsus longest (relative length of tarsomeres 2.6–1–1.8–1.3–1.3), with one spine-like long curved seta on outer edge, and with six ventral spine-like setae of different sizes; second protarsomere shortest, with one spine-like long curved seta on outer edge, and with one short ventral spine-like seta; third to fifth protarsomeres covered with fine longish setae; claws very slender, curved.

Mid-leg. Mesocoxa stout, conical, rather short. Mesotrochanter similar in structure to that of foreleg. Mesofemur elongate (ca. 0.8 mm), slender; covered dorsally with long setae. Mesotibia long (ca. 0.9 mm), slender; covered with dense long setae with their apices inclined towards tibia apex, and with several long stronger almost perpendicular setae at tibia middle, and at apex forming apical collar of ≥ five strong setae. Mesotarsus similar to metatarsus.

Hind leg. Metacoxa similar to metacoxa. Metatrochanter short. Metafemur elongate, slender; covered with long setae. Metatibia long (ca. 1.5 mm), slender; covered with dense long setae with their apices inclined towards tibia apex, and with several long stronger almost perpendicular setae before tibia end, and at apex forming apical collar of ≥ seven long strong setae. Metatarsus thin, long (ca. 0.8 mm), covered with very dense fine setae; relative length of tarsomeres 6.2–1.9–1.1–1.1–1.

Abdomen oval, rather stout; terminal segments without visible processes and projections (no clear hypocaudae and pseudohypocaudae). Segmentation and finer structure of terminal segments unclear (Fig. 3).

Forewing broadly-oval, 3.65 mm long, 1.7 mm wide (left forewing). Costal space relatively broad, especially at proximal one third and distad fusion of ScP, RA. Most subcostal veinlets once forked, relatively shallowly; six-seven veinlets simple. Humeral plate elongated, ellipsoid. Humeral veinlet recurrent, with two very short simple branches. Subcostal space broad; proximal crossvein (1scp-r) located much distad origin of RP. Presumable ScA well developed, very short connecting origin of costal vein with ScP (Fig. 5). ScP, RA fused apically. ScP+RA entering wing margin before apex, with four-five forked veinlets. RA space generally slightly wider than subcostal space, with two crossveins proximad fusion of ScP, RA, none distad. RP originated far from wing base, with three branches originated proximad 3ra-rp. Stem of RP, RP1, RP2 similarly dichotomously branched distally; RP3 shallowly forked: once in left wing, twice in right wing. No crossveins between branches of RP. Two crossveins between RP, M: proximal crossvein 2r-m connecting stem of RP, MA; distal crossvein 4r-m (belonging to outer series) connecting RP1 before branching and anterior branch of MA. M basally not fused with R; forked slightly distad origin of RP. MA, MP dichotomously branched similar to branching of RP1. One crossvein (4im) belonging to outer series between MA, MP. Three crossveins between M, Cu: 1m-cu ('M5') connecting M, CuA; 2m-cu connecting MP, CuA proximad its branching; 4m-cu connecting MP proximad its branching, CuA much distad origin of CuA1. Cu divided into CuA, CuP rather close to wing base. CuA pectinately branched, with two branches; CuA1 shallowly dichotomously branched distally. CuP deeply forked: anterior branch shallowly dichotomously branched, posterior branch shallowly twice forked. One crossvein (2icu) between CuA, CuP connecting CuA proximad 2m-cu, anterior branch of CuP. Basal 'anal bridge' between Cu, AA1 well developed. One crossvein (1cu-aa) between Cu, AA1 connecting CuP, AA1 much proximad branching. AA1 pectinately branched, with four short branches; proximal-most branch forked. AA2 pectinate, with three simple branches. AA3 stout for most length, probably with one short branch (poorly preserved). One crossvein (1aa1-aa2) between AA1, AA2 located proximad 1cu-aa. Jugal lobe rather poorly developed. Setae on veins rather long. Marginal setae arranged in bunches at end of veins and trichosors, very long (especially along jugal lobe). Trichosors prominent along entire wing margin (except basally where these are not so distinct). Wing membrane hyaline, with following dark brown maculation: narrowly margined crossveins 3ra-rp, 4im; two rather large semi-round spots at anterior part of 2r-m, 1cu-aa; two spots along hind margin (at end of CuA1 and posterior branch of CuP); and spots at primary forks (inside) of stem of RP, RP1, RP2.

Hind wing 3.3 mm long, 1.3 mm wide (left hind wing). Costal space strongly narrowed medially, dilated proximally and distally, especially distad fusion of ScP, RA. Subcostal veinlets poorly preserved; few preserved veinlets in narrow medial part simple, rather close spaced. Humeral plate elongate, narrow. Subcostal space broad, basally appears narrowed; no crossvein detected. ScP, RA fused apically. ScP+RA entering wing margin before apex, with four distal veinlets, two of these sinuous, branched (proximal veinlets poorly preserved). RA space wider than subcostal space, with two crossveins proximad fusion of ScP, RA, none distad. RP originated rather far from wing base, with three branches originating proximad 3ra-rp. Stem of RP twice rather shallowly forked; RP1, RP2 similarly dichotomously branched distally; RP3 once shallowly forked. No crossveins between branches of RP. One crossvein between RP, M (4r-m) connecting RP1, MA before their branching; basal 1r-m not detected, most probably absent. M basally not fused with R; forked distad origin of RP and at level of 2icu. MA, MP parallel, dichotomously branched (similar to branching of RP1). One crossvein (4im) belonging to outer series between MA, MP. Two crossveins between M, Cu: 1m-cu ('M5') connecting M, Cu before fork; 4m-cu connecting MP proximad its branching, CuA distad diastal-most branch of CuA. Cu dividing into CuA, CuP slightly distal to wing base than in forewing. CuA long, running rather close to hind margin medially, pectinately branched with four branches; CuA1 twice forked. CuP running very close to hind margin in distal half, pectinately branched with seven simple branches. One crossvein (2icu) between CuA, CuP. Basal 'anal bridge' between Cu, AA1 and claval fold well developed. No crossveins between Cu, AA1 detected. AA1 pectinately branched, with three short branches. AA2 pectinately branched, rather short, with two simple branches. AA3 short, simple. Crossveins between anal veins not detected. Jugal lobe poorly developed. Setae on veins rather long. Marginal setae arranged in bunches at end of veins and trichosors; very long along hind margin (especially along jugal lobe), shorter along costal margin. Trichosors prominent along entire wing margin (except basally and along anterior margin where these are not distinct). Wing membrane hyaline, without maculation.

Characteristics of Paraberothinae

Makarkin & Kupryjanowicz (2010) characterized the subfamily Paraberothinae by a combination of the following character states: [1] small berothids (forewing 2.9–4.0 mm long); [2] postocular lobe reduced; [3] scapus long to very long (up to 10 times longer than pedicel); [4] forelegs raptorial; [5] tarsus of male 5-segmented; [6] tibia with numerous spine-like setae on inner edge; [7] Sc and R1 fused distally in both wings; [8] intermediate subcostal crossvein 2sc-r1 absent in the forewing; [9] the basal crossvein 1r-m straight and [10] CuP present in the hind wing. Since then three genera were added to the subfamily: *Raptorapax* Petrulevičius *et al*., 2010, *Micromantispa*, and *Creagroparaberotha* **gen. nov.** (Petrulevičius *et al*. 2010; Makarkin 2015; this paper). Therefore, it is reasonable to consider the diagnosis again, and revise it if needed.

Character [1]. The length of the forewing of *Micromantispa cristata* (i.e., 4.19 mm) is slightly beyond a range given in the diagnosis.

Character [2]. The postocular lobe of these three genera is similarly constructed to other Paraberothinae.

Character [3]. The length of the scapus of *Micromantispa cristata* is impossible to determine with accuracy due to the position of the specimen, but it is likely rather short, probably similar in the length to the scapus of *Scoloberotha necatrix*. The scapus of the other two genera is long.

Character [4]. The raptorial forelegs are mainly characteristic of the berothoid clade (Yang *et al*., 2012; Makarkin *et al*. 2013), i.e., Mantispidae, Dipteromantispidae, and some Berothidae (Paraberothinae, Rhachiberothinae, and Mesithoninae). This character state is possibly a synapomorphy of this clade, although it is sometimes considered as originating independently, at least in Mantispidae and Rhachiberothinae (e.g., Aspöck & Mansell 1994).

Character [5]. The protarsus of all species of Paraberothinae are 5-segmented (both males and females: see below under 'Genital segments'). The spine-like setation in *Creagroparaberotha* **gen. nov.** is especially well developed. Two basal tarsomeres of all species of Paraberothinae from Burmese amber (including the new genus), *Rhachibermissa splendida*, and *Albertoberotha leuckorum* each bear one terminal curved spine-like seta on outer (dorsal) edge (Fig. 6). One undescribed specimen from Burmese amber bears such a seta only on the basitarsus (pers. obs.). Other known species of Paraberothinae lack these dorsal spine-like setae.

Most species of Paraberothinae bear spine-like setae on the inner (ventral) edge of the probasitarsus, i.e., one seta in *Rhachibermissa splendida*; two setae in *Micromantispa cristata*; three in *Paraberotha acra*; and five-six in *Albertoberotha leuckorum*, *Spinoberotha mickaelacrai* and *Creagroparaberotha groehni* **sp. nov.** Setae in *S. mickaelacrai* are long and relatively thin. *Raptorapax terribilissima* and *Chimerhachiberotha acrasarii* probably lack these ventral setae.

In most of the genera that possess setae on the basitarsus (except *Rhachibermissa splendida* and *Micromantispa cristata*), the second tarsomere bears one-two ventral spine-like setae.

Character [6]. Most species of Paraberothinae possess numerous long spine-like setae on the inner (ventral) edge of the protibia. These range from 12 in *Paraberotha acra* and *Creagroparaberotha groehni* **sp. nov.** to 42 in *Raptorapax terribilissima* Petrulevičius *et al*., 2010. Those in *Chimerhachiberotha acrasarii* Nel *et al*., 2005a are very short, an obvious apomorphic state (considered as an autapomorphy of the genus by Nel *et al*., 2005a). The number of these spine-like setae are reduced to three distal in *Scoloberotha necatrix* and *Micromantispa cristata*, four distal in *Rhachibermissa splendida*, and even only two distal in one undescribed specimen from Burmese amber (pers. obs.). The presence of spine-like setae on the inner edge of the protibia is considered a synapomorphy of Paraberothinae (Nel *et al*. 2005a; Makarkin & Kupryjanowicz 2010).

The structure of the protibia in the Jurassic to Early Cretaceous Mesithoninae is poorly known. The preserved distal half of one of the protibia in an undescribed specimen from the Middle Jurassic Daohugou bears no spine-like setae (pers. obs.). Details of the forelegs of the single known specimen of the genus *Berothone* with a preserved body (i.e., *Berothone gracilis* (Panfilov, 1980)) are very unclear. The forelegs in the single known specimen of *Oloberotha sinica* Ren et Guo, 1996 are missing. Other Mesithoninae are known only from wings.

In Dipteromantispidae, the protibia of *Mantispidiptera enigmatica* Grimaldi, 2000 bears no spine-like setae (Grimaldi 2000: Fig. 12). The setation of the two other species of the family (*M. henryi* Grimaldi, 2000 and *Dipteromantispa brevisubcosta* Makarkin *et al*. 2013a) is unknown (Grimaldi 2000: Fig. 13; Makarkin *et al*. 2013a: Fig. 1).

All species (both fossil and extant) of Rhachiberothinae and Berothidae with cursorial legs bear no spine-like setae or prostrate setae on the inner edge of the protibia (Fig. 7).

All species of Mantispidae bear no spine-like setae on the inner edge of the protibia. However, the minute closely spaced strong setae (so called 'prostrate setae') on the edge of the protibia, forming a lateroventral ridge, are present in Symphrasinae, Drepanicinae, and Calomantispinae (Tjeder 1959: Fig. 247; Lambkin 1986: Figs 21, 22; Willmann 1990: Fig. 12), but absent in Mantispinae. These prostrate setae are strongly specialized (see Poivre 1978: Figs 4A, B), and are considered a synapomorphy of Mantispidae (Liu *et al*. 2015). These are also detected in the Middle Jurassic to Early Cretaceous subfamily Mesomantispinae (see Jepson *et al*. 2013: Figs 2C, 3B, 6B, 7B; Khramov 2013: Figs 4, 8). "Peg-like protrusions" on inner edge of the protibia in the Burmese amber mantispid *Doratomantispa burmanica* Poinar et Buckley, 2011 are quite similar to the prostrate setae of Mesomantispinae but slightly larger (see Poinar & Buckley 2011: Figs 4, 5). These structures might be homologies of prostrate setae; Liu *et al*. (2015) consider them as enlarged prostrate setae.

It is unclear yet if prostrate setae of Mantispidae are homologous with the spine-like setae of Paraberothinae, but it is very probable that both conditions evolved from ordinary fine setae independently.

Character [7]. The fusion of ScP and RA occurs in all species of the subfamily including the three genera that have been added since 2010.

Character [8]. The loss of the intermediate subcostal crossvein (2scp-r) in the forewing of Paraberothinae is considered apomorphic at the family level (Makarkin & Kupryjanowicz 2010). This character state distinguishes Paraberothinae from other berothoids with raptorial legs (most Mesithoninae and Rhachiberothinae) and Mantispidae, which possess this crossvein (at least plesiomorphically).

Character [9]. The basal crossvein 1r-m in the hind wing is straight (i.e., *Paraberotha acra* Whalley, 1980, *Rhachibermissa splendida* Grimaldi, 2000, and *R. phenax* Engel et Grimaldi, 2008) or lost (i.e., *Spinoberotha mickaelacrai* Nel *et al*., 2005a, *Scoloberotha necatrix*, and *Creagroparaberotha groehni* **sp. nov.**). Its structure is unknown in other species. A plesiomorphic condition at the level of the family and order (i.e., 1r-m sinuous) is not documented in any species.

Character [10]. The presence of CuP in the hind wing is a plesiomorphic condition at the family level. This condition is present in Paraberothinae, some other Berothidae with cursorial legs, and probably in Mesithoninae. It is partly reduced in all Rhachiberothinae, and strongly reduced in most Mantispidae (except Symphrasinae) and most Berothidae (see also Makarkin & Ohl 2015). The hind wings of Dipteromantispidae are modified into small halter-like structures.

Humeral veinlet. This veinlet is similarly configured in three species: slightly recurrent with one (*Paraberotha acra*) or two short branches (*Raptorapax terribilissima* and *Creagroparaberotha groehni* **sp. nov.**). The humeral veinlet in other species of Paraberothinae is not branched or the basal portion of the costal space is poorly preserved. The humeral veinlet is strongly recurrent and branched in Mesithoninae and the basal Mantispidae (e.g., Mesomantispinae, Symphrasinae).

Genital segments. The structure of genital segments in Paraberothinae is in general unclear, mainly due to incomplete descriptions or poor preservation. *Albertoberotha leuckorum* McKellar et Engel, 2009 is a male, with "protrusion of two talon-shaped paramere-mediunci" (p. 119). *Raptorapax terribilissima* Petrulevičius *et al*., 2010 was thought to be a female by the authors of the species, but its abdominal apex bears two talon-shaped structures (probably similar to those of *A. leuckorum*) located up to 9th sternite (Petrulevičius *et al*. 2010: Fig. 4), implying that this is a male. The holotype of *Micromantispa cristata* is the only specimen among known Paraberothinae that may be more or less confidently interpreted as a female, with "9th tergite with ventroposterior region protruded. Ectoproct dorsoventrally elongated" (p. 420) (Shi *et al*. 2015a: Figs 4, 5a). The holotype of *Spinoberotha mickaelacrai* is thought to be a female, "with each lateral gonapophyse bearing a long hypocauda" (Nel *et al*., 2005a: p. 76). However, this 'hypocauda' is caudally directed (Nel *et al*., 2005a: Fig. 16), but true hypocaudae are usually directed anteriorly or ventrally. Therefore, judging from the figure this 'lateral gonapophyse' may well be interpreted as an ectoproct, and therefore the holotype may be a male. Although *Eorhachiberotha burmitica* is indicated as a male in the original description, and *Rhachibermissa phenax* Engel et Grimaldi, 2008 and *Scoloberotha necatrix* as females, no evidence is given in either the text or the figures about their sex. It can be assumed that the method for determining the sex of the species was based on the number of segments of the protarsus: females possessing a 5-segmented protarsus, and males with a 4-segmented protarsus (i.e., regarding *E. burmitica*). This is because all of them were originally considered as belonging to Rhachiberothinae, which exhibits this kind of sexual dimorphism in the structure of the protarsus. However, the actual number of tarsomeres in the *Eorhachiberotha burmitica* holotype is unclear.

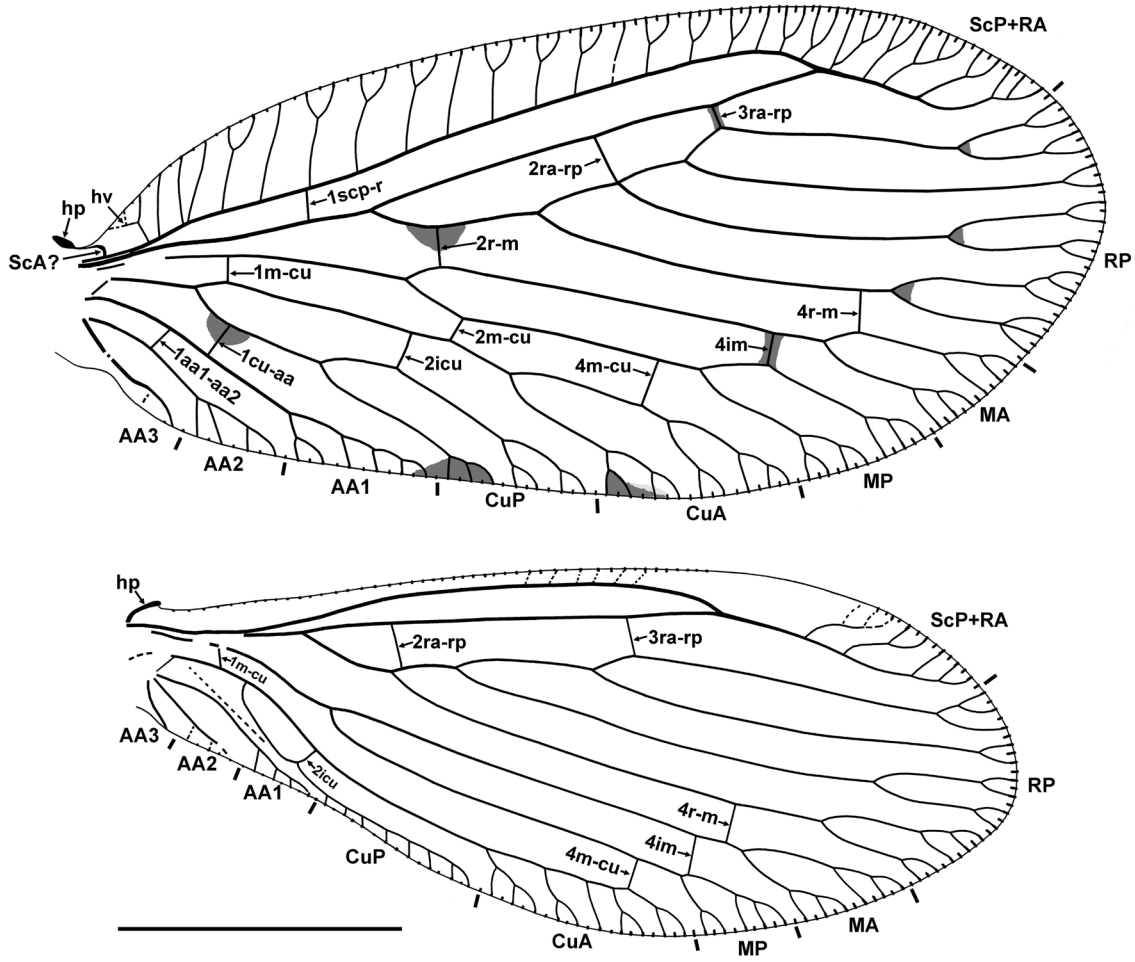

FIGURE 4. *Creagroparaberotha groehni* **gen. et sp. nov.**, wing venation of the holotype GPIH Typ. Kat. Nr. 4568. A, left forewing. B, left hind wing. Both converted to standard dorsal view. Scale bar = 1 mm.

In summary, the sex of only three specimens may be confidently interpreted: one female (i.e., *Micromantispa cristata*) and two males (i.e., *Albertoberotha leuckorum* and *Raptorapax terribilissima*).

Revised diagnosis of Paraberothinae. The above analysis shows that the diagnosis of the subfamily is insufficiently changed after the addition of the three genera. The revised diagnosis of Paraberothinae is as follow: [1] small berothids (forewing 2.9–4.2 mm long); [2] postocular lobe reduced (at least not inflated); [3] scapus long to very long (about 2.5 to 10.0 times longer than wide); [4] forelegs raptorial; [5] protarsus of both female and male 5-segmented; [6] protibia at least with two spine-like setae on inner edge (usually with numerous spine-like setae) (synapomorphy); [7] ScP and RA fused distally in both wings; [8] intermediate subcostal crossvein 2scp-r lost in the forewing; [9] humeral veinlet relatively short, not or few branched (with 1–2 branches) in the forewing; [10] basal crossvein 1r-m straight (if present) in the hind wing; [11] CuP present in the hind wing.

Dorsal spine-like seta on the probasitarsus of Paraberothinae and its probable homologues in Rhachiberothinae (Berothidae) and Symphrasinae (Mantispidae)

The structure and placement of a dorsal spine-like seta on the probasitarsus of Paraberothinae is important for understanding the evolution of a peculiar probasitarsus armament of younger Rhachiberothinae and Symphrasinae. Such a probasitarsus armament is only characteristic of these three groups of the berothoid clade, which includes the Jurassic to Recent Berothidae and Mantispidae, and the Cretaceous Dipteromantispidae.

Is the apical spine of Symphrasinae homologous with a dorsal spine-like seta of Paraberothinae and Rhachiberothinae (i.e., their similarity is based upon their origin from a common ancestor that possessed such a proto-structure), or does it represent a homoiology (parallelism), i.e., convergent modifications of a homologous

structure (Bechly 2005)? I agree with Bechly (2005) in that the term parallelism is superfluous, as "the decision where to draw a line between homoiology and parallelism is subjective" (Waegele 2005, p. 121).

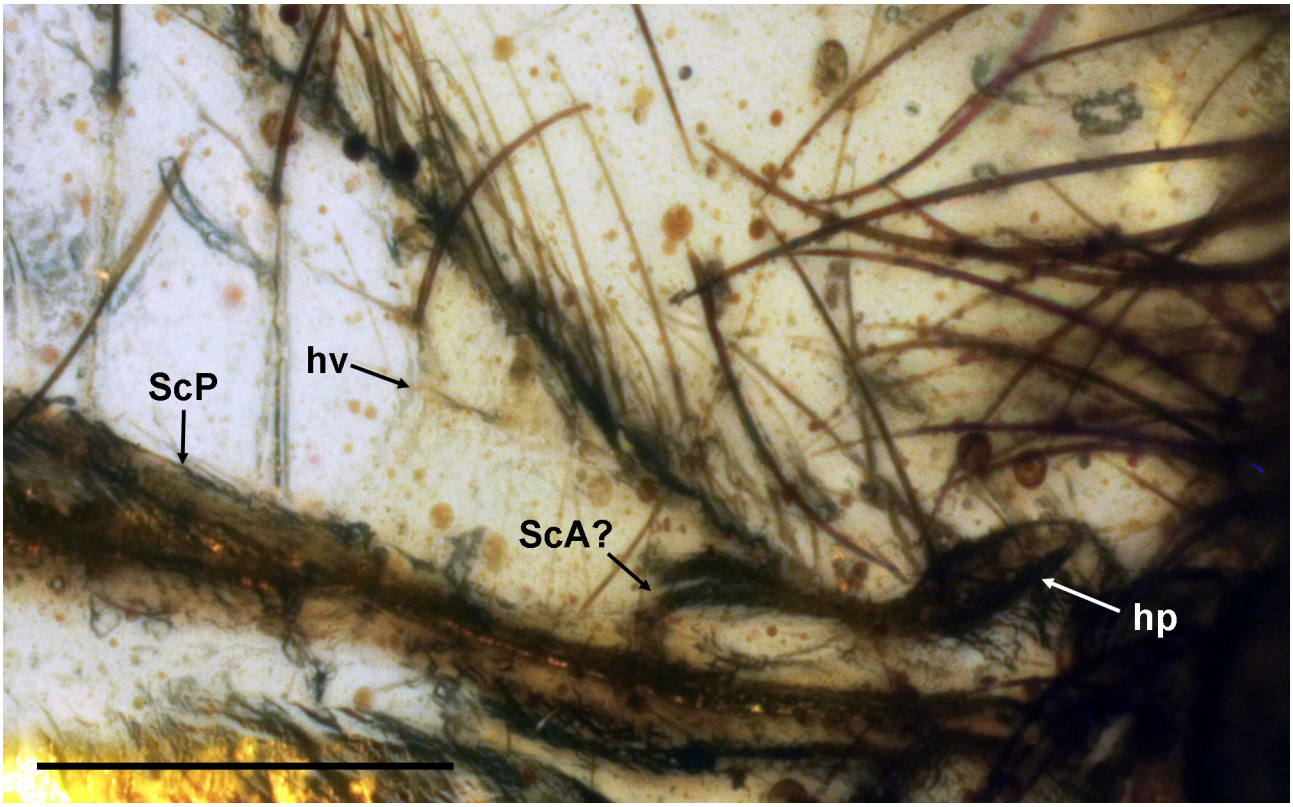

FIGURE 5. *Creagroparaberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4568. Basal portion of the left forewing costal space. Scale bar = 0.2 mm.

All males of Rhachiberothinae possess a 4-segmented protarsus and a terminal spur-like spine on the basitarsus, whereas the females have a plesiomorphic 5-segmented protarsus without any spines or spine-like setae. A probasitarsus spine-like seta is observed in *Whalfera* Engel, 2004 arising from the outer (dorsal) terminal edge (Willmann 1994: Fig. 4; Makarkin & Kupryjanowicz 2010: Fig. 2); its articulation is clearly visible at least in *W. wiszniewskii* Makarkin et Kupryjanowicz, 2010 (see Fig. 7). A similar configuration is found in the extant *Rhachiberotha sheilae* Aspöck et Mansell 1994 (Aspöck & Mansell 1994: Fig. 12). However, in *R. sheilae* there is a distal protruding process ended by a strong seta, so that the remaining protarsus arises near the base of the protruding process and much proximal to the articulation of a seta. A probasitarsus armament of *Mucroberotha* Tjeder, 1959 is more diverse, from an inner terminal protruding process in *M. vesicaria* Tjeder, 1968 (Tjeder 1968: Fig. 1) to a strong dorsal seta in the apical half in *M. minteri* Aspöck et Mansell, 1994 (Aspöck & Mansell 1994: Fig. 38).

Both sexes of all species of Symphrasinae have a specialized 4-segmented protarsus: the basitarsus is enlarged ending in an apical pointed spine; the remaining three tarsomeres are small in size, arising from nearly the middle of the basitarsus at its inner edge (see Tjeder 1959: Figs 247, 250; Willmann 1990: Figs 12, 19; Ardila-Camacho & García 2015: Figs 1b, d, 4e, 6e, f, 12d). The strongly specialized protarsus of Symphrasinae is considered one of the synapomorphies of this subfamily (Lambkin 1986). Other taxa of Mantispidae have a 5-segmented protarsus and their basitarsus do not bear setae that might be homologous with the dorsal spine-like setae of berothids.

The evolution of such a specialized protarsus might have occurred in the following way: a condition of Paraberothinae → a condition of Rhachiberothidae → a condition of Symphrasinae (Fig. 8). Of course, this transformation series does not represent a phylogenetic reconstruction; these conditions could be present in the ancestors of these taxa, i.e., the series shows how the apical spine of Symphrasinae might have arisen. According to this evolutionary hypothesis, the protarsus becomes 4-segmented from 5-segmented, and the basitarsus is fused with the dorsal spine-like seta.

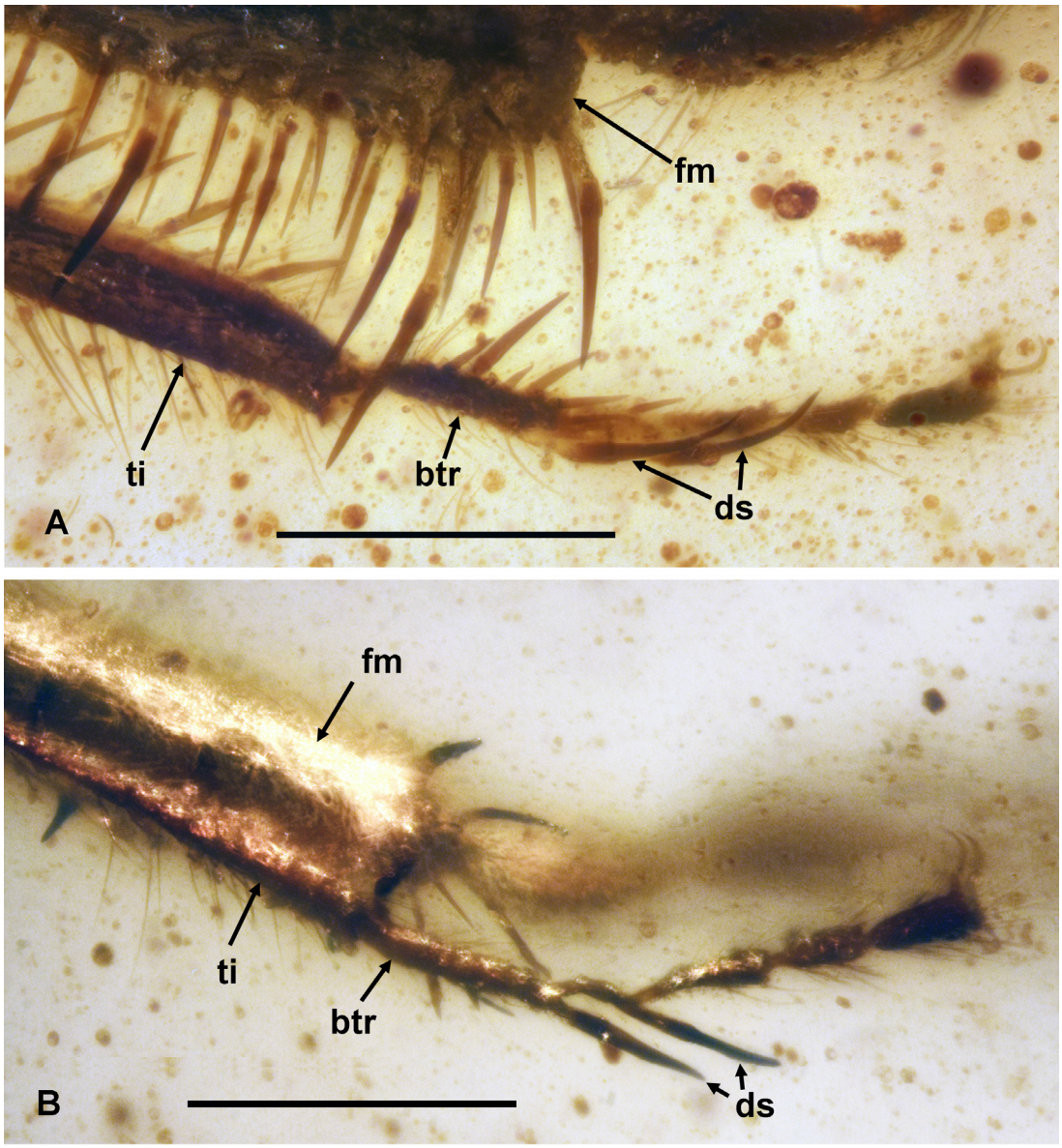

FIGURE 6. *Creagroparaberotha groehni* **gen. et sp. nov.**, details of forelegs of the holotype GPIH Typ. Kat. Nr. 4568. A, left protarsus (outer lateral view). B, right protarsus (dorsal view). btr, basitarsus; ds, dorsal spine-like setae; fm, femur; ti, tibia. Scale bars = 0.2 mm.

FIGURE 7. *Whalfera wiszniewskii* Makarkin et Kupryjanowicz, 2010, right foreleg of the holotype MZ 24203 (inner lateral view). btr, basitarsus; ds, dorsal spine-like seta; tr, tarsus. Scale bar = 0.5 mm.

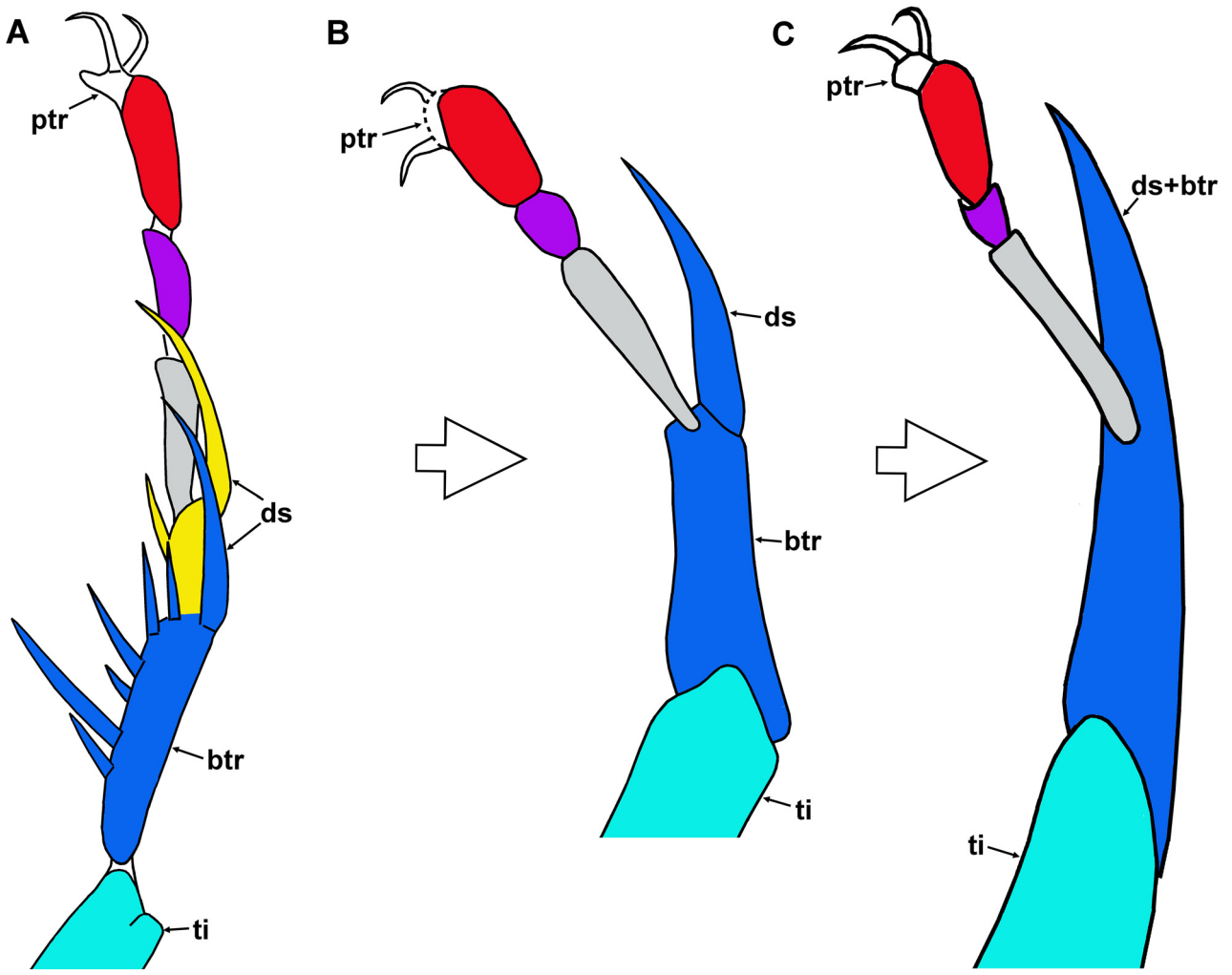

FIGURE 8. The evolution of the protarsus structure in berothoids with raptorial forelegs. A, *Creagroparaberotha groehni* **gen. et sp. nov.** (Berothidae: Paraberothinae; earliest Cenomanian). B, *Whalfera wiszniewskii* Makarkin et Kupryjanowicz, 2010 (Berothidae: Rhachiberothinae; late Eocene). C, *Trichoscelia* sp. (Mantispidae: Symphrasinae; Recent). Outer (A), inner (B, C) view. All slightly schematized, not to scale; presumable homologous segments are shown by the same color. btr, basitarsus; ds, dorsal spine-like (spur-like) seta; ptr, pretarsus; ti, tibia.

The oldest known (Jurassic) taxa of Berothidae and Mantispidae bear no such setae on the protarsus. The dorsal spine-like setae first appear in the Cretaceous Paraberothinae. The protarsus in this subfamily is rather generalized, 5-segmented in both sexes, and dorsal spine-like setae are not present in all genera: the oldest Paraberothinae (i.e., from Lebanese amber) lack any spine-like setae, including dorsal. Therefore, it may be reasonably assumed that these structures evolved within Paraberothinae. However, it is theoretically possible that there are older (still to be discovered) paraberothine taxa that bear spine-like setae. Currently, Paraberothinae possessing protarsus dorsal spine-like setae are only known from the taxa in the Late Cretaceous, occurring from the earliest Cenomanian to Campanian.

In Rhachiberothinae, the male specialized 4-segmented protarsus with an apical spine-like seta occurs in their earliest known genus, the Eocene *Whalfera*. However, rhachiberothines cannot be considered direct descendants of paraberothines. In particular, the latter have the apomorphic character state of a straight basal crossvein 1r-m in the hind wing (this is reduced in some species, e.g., *Creagroparaberotha groehni* **sp. nov.**), whereas in all Rhachiberothinae the plesiomorphic state is observed, i.e., long and sinuous. Therefore, Paraberothinae and Rhachiberothinae are most probably sister groups (Makarkin & Kupryjanowicz 2010).

The Symphrasinae represent the next stage of evolution of the protarsus: 4-segmented in both sexes with an apical acute spine on the large basitarsus. Although fossil evidence of the foreleg structure in Symphrasinae is absent, the most reasonable hypothesis is that the apical spine resulted from the fusion of an apical dorsal spine-like

seta and basitarsomere. It is interesting that Symphrasinae is the only subfamily among Mantispidae which has a plesiomorphic sinuous 1r-m in the hind wing similar to that of Rhachiberothinae.

The precise phylogenetic relationships within the berothoid clade are as yet unclear, especially the position of Rhachiberothinae and Symphrasinae, which represent the most isolated taxa within Berothidae and Mantispidae, respectively. Based on the current knowledge, it is more correct to interpret the specialized probasitarsi in Paraberothinae, Rhachiberothinae, and Symphrasinae as a homoiology (parallelism), not a true homology. Theoretically, however, these might be homologous, especially if fossil taxa of the stem-group Berothidae + Mantispidae were to be discovered possessing a dorsal spine-like seta on the basitarsus.

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