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The first fossil hanging flies (Insecta: Mecoptera: Raptipedia: Cimbrophlebiidae and Bittacidae) from the limestones of Solnhofen and Nusplingen (Upper Jurassic, Germany)

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With 8 figures

Summary

A new fossil hanging fly, *Malmocimbrophlebia buergeri* n. g. n. sp., is described after two complete specimens as first record of Raptipedia – Cimbrophlebiidae from the Upper Jurassic Solnhofen Lithographic Limestones in Bavaria. A second new genus and species of fossil Raptipedia from there is briefly described but not yet named. Furthermore, an unnamed fossil Bittacidae is described after an isolated wing from the Upper Jurassic Lithographic Limestone of Nusplingen (Swabian Alb). These four specimens represent the first fossil records of hanging flies in the Upper Jurassic of Germany. The phylogeny of fossil Raptipedia is discussed and a revised phylogenetic classification is suggested.

Zusammenfassung

Ein neuer fossiler Mückenhaft, *Malmocimbrophlebia buergeri* n. g. n. sp., wird nach zwei vollständigen Exemplaren als erster Nachweis der Raptipedia – Cimbrophlebiidae aus den oberjurassischen Solnhofener Plattenkalken Bayerns beschrieben. Eine zweite neue Gattung und Art fossiler Raptipedia von dort wird kurz beschrieben aber noch nicht benannt. Desweiteren wird eine unbenannte fossile Bittacidae nach einem isolierten Flügel aus dem oberjurassischen Plattenkalk von Nusplingen (Schwäbische Alb) beschrieben. Diese vier Exemplare sind die ersten Fossilnachweise der Mückenhafte im Oberen Jura von Deutschland. Die Phylogenie der fossilen Raptipedia wird diskutiert, und eine revidierte, phylogenetische Klassifikation wird vorgeschlagen.

1. Introduction

Raptipedia is today only represented by the family Bittacidae, which is a basal but highly specialized family of Mecoptera, with world-wide distribution (except for the northern Holarctic), including about 15 extant genera and 130 extant species. The adults are predators on other insects and mostly found on vegetation in sheltered

places, while the larvae are ground-dwelling scavengers pupating beneath the surface. The vernacular name „hanging flies" and the scientific name Raptipedia refer to the curious habits of adult bittacids that hang on small branches with their forelegs and catch flying insects with their raptorial hindlegs. Until recently only few fossil hanging flies had been known to science: WILLMANN (1978) listed only 4 genera with 6 species. According to WILLMANN (1978) the holotype of *Bittacus reticulatus* HEER, 1849 from the Miocene of Radoboj does not represent a Mecoptera at all, and also *Electrobittacus antiquus* (PICTET, 1854) may not be a Mecoptera and thus should better be regarded as a nomen dubium. CARPENTER (1992) synonymized *Electrobittacus* with *Bittacus* without explanation or discussion. BACHOFEN-ECHT (1949, 1996: Abb. 124–125) figured *Bittacus* sp. in Baltic amber (SPAHR 1989), and WEITSCHAT & WICHARD (1998: 188–189, Taf. 74e+f) featured *Bittacus* cf. *fossilis* from Baltic amber, too. JARZEMBOWSKI (1980) redescribed *Bittacus veternus* (COCKERELL, 1921) and described an unnamed second species of *Bittacus* from the Oligocene Bembridge Marl of England (also mentioned by CARPENTER 1992). NOVOKSCHONOV (1993) described *Bittacus biamensis* from the Oligocene of east Asia, but the attribution of the mentioned fossil species to the extant genus *Bittacus* seems to be rather questionable. PETRULEVICIUS (1998) mentioned a first fossil hanging fly from the Tertiary of Argentina. It is remarkable that no Raptipedia have yet been recorded from the very rich fossil insect fauna of the Lower Cretaceous Crato Formation in NE Brazil (BECHLY 1998a).

The only Mesozoic bittacid mentioned by WILLMANN (1978) is *Probittacus avitus* MARTYNOV, 1927 from the Upper Jurassic of Karatau (Kazakhstan), which is based on an isolated forewing. However, the recognition of „Neorthophlebiidae" as close relatives or even members of Bittacidae within Raptipedia significantly increased the number of known Mesozoic hanging flies, mainly from the Lower Jurassic (Lower Toarcian) of Germany, England, and Central Asia. The oldest known representative of Raptipedia is *Archebittacus exilis* from the Upper Triassic of Australia (RIEK 1955). Recently, numerous new fossil Raptipedia have been described from the Jurassic and Cretaceous of Eurasia (SUKATSHEVA 1985, 1990; NOVOKSCHONOV 1993a, 1993b, 1996, 1997a, 1997b; REN DONG 1993, 1997; ANSORGE 1996). WILLMANN (1977) described *Cimbrophlebia bittaciformis* from the Upper Palaeocene/Lower Eocene Moler Formation of Denmark as a new family Cimbrophlebiidae within Raptipedia. ANSORGE (1996) mentioned the discovery of an undescribed forewing (length about 25 mm) of a new genus of Cimbrophlebiidae from the Upper Liassic of Grimmen in Germany, and *Telobittacus fragosus* ZHANG, 1993 from the Lower Cretaceous of China seems to be a further Mesozoic representative of Cimbrophlebiidae (NOVOKSCHONOV 1997b: 115; ANSORGE, pers. comm.). ANSORGE (in prep.) also attributes *Plesiobittacus* NOVOKSCHONOV 1997b (Plesiobittacinae) to Cimbrophlebiidae, since he regards the three-branched RP1 as a putative synapomorphy.

Here we describe a new fossil species of Raptipedia – Cimbrophlebiidae from the Solnhofen lithographic Limestone, an unnamed Raptipedia incertae sedis from the Solnhofen lithographic Limestone, too, and an unnamed fossil Bittacidae from the Nusplingen Limestone in South Germany. It is the first record of Raptipedia for these Upper Jurassic localities and only the second record of Mecoptera for the Solnhofen Limestone after the recent description of *Orthophlebia lithographica* by WILLMANN & NOVOKSCHONOV (1998a) (also see FRICKHINGER 1999: 64, fig. 112).

Methods

All drawings were made with a camera lucida and a binocular microscope (Figs 1, 4 and 6). The photos have been made with a 35 mm SLR camera by K. A. FRICKHINGER (Fig. 3), G. SCHWEIGERT (Fig. 7), and by G. BECHLY (Fig. 2).

2. Systematic Palaeontology

Class Insecta LINNAEUS, 1758 (= Hexapoda LATREILLE, 1825)
Pterygota BRAUER, 1885
Order Mecoptera PACKARD, 1886
Raptipedia WILLMANN, 1987
Family Cimbrophlebiidae WILLMANN, 1977

Genus *Malmocimbrophlebia* n. g.

Type species: *Malmocimbrophlebia buergeri* n. g. n. sp. (present designation).
Derivation of name: After the Malm age and the genus *Cimbrophlebia*.

Diagnosis. – See type species, since monotypic.

Malmocimbrophlebia buergeri n. sp.
Figs 1–3

Holotype: A complete female specimen (Figs 1–2), housed in the collection of the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS no. 63858, ex coll. BÜRGER 1999).

Type locality: Eichstätt area, near Solnhofen, southern Franconian Alb, Bavaria, SW Germany.

Type horizon: Solnhofen Formation (Solnhofen Lithographic Limestone, „Malm ζ 2b“). Upper Jurassic, Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone.

Derivation of name: Named in honour of Mr PETER BÜRGER (Bad Hersfeld) who kindly donated the important holotype from his private collection to SMNS.

Further Material: One specimen (Fig. 3) without collection number is present in the private collection of Mr PETER BÜRGER (Bad Hersfeld). It agrees with the holotype in all visible characters (incl. the expanded anal area with branched AA2), but the more slender abdomen suggests that it is a male specimen, so that it could represent a putative allotype.

Diagnosis. – This new genus and species is distinguished from most other fossil and extant Mecoptera by its very large size, the presence of long raptorial legs, the widened anal area with a branched vein AA2, and the shape of the forewings that are basally stalked and distally very strongly broadened. Within Mecoptera the size of this new species is only matched by *Cimbrophlebia bittaciformis* WILLMANN, 1977, *Orthobittacus* WILLMANN, 1989, *Orthophlebia elenae* WILLMANN & NOVOKSCHONOV, 1998b, and the giant extant bittacid *Neobittacus blancheti* PICTET, 1836. This new taxon is most similar to the Tertiary *Cimbrophlebia*, but is about 100 Mio. years older.

The present species differs from the unnamed second large Raptipedia taxon (described below) from the same locality by the expanded anal area of the forewings with a multibranched vein AA2, and the strong distal broadening of the forewings. Because of its size, the presence of four wings, and the curious cranefly-like habitus, this fossil taxon can easily be distinguished from all other fossil insects from the same locality, including the few known fossil tipulomorph Diptera, viz. *Tipularia teyleri* WEYENBERGH, 1869, *Crenoptychoptera bavarica* KRZEMINSKI & ANSORGE,

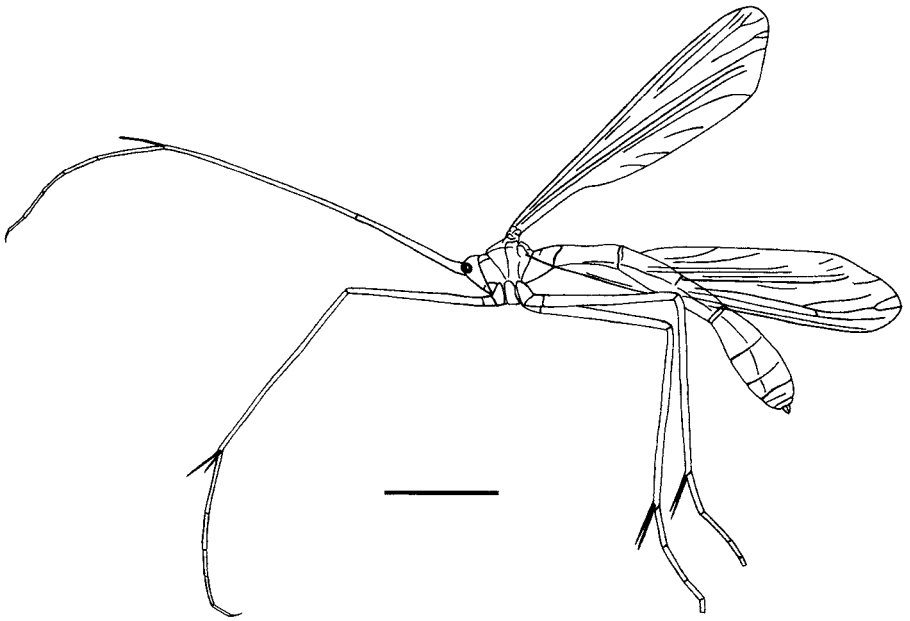

Fig. 1. *Malmocimbrophlebia buergeri* n. g. n. sp., Holotype. Solnhofen Lithographic Limestones, Eichstätt area. Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone. SMNS no. 63858. Scale 10 mm.

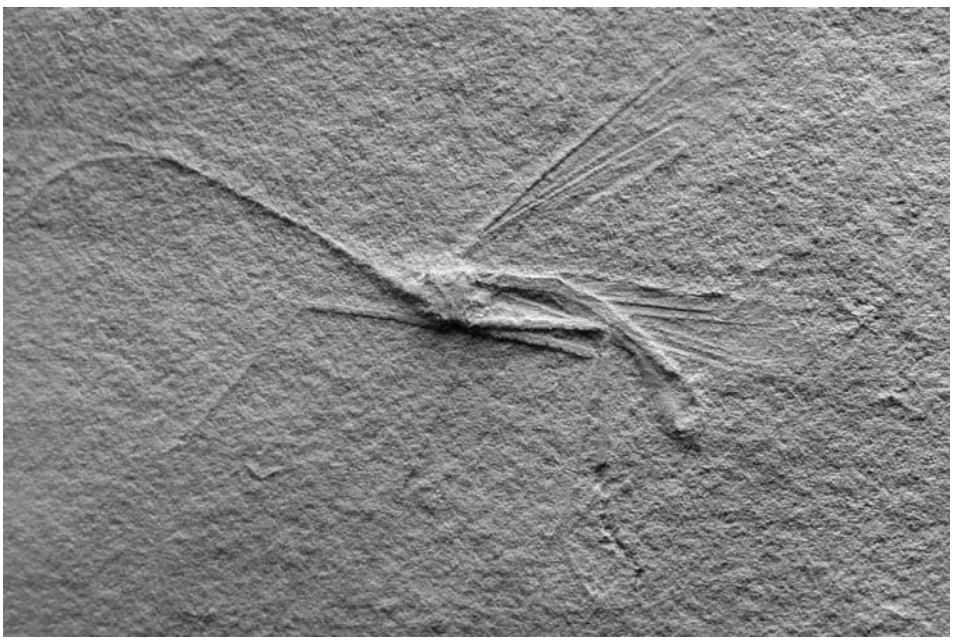

Fig. 2. *Malmocimbrophlebia buergeri* n. g. n. sp., Holotype. Solnhofen Lithographic Limestones, Eichstätt area. Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone. SMNS no. 63858. Without scale (photo G. BECHLY).

1995, and *Tipunia intermedia* KRZEMINSKI & ANSORGE, 1995 (also figured as „unbenannter Zweiflügler" in FRICKHINGER, 1999, fig. 124). However, the type specimen of *Tipularia teyleri* has been regarded by HANDLIRSCH (1906) as an unidentifiable fossil insect, so that this taxon is in need of a revision, but probably represents a nomen dubium.

Description (holotype). – An imprint of a complete female specimen of Raptipedia. On the backside of the plate there are numerous small planctonic crinoids of the genus *Saccocoma*. A counterplate most probably exists, but its current deposition is unknown.

Body: The head is poorly preserved in the holotype, but the second specimen clearly shows a long beak. The thorax is dorsally widened; max. length, 4.6 mm; max. width, about 4.3 mm. The abdomen is 27.5 mm long and distally distinctly expanded (basal width, 1.6 mm; max. distal width, 3.8 mm). The anal appendages are very short (length, 0.7 mm) and spine-like. The shape of the distal part of the abdomen and the anal appendages strongly suggest that the holotype is a female specimen (compare MICKOLEIT & MICKOLEIT 1978, fig. 2). The forelegs and hindlegs are well preserved, but the mesothoracic pair of legs is completely missing except for the coxa (length, 2.1 mm). Length of procoxa, 2.0 mm; length of protrochanter, 1.0 mm; length of profemur, 11.9 mm; length of protibia, 17.7 mm (there is a pair of long spines at the distal end of the protibia; max. length, about 3.9 mm); length of protarsus, 15.7 mm. The protarsus is five-segmented with the first tarsomere being the longest (length,

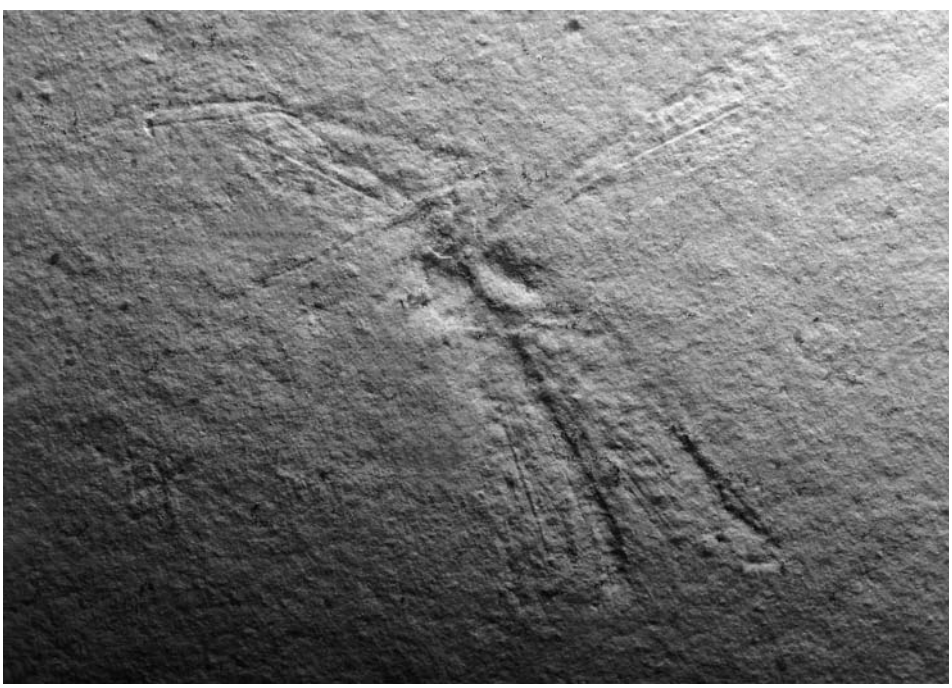

Fig. 3. *Malmocimbrophlebia buergeri* n. g. n. sp., Solnhofen Lithographic Limestones, Eichstätt area. Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone. Specimen (potential allotype) in coll. BÜRGER. Without scale (photo K. A. FRICKHINGER).

5.7 mm), and there is only a single tarsal claw visible. Length of metacoxa, 1.9 mm; length of metatrochanter, 1.4 mm; length of metafemur, 11.3 mm; length of metatibia, 15.6 mm (there is a pair of very long spines at the distal end of the metatibia; length, about 4.3 mm). The tarsus is incompletely preserved (length of the preserved part, 9.9 mm) and only shows the basal three to four segments.

Wings: The (right) forewing is 28.6 mm long. The apparently larger length of the left forewing is most probably caused by a detachment from the pterothorax. The forewing is basally very narrow and distinctly stalked (length of petiole, about 6.7 mm), while it is distally strongly broadened (max. width 6.8 mm). The wing venation is incompletely preserved, but the visible parts agree with the general wing venational pattern of Raptipedia. The Subcosta ScP is very long, and running closely parallel to the first Radius RA along the costal margin. Unfortunately, the number of branches of the Radiussector (RP1 and RP2), Media (MA and MP) cannot be determined. CuA and CuP are unbranched, very long and closely parallel. The anal area is wide and the anal vein AA2 is multibranched, even though the branches of the anal vein are only weakly visible with strong side light in both specimens. The hindwings are not preserved or concealed beneath the forewings in the holotype, but at least one hindwing is visible in the second specimen.

Systematic position. – The following combination of diagnostic characters clearly identifies this new taxon as a representative of Mecoptera – Raptipedia: Four narrow subpetiolate membraneous wings; extremely long legs with very long tibial spines and a very elongated tarsus that bears only a single claw; head with beak; relatively small and conical thorax; long and slender abdomen with small anal appendages; cranefly-like general appearance. The very long Subcostal vein ScP is a symplesiomorphy with Cimbrophlebiidae and Plesiobittacinae. The very narrow parallel course of veins ScP and RA along the costal margin is most similar to Cimbrophlebiidae and Plesiobittacinae, too, but the polarity of this character is unclear. The widened anal area of the wings and the large size are further derived similarities with Cimbrophlebiidae. Finally, the apparent branching of the Anal vein AA2 that is faintly indicated in both specimens would be a unique putative synapomorphy with Cimbrophlebiidae. Also the long and closely parallel course of CuA and CuP along a medio-longitudinal axis of the wing is quite typical of Cimbrophlebiidae (Ansorge, pers. comm.). Thus, the character pattern strongly suggests an attribution to Cimbrophlebiidae within the basal stemgroup of Bittacidae. Unfortunately, the poor preservation of the wing venation in both specimens does not yet allow a very well-founded differential diagnosis for the new genus compared to *Cimbrophlebia*, but the much older age in our view justifies a separate genus as well.

Raptipedia family indet.

Unnamed n. gen. n. sp.

Figs 4–5

Material: Specimen no. 213a is present in the private collection of the fossil trader Mr Jürgen Schmitt (Frankfurt a. M.). The latter specimen was figured by Frickhinger (1994: 166, fig. 354) as a supposed tipulid under the incorrect name *Tipularia teyleri* Weyenbergh, 1896, and it was mentioned by Krzeminski & Ansorge (1995) as a „tipulomorph-like fly". The left hindwing of this specimen was erroneously interpreted as abdomen by Frickhinger (1994), who overlooked the faint impression of the true abdomen and the wing venation of the alleged „abdomen", and who consequently regarded the insect as dipterous.

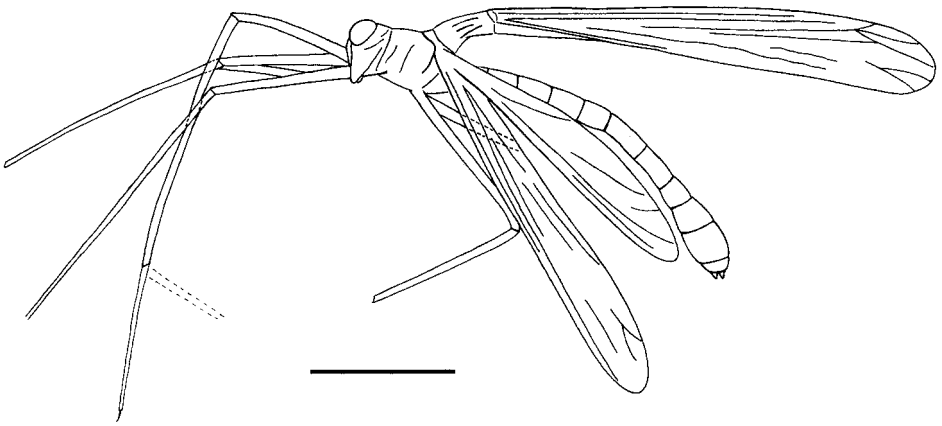

Fig. 4. Raptipedia fam. indet., n. gen. et n. sp. innom., Solnhofen Lithographic Limestones, Eichstätt area. Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone. Specimen in coll. SCHMITT. Scale 10 mm.

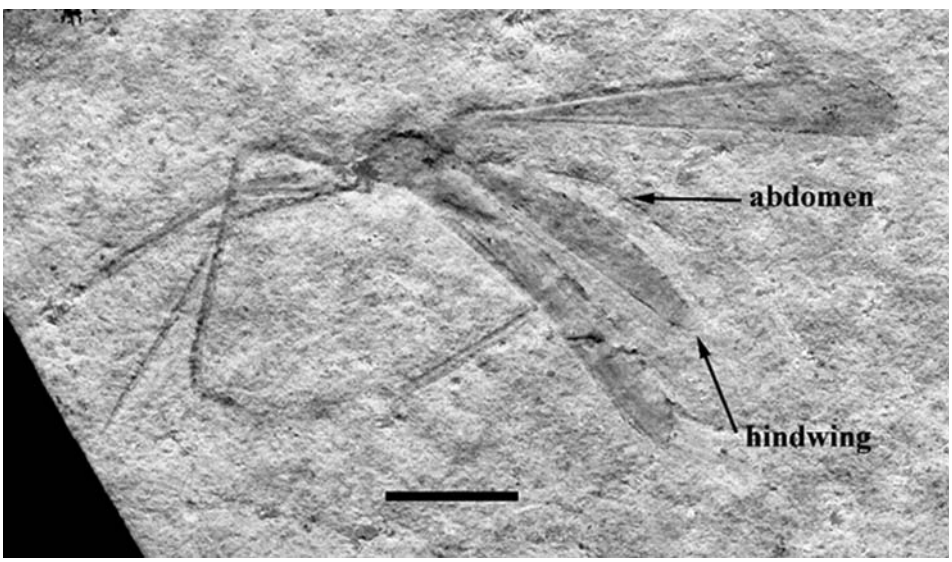

Fig. 5. Raptipedia fam. indet., n. gen. et n. sp. innom., Solnhofen Lithographic Limestones, Eichstätt area. Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone. Specimen in coll. SCHMITT. Scale 10 mm (direct scan of the fossil with a flatbed scanner by G. BECHLY).

Locality: Eichstätt area, near Solnhofen, southern Franconian Alb, Bavaria, SW Germany.

Horizon: Solnhofen Formation (Solnhofen Lithographic Limestone, „Malm ζ 2b“). Upper Jurassic, Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone.

Description. – A rather complete female specimen of Raptipedia (parts of the body and the wings are covered with coating).

Body: The head is poorly preserved, but faintly shows a beak and the globular compound eyes. The thorax is max. 4.6 mm long and max. 4.0 mm wide. The abdo-

men is about 25.5 mm long and distally somewhat widened (min. width, 1.4 mm; max. width, 2.7 mm). The anal appendages are very short (length, 0.53 mm) and spine-like. The shape of the distal part of the abdomen and the anal appendages suggest that this specimen is a female, too. All six legs are present and strongly elongated, but except for one foreleg these legs are only partly preserved. Length of protibia, 18.6 mm (the raptorial spines are not preserved); length of protarsus, 10.3 mm. The segmentation of the protarsus is not preserved but there seems to be only one tarsal claw.

Forewings: The right forewing is 31.4 mm long, while the left forewing seems to be only 27.7 mm long. This curious unequal length of the two forewings is certainly due to an artifact of preservation (e.g. a detachment of the right forewing and/or a basal twisting and folding of the left forewing). The forewing is basally narrow (width 1.8 mm) but not stalked, and it is distally smoothly broadened (max. width 4.6 mm). The wing venation is very incompletely preserved, but the visible parts agree with the general wing venational pattern of Raptipedia. The Subcosta ScP is very long, and running closely parallel to the first Radius RA along the costal margin. Unfortunately, the number of branches of the Radiussector (RP1 and RP2), Media (MA and MP) cannot be determined. CuA is basally fused with MP. The cubitoanal area is narrow and the veins CuA, CuP, and AA2 seem to be unbranched.

Hindwings: Only the left hindwing is preserved. It is 22.0 mm long and max. 3.6 mm wide. The wing is basally narrowed (min. width, 0.9 mm), the wing venation is rather poorly preserved.

Discussion. – The character pattern clearly identifies this specimen as a member of a new genus of Raptipedia, which is distinguished by its very large size, the long and narrow forewings and the shortened hindwings. Since the specimen is still in private possession and the wing venation is rather poorly preserved we here refrained from a formal description and scientific naming of this new taxon, especially since it cannot be totally excluded that *Tipularia teyleri* WEYENBERGH, 1869 indeed refers to this taxon rather than to a genuine tipulid. However, the owner plans to sell his complete Solnhofen collection, including this specimen, so that it might be formally described in case that this collection should be acquired by a public natural history museum and no better preserved specimens should be discovered. Generally, public and private collections of Solnhofen fossils should be carefully checked for further specimens that may have been potentially misidentified as tipulids, too.

Family Bittacidae HANDLIRSCH, 1906
Subfamily „Neorthophlebiinae“ HANDLIRSCH, 1920
(or Bittacinae? HANDLIRSCH, 1906)

Gen. et sp. indet.
Figs 6–7

Material: Plate and counterplate of a forewing fragment, housed in the collection of the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS no. 64215). The specimen was discovered during an excavation of SMNS in July 1999 by Mr JÖRN DIETL (Stuttgart).

Locality: Nusplingen quarry, Westerberg, „Gewann Taubenloch“, SW Swabian Alb, Baden-Württemberg, Germany, see DIETL et al. 1998.

Horizon: Nusplingen Lithographic Limestone (layer „G“, 10–20 cm from above, see section in DIETL et al. 1998). Upper Jurassic (Malm ζ), Upper Kimmeridgian, Beckeri Zone, Ulmense Subzone.

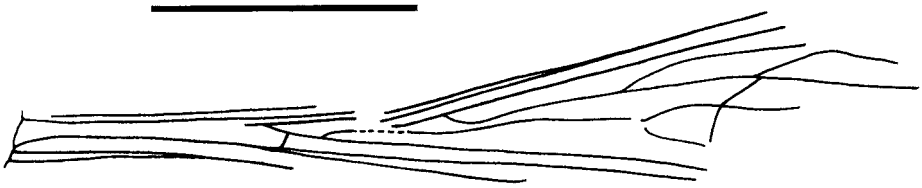

Fig. 6. Bittacidae („Neorthophlebiinae“) gen. et sp. indet., Nusplingen Lithographic Limestone, Nusplingen quarry. Upper Kimmeridgian, Beckeri Zone, Ulmense Subzone. SMNS no. 64215. Scale 5 mm.

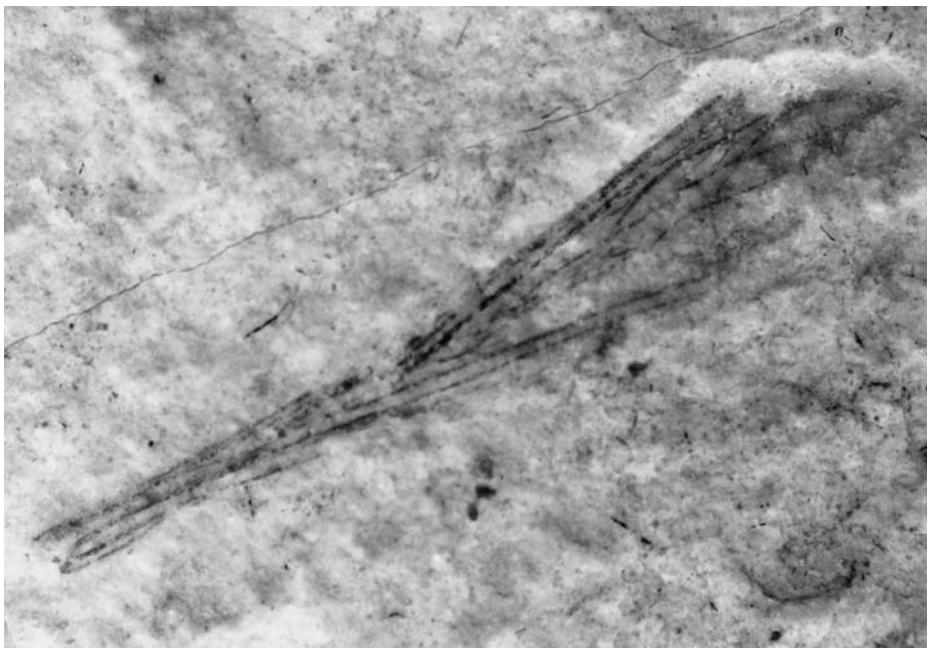

Fig. 7. Bittacidae („Neorthophlebiinae“) gen et sp. indet., Nusplingen Lithographic Limestone, Nusplingen quarry. Upper Kimmeridgian, Beckeri Zone, Ulmense Subzone. SMNS no. 64215. Without scale (photo G. SCHWEIGERT).

Description. – An isolated forewing with the distal third being destroyed. When the fossil is covered with alcohol one can see with large magnification that the wing membrane is covered with numerous tiny hairs (microtrichiae) and less frequent short bristles (macrotrichiae). The wing is strongly petiolated at the base; the fragment is 17.1 mm long, which suggests a total wing length of about 22.0 mm. The bases of AA, CuP and CuA are visible; CuA is basally fused with M, and only connected to CuP by a weakly oblique veinlet near the beginning of the petiole; there is a distinct „bittacid cross“ („Kreuz der Bittaciden“) formed by an oblique crossvein between the base of the RP2-fork and MA, and an aligned transverse crossvein between MA and MP; RP and RA have a common stem; the apex is not preserved, so that the number of branches of R and M is unknown. The presence of a crossvein-like base of CuA shows that it is a forewing, since this veinlet is absent in the hindwings of all known fossil and extant representatives of Raptipedia.

Discussion. – The combination of a well-defined „bittacid cross“ and a weakly oblique base of CuA suggests that this specimen belongs to the „neorthophlebiine“ grade within Bittacidae. All the other preserved parts of the wing venation completely agree with such an attribution as well.

3. Remarks on the preservation of the bittacid specimens

Even though fossil excavations took place in the Nusplingen Lithographic Limestone since the middle of the 19th century, the bittacid wing is only the sixth fossil insect and the first non-dragonfly found at this locality (DIETL et al. 1997; SCHWEIGERT et al. 1997; BECHLY 1998b). Three of the dragonflies (*Urogomphus nusplingensis*, *Aeschnidium densum*, and *Cymatophlebia longialata*) come from the kerogen-rich layer „D“ which provides an exceptional preservation of organic matter. Also, the layer „G“, which yielded the bittacid and two isolated wings of the dragonfly *Aeschnidium densum*, is partly bituminous and preserved the completely dark coloration of the most recently discovered wing of *Aeschnidium*.

The deposition place of the Nusplingen Lithographic Limestone is formed by an up to 80 m deep marine basin surrounded by sponge-microbial reefs, small islands, and shallow water areas. A lot of well-preserved land plants were washed in from these islands into the basin. The bittacid was not found on a sedimentary surface but within the rock. The finding layer is extremely rich in plant debris and coprolites. Hence, we assume the bittacid wing was transported in a suspension stream. The accumulated plant material and soil was most likely washed into the lagoonal basin during heavy rainfalls. Besides the xerophytic conifers, some benettitaleans and seed ferns, but also equisetaleans rarely occur. Together with the dragonflies the latter most probably indicate the presence of wet and boggy areas on some of the islands. Another circumstance might also suggest the proximity of larger islands with freshwater habitats and vegetation: Four of the five discovered dragonflies belong to the family Aeschnidiidae, which is characterized by adaptations for gliding flight and reductions of structures that are necessary for swift active flight (BECHLY 1998b).

The Tithonian Solnhofen Lithographic Limestones, from which the *Malmocimbrophlebia* n. g. and unnamed Raptipedia specimens come, was deposited much closer to the Late Jurassic coast. On the other hand, like in Nusplingen, islands were present in the near surroundings, on which freshwater habitats were developed (VIOHL 1998). The holotype specimen of *Malmocimbrophlebia* n. g. lies directly on the surface of a limestone bed, together with the planctonic crinoid *Saccocoma*. Both must have sunk down slowly from the water column to the seafloor. The preservation of this finding is therefore almost perfect, in contrast to the transported bittacid wing from Nusplingen.

4. Discussion

Even though extant Bittacidae have often been regarded as typical dwellers of shady and moist habitats, like gallery forests, MICKOLEIT & MICKOLEIT (1978) demonstrated that at least some species (e.g. *Bittacus italicus*) can also be found in open dry meadows. Because of this obvious ecological tolerance, the present discovery of the

first fossil stemgroup representatives of Cimbrophlebiidae and Bittacidae from the lithographic limestones of Solnhofen and Nusplingen are of limited importance for the reconstruction of the referring paleoenvironment. Also, fossil Raptipedia from this age have been known before, and the occurrence of this taxon in Late Jurassic times would have to be expected from its basal phylogenetic position within the old order Mecoptera anyway. Nevertheless, the first record of Raptipedia from the two mentioned outcrops adds to our knowledge of these famous fossil localities, as well as to our knowledge of the evolutionary history and paleobiogeography of Raptipedia.

5. Phylogenetic Systematics of Raptipedia

„Neorthophlebiidae" has been regarded as paraphyletic stemgroup of Bittacidae by WILLMANN (1987, 1989), ANSORGE (1993), and NOVOKSCHONOV (1993b). ANSORGE (1996) restricted Neorthophlebiinae to four genera (*Neorthophlebia*, *Protobittacus*, *Probittacus*, and *Scharabittacus*) and claimed that his Neorthophlebiinae has to be regarded as sistergroup of Bittacinae within Bittacidae. However, this statement is in conflict with phylogenetic systematic reasoning, since he did not demonstrate the monophyly of his (restricted) Neorthophlebiinae by any autapomorphies. Even the cited support for the monophyly of Bittacinae seems to be somewhat doubtful, since it only relies on two weak characters: Media four-branched in forewings (weak because only a reduction); base of CuA transverse (weak because homoplastic, since the base of CuA is distinctly oblique in fossil representatives of *Orobittacus*, that are included by ANSORGE in Bittacinae). Furthermore, the cladogram of fossil Raptipedia by ANSORGE (1996) differs considerably from the cladogram by NOVOKSCHONOV (1993b), which suggests that their phylogenetic relationships may still be far from settled (this is also suggested by our cladistic analysis). Out of these reasons, and since „Neorthophlebiidae" shares with extant bittacids the main apomorphies in the wing venation and body groundplan, e.g. even including the raptorial forelegs according to TILLYARD (1933) and SUKATSHEVA (1985), we preliminarily concur with the synonymization of „Neorthophlebiidae" HANDLIRSCH, 1920 (nec 1925) with Bittacidae by NOVOKSCHONOV (1993b).

According to WILLMANN (1977), Cimbrophlebiidae from the Eocene Fur Formation (Moler or Mo-clay) of Denmark might be closer related to Bittacidae than most „Neorthophlebiidae", but could also be derived from a subgroup of „Neorthophlebiidae" (ANSORGE 1993). CARPENTER (1992) regarded *Cimbrophlebia* as apparently related to Bittacidae, but too poorly known to permit assignment to a family. ANSORGE (1996) proposed an unresolved polytomy of *Archebittacus*, *Parabittacus*, *Cimbrophlebia*, *Orthobittacus*, and Bittacidae (incl. Neorthophlebiinae sensu ANSORGE). Currently, ANSORGE (pers. comm.) supposes that Plesiobittacinae could be a synonym of Cimbrophlebiidae, which is neither supported nor ruled out by our phylogenetic analysis (see below).

The genus *Permotipula* TILLYARD, 1929 has previously been classified in a separate family Permotipulidae TILLYARD, 1929, and the genus *Robinjohnia* MARTYNOVA, 1948 has originally been classified in the separate family Robinjohniidae MARTYNOVA, 1948 as well, but the latter is now mostly regarded as a close relative or even synonym of Nannochoristidae (WILLMANN 1978, 1987). The similarity of both

mentioned genera is documented by their confusion by several authors that is enumerated in WILLMANN (1978). CARPENTER (1992) regarded the position of both genera as doubtful. However, both genera differ considerably from the wing venation of the extant genus *Nannochorista*, while they do share several putative wing venational synapomorphies with Raptipedia (e.g. wings basally subpetiolate or petiolate, and RP2 with asymmetrical dichotomic branching). The two genera also share a few derived characters (see data matrix), including a strongly shortened ScP. We therefore tentatively attribute *Robinjohnia* to Permotipulidae and regard this family as sistergroup of Raptipedia. The genus *Bittacopanorpa* ZALESSKY, 1935 is only known by the wingbase, which is very similar to the two mentioned genera, and also shares the shortened ScP. A further similarity, and strong difference to other Raptipedia, is the proximity of the branchings of RA/RP and M/CuA. We therefore preliminarily transfer this genus from Neorthophlebiidae to the family Permotipulidae sensu nov.

Even though we endorse consequent phylogenetic systematic methods (sensu HENNIG) rather than mainstream computer cladism, we performed a cladistic analysis of a data matrix of 34 taxa and 20 characters with Hennig86 and TreeGardener2.2 to document the highly homoplastic character distribution that still prohibits a well-founded phylogenetic reconstruction of Mesozoic hanging flies. An all-zero hypothetical ancestor was chosen as outgroup, since the characters have been a priorily polarized by an outgroup comparison with numerous other fossil and extant Mecoptera, and the plesiomorphic state was generally coded as „0“, while the apomorphic states were coded as „1-x“, and an unknown or inapplicable state was coded as „?“. Furthermore, the fossil Mecoptera genus *Orthophlebia* was included as additional outgroup taxon. Multistate characters have been ordered and treated as additive, except for character 17 (unordered and non-additive). We used the heuristic search options „mhennig*;bb*“ which found 2649 trees with a minimum length of 88 steps (CI = 0.34, RI = 0.66). Also an additional heuristic search with PAUP did not yield shorter trees. The referring strict consensus tree (computed with Hennig86 command „nelsen“) is shown in Fig. 8. The rather low CI demonstrates a high degree of homoplasy in the characters, which is also indicated by the prevailing polytomies. The low number of characters (compared to the number of taxa) and the numerous missing entries also contributed to this poor resolution. Anyway, in many of the most parsimonious trees (not necessarily in the consensus tree!) there is considerable agreement with some phylogenetic conclusions of our „manual“ analysis that is based on an a priori weighting of the characters according to their complexity and congruence: *Robinjohnia* and *Permotipula* are putative sistergroups; Permotipulidae (incl. *Robinjohnia* and maybe *Bittacopanorpa*) constitutes a monophylum with Raptipedia (see above); „Plesiobittacinae“ and Cimbrophlebiidae are very basal groups within Raptipedia, which is documented by their unique symplesiomorphy of a retained three-branched RP1; *C. buergeri* n. sp. belongs to Cimbrophlebiidae (*Cimbrophlebia* and *Telobittacus*); there are no synapomorphies for the two species of *Plesiobittacus*, which implies the potential paraphyly of *Plesiobittacus* and Plesiobittacinae; *Karataccus*, *Archebittacus*, *Parabittacus*, and *Orthobittacus* have to be regarded as basal genera within Raptipedia, too; „Neorthophlebiinae“ sensu ANSORGE (1996) is likely paraphyletic, but Bittacinae sensu ANSORGE (1996) is weakly supported as monophylum, except for the placement of *Mesobittacus* and the Mesozoic „*Orobittacus*“ species (the single-branched RP1 could more likely represent a convergence to extant *Orobittacus*). Based on our „manual“ analysis (not the computer

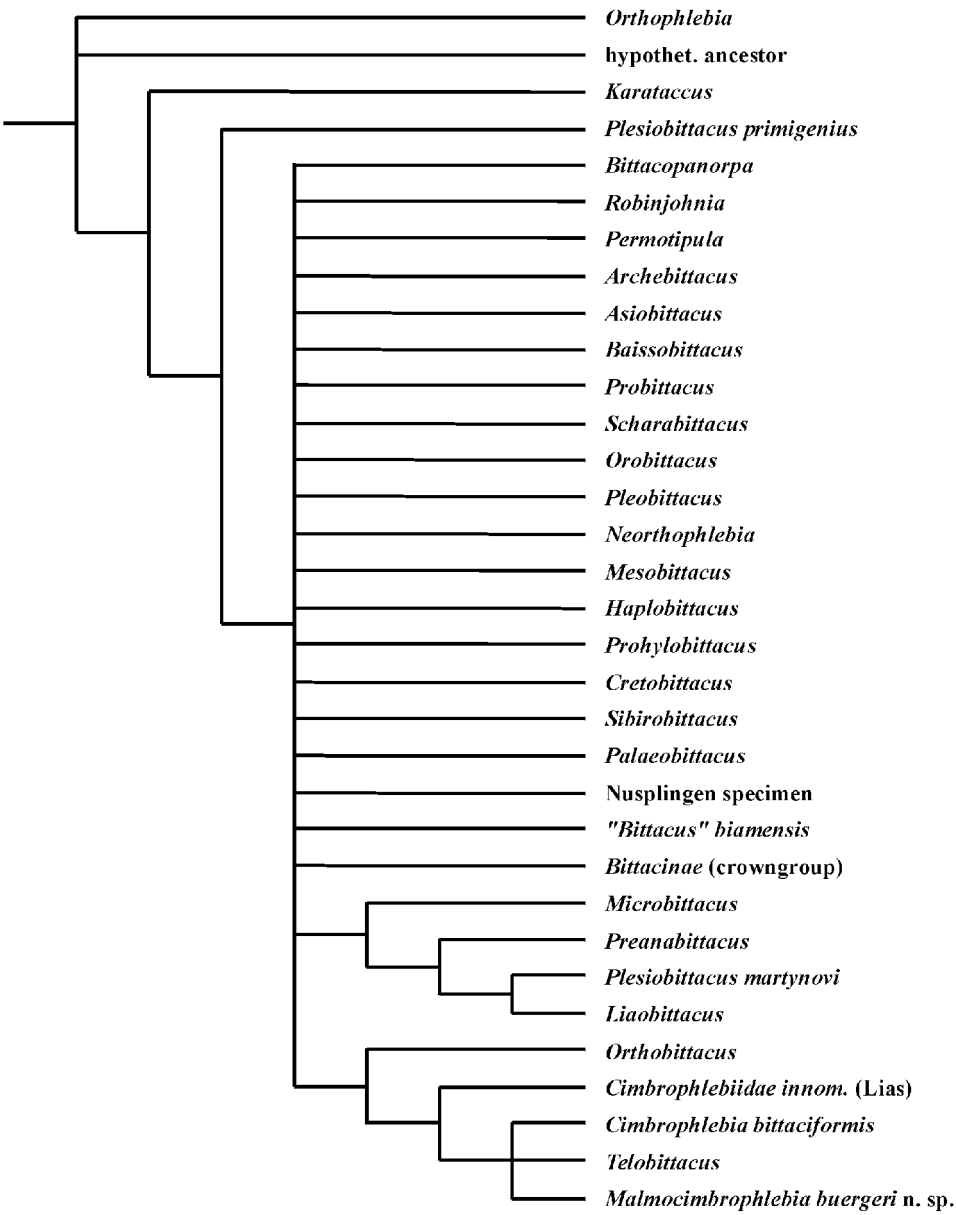

Fig. 8. Strict consensus tree of 2649 most parsimonious trees (20 characters, 88 steps, CI = 0.34, RI = 0.66) calculated with Hennig86 (mhennig*;bb*) and TreeGardener 2.2.

analysis!) we therefore propose the following phylogenetic reclassification of raptiped Mecoptera, which is still rather „conservative“ and preliminary, because of the low phylogenetic significance of many characters:

Raptipediomorpha taxon nov.
- Permotipulidae sensu nov.
  - *Bittacopanorpa* incertae sedis
  - *Permotipula*
  - *Robinjohnia* pos. nov.
- Raptipedia
  - *Karataccus* incertae sedis
  - *Archebittacus* incertae sedis
  - „Plesiobittacidae“ stat. nov. sedis mutabilis
  - Cimbrophlebiidae sedis mutabilis
    - Unnamed genus (Liassic Cimbrophlebiidae) sedis mutabilis
    - *Telobittacus* sedis mutabilis
    - *Malmocimbrophlebia* n. g. sedis mutabilis
    - *Cimbrophlebia* sedis mutabilis
  - Bittacidae sedis mutabilis
    - *Orthobittacus* sedis mutabilis
    - *Parabittacus* sedis mutabilis
    - Taxon innom. sedis mutabilis
      - *Protobittacus* sedis mutabilis
      - *Baissobittacus* sedis mutabilis
      - *Asiobittacus* sedis mutabilis
      - *Neorthophlebia* sedis mutabilis
      - *Pleobittacus* sedis mutabilis
      - *Mesobittacus* sedis mutabilis
      - *Scharabittacus* sedis mutabilis
      - *Probittacus* sedis mutabilis
      - „*Orobittacus*“ (Mesozoic species) sedis mutabilis
      - *Sibirobittacus* sedis mutabilis
      - Taxon innom. sedis mutabilis
        - *Haplobittacus*
        - *Prohylobittacus*
      - *Praeanabittacus* sedis mutabilis
      - *Microbittacus* sedis mutabilis
      - Bittacinae sensu nov. (incl. extant *Orobittacus*) sedis mutabilis
        - *Liaobittacus* sedis mutabilis
        - *Palaeobittacus* sedis mutabilis
        - *Cretobittacus* sedis mutabilis
        - „*Bittacus*“ *biamensis* sedis mutabilis
        - Bittacini (extant genera) stat. nov. sedis mutabilis

List of polarized characters

The coding of *Telobittacus* and the undescribed Liassic Cimbrophlebiidae is based on unpublished drawings of Ansorge (pers. comm.).

1. Raptorial legs with elongated tarsi and a single tarsal claw: no = 0; yes = 1.
2. Wings slender and basally narrowed (subpetiolate): no = 0; yes = 1.
3. Wing length distinctly larger than 25 mm: no = 0; yes = 1.
4. Length of ScP in the forewing (ordered multistate): very long (reaching or surpassing MA-fork) = 0; distinctly longer than half wing length (but not reaching MA-fork) = 1; about half wing length = 2; distinctly shorter than half wing length = 3.
5. RA makes a kink at the basal end of the stigma: yes = 0; no = 1.
6. The stigmal part of RA (beneath the stigma) is extremely curved or kinked: no = 0; yes = 1.
7. Number of crossveins beneath the stigmal part of RA (ordered multistate): none = 0; one = 1; two = 2.
8. Number of terminal branches of RP1 (ordered multistate): three or more (long branches) = 0; two long branches = 1; two very short branches = 2; only one branch = 3.
9. Branching of RP2: symmetrical = 0; asymmetrical = 1.

10. Length of branching of RP2 compared to branching of MA: RP2 fork as long or longer as MA fork = 0; RP2 fork shorter than MP2 fork = 1.
11. Number of branches of MA: two = 0; multiple = 1.
12. Number of branches of MP: three (or more) branches = 0; two branches = 1.
13. Connection between CuA and CuP retained in hindwing: yes = 0; no = 1.
14. Base of CuA (ordered multistate): strongly oblique = 0; weakly oblique = 1; transverse = 2. The state is unknown in *Cretobittacus*, *Karataccus*, and *Microbittacus*, which are only known by the hindwing, and for *Sibirobittacus* of which the wingbase is unknown. Since the CuA is originally branching from CuP (compare the state in *Orthophlebia*), an oblique base probably represents the plesiomorphic state.
15. Distinct oblique veinlet between A1 and A2: absent = 0; present = 1. The derived state is only known from *Orthobittacus abshiricus* and the Liassic Cimbrophlebiidae, while it is absent or unknown in other Raptipedia; the character is not preserved in the other species of the two mentioned genera.
16. Second Anal vein AA2: short and unbranched = 0; long and multibranched = 1.
17. Crossvein that forms the anterior part of „bittacid cross“ between RP2b and MA (unordered multistate): transverse = 0; distinctly oblique = 1; with reversed obliquity = 2; totally absent = 3.
18. Crossvein that forms the posterior part of „bittacid cross“ between MA and MP: present = 0; absent = 1.
19. Both crossveins that form the „bittacid cross“ (ordered multistate): present and non-aligned = 0; present and weakly aligned = 1; present and aligned = 2; one or both crossveins are totally absent = ? (inapplicable). This character is homoplastic and thus not very strong, since a non-aligned ‚bittacid cross“ also occurs as reversal (?) in a few extant Bittacidae (e.g. *Bittacus latipennis*).
20. Longitudinal veins at crossvein junctions (ordered multistate): straight = 0; at least weakly kinked = 1; strongly kinked = 2.

Datamatrix of fossil and extant genera of Raptipedia

Taxa / Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
hypothetical ancestor (outgroup)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
„*Orthophlebia*“ (outgroup)	0	0	0/1	0–1	0	0	0	0	0	0	0	0/1	0	0	0	0	3	1	?	0
Robinjohnia	?	1	0	2–3	1	0	0/1	2	1	0	0	1	0	2	?	0	3	1	?	0
Permotipula	0?	1	0	2	1	0	0/1	3	1	1	0	1	?	0	?	0	3	1	?	0
Bittacopanorpa	?	1	0	3	?	?	?	?	?	?	?	?	?	0?	?	?	?	?	?	?
Plesiobittacus martynovi	?	?	0	0	0	0	2	0	1	0	1	0	?	?	?	?	0	0	0	2
Plesiobittacus primigenius	?	1	0	0	0	0	?	0	1	0	?	?	?	0	?	?	1	?	?	0?
Cimbrophlebia bittaciformis	1	1	1	0	0	0	0	0/1	1	1	0	1	?	?	?	1	1?	0	1?	0
Cimbrophlebiidae n. g. (Lias)	?	1	0–1	0	0	0	0	0	1	0	0	1	?	2	1	1	1	0	2	1
***Malmocimbrophlebia buergeri* n. g. n. sp.**	1	1	1	0?	?	?	?	0/1	?	?	?	?	?	?	?	1	?	?	?	0?
Telobittacus	?	1	?	0	0	0	0	0	1	1	0	1	?	?	?	1	1	1?	?	0
Karataccus	?	1	0	0	?	?	?	?	1	0	0	0	?	?	0	0	0?	?	?	0
Archebittacus	?	1	0	0–1	?	?	?	?	1	0	0	0	?	0	0?	0	3?	1?	?	0
***Parabittacus* (= *Polydicrobittacus*)**	?	1	0	0–1	0	0–1	0	1	1	0	0	0	?	0	0	0	3	1	?	0
Orthobittacus	?	1	1	0	0	0	0	1	1	0	1	0	?	0	1	0	3	1	?	1
Protobittacus liassicus	?	1	0	0–1	0	0	1	1	?	0	0	0	?	0	0	0	1	1?	?	1
Pleobittacus	?	1	0	2	1?	0	1?	1	1	0	0	0?	?	?	0?	0	1	0?	1?	0?
Asiobittacus	?	1	0	3	0	0	1	1	1	0	0	0	?	0	0	0	0	0	0–1	1
***Mesobittacus* (= *Auxobittacus*)**	1	1	0	3	1	0	0	1	1	0	0	0	1	2	0	0	0	0	1	1
***Neorthophlebia* (= *Metaxybittacus*)**	1	1	0	2	0	0	0	1	1	0	0	0	1	0	0	0	1	0	2	1
Probittacus	?	1	0	1	0	1	1	1	1	0	0	0	?	1	0	0	1	0	2	2
Scharabittacus	?	1	0	1	0	1	1	1	1	0	0	0	?	0	0	0	1	1	?	2
***Orobittacus* (fossil)**	?	1	0	2	1	0	0	3	1	0	0	1	1	0	0	0	0	0	1/0	2
Baissobittacus	?	1	0	1	0	0	1	1	1?	0	0	1	1	?	0	0	1	0	2	0
Nusplingen specimen	?	1	0	?	?	?	?	?	?	?	?	?	?	1	?	0	1	0	2	?
***Microbittacus* stat. rest.**	?	1	0	?	0	0	1?	1	0?	0	0	1	1	?	0	0	1	0	1	1–2
Haplobittacus	?	1	0	3	1?	0?	1?	1	1	0	0?	0?	?	?	?	0	2	0	1?	0
Prohylobittacus	?	1	0	3	0	1	1	1	1	0	0	1	?	2	0	0	2	0	2	0–1
Preanabittacus	?	1	0	1	1	0	1	1	1	0	0	1	?	1	0	0	0	0	0	2
Sibirobittacus	?	1	0	1	0	1	1	1	1	0	0	1	?	?	?	?	1	0	2	1–2
Liaobittacus	1	1	0	0	0	1	2	1	1	0	0	1	1	1	0	0	0	0	0	0
Cretobittacus	?	1	0	1	0	1	2?	1	1	0	0	1	1	?	0?	0	1	0	2	2
Palaeobittacus	?	1	0	2	0	1	2	1	1	0	0	0?	?	2	0	0	1	0	2	1
„*Bittacus*“ *biamensis*	?	1	0	?	0	1	2	1	1	0	0	1	1	?	1?	0	1	0	2	2
crowngroup Bittacinae	1	1	0/1	1/2	0	1	2/1	1–3	1	0	0	1	1	2/1	0	0	1	0	2/0	1/2

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