

New hymenopterous insects (Insecta: Hymenoptera) from the Lower Toarcian (Lower Jurassic) of Germany

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With 13 figures

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Abstract: Three new hymenopteran species are described from different Lower Toarcian localities of Northern Germany. *Xyelula benderi* (Sepulcidae, Symphyta) is based on three isolated fore-wings. Wingless bodies of six females and one male are tentatively attributed to this species. *Brigittepterus brauckmanni* n. g. n. sp. and *Thilopterus lampei* n. g. n. sp. are representatives of Ephialtitidae (Apocrita). A second specimen of *Liadobracona raduhna* ZESSIN 1981, previously only known from Dobbertin, is recorded from Schandelah. *Symphytopterus liasinus* (ZESSIN 1985) is revised, considering *Sippelipterus* ZESSIN 1985 as a new junior synonym of *Symphytopterus* RASNITSYN 1975. The extreme rarity of Hymenoptera in the Lower Toarcian marine taphocoenoses of Middle Europe may be the result of unknown taphonomic processes.

Zusammenfassung: Drei neue Hymenopteren Arten werden aus dem Unteren Toarcium von Deutschland beschrieben. *Xyelula benderi* n. sp. (Symphyta: Sepulcidae) wird auf der Basis von drei isolierten Vorderflügeln beschrieben. Flügellose Körper von sechs weiblichen und einem männlichen Tier aus Dobbertin, Schandelah und Mistelgau werden unter Vorbehalt zu dieser Art gerechnet. *Brigittepterus brauckmanni* n. g. n. sp. (Dobbertin) und *Thilopterus lampei* n. g. n. sp. (Schandelah) sind Vertreter der Ephialtitidae (Apocrita). Ein zweites Exemplar von *Liadobracona raduhna* ZESSIN 1981, bisher nur aus Dobbertin bekannt, wird aus Schandelah beschrieben. *Symphytopterus liasinus* (ZESSIN 1985) aus Schandelah wird revidiert, danach ist *Sippelipterus* ZESSIN 1985 ein jüngeres Synonym von *Symphytopterus* RASNITSYN 1975. Neben einer generellen Seltenheit von Hymenopteren im Oberen Lias dürfte ihre Seltenheit in den marinen Insekten-Taphozoenosen des Unteren Toarcium Mitteleuropas auf bisher unbekannte taphonomische Ursachen zurückzuführen sein.

Introduction

Hymenopterous insects entered the fossil record in the Upper (or perhaps the Middle) Triassic of Australia, South Africa and Central Asia, and became diverse and not extremely rare toward the upper Lower Jurassic (RIEK 1955, RASNITSYN 1980, ANDERSON et al. 1998, SCHLÜTER 2000). It is paradoxical that not a single hymenopterous fossil occurs in the huge and comparatively well studied collections of Lower Toarcian insects from Northern Germany that were accumulated in various museums at the beginning of the twentieth century (HANDLIRSCH 1906-08, 1939; BODE 1953).

Less than twenty years ago the first two fossil hymenopterans were described from Dobbartin and Schandelah, both belonging to new genera of extinct Ephialtitidae (ZESSIN 1981, 1985). Since that time some thousand fossil insects were collected in various Lower Toarcian localities of Germany. Several additional hymenopterans were recorded from this material that has considerably enlarged our knowledge of the earlier Jurassic hymenopterans in Europe.

The material presented here was collected in four Lower Toarcian localities in Germany: Dobbartin (Mecklenburg), Klein Lehmhagen near Grimm (Western Pomerania), Schandelah near Braunschweig (Lower Saxony) and Mistelgau in Franconia (for details see ANSORGE 1996, 2002). The fossils are preserved in carbonate concretions which are intercalated either in marine clay of the "Green Series" or Posidonia shale of the *falci-ferum*-zone.

The insects of Grimm and Dobbartin lived on the Scandinavian mainland or on offshore islands in the north. The insects of Schandelah are derived either from the Bohemian or the Rhenic Massifs and the insects of the Mistelgau taphocoenosis lived on the Bohemian one.

Systematics

Suborder	Siricina BILLBERGH 1820 (LATREILLE 1802)
Superfamily	Cephoidea NEWMAN 1834
Family	Sepulcidae RASNITSYN 1968
Subfamily	Xyelulinae RASNITSYN 1993
Genus	<i>Xyelula</i> RASNITSYN 1969

Xyelula benderi n. sp.

Fig. (1-7)

Derivatio nominis: In honour of the collector of the holotype, Mr. Bodo Bender, Elmenhorst (Nordvorpommern, Germany).

Holotypus: Isolated wing LGB 112 (part and counterpart) in the collection Bodo Bender, Elmenhorst, later Museum für Naturkunde der Humboldt Universität, Berlin (Palaeontological Institute).

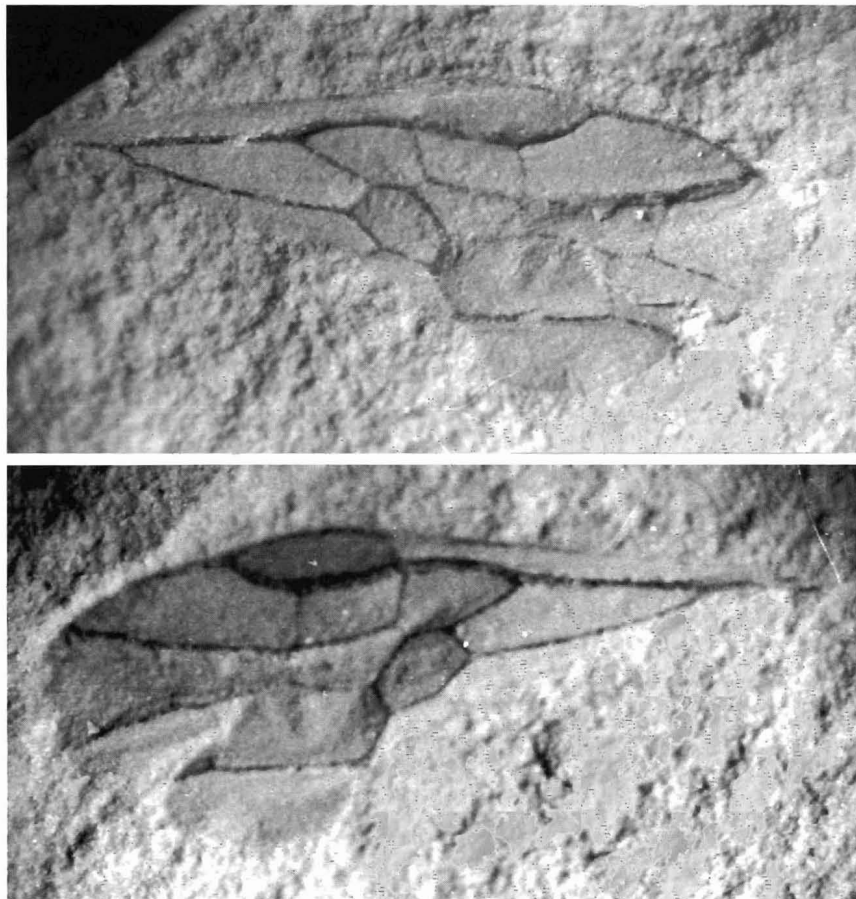


Fig. 1. *Xyelula benderi* n. sp. - holotype LGB 112, isolated fore-wing Lower Toarcian of Grimmen Western Pomerania, Germany).

Locus typicus: Clay pit Klein Lehmhagen in the vicinity of Grimmen (Western Pomerania/NE-Germany).

Stratum typicum: Limestone concretions within the Lower Toarcian "Green Series", ammonite zone of *Harpoceras falciferum*.

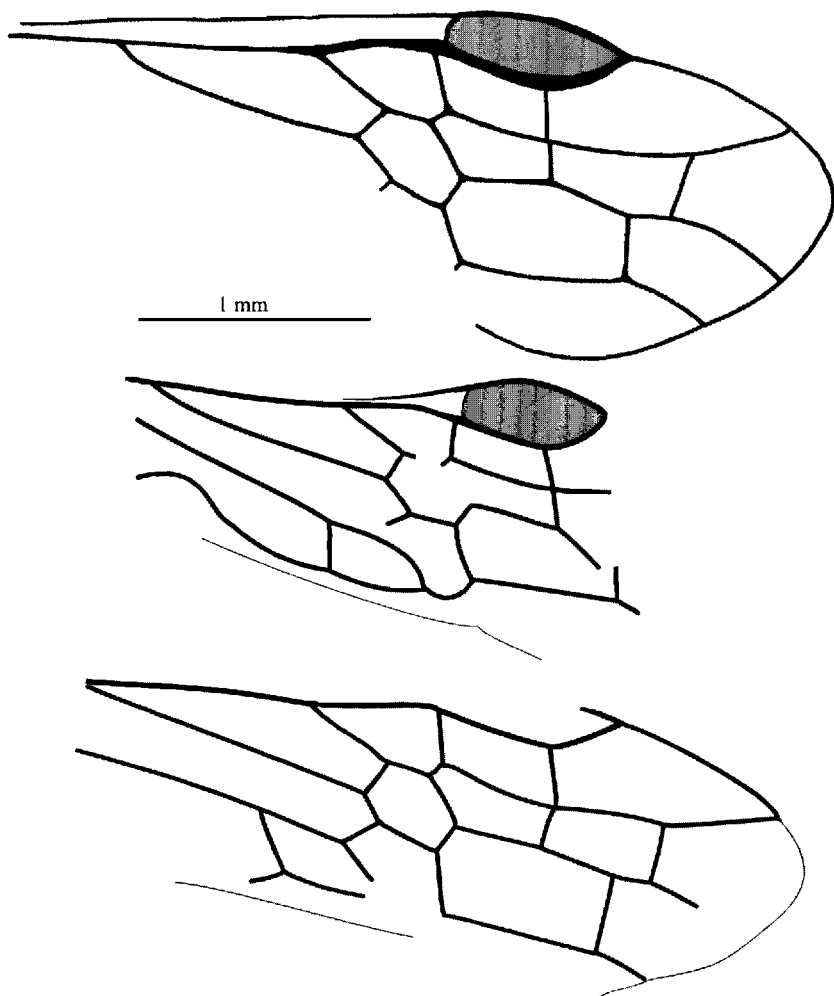


Fig. 2. *Xyelula benderi* n. sp. - isolated fore-wings. **A:** Holotype LGB 112 Lower Toarcian of Grimmen (Western Pomerania, Germany). **B:** Paratype LD 2468, Lower Toarcian of Dobbartin (Mecklenburg, Germany). **C:** Paratype LDA 445, Lower Toarcian of Dobbartin (Mecklenburg, Germany).

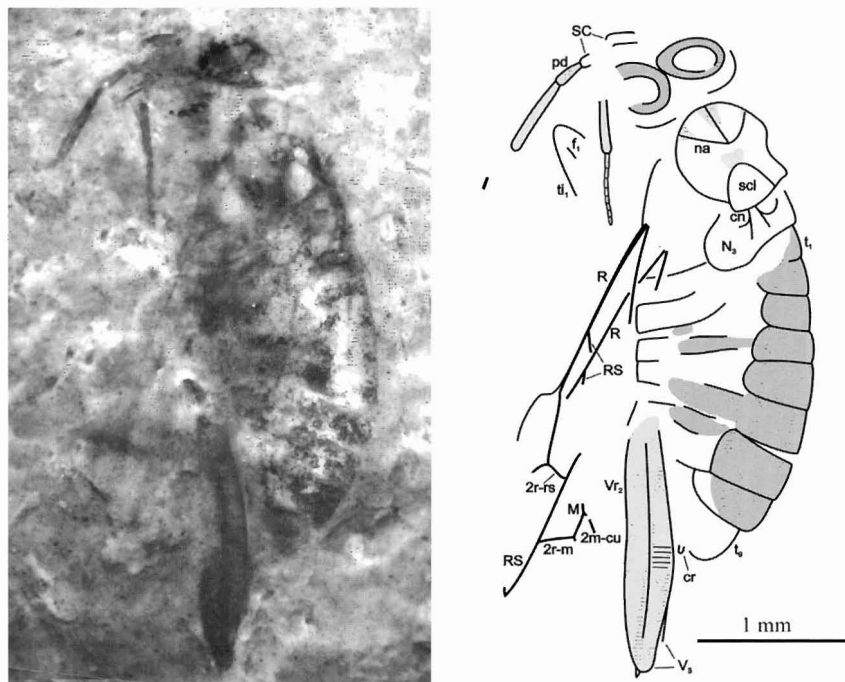


Fig. 3. *Xyelula benderi* n. sp. - female. LDA 515, Lower Toarcian of Dobbertin (Mecklenburg, Germany).

Paratypes: Isolated fore-wings LDA 445 1/2 (coll. J. Ansorge) and LD 2468 1/2 (coll. W. Zessin) both from the former clay pit of Schwinz near Dobbertin (Mecklenburg), later Museum für Naturkunde der Humboldt Universität, Berlin (Palaeontological Institute).

Additional material: Two isolated female bodies from Schandelah (PIN 4779/1-2), collected by Yuri A. Popov (PIN Moscow) in 1986, one male body coll. Thilo Lampe, three isolated female bodies from Dobbertin (coll. J. Ansorge LDA 1027 1/2, LDA 1102, LDA 515 with incomplete wings) and one from Mistelgau (coll. J. Ansorge M 162), later Museum für Naturkunde der Humboldt Universität, Berlin (Palaeontological Institute).

Diagnosis: The new species differs clearly in wing venation from the three other species in the genus, the type *X. hybrida* RASNITSYN 1969 from the Upper Jurassic of Kazakhstan *X. xiphophora* (RASNITSYN 1969) of the same origin, and *X. bakharensis*

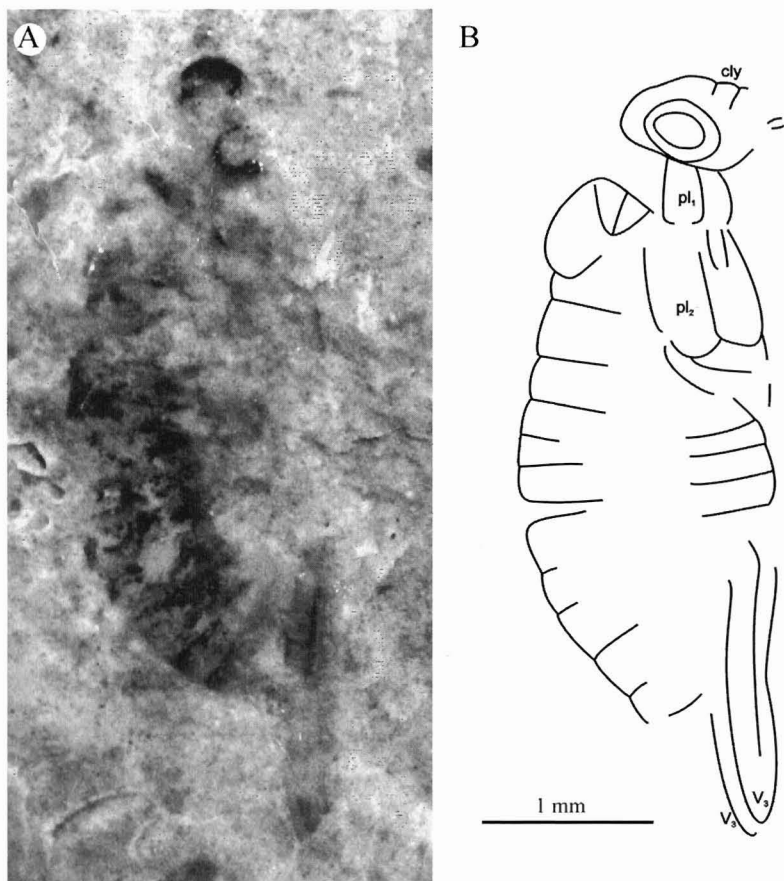


Fig. 4. *Xyelula benderi* n. sp. - female. Lower Toarcian of Dobbertin (Mecklenburg, Germany). A: LDA 1102. B: LDA 1027.

RASNITSYN 1993 from the Middle Jurassic of Mongolia (RASNITSYN 1993), in that the crossveins 2r-rs and 2r-m coincide on RS or almost so (in the type species 2r-rs is much apicad of 2r-m; in the two other species the reverse is true). In body structure, assuming that the wings and the bodies described below do belong to the same species, the new species differs from *X. xiphophora*, the only other known for the female sex and antennal structure, in that the flagellum is short, 8- instead of 11-segmented, and the ovipositor is shorter (2 mm in contrast to 3.3 mm in

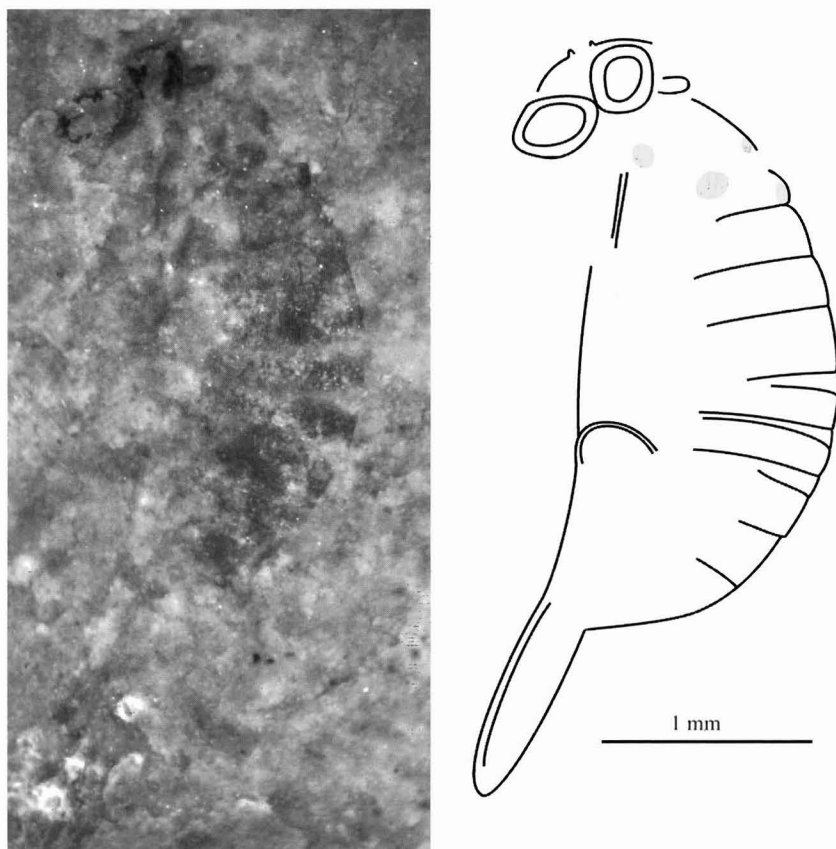


Fig. 5. *Xyelula benderi* n. sp. - female. M 162, Lower Toarcian of Mistelgau (Frankonia, Germany).

xiphophora), extending beyond the abdominal apex for less than half its length (more than half in *xiphophora*), and more tapering toward the apex.

Description: Female. Colour predominantly light, internal ocular apodemes ("eye rings", abdominal terga and, to a lesser extent, antenna except scape, mesonotal spots (along medial mesoscutal sulcus, at anterior ends of notauli and before scutellum) and ovipositor darker. No surface sculpture discernible. Eyes of moderate size (0.4 mm), otherwise no taxonomically

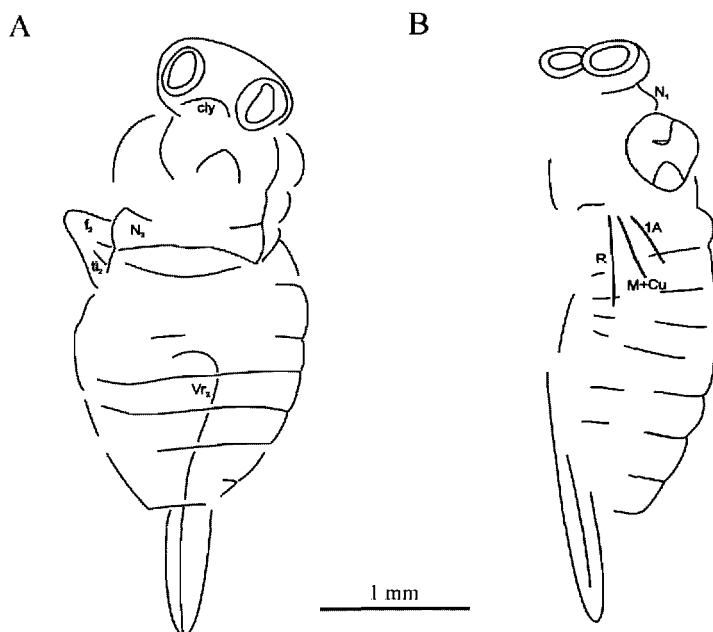


Fig. 6. *Xyelula benderi* n. sp. - female. Lower Toarcian of Schandelah (Lower Saxony, Germany). A: PIN 4779/2. B: PIN 4779/1.

important body structures discernible except ovipositor. Fore-wing with long and wide pterostigma, 2r-rs issuing beyond its midlength. First section of RS as long as, or slightly shorter than, cell 1mcu. RS + M not reaching midlength of cell 1mcu. 2r-rs and 2r-m reaching RS at the same point or almost so. 3r-m reaching RS at about the same distance from both 2r-m and apex of cell 3r. 1m-cu about half as long as section of Cu distad of it. 2m-cu reaching M well beyond midlength of cell 3rm. Crossvein cu-a variable in joining cell 1mcu before, at, or beyond its midlength. Ovipositor about 0.6 times as long as forewing, extending beyond abdominal apex for about 0.45 times its length, moderately wide (about 0.1 times as wide as long), parallel-sided to about 0.6-0.7 times its length, then symmetrically tapering toward rounded apex. Length of body without ovipositor 3.2 mm, of fore-wing 3.3-3.6 mm, of ovipositor 1.9-2.0 mm.

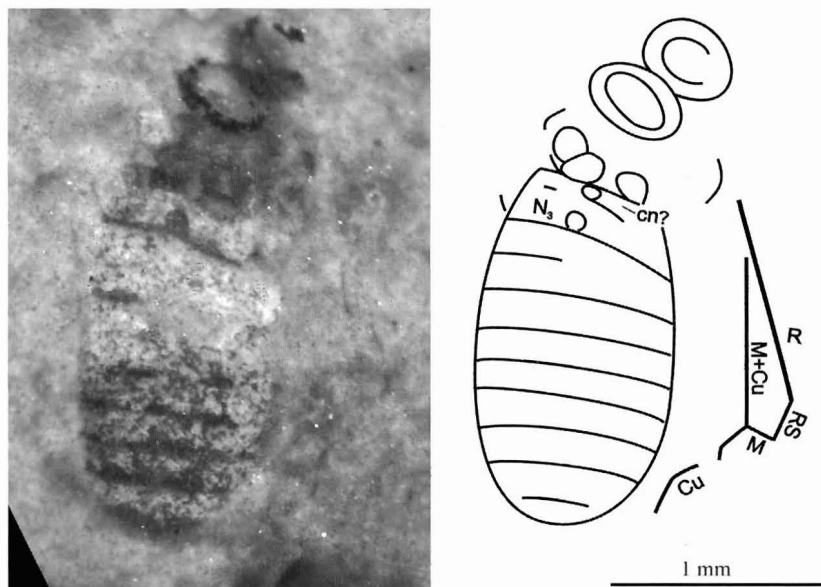


Fig. 7. *Xyelula benderi* n. sp. - male. coll. Thilo Lampe, Lower Toarcian of Schandelah (Lower Saxony, Germany).

Male (based on incomplete body with badly deformed thorax and partial fore-wing) differing from female, besides absence of ovipositor, in its small size (common in sawflies), with abdomen, as preserved, ca. 1.4 mm long (1.8-2.3 mm in females). A visible difference in wing venation, viz., comparatively short 1st section of RS, may be the result of wing deformation.

Remarks: The ten specimens listed above are attributed to the same species because of the essential similarity of the three wing impressions, because the six wingless female bodies agree with the wings in size, and because the only available male fossil is similar to females in general appearance, comparable in size (identical in the case of ocular discs) and has a similar colour pattern. The great similarity of the bodies to *X. xiphophora* in their basic features and the general appearance of the body and ovipositor also indicate that they belong to *Xyelula*.

Suborder	Vespina LAICHARTING 1781
Superfamily	Ephialtitoidea HANDLIRSCH 1906
Family	Ephialtitidae HANDLIRSCH 1906
Subfamily	Ephialtitinae HANDLIRSCH 1906

Genus *Thilopterus* n. g.

Species typica: *Thilopterus lampei* sp. nov. from the Lower Toarcian of Germany.

Derivatio nominis: In honour of Mr. Thilo Lampe, Vechelde, who collected the material in which JA found the type specimen.

Diagnosis: Fore-wing with complete set of crossveins (2r-rs, 2r-m, 3r-m, 1m-cu, 2m-cu, cu-a, 1a-2a) except lacking even rudimentary 1r-rs. First section of RS almost as long as that of M, directed posteroapically, almost aligned with RS + M. Crossvein cu-a coinciding with base of cell 1mcu. 2A complete (possibly except basally).

Remarks: The new genus belongs to the subfamily Ephialtitinae because of the proximal position of cu-a. Within the subfamily and the family in general it is uniquely plesiomorphic in having the basal section of RS both long and directed posteroapically, thus approaching the state recorded in *Proapocritus* RASNITSYN (Karatavidae) (RASNITSYN 1975). Other Ephialtitidae have this section either short (*Brigittepterus* n. g., *Parephialtites* RASNITSYN), or short and subvertical to R (*Stephanogaster* RASNITSYN and *Asiephialtites* RASNITSYN), or directed posterobasally. The long 2A is unique in Ephialtitinae.

Thilopterus lampei n. g. n. sp.

(Fig. 8)

Derivatio nominis: The species is also named after Mr. Thilo Lampe, Vechelde.

Holotypus: Isolated fore-wing (coll. Thilo Lampe, Pt 60/1-20 Schandelah/bore), later Museum für Naturkunde der Humboldt Universität, Berlin (Palaeontological Institute).

Locus typicus: Former marl pit of Schandelah near Braunschweig (Lower Saxony).

Stratum typicum: Limestone *boreale*-concretions within the Lower Toarcian Posidonia shale, ammonite zone of *Harpoceras falciferum*.

Diagnosis: As for the genus.

Description: Fore-wing 2.9 mm long, with RS + M reaching 1m-cu and about 1.5 times as long as 1m-cu. 2r-rs meeting pterostigma near its mid-length, meeting M slightly before 2r-m. Cells 2rm and 3rm of subequal length, 3rm 1.5 times as long as high. 2r-m and 3r-m nearly straight, sub-

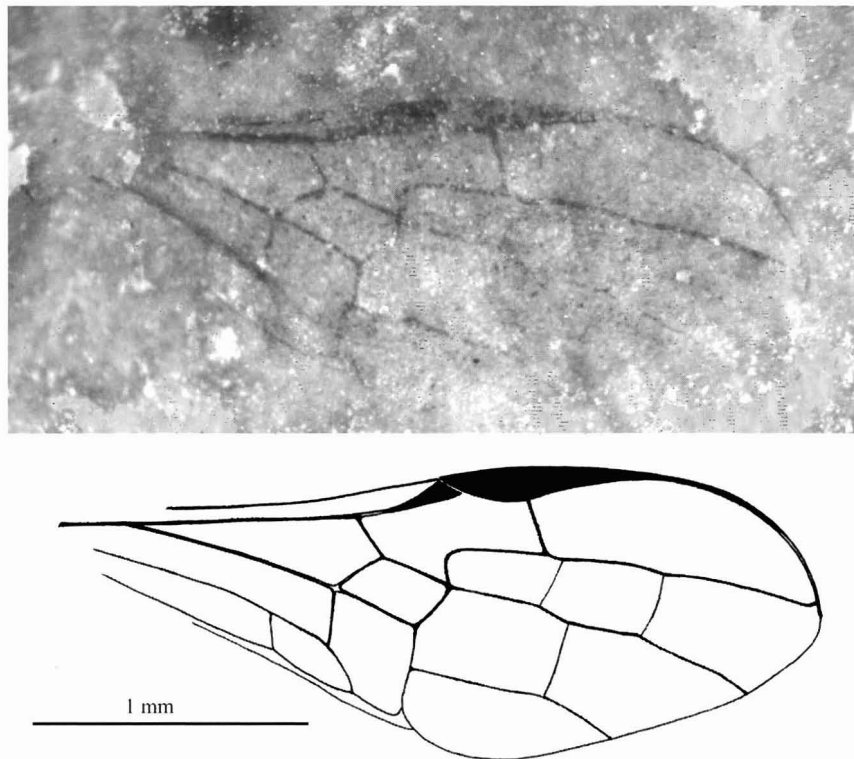


Fig. 8. *Thilopterus lampei* n. g. n. sp. - isolated fore-wing (Pt 60/1-20 Schandelah/bore), holotype Lower Toarcian of Schandelah (Lower Saxony, Germany).

vertical, 3r-m 1.5 times as distant from apex of cell 3r as from 2r-m. 2m-cu meeting M at about 0.35 times length of cell 3rm.

Subfamily Symphytopterinae RASNITSYN 1980

Genus *Brigittepterus* n. g.

Species typica: *Brigittepterus brauckmanni* n. g. n. sp. from the Lower Toarcian of Germany.

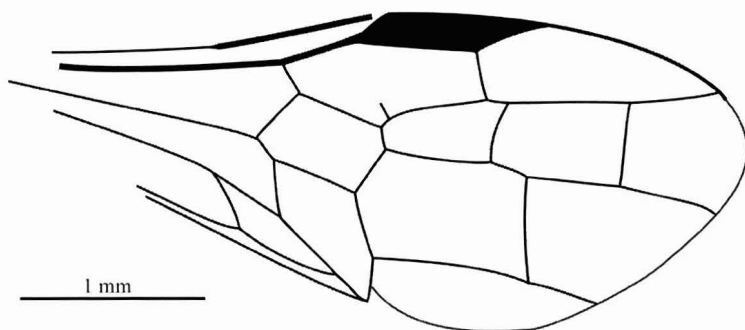
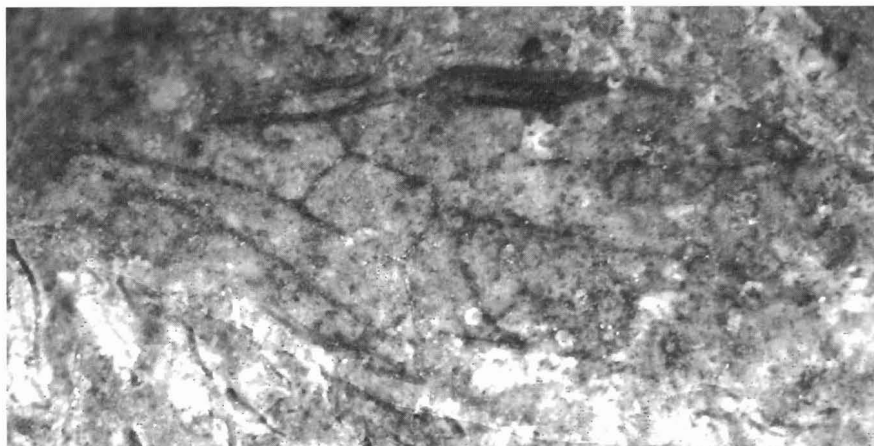


Fig. 9. *Brigittepterus brauckmanni* n. g. n. sp. - isolated fore-wing. holotype LD 2453 1/2, Lower Toarcian of Dobbertin (Mecklenburg, Germany).

Derivatio nominis: In honour of Mrs. Brigitte Brauckmann, Clausthal-Zellerfeld.

Diagnosis: Fore-wing with complete set of crossveins (2r-rs, 2r-m, 3r-m, 1m-cu, 2m-cu, cu-a, 1a-2a and rudimentary 1r-rs). First section of RS short, directed posteroapically, almost aligned with RS + M. Crossveins 2r-rs and 3r-m subvertical, cu-a distant from base of cell 1mcu by about 0.3 times its length. 2A complete (possibly except basally).

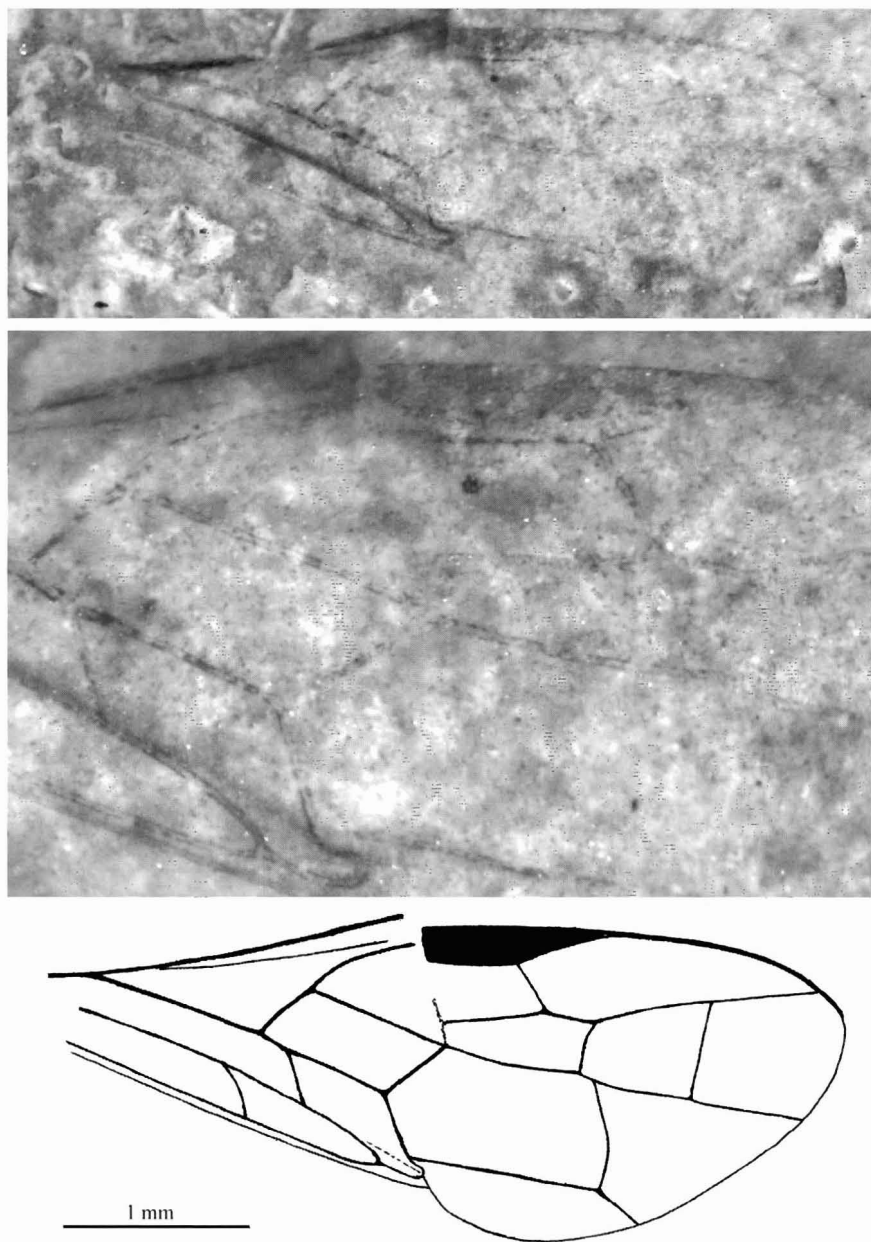


Fig. 10. *Symphytopterus liasinus* (ZESSIN 1985) - isolated fore-wing. LS 18 Lower Toarcian of Schandelah (Lower Saxony, Germany). A: Holotype. B: Detail of 1rs-cell. C: Drawing.

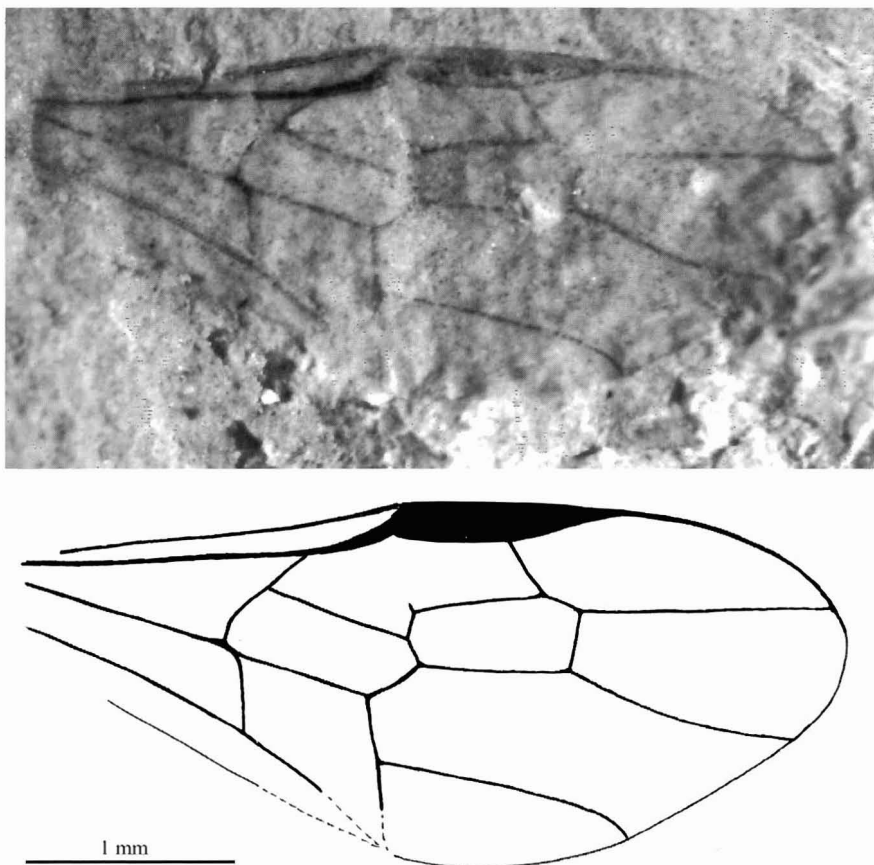


Fig. 11. *Liadobracona raduhna* ZESSIN 1981. - isolated fore-wing, holotype LD 1127, Lower Toarcian of Dobbertin (Mecklenburg, Germany).

Remarks: The new genus belongs to the subfamily Symphytopterinae because of the distal position of cu-a. Its complete venation, including the well developed 2A, approaches only that of *Karataus* RASNITSYN 1977, *Microphialtites* RASNITSYN 1975, and *Symphytopterus* RASNITSYN 1975 (= *Sippelipterus* ZESSIN 1985) (cf. RASNITSYN 1975, 1980; ZESSIN 1985). Unlike these and all other Ephialtitidae (except *Stephanogaster* RASNITSYN

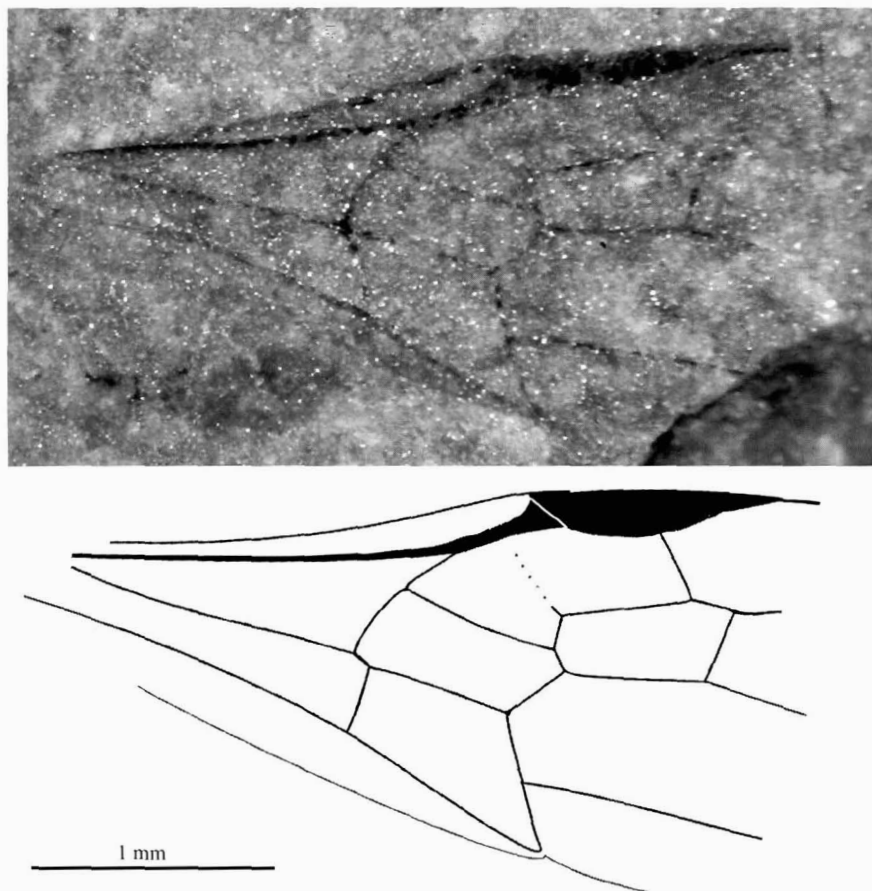


Fig. 12. *Liadobracona raduhna* ZESSIN 1981. - isolated fore-wing. LSV 1-1, Lower Toarcian of Schandelah (Lower Saxony, Germany)

1975, *Asiephialtites* RASNITSYN 1975, *Parephialtites* RASNITSYN 1975 and *Thilopterus* gen. nov.) this new genus has the base of RS directed postero-apically rather than posterobasally. This new genus differs from the last four genera in the more distal position of cu-a with respect to the fork of M + Cu. It is plesiomorphic within the family in the majority of its character states. Moreover, the first section of RS almost aligned with RS + M is similar to

Karatavidae, like *Thilopterus* n. g.. The only undoubted autapomorphy of the genus is the short first section of RS.

Brigittepterus brauckmanni n. g. n. sp. (Fig. 9)

Derivatio nominis: The species is named after the palaeontologist Prof. Dr. Carsten Brauckmann, Clausthal-Zellerfeld.

Holotypus: Isolated fore-wing LD 2453 1/2 in the collection Wolfgang Zessin, Jasnitz, later Museum für Naturkunde der Humboldt Universität, Berlin (Palaeontological Institute).

Locus typicus: Former clay pit of Schwinz near Dobbertin (Mecklenburg).

Stratum typicum: Limestone concretions within the Lower Toarcian "Green Series", ammonite zone of *Harpoceras falciferum*.

Diagnosis: As for the genus.

Description: Fore-wing, 4.0 mm long, with first section of RS half as long as first section of M. RS + M distant from lm-cu by about 0.3 times length of 1m-cu. 2r-rs meeting pterostigma at about 0.6 times its length, meeting M slightly before 2r-m. Cells 2rm and 3rm of subequal length, both less than twice as long as high. 3r-m separated from apex of cell 3r by slightly less than length of 3r-m. Cell 1mcu about 1.5 times as long as high, with its sides subparallel. 2m-cu meeting M at about 0.3 times length of cell 3rm.

Genus *Symphytopterus* RASNITSYN 1975

* 1975 *Symphytopterus*. – RASNITSYN: 42.

1985 *Sippelipterus*. – ZESSIN: 133 syn. nov.

Species typica: *Symphytopterus nigricornis* RASNITSYN 1975 – Upper Jurassic of Karatau (Kazakhstan).

Remarks: Re-examination of the holotype of *Sippelipterus liasinus* ZESSIN 1985 suggest some minor changes of the original drawing of ZESSIN (1985) which concern the shape of cell 1rs and the partially reduced 1r-rs cross-vein. Because of their identical fore-wing venation, *Sippelipterus* ZESSIN 1985 should be regarded as a junior synonym of *Symphytopterus* RASNITSYN 1975.

Symphytopterus liasinus (ZESSIN 1985) comb. nov. (Fig. 10)

v* 1985 *Sippelipterus liasinus*. – ZESSIN: 133, fig. 2; pl. 1-2.

Holotypus: Isolated fore-wing LS 18/2-1 (coll. Zessin) Museum für Naturkunde der Humboldt Universität, Berlin (Palaeontological Institute).

Locus typicus: Former marl pit of Schandelah near Braunschweig (Lower Saxony).

Stratum typicum: Limestone concretions within the Lower Toarcian Posidonia shale, ammonite zone of *Harpoceras falciferum*.

Ephialtitidae incertae subfamiliae

Genus *Liadobracona* ZESSIN 1981

Species typica: *Liadobracona raduhna* ZESSIN 1981.

Remarks: *Liadobracona* cannot be assigned to a subfamily with any certainty, because its ovipositor length (short in Symphytopterinae, long in Ephialtitinae) is unknown, and the position of cu-a (distad of the fork of M + Cu by less than 0.3 times its length) is borderline between Symphytopterinae (0.5 times its length or more apicad) and Ephialtitinae (0.25 times length of cu-a or less apicad). *Liadobracona* differs from all other Ephialtitidae except *Parephialtites* RASNITSYN in lacking both 3r-m and 2m-cu, and differs from *Parephialtites* in having the first section of RS directed postero-basally and so aligned with the first section of M, in having cu-a shifted distad of the fork of M + Cu, and in lacking an enclosed anal cell.

Liadobracona raduhna ZESSIN 1981

(Fig. 11-12)

v* 1981 *Liadobracona raduhna* n. s. - ZESSIN: 714, pl. 1.

1985 *Liadobracona raduhna* ZESSIN, 1981. - ZESSIN: 134, Fig. 3.

Holotypus: Isolated fore-wing LD 1127 (coll. Zessin) Museum für Naturkunde der Humboldt Universität, Berlin (Palacontological Institute).

Additional material: Isolated fore-wing LSV 1-1, former marl pit in Schandelah near Braunschweig (Lower Saxony, Germany), housed in the collection of Bernd-Wolfgang Vahldiek (Böhme), later Zoological Museum of University of Göttingen, Germany.

Description: Incomplete fore-wing, 3.2 mm long as preserved, supposedly 4.2 mm life size; with RS + M nearly 1.5 times closer to base of RS than to base of M; 2r-rs meeting pterostigma near its midlength, meeting M as far from 2r-m as about half length of 2r-rs; 1m-cu meeting M as far from RS + M apex as almost 0.4 times its length, meeting Cu as far from distal Cu kink as almost its length; cu-a meeting Cu as far from M as 0.3 its length; rudiment of 1r-rs short but distinct.

Discussion: The second specimen from Schandelah has the same size and identical venation as the type from Dobbertin.

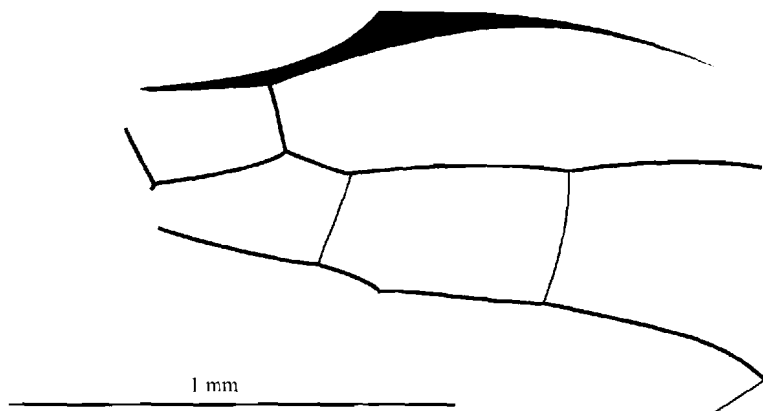


Fig. 13. Ephialtitidae incertae sedis. - fore-wing fragment. LDA 778, Lower Toarcian of Dobbertin (Mecklenburg, Germany).

Ephialtitidae incertae sedis

(Fig. 13)

Material: Apical part of an isolated fore-wing from the Lower Toarcian of Dobbertin, LDA 778 (coll. Ansorge) later Museum für Naturkunde der Humboldt Universität, Berlin (Palaeontological Institute).

Description: Fore-wing apical fragment 1.4 mm long. Preserved are the two radial and three medial cells, with 1 r-rs (incomplete but long), 2 r-rs, 2 r-m, 3 r-m present and position of 2 m-cu indicated by kink of M.

Remarks: Of the Ephialtitidae found in the German Liassic, the fragment fits both, *Symphytopterus* and *Brigittepterus*, but is more similar to the latter because of the presence of 1 r-rs. However, the similarity is not conclusive because the fragment does not show enough details to place it taxonomically with any certainty.

Discussion

The Lower Toarcian hymenopteran fauna of Germany is not diverse, with only five genera in two families known up to now.

The sawfly *Xyelula benderi* is present in all major Lower Toarcian insect localities of Germany and is one of the oldest representatives of Sepulcidae. Only *Sogutia liassica* from the lower Lower Jurassic of Soguty, Issyk Kul Lake in Kirghizia, is older. Recent sawfly species often strictly depend on a particular host plant, so it can be supposed that the host plant of *X. benderi* was also widespread. On the other hand, differences in the hemipterous plant sucking insects of Grimmen, Dobbartin and Schandelah can probably be explained by the presence of different host plants in the northern and southern source areas of the insects (ANSORGE 2002).

The suborder Vespina (= Apocrita) entered the fossil record in the Liassic, and the four species in four genera of Ephialtitidae, are among the oldest, if not the oldest, apocritans. Indeed, only two other apocritans are comparable in age, viz. *Proapocritus praecursor* RASNITSYN 1975 from Sagul in Kirghizia and *Cleistogaster buriatica* RASNITSYN 1975 from Novospasskoye in Transbaikalia. However, their stratigraphic position cannot yet be specified more precisely than upper Lower or lower Middle Jurassic (RASNITSYN 1975); they may actually be older, younger or of the same age as those from the German Liassic.

It is of interest that, in spite of their age, the German Liassic Ephialtitidae are not particularly archaic. Of the four genera recorded, only two (*Brigittepterus* and *Thilopterus*) have a relatively basal position within the family because of the complete venation combined with the plesiomorphic position of the first section of RS. *Symphytopterus* is moderately advanced (venation is complete but the position of the first section of RS is apomorphic), while *Liadobracona* is highly advanced because of its reduced venation. However, the comparatively small size of these fossils (fore-wing 2.9-4.4 mm long) makes all of them, even the venationally plesiomorphic *Brigittepterus* and *Thilopterus*, advanced in that respect. This is because the majority of Ephialtitidae, like their probable ancestral taxa, Karatavitidae and siricoid woodwasps, are generally larger.

The apparently low diversity of hymenopterans in the Lower Toarcian is also reflected in the marine taphocoenoses. In Grimmen only one hymenopteran wing was detected among ca. 3000 insect remains [0.033 %]. From Dobbartin eight hymenopterans (three species) are known out of ca. 6700 insects [0.12 %]. Six specimens (four species) were recorded in Schandelah of about 3000 insects [0.2 %]. HENROTAY et al. (1998) mentioned the presence of Hymenoptera in the Lower Toarcian of Bascharage (Luxembourg), but according to NEL (pers. communication), there is only one fragmentary hymenopteran wing in 2000 insects from Luxembourg.

The low percentage of Hymenoptera in the Lower Toarcian marine taphocoenoses is hard to explain. ANSORGE (1996) stated that the fossil record reflects the actual rarity of Hymenoptera in the Lower Jurassic biota. How-

ever, it is possible that unknown selective taphonomic processes reduced the number of hymenopterans considerably before they were buried in the Lower Toarcian taphocoenoses.

There are two other Mesozoic and one Cainozoic marine insect taphocoenoses where hymenopterans are absent or only present with low diversity. In the Lower Liassic (Sinemurian) of Dorset (England) no hymenopterans have yet been recorded (WHALLEY 1985). In the rich material from the Upper Jurassic (Lower Tithonian) Solnhofen lithographic limestone only species of *Myrmecium* WESTWOOD 1854 (Pseudosiricidae HANDLIRSCH 1906) have been found.

In the Lower Tertiary Fur Formation (Lower Palaeocene/Upper Eocene) of Denmark, hymenopterans are mostly represented by female Ichneumonidae (RUST 1990, ANSORGE 1993). Other taxa are present, although with extremely low diversity. The predominance of female ichneumonids was explained by their active dispersion flights over the sea (ANSORGE 1993). In the Upper Palaeocene Ølst Formation (Denmark) winged ants (*Pachycondyla rebekkae* RUST & ANDERSEN 1999) are quite common, which was explained by active migration, associated with mating and/or colony founding swarms dominated by females (RUST & ANDERSEN 1999). Hence it seems likely that hymenopterans, if they were not victims of their own active flights over the sea, were part of the aerial plankton. The predominance of female hymenopterans in marine taphocoenoses seems also to be true in the Upper Liassic of Germany, where all but one of the hymenopteran bodies are females of *Xyelula benderi*.

The low number of hymenopterans in the Upper Liassic of Germany is in contrast to their abundance in various Mesozoic assemblages of non-aquatic (allochthonous) insects in limnic-lacustrine sediments. The hymenopteran percentage varies from 0.4 % to 5 % in some rich Asian localities of the former Soviet Union (RASNITSYN, 1980, table 4):

- Middle - Upper Triassic of Dzhayloucho (Kirghizia) - 0.4 %
- Lower Liassic (Sinemurian) of Sogyuty & Kyzyl-Kiya (Kirghizia) - 0.6 %
- Lower - Middle Jurassic of Sagul (Kirghizia) - 0.6 %
- Lower - Middle Jurassic of Novospasskoye (Transbaikalia, Russia) - 2.6 %
- Upper Jurassic of Karatau (Kazakhstan) - 2.5 %
- Lower Cretaceous of Baissa (Transbaikalia, Russia) - ca. 5 %
- Lower Cretaceous of Unda & Daya (Transbaikalia, Russia) - 0.7 %
- Upper Cretaceous (Turonian) of Kyzyl Zhar (Kazakhstan) - 2.0 %

BECHLY (1998) recognized 2 % Hymenoptera in the non-marine Lower Cretaceous Santana Formation of Brazil. In the Lower Barremian of Montsec (Spain) the percentage of Hymenoptera is considerably higher, about 7 % (personal observation of J. A.).

From the above, it is evident that the low percentage of hymenopterans in the German Upper Liassic insect assemblages might result, at least in part, from its marine origin. This is not the case with their generally small body size, because in other marine assemblages (e.g., Solnhofen and Ølst) hymenopteran fossils are often large.

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