FIRST RECORDS OF FOSSIL TREMECINE
HYMENOPTERANS

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ABSTRACT. Two Hymenoptera, from the Upper Oligocene of Enspel (Germany) and the Upper Pliocene of Willershausen (Germany), are described and their systematic position is discussed. The fossil from Enspel shows parts of the body and almost the complete wing venation. After analysis of the phylogeny of Tremecinae (Siricidae) it could be placed near *Eriotremex* and *Afrotremex*. The specimen from Willershausen has only the apical part of one forewing preserved and belongs to *Tremex*.

THE earliest representatives of hymenopterous insects are from the Triassic of Australia (Riek 1955) and Russia (Rasnitsyn 1980, 1988). They are exclusively members of the Xyelidae. Only in the Jurassic do more hymenopterous taxa (Rasnitsyn 1988) appear. Many of these belong to the Siricidae or their stem-group. One of the oldest records of a stem-group member of the Siricidae is that of *Sinosirex* Hong, 1975 from the Upper Jurassic or Lower Cretaceous of China (Königsmann 1977). Myrmiciidae (= Pseudosiricidae) from the Upper Jurassic and Cretaceous was synonymized with Siricidae by Rasnitsyn (1988) because the thorax shows features typical of siricids. Perhaps these fossils belong to the stem-group of the Siricidae, too. The Auliscinae from the Upper Jurassic of Karatau are placed in Siricidae by Rasnitsyn (1969, 1980), but Königsmann (1977) considered this placement to be problematical. The Praesiricidae from Lower Cretaceous of Transbaikalia and from the Upper Jurassic of Kazakhstan have been removed from the Siricidae (Rasnitsyn 1983).

The extant Siricidae consist of the Siricinae (not necessarily a monophyletic group) and the Tremecinae. The oldest fossil siricine is from the Lower Cretaceous of eastern Russia; it is possibly related to *Xeris* Costa, 1894 and *Eoxeris* Maa, 1949 (Gromov *et al.* 1993). The oldest Tertiary find is *Urocerus patagonicus* Fidalgo and Smith, 1987, described from Paleocene shales in Patagonia (Fidalgo and Smith 1987); *Urocerus ligniticus* (Piton, 1940) and two other *Urocerus* fossils are recorded from the Paleocene of Menat, Puy-de-Dôme, France (Nel 1988). *Eoxeris klebsi* (Brues, 1926) is known from Baltic amber (Brues 1926). Other fossil Siricinae were mentioned by Nel (1991) from Oligocene and Miocene shales in France. *Urocerites spectabilis* Heer, 1867 has been described from the Miocene shales of Radoboj, Croatia.

The two fossils described here are the first reports of Tremecinae in the geological record. One fossil was found in the lake deposits of Enspel (*c.* 25 Ma; Storch *et al.* 1996; Wuttke 1997), near Bad Marienberg, Westerwald Mountains, Rheinland-Pfalz, Germany. The second fossil is from the lake deposits (Upper Pliocene) of Willershausen near Osterode in the Harz Mountains, Lower Saxony, Germany.

Before determining the exact systematic position of a fossil species or higher taxon, the phylogenetic relationships among the related extant taxa should be clarified. So far only Gauld and Mound (1982) have attempted to reconstruct the phylogeny of Siricidae. A new evaluation of characters has led to the reconstruction of phylogenetic relationships presented here.

EXTANT MATERIAL

I examined the venation of the forewings of the following extant material from the general collection of the Muséum National d'Histoire Naturelle in Paris: *Eriotremex insignis* Smith, 1859: 2 ♀; *Tremex*

alchymista Mocsáry, 1886: 3 ♂, 2 ♀; *Tremex columba* (Linnaeus, 1763): 1 ♂, 9 ♀; *Tremex fuscicornis* (Fabricius, 1787): 4 ♂, 4 ♀; *Tremex longicollis* Konow, 1896: 1 ♀; *Tremex magus* (Fabricius, 1787): 1 ♂, 2 ♀; *Tremex pandora* Westwood, 1874: 1 ♂. The following material was borrowed for further study: *Eriotremex insignis*: 1 ♀; *Tremex alchymista*: 2 ♀; *Tremex columba*: 3 ♀; *Tremex fuscicornis*: 1 ♂, 3 ♀; *Tremex magus*: 1 ♀.

PHYLOGENY OF TREMECINAE

Siricidae

Siricidae is very probably a monophyletic group (Königsmann 1977). There are several autapomorpic features for this taxon (Text-fig. 1, characters 1–6): Both the labium and maxilla are very hairy, the maxillary palp is 1-segmented (Ross 1937). The mesonotum has two diagonal grooves separating off side lobes (Ross 1937; Benson 1938). This feature seems not to be present in *Sinosirex* (Hong 1975), which can be interpreted either as a plesiomorphic feature or as an apomorphic loss in *Sinosirex*. Apomorphic characters of the wing venation are the basad inclined first part of Rs (Königsmann 1977; Rasnitsyn 1988) and the short fused part of Rs+M (Königsmann 1977). The last abdominal segments of both sexes are modified: in the female tergite 9 is short with a distinct precornal basin, tergite 10 is long, horn-like and strongly protruding caudad (Maa 1949). In the male the ninth tergite is divided into two triangular plates and the last sternite is drawn out pointedly (Königsmann 1977).

Extant Siricidae are divided into two groups, Siricinae and Tremecinae (Ashmead 1898). In this investigation the classification of Rohwer (1911) is followed.

Siricinae

The Siricinae are not necessarily monophyletic because no autapomorpic characters are known. The 3-segmented labial palp is a plesiomorphic character which is shared with Orussidae, Anaxyelidae, most Xiphydriidae and other taxa (Ross 1937). Another plesiomorphic feature is the long, slender, multi-segmented antenna. Further characters used to separate Siricinae from Tremecinae are the attachment of the larvae of Siricinae to conifers, short distance between the antennae, ratio of width to length of eyes being not more than 1·5 and contraction of the anal cell from about the middle (Benson 1943). These characters are not present in all genera of Siricinae or not only in genera of Siricinae. Gauld and Mound (1982) regarded the contraction of the anal cell from about the middle as an autapomorphic feature of Siricinae without *Siricosoma* Forsius, 1933. But, this is a rather vague character which is present also in *Teredon* (Bradley 1913, text-fig. 10), and therefore I consider this feature to be unsuitable to confirm the monophyly of Siricinae without *Siricosoma*. Further investigations are necessary to resolve the phylogenetic relationships of these taxa.

Gauld and Mound (1982) established a sister-group relationship between *Siricosoma* and Tremecinae (*sensu* Rohwer 1911) because these taxa have only one hind tibial spur (termed the mid tibial spur by Gauld and Mound (1982)). However, in *Xeris* Costa, 1894 and in the closely related *Neoxeris* Saini and Singh, 1987, there is only one spur present, too, which is rated as a convergent development by Gauld and Mound (1982). Even in *Urocerus flavicornis* Fabricius, 1781, about 10 per cent. of the males possess only a single spur on the hind tibia (Bradley 1913), which is why I consider this character to be very weak. As a second autapomorphic feature for *Siricosoma*+Tremecinae the shape of the distal flagellar segments is listed (Gauld and Mound 1982), a feature which is not defined more closely. The third apomorphy of Gauld and Mound (1982) is that the antennal bases of *Siricosoma* and of the taxa belonging to the Tremecinae are set far apart. This character is also found in *Sirotremex* Smith, 1988, which is placed currently in the Siricinae (Smith 1988). As stated before, it is necessary to investigate many more characters before a well-founded analysis of phylogenetic relationships is possible.
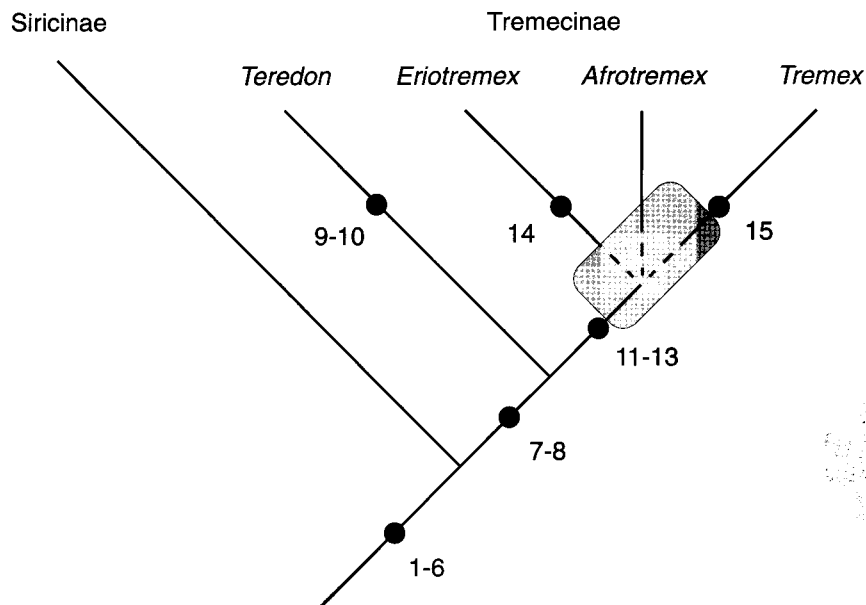
TEXT-FIG. 1. Phylogenetic relationships of extant Siricidae. The shaded area shows the possible phylogenetic position of Eriotremex or Afrotremex sp. from Enspel. The numbers refer to the following list of apomorphic characters. 1, labium and maxilla very hairy. 2, maxillary palp 1-segmented. 3, mesonotum with two diagonal grooves setting off side lobes. 4, first part of Rs directed diagonally towards wing base. 5, fused part of Rs and M very short. 6, abdominal segments 9 and 10 modified. 7, labial palp two-segmented. 8, vein 1r-m in hindwing shifted apically and located near middle of cell 1M. 9, antenna with five or six segments. 10, hindleg of male widely dilated. 11, vein 2r-m absent in forewing. 12, hindwing without closed anal cell. 13, veins M and cu-a of forewing (almost) in line. 14, disc on ninth abdominal tergite convex in the middle and hairy. 15, apical position of vein 2r-rs in forewing.

Tremecinae

Tremecinae sensu Rohwer (1911) comprises Teredon, Eriotremex, Afrotremex and Tremex. This taxon is most probably monophyletic. A synapomorphic feature of the Tremecinae is probably the 2-segmented labial palp (Text-fig. 1, character 7) which is present in Teredon (Konow 1905), Tremex (Bradley 1913; Benson 1943), Eriotremex (Benson 1943) and Afrotremex (David R. Smith, pers. comm.).

In the hindwing, vein 1r-m (nomenclature after Ross 1936) is shifted towards the apex so that it is located at about the middle of cell 1M at least in the following species: Teredon latitarsis (Bradley 1913, fig. 10), Eriotremex formosanus (Matsumura 1930, pl. 6, fig. 4; Smith 1975, fig. 1), E. smithi (Kirby 1882, pl. 15, fig. 1), E. yamasakii (Togashi 1990, fig. 1) and E. insignis, Afrotremex hyalinatus (Guiglia 1937, pl. 15), Tremex apicalis (Matsumura 1930, pl. 6, fig. 7), T. chujoi (Sonan 1938, fig. 5), T. longicollis (Matsumura 1930, pl. 6, fig. 3), T. niger (Sonan 1938, fig. 4), T. pandora (Westwood 1874, pl. 21, fig. 9), T. rugicollis (Westwood 1874, pl. 20, fig. 9), T. columba, T. fuscicornis and T. magus. In Siricinae and in many taxa whose wing venation is considered to be rather primitive, e.g. Xyelidae (Königsmann 1977), vein 1r-m is located at the basal part of cell 1M. Thus, the apical position of vein 1r-m is probably another synapomorphic feature of the Tremecinae (Text-fig. 1, character 8).

Bradley (1913) mentioned the loss of cerci in Tremecinae. This could be another apomorphic character of Tremecinae, since in Teredon (David R. Smith, pers. comm.), Afrotremex (David R. Smith, pers. comm.) and Tremex (Benson 1943) cerci are entirely absent. However, species of

TEXT-FIG. 2. *Eriotremex* or *Afrotremex* sp.; Landesamt für Denkmalpflege Rheinland-Pfalz No. 9604; Enspel, Germany, Upper Oligocene; whole fossil; × 3·3.

Eriotremex possess cerci (Benson 1943). On condition that loss of cerci is apomorphic for Tremecinae the presence of cerci in *Eriotremex* would have to be rated as a reversal. This would be an autapomorphic feature of *Eriotremex*. The alternative is to assume independent loss of cerci in *Teredon*, *Afrotremex* and *Tremex*. This could support a sister group relationship of *Afrotremex* and *Tremex*.

The attachment of Tremecinae to angiosperm trees (Benson 1943) is not necessarily apomorphic for the Tremecinae since the larval host plants of *Teredon* and of *Afrotremex* are not known. One species of *Eriotremex* is associated with angiosperm plants and the larvae of *Tremex* species seem to live exclusively in angiosperm trees (Smith 1978).

Teredon

The two species of *Teredon* have the following apomorphic characters (Text-fig. 1, characters 9–10): The antennae are 5- or 6-segmented. The hindleg of the male has a widely expanded tibia and basitarsus (Cresson 1865).

Eriotremex + Afrotremex + Tremex

The taxa *Eriotremex*, *Afrotremex* and *Tremex* probably form a monophylum. In these taxa vein 2r-m is absent, M and cu-a almost are in line in the forewing, and the hindwing lacks a closed anal cell (Text-fig. 1, characters 11–13).

There are several diagnostic characters for *Eriotremex* (Benson 1943). The basal position of vein 2r-rs in the forewing is a plesiomorphic feature and the rating of the presence of cerci is not clear (see above). The only possible apomorphic feature of *Eriotremex* is that the disc on the ninth abdominal tergite is convex in the middle and hairy (Text-fig. 1, character 14). In *Teredon*, *Afrotremex* and *Tremex* this disc is flat and bald (Pasteels 1951; David R. Smith, pers. comm.) as in the Siricinae.

The diagnostic features of *Afrotremex* are the basal position of vein 2r-rs in the forewing, a flat ninth abdominal tergite, and the presence of a genal carina (Pasteels 1951). Probably all of these character states are plesiomorphic since they can be found in several taxa of Siricinae, too. A genal carina is absent in *Eriotremex*, *Tremex* and some taxa of the Siricinae. The state of this character is not known for *Teredon*. Independent loss could have occurred easily.

Tremex has an apomorphic character in the apical position of vein 2r-rs in the forewing (Text-fig. 1, character 15).

The phylogenetic relationships between *Eriotremex*, *Afrotremex* and *Tremex* cannot be resolved with the characters presently available.

Characters of the wing venation should be used with caution. Because of potential variability of the wing venation of lower Hymenoptera (Kloiber 1936; Zirngiebl 1939; Jansen 1987) and especially of woodwasps (Cockerell 1921), 28 individuals of six species of *Tremex* and two specimens of *Eriotremex insignis* were examined. Although there were several aberrations, no significant variability in the above mentioned characters of the wing venation could be detected. Thus, the use of the venational characters is justified.

Altogether, this phylogenetic analysis is based on characters for which homoplasy is possible. It is desirable to find many more additional characters to test the proposed relationships.

SYSTEMATIC PALAEONTOLOGY

Genus ERIOTREMEX Benson, 1943 or AFROTREMEX Pasteels, 1951

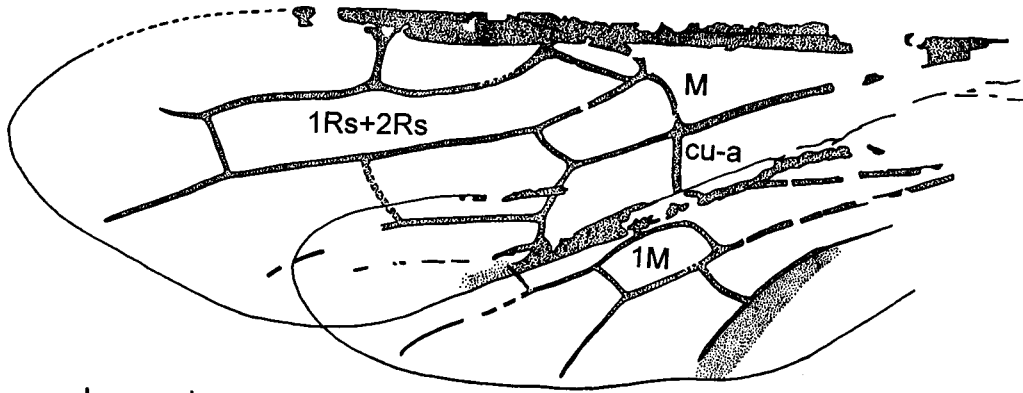*Eriotremex* or *Afrotremex* sp.

Text-figures 2–4

Material. Collection-no. 9604, deposited in the Landesamt für Denkmalpflege Rheinland-Pfalz, Referat Erdgeschichtliche Denkmalpflege, Mainz, Germany.

Locality. Enspel, near Bad Marienberg, Westerwald Mountains, Germany. Fossil site 6, horizon 16.

Age. Upper Oligocene, c. 25 Ma (Storch *et al.* 1996; Wuttke 1997).

Preservation. The fossil is seen from the ventral side. The body is fragmentarily preserved (Text-fig. 2). In the head the lower parts of the two eyes are visible. Fragments of the antennae are preserved in front of the head. The thorax shows no detailed structures. The left forewing is only partly present (Text-fig. 2). On the right side both wings can be seen clearly (Text-fig. 3). The abdomen is fragmentarily preserved. From the presence of an ovipositor the fossil can be determined as female.

Morphology. Length 33 mm from head to tip of ovipositor. Forewing 19 mm long. Lower part of forewing and upper part of hindwing overlap, veins in this area cannot be seen (Text-fig. 3). In forewing, 2r-rs is located basally, 2r-m absent with 1Rs and 2Rs united, and M and cu-a in line (Text-fig. 3). Vein 1r-m seems shifted backwards in hindwing, no trace of it above proximal part of cell M, possibly located at middle of upper margin of cell M. Hindwing lacks closed anal cell. Dark shadow below vein A1 in hindwing, probably caused

TEXT-FIG. 3. *Eriotremex* or *Afrotremex* sp.; Landesamt für Denkmalpflege Rheinland-Pfalz No. 9604; Enspel, Germany, Upper Oligocene; *Camera lucida* drawing of right wings. Scale bar represents 2 mm. For abbreviations see text.

TEXT-FIG. 4. *Eriotremex* or *Afrotremex* sp.; Landesamt für Denkmalpflege Rheinland-Pfalz No. 9604; Enspel, Germany, Upper Oligocene; *Camera lucida* drawing of hind part of abdomen. Scale bar represents 2 mm. rv = rami valvularum, v3 = third valvulae.

by folded wing membrane (Text-fig. 3). Semicircular structures at base of ovipositor (Text-fig. 4) are rami valvularum (Snodgrass 1935). Ovipositor length 15 mm from base to tip, but it is unclear if ovipositor is completely preserved. Ratio length of forewing/length of ovipositor 1·27.

Systematic position. The fossil belongs to the monophyletic group *Eriotremex + Afrotremex + Tremex* because in the forewing 2r-m is absent, M and cu-a are almost in line and the hindwing lacks a closed anal cell (complex of apomorphic features 11–13 in Text-fig. 1). The fossil can be distinguished from *Tremex* by having 2r-rs in a basal position (Text-fig. 3). This is the plesiomorphic condition which is present in *Eriotremex* and *Afrotremex*. The appearance of the disc on the ninth abdominal tergite is not visible in the fossil. Consequently, the phylogenetic position must be within the monophylum consisting of *Eriotremex + Afrotremex + Tremex*, whilst *Tremex* can be excluded. In Text-figure 1 the area of possible phylogenetic positions is shaded.

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Genus TREMEX Jurine, 1807

Tremex sp.

Text-figure 5

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Material. Collection-no. 27670, Staatliches Museum für Naturkunde in Stuttgart, Germany.

Locality. Willershausen near Osterode, Harz Mountains, Lower Saxony, Germany. No further data available.

Age. Upper Pliocene.

Preservation. Only one forewing (Text-fig. 5) is present. The basal part of the wing is missing. The venation is almost completely preserved. Parts of the veins are not dark but can be recognized because they are raised.

Morphology. Wing length 14 mm. Membrane apically undulated. Vein 2r-rs in apical position, M and cu-a in line. Vein 2rm absent, resulting in fusion of cells 1Rs and 2Rs. In cell 2M, veins M and Cu1a are parallel to each other (Text-fig. 5).

Systematic position. The fossil belongs to *Tremex* because of the apical position of vein 2r-rs in the forewing. This position of 2r-rs is an autapomorphic feature of *Tremex* (Text-fig. 1, character 14). A determination of the species is not possible since there are no known significant differences in the wing venation of *Tremex* at species level.

ZOOGEOGRAPHICAL AND EVOLUTIONARY CONSIDERATIONS

The two extant species of *Teredon* occur only in Cuba (Smith 1978). There are 11 recent species of *Eriotremex* which are native to the Oriental Region (Maa 1956; Smith 1978; Togashi 1991). One species also occurs in Papua-New Guinea (Smith 1978). *E. formosanus* was recently introduced in North America (Smith 1975, 1996). The two species of *Afrotremex* are native to Central Africa (Guiglia 1937; Pasteels 1951). Currently, there are 23 species of *Tremex* (Smith 1978; Togashi 1979). One species occurs in North America, but most species occur in the Palaearctic Region and a few species are confined to the Oriental Region (Smith 1978). The present geographical pattern of Tremecinae can be interpreted as a relict distribution. Probably the Tremecinae formerly were much more widely distributed than today.

For Siricinae, a formerly much wider distribution is proven by the discovery of a fossil *Urocerus*-species in Paleocene shales in Argentina (Fidalgo and Smith 1987). Today there are no Siricidae native in South America.

The specimen from the Upper Oligocene of Enspel belongs to the monophyletic group consisting of *Tremex + Afrotremex + Eriotremex*. If the reconstruction of the phylogenetic relationships
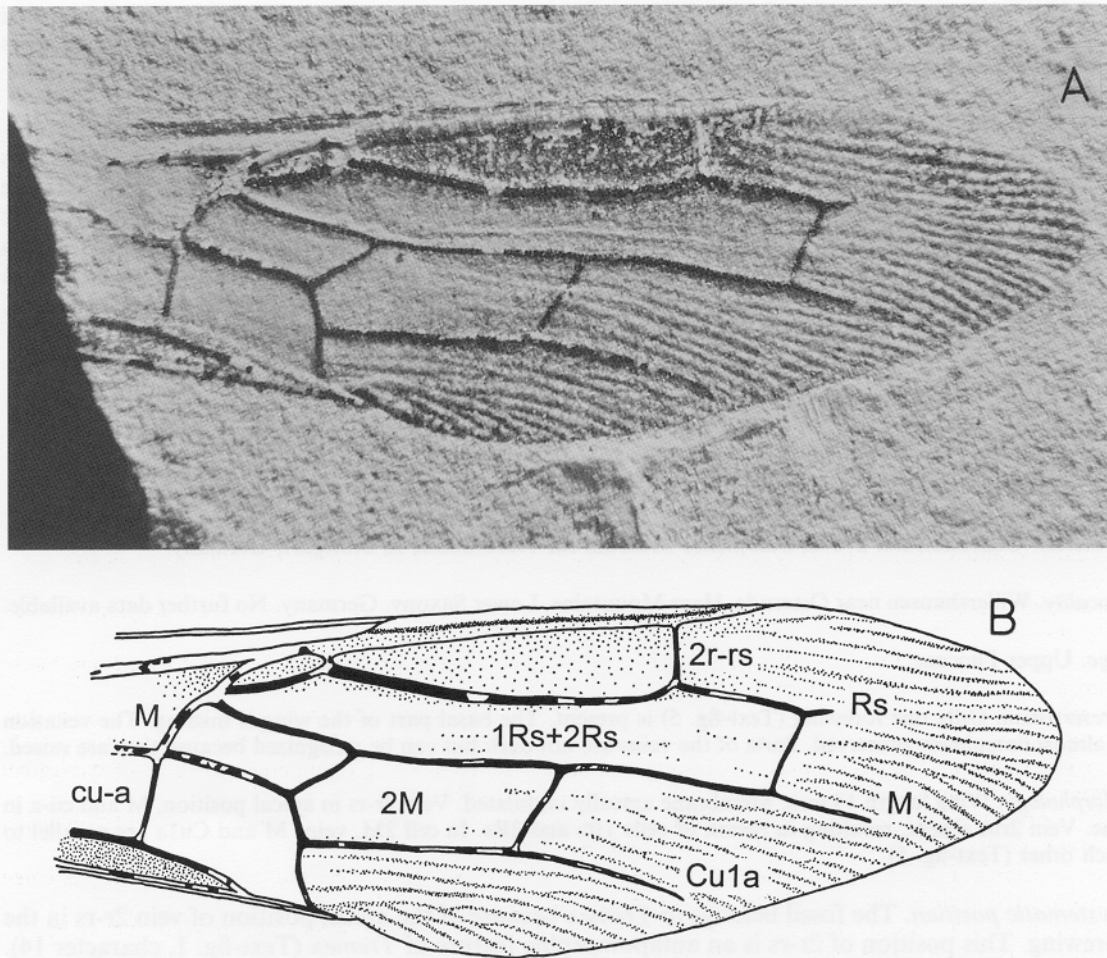
TEXT-FIG. 5. *Tremex* sp.; Staatliches Museum für Naturkunde Stuttgart, No. 27670; Willershausen, Germany, Upper Pliocene. A, photograph of whole fossil; B, *Camera lucida* drawing. Scale bar represents 2 mm. For abbreviations see text.

presented above is correct, not only must *Tremex + Afrotremex + Eriotremex* have been present in Upper Oligocene times, but also *Teredon* as its supposed sister taxon.

The zoogeographical implications of the fossil from Enspel are unclear. It is possible that the fossil does not belong to *Eriotremex* or *Afrotremex* but to the stem-lineage of *Tremex +* *Afrotremex + Eriotremex* or to the stem-lineage of one of these three taxa (Text-fig. 1).

The Pliocene *Tremex* from Willershausen indicates the minimum age for *Tremex*, but the taxon probably is much older.

Willershausen fossil. Drs A. Nel and J. Casevitz-Weulersse (both Paris) were so kind as to make a loan of the extant material possible. This study was supported financially by the Deutsche Forschungsgemeinschaft (TR 262/3-1).

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