
TERTIARY SAWFLIES OF THE TRIBE XYELINI (INSECTA: VESPIDA = HYMENOPTERA: XYELIDAE) AND THEIR RELATIONSHIP TO THE MESOZOIC AND MODERN FAUNAS

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ABSTRACT. Ten Tertiary species of Xyelini are currently known. One of them, *Enneoxyela? cenozoica* (Zhang, 1989) comb. nov., from the Middle Miocene of China, is a Late Tertiary relic of a mid-Mesozoic group, being a member or at least a close relative of the otherwise Late Jurassic genus. All other Tertiary Xyelini are of Oligocene age and belong to the genus *Xyela* Dalman, 1819. Subgenus *Pinicolites* Meunier, 1920, stat. nov. is represented by only one species, *X. (P.) graciosa* (Meunier, 1920). Subgenus *X. (Xyela)* is represented by eight fossil species, including *X. (X.) magna* Statz, 1936, which belongs to the *X. minor* group and is most closely related to living North American species. The others are all attributed to the *X. julii* group. Four are extinct—*X. (X.) latipennis* Statz, 1936, *X. (X.) angustipennis* Statz, 1936, *X. (X.) florissantensis* sp. nov., and *X. (X.) micrura* sp. nov.—whereas *X. (X.) cf. menelaus* Benson, 1961, and *X. (X.) cf. julii* Brébisson possibly represent the two living European species. All known Tertiary *Xyela* come from the highest Upper Oligocene Rott Formation of Germany, except *X. (X.) florissantensis*, from the Lower Oligocene Florissant Formation of Colorado, USA. All known Tertiary Xyelini were buried in lacustrine, tuffaceous deposits.

INTRODUCTION

The sawfly family Xyelidae has special significance for the history of hymenopterous insects (order Vespida; see Rasnitsyn, 1988, and references therein for name justification). It appeared in the fossil record as early as the Middle or early Late Triassic, whereas other hymenopteran fossils are unknown before the earliest Jurassic (Rasnitsyn, 1988). Xyelid morphology suggests an ancestral position for the family with respect to other Hymenoptera, although this claim is not entirely accepted (compare Königsman, 1976, and Rasnitsyn, 1980).

The three subfamilies of Xyelidae are comparable in size and diversity. The ancestral Archexyelinae Rasnitsyn, 1964, is known only from the Triassic, while the Macroxyelinae Ashmead, 1898, and Xyelinae Newman, 1834, range from the Early Jurassic to the present. During Mesozoic time, the Xyelidae was a prominent hymenopteran family, especially in areas with relatively cooler climates, where it often was dominant.

In the Tertiary (or perhaps the Late Cretaceous; there are insufficient data for that period), the pattern changed radically. Xyelidae became a rare group with a poor fossil record, confined mostly to the temperate regions of the Northern Hemisphere. Only 17 Tertiary specimens are known worldwide.

Thirteen belong to *Xyela* Dalman, 1819, *s.l.*; of these, 10 were described by Statz (1936) (paralecotype 4019 of *Xyela latipennis* is not a hymenopteran but a possible trichopteran) and 3 were described by Meunier (1920) and Zhang (1989) and in the present paper. Three are members of *Megaxyela* Ashmead, 1898: one was described by Brues (1908; redescribed by Zhelochovtzev and Rasnitsyn, 1972), the second by Zhang (1989), and the third is an undescribed species of *Megaxyela* from the Lower Miocene of Sikhote-Alin, Maritime Province, kept in the Paleontological Institute, Russian Academy of Sciences, Moscow. One specimen belongs to *Xyelecia* Ross, 1932 (Zhang, 1989). The Lower Cretaceous deposits of Siberia and Mongolia have yielded more than 80 xyelid specimens, now housed at the Paleontological Institute in Moscow.

Unlike the Jurassic and Cretaceous xyelid faunas, which were composed of comparable diversities of both Xyelinae and Macroxyelinae, the Tertiary fauna was strongly dominated by Xyelinae, particularly *Xyela* Dalman. There are only three known species of *Megaxyela* Ashmead and one of *Xyelecia* Ross belonging to Tertiary Macroxyelinae. The dominance of *Xyela* among the Tertiary Xyelidae is similar to the contemporary fauna which comprises a total of 48 xyelid species, 31 of which belong to *Xyela* (Smith, 1978).

The distribution of the fossils is enigmatic. The larval stage of *Xyela* develops within staminate cones of pines and feeds on the unripe pollen. The adults readily visit other, flowering plants for pollen, but

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nevertheless they spend much of their time on pine trees. These habits have persisted since at least the Early Cretaceous (Krassilov and Rasnitsyn, 1982). *Xyela* are intimately associated with the genus *Pinus* Linné, 1753, both genera being widespread over the Northern Hemisphere. *Xyela* is particularly abundant and diverse in southwestern North America (Burdick, 1961; Rasnitsyn, 1971), where pine trees are also common and represented by a number of species. Still, the Tertiary fossil record is poor for *Xyela* in the above region. A single *Xyela* specimen has been found among the tens of thousands of fossils collected at Florissant, Creed, and Green River. Even more unexpected, the only known Tertiary fauna rich in *Xyela* comes from the Rott Formation (latest Oligocene diatomite deposits accumulated in a mountain lake at Rott near Bonn in Germany), which is poor in *Pinus* fossils (Weyland, 1937, 1948). Nevertheless, the Rott hymenopteran assemblage is even richer in xyelids than most Cretaceous ones, being represented by 11 specimens among 14 sawflies (79%) and 76 solitary hymenopterans (14.5%; figures from Statz, 1936). It is unlikely that the rare local pine trees could have housed all of them, and the diversity of *Xyela* suggests a considerable diversity of host pine tree species. Indeed, the extant closely related species of *Xyela* rarely exploit the same host plant species (Burdick, 1961; Rasnitsyn, 1965, 1971). The insects may have been transported to the Rott lake by winds from nearby mountains as has been described for extant *Xyela* (Fridolin, 1936).

The above considerations do not fully explain the composition of the Rott assemblage, however, because there are many other mountain lake deposits with rich insect assemblages but few, if any, *Xyela*. Yet this is not the most perplexing aspect of the fossil record of the group. Even more difficult to explain is the absence of *Xyela* among hundreds of thousands of insect inclusions in Baltic amber, a fossil pine resin. Their absence from Baltic amber could not be because these insects are able to escape entrapment. Indeed, I have identified two specimens of *X. ussuriensis* Rasnitsyn in spruce resin collected at the Sikhote-Alin Mountains (cf. Zherikhin and Sukacheva, 1989).

Also enigmatic is the appearance of a representative of the otherwise Late Jurassic genus *Enneoxyela* Rasnitsyn, 1966, or a closely related genus, in the Tertiary (Middle Miocene) of China (see below).

The above review of the *Xyela* fossil record shows that it deserves exploration. This became possible after a visit to the Natural History Museum of Los Angeles County (Los Angeles, California) and the National Museum of Natural History (Washington, D.C.) in 1989–1990. The first institution keeps the Georg Statz collection of the Rott insect fossils (Sphon, 1973); the latter has the only specimen of *Xyela* from the Lower Oligocene of Florissant, Colorado.

SPECIMENS EXAMINED

Material utilized in the study is from the following collections: Invertebrate Paleontology Section, Natural History Museum of Los Angeles County, Los Angeles, California (LACMIP); Arthropoda Laboratory, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia (PIN); Department of Entomology, U.S. National Museum of Natural History, Washington, D.C. (NMNH); and Linqu Paleontological Museum, Linqu, Shandong Province, P.R. China (LPM) (only a photograph of the Chinese specimen was examined).

TAXONOMY

I am following a moderately splitting approach to *Xyela* taxonomy developed in my earlier publications (Rasnitsyn, 1965, 1971). I consider the widespread synonymization of allopatric species by Benson (1961, 1962) as possibly correct but premature given the present state of our knowledge. In my opinion, more data on *Xyela* morphology and distribution should be accumulated before these geographically disjunct populations with slight morphological differences are lumped together. Otherwise we risk mixing and losing important information.

Family Xyelidae Newman, 1834
Subfamily Xyelinae Newman, 1834
Tribe Xyelini Newman, 1834
Genus *Xyela* Dalman, 1819
Subgenus *Pinicolites*
Meunier, 1920, stat. nov.

Pinicolites: Meunier, 1920: 896; Burdick, 1959: 121; Rasnitsyn, 1971: 192. Type species: *Pinicolites graciosus* Meunier, 1920: 896; monobasic.
Pleroneura (partim): Statz, 1936: 262; Sphon, 1973: 60.

DIAGNOSIS. *Pinicolites* (Figs. 1–4) similar to *X. (Mesoxyela)* Rasnitsyn, 1965 (Fig. 4), *Xyela (Xyela)* (Figs. 5–20), and *Pleroneura* Konow, 1897. Differs from the largely Mesozoic genera *Eoxyela* Rasnitsyn, 1965, *Enneoxyela*, and *Spathoxyela* Rasnitsyn, 1969 in having R sinuate resulting in costal space widened at midlength, and probably also in having mesonotum impunctate (in that respect similar additionally to *Spathoxyela*). Similar to *Xyela (Xyela)* and *X. (Mesoxyela)* and differing from *Pleroneura* in having thin and flat (saw-like instead of needle-like) ovipositor and short or lacking 1 r-m in forewing (RS and M scarcely or not at all separated). Similar to *X. (Mesoxyela)* and *Pleroneura* in having wide pterostigma. Similar to *Xyelisca* Rasnitsyn, 1969, *Pleroneura*, and *X. (Mesoxyela)* and differing from *Eoxyela*, *Enneoxyela*, *Spathoxyela*, and *X. (Xyela)* in having antennal funicle shorter than segment 3. Similar to all Xyelini except *Xyela s.str.* in having free SC stalk in forewing and, except *Xyela s.str.* and *Pleroneura*, in having fore SC branch long, reaching level of RS base. Similar to *Pleroneura* and unlike all other Xyelini in having 2r cell short in the forewing. Similar to many *X. (Xyela)* and differing from *Pleroneura* in color pattern of meso-

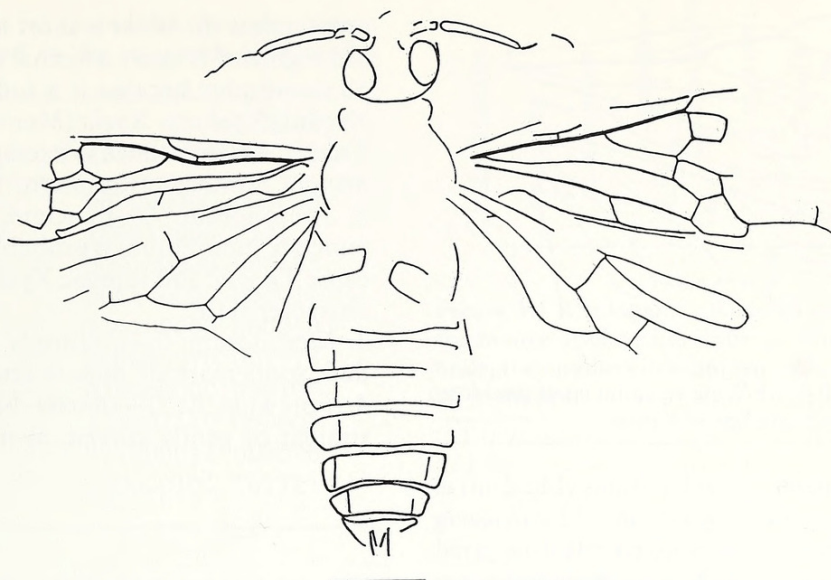


Figure 1. Line drawing of *Xyela (Pinicolites) graciosa* (Meunier, 1920) traced after photograph of holotype, with forewings displaced to show venation of the hind pair. Scale bar = 1 mm.

notum, which, instead of being almost uniformly dark, is light with dark spots marking areas of muscle attachment. Similar to all Xyelini except *Pleroneura* in having hindwing lacking free apex of A_1 (unknown for *Xyelisca*).

SPECIES INCLUDED. Type species only.

SYSTEMATIC AND PHYLOGENETIC POSITION. The characters used to identify the systematic and phylogenetic position of *Pinicolites* within the tribe Xyelini are presented in the following list; their distribution is shown in Table 1:

1. Antennal funicle: 0—short (shorter than 3rd seg-

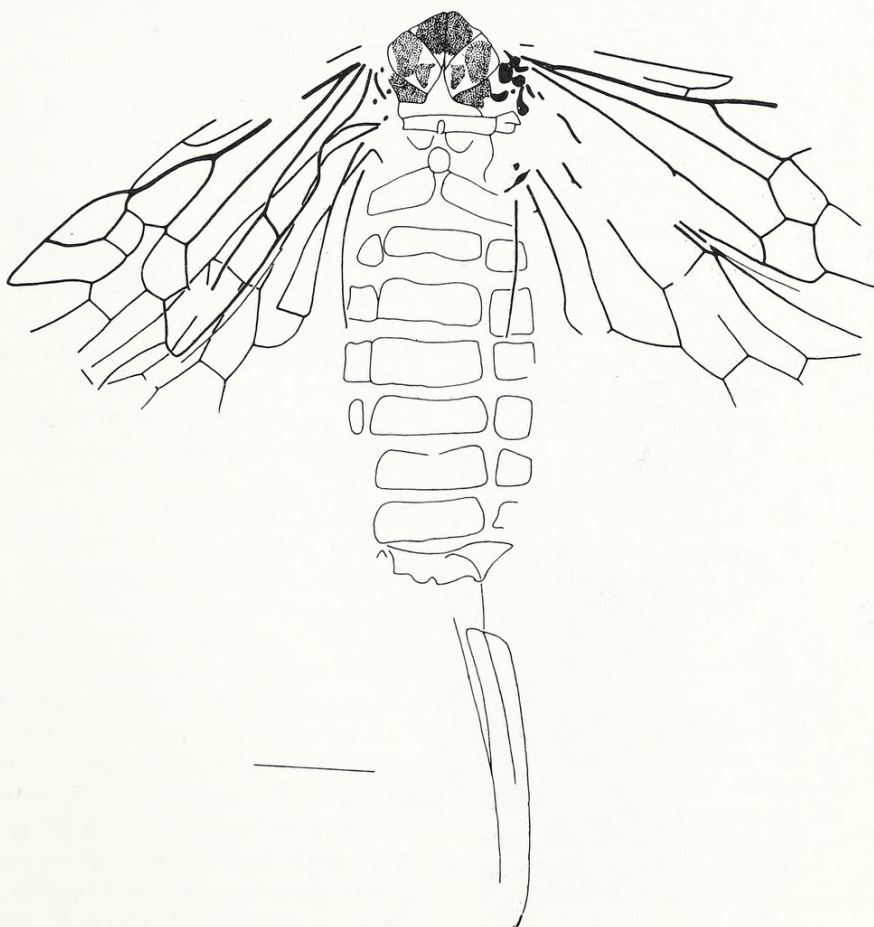


Figure 2. LACMIP 4010: Line drawing of the fossil. Scale bar = 1 mm.

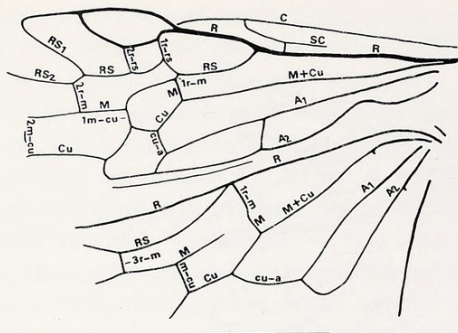


Figure 3. LACMIP 4010: Wing venation combined from left and right wings. Scale bar = 1 mm.

ment unless the latter is short itself), 1—longer than 3rd segment. A short antennal funicle is considered plesiomorphic because it is found in less advanced Xyelini [*Xyelisca*, *Xyela* (*Mesoxyela*)], as well as in Triassic Archexyelinae as exemplified by *Dinoxyela armata* Rasnitsyn (Rasnitsyn, 1969, Fig. 24).

2. Mesonotum: 0—punctate, 1—impunctate. A punctate mesonotum is probably plesiomorphic because Triassic and Jurassic Xyelidae all retained this character state.

3. Mesonotum: 0—uniformly dark, 1—light with dark spots marking muscle attachment sites.

4. Forewing R: 0—sinuate before RS base, 1—straight or gently curved, at most slightly bent at



Figure 4. LACMIP 4010: Photograph of impression. Scale bar = 1 mm.

Table 1. Data matrix for groundplan characters of taxa of Xyelini as discussed in the text, with Liadoxyelini taken as an outgroup.

	111111	
	123456789	012345
Ancestor	000000000	000000
Liadoxyelini	100010000	01????
Eoxyela	000100000	00010?
Enneoxyela	000100000	000010
Spathoxyela	110100000	000010
Xyelisca	0000000?0	00????
Mesoxyla	010000000	00010?
Xyela	111001110	000000
Pinicolites	011000011	000020
Pleroneura	010000101	101121

RS base. A sinuate R is considered plesiomorphic because it is characteristic for the oldest xyelid group, the Triassic Archexyelinae. It is also found in most of the predominantly Jurassic Liadoxyelini Rasnitsyn, 1966 (Xyelinae), and the majority of Macroxyelinae (Rasnitsyn, 1969).

5. Forewing SC: 0—free, 1—appressed to R except apically. A free SC is considered plesiomorphic because it is a groundplan character state for Pterygota. It is present also in the majority of Xyelidae, including most Archexyelinae, Macroxyelinae, and Liadoxyelini.

6. Forewing SC: 0—reaching, 1—far from reaching level of RS base. The first character state is probably plesiomorphic because it is present in most Paleozoic insects and most Xyelidae, including most Archexyelinae, Macroxyelinae, and Liadoxyelini.

7. First abscissa of forewing RS: 0—much longer than, 1—subequal to 1st abscissa of M. A long first abscissa of RS is considered plesiomorphic because archetypically holometabolous insects have RS and M connected by an r-m crossvein positioned distad of RS and M bases. Only secondarily have these veins become fused, and when becoming longer, the fusion often results in shortening of the basal abscissa of RS.

8. Pterostigma: 0—narrow, 1—wide. The pterostigma is narrow in all Triassic and Jurassic Xyelidae except the aberrant Jurassic *Lydoxyela* Rasnitsyn, 1966 (Liadoxyelini). Thus, it is considered here as the plesiomorphic character state.

9. Forewing cell 2r: 0—long, 1—short. A long 2r is found in all Xyelidae except *Pinicolites* and *Pleroneura* and, thus, is considered plesiomorphic.

10. Forewing crossvein 1r-m: 0—short or absent, 1—long (cells 1r and 1m-cu distant). A long 1r-m widely separating RS and M is undoubtedly the groundplan character state in holometabolous insects. However, the same is not necessarily true in the Hymenoptera, in which *Pleroneura* is practically unique in having 1r-m long. Another example

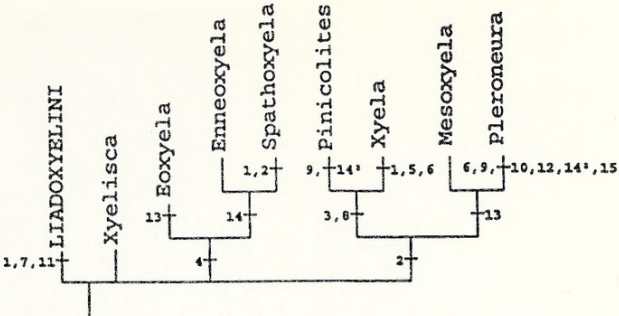


Figure 5. Cladogram calculated using Hennig86 from the matrix displayed in Table 1. When present below a node, the numbers indicate syn- and autapomorphies listed in the text.

is the highly modified wing venation of the horntail genus *Sirex* Linné. A reversion may have taken place here, with the result that the short or absent 1r-m is plesiomorphic, and *Pleroneura* and *Sirex* are considered homoplastically apomorphic instead of symplesiomorphic.

11. Forewing crossvein 1m-cu: 0—long, 1—short. A long 1m-cu correlates with the less angulated Cu, which is evidently plesiomorphic for the winged insects.

12. Hindwing A₁: 0—lacking free apex, 1—with free apex. This case is similar to that of the crossvein 1r-m (No. 10, above). A free A₁ is undoubtedly a groundplan character state for the winged insects in general and for Xyelidae in particular (found in the Triassic Archexyelinae; Rasnitsyn, 1969, figs. 36, 39, 41). However, it is not found in higher Xyelidae (Xyelinae + Macroxyelinae) except in *Pleroneura*, which is otherwise a relatively specialized form, and it is unlikely that this character state was inherited directly from the Triassic ancestor. Instead, I hypothesize that the free A₁ apex has been re-acquired here.

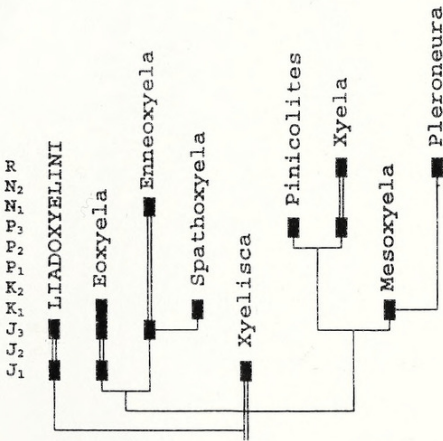


Figure 6. Phylogenetic tree of the subfamily Xyelinae. Black boxes show the fossils recorded for the respective time intervals, double lines designate the hypothesized (not confirmed by fossils) existence of taxa, and thin lines indicate ancestry. Geochronological units are abbreviated as follows: J₁ = Early Jurassic, J₂ = Middle Jurassic, J₃ = Late Jurassic, K₁ = Early Cretaceous, K₂ = Late Cretaceous, P₁ = Paleocene, P₂ = Eocene, P₃ = Oligocene, N₁ = Miocene, N₂ = Pliocene, R = the present time.

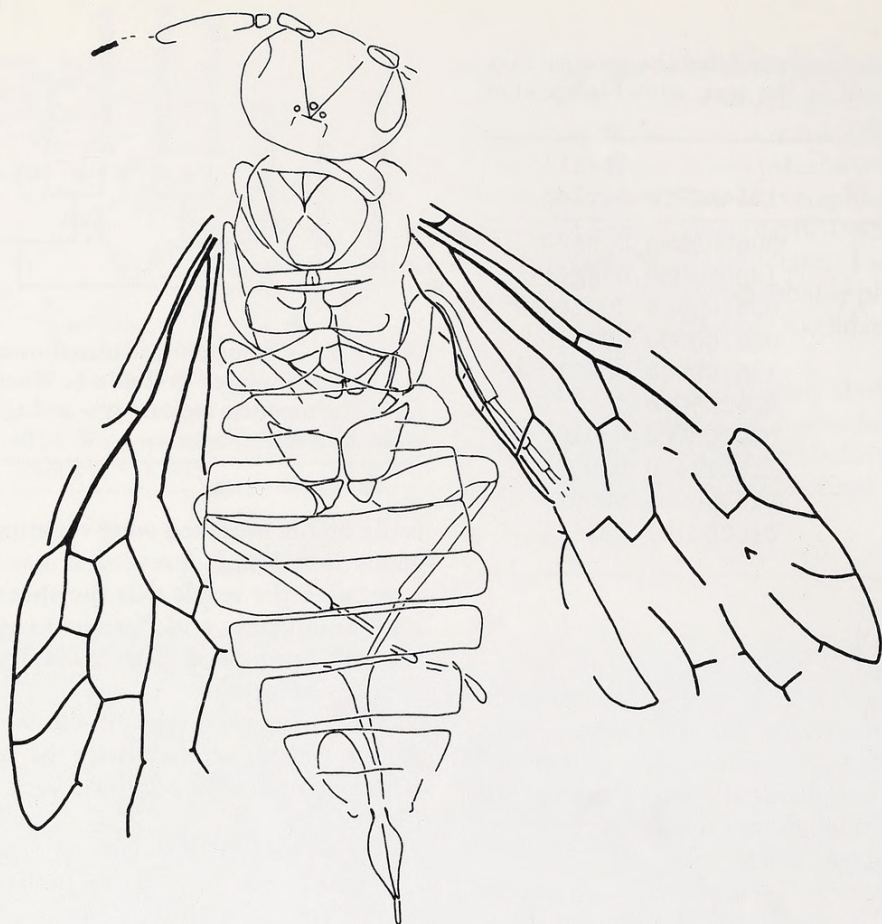
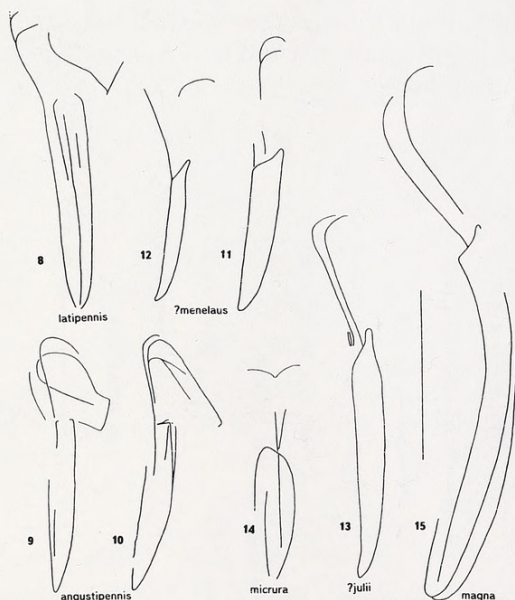


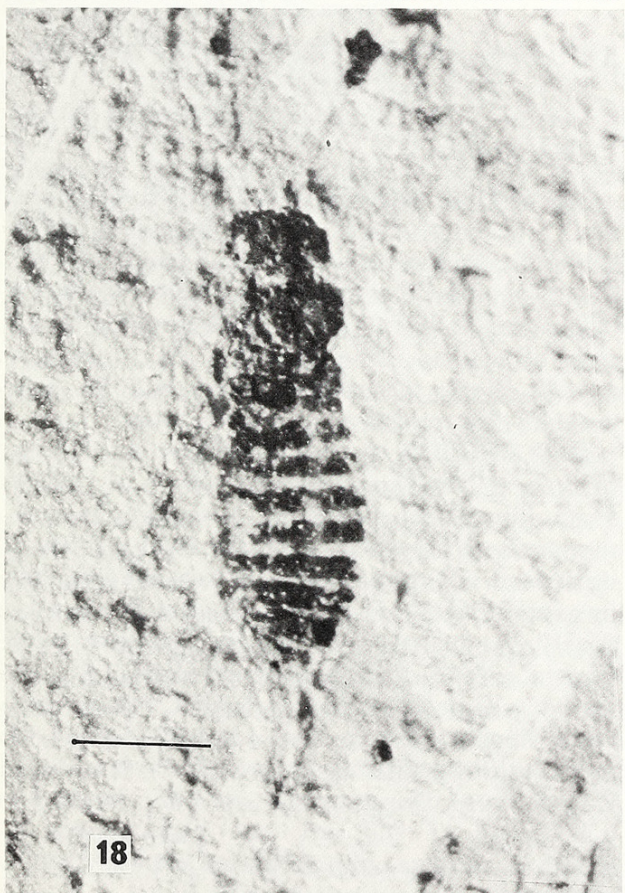
Figure 7. *Xyela (Mesoxyela) mesozoica* Rasnitsyn, 1965, PIN 3064/1924; Eastern Siberia, upper Vitim River in 45 air km upstream from Romanovka Village, Baissa Locality, Bed 31; Neocomian, Lower Cretaceous, Zaza Formation.



Figures 8–15. Line drawing of ovipositor of lectotype of *Xyela (Xyela) latipennis* Statz, 1936 (8), paralectotypes of *X. (X.) angustipennis* Statz, 1936 (LACMIP 4012 and 4014, respectively) (9, 10), *X. (X.)* sp. cf. *menelaus* Benson, 1960 (11 = LACMIP 4017, 12 = LACMIP 4016), *X. (X.)* cf. *julii* (Brébisson, 1818) (LACMIP 4018) (13), holotype of *X. (X.) micrura* sp. nov. (14), and holotype of *X. (X.) magna* Statz, 1936 (15).

13. Ovipositor: 0—saw-like, 1—needle-like. A saw-like ovipositor probably is plesiomorphic because it is the only ovipositor type found in the Mesozoic Xyelidae. The mechanically more efficient needle-like ovipositor is typical for hymenopterans boring shoots and wood. It is uncommon among those developing in the pine tree staminate cones, such as *Xyela (Mesoxyela)* and *X. (X.) alpigena*, *X. (X.) concava*, *X. (X.) linsleyi*, and *X. (X.) longula* groups. **14. Ovipositor:** 0—downcurved, 1—straight, 2—upcurved. An upcurved ovipositor is considered the most apomorphic in the transformation series because it is not found in the Mesozoic Xyelidae and is known only for a few Cenozoic forms [*Pleroneura*, *Pinicolites*, and *X. (X.) concava* group]. For the two other character states, a straight ovipositor is present in Triassic Archexyelinae, while the otherwise less advanced Xyelini, including *X. (Mesoxyela)*, have it downcurved. *Eoxyela* is among the genera with a straight ovipositor.

15. Larva: 0—feeding on pollen in staminate cones of pine trees, 1—boring fir shoots. The former character state is considered plesiomorphic for the reasons I have discussed previously (Rasnitsyn, 1980, 1988). For fossils, the forms with a saw-like ovipositor are hypothesized to feed in the staminate



Figures 16–19. 16. *Xyela (Xyela) latipennis* Statz, 1936, photograph of lectotype. 17–19. *Xyela (Xyela) angustipennis* Statz, 1936, photographs of LACMIP lectotype 4011 (17), LACMIP paralectotype 4012 (18), and LACMIP paralectotype 4014 (19).

cones, whereas the shoot-borers normally have a needle-like ovipositor.

Based on the data from Table 1, a cladogram has been derived using the "ie" option of Hennig86 (Farris, 1988). When no *a priori* weighting is applied, the result is an overflow of trees (tree length 25, consistency index 0.64, retention index 0.50) and a completely unresolved consensus tree, showing no subclades except the terminal groups. In contrast, when a weight of 2 is applied *a priori* to character 4, and the only multistate character (No. 14) is coded as nonadditive, the result is a single cladogram (tree length 24, consistency index 0.70, retention index 0.61). This cladogram essentially agrees with my intuitive assessment of the relationships within the group (Fig. 5). The phylogenetic tree (Fig. 6) is modified from the cladogram to reflect the geological succession of the taxa involved, as well as the fact that some of them seemingly lack autapomorphies. Until autapomorphies are found, these taxa are considered to be paraphyletic.

I consider paraphyletic taxa to be legitimate (Rasnitsyn, 1987, 1988, and references therein) and feel no need to discard *Xyelisca*, *Enneoxyela*, *Mesoxyela*, and *Xyela s.l.* or to reduce any of them to a parataxon *plesion* (Patterson and Rosen, 1977). I feel also that *Pinicolites* is roughly equidistant phenetically from *Xyela s.str.* and *Mesoxyela* and more distant from *Pleroneura*. That is why I prefer to reduce *Pinicolites* to subgeneric rank rather than to make *Mesoxyela* a full genus or to lump *Pleroneura* under *Xyela s.l.* Either of the latter two decisions would obscure the close similarity among the three subgenera of *Xyela* and the phenetically distant position of *Pleroneura*.

Pinicolites graciosus Meunier, 1920

Figures 1–4

Pinicolites graciosus Meunier, 1920: 896, figs. 4, 5; Burdick, 1959: 121; Rasnitsyn, 1969: 38, fig. 60. *Pleroneura graciosus*: Statz, 1936: 262, Abb. 1.

MATERIAL EXAMINED. Published photograph of the holotype (Meunier, 1920, fig. 5), and LACMIP 4010 described and figured by Statz (1936); Rott Formation, Rott near Bonn, Germany, Latest Oligocene.

DESCRIPTION. Structure as figured (Figs. 1–3). Wing: ovipositor ratio 0.8:1, sheath: basal plate ratio 3.4:1. In LACMIP 4010, length of body without head as preserved (inflated because of postmortem decomposition) 7.5 mm, forewing about 4 mm, ovipositor 3.1 mm, sheath 2.4 mm. According to Meunier (1920), length of holotype body 5.5 mm, calculated forewing length about 3.5 mm.

The two known specimens differ slightly in their forewing length; more significantly, there are differences in the position of the hindwing crossvein 1r with respect to the RS base and possibly also in the form of the forewing pterostigma and 2r cell.

These do not seem sufficient, however, to rule out their conspecificity.

Subgenus *Xyela* Dalman, 1819

Rasnitsyn (1965) subdivided this subgenus into species groups and later (Rasnitsyn, 1971) transformed them into sections. One of these sections, which was based on the relatively short wings and long body, comprised all fossil species known up to that time. This distinction seems to be partially real and partially the result of different postmortem changes in both living and fossil specimens. Pinned museum specimens have the abdomen shortened because of desiccation, while fossils usually have it inflated because of decomposition. As a result, this character has been proven to be misleading. Other diagnostic characters of the section are not known, so the latter has to be discarded. The position of the included species is discussed below.

According to the suggestion by the editorial adviser, I abandon here the concept of the section which is not accepted by the ICZN and return to the species group.

cf. *Xyela julii* Group

Xyela (Xyela) latipennis Statz, 1936

Figures 8, 16

Xyela latipennis Statz, 1936: 263, Abb. 2; Burdick, 1959: 121; Sphon, 1973: 60.

Xyela (Xyela e.g. magna) latipennis: Rasnitsyn, 1965: 491, fig. 6.

MATERIAL EXAMINED. LACMIP lectotype 4015 [specimen described and figured by Statz (1936); designated (as holotype) by Sphon (1973)]; Rott Formation, Rott near Bonn, Germany, Latest Oligocene. Note: Two of the paralectotypes ("paratypes" by Sphon, 1973) proved to belong in part to other *Xyela* species (see below), and the third probably is a caddisfly (see Introduction).

DESCRIPTION. Structure similar to that figured by Statz (1936), though wing venation as well as some other details is difficult to confirm because the specimen has since faded. Antennal segment 3 light, head and mesonotum with characteristic color pattern (Fig. 2). Ovipositor flat (saw-like), wide, gently downcurved, sheath with sides almost straight, weakly converging caudally, roundly narrowed subapically toward subacute, symmetrical apex. Wing: ovipositor ratio 1.6–1.9:1. Length of body with ovipositor, as preserved, 4.8 mm, forewing 3.3 mm, ovipositor 1.8–2.1 mm, sheath 1.3 mm. Length of ovipositor basal plate, as well as sheath: basal plate ratio cannot be determined with certainty.

TAXONOMIC POSITION. The flat, gently downcurved ovipositor is typical for the subgenus *Xyela*. Assignment of the species should be considered only tentative, because the characters most

reliable for group discrimination, viz. those dealing with the fine structure of the ovipositor stylets, are not preserved in the fossil. This is true for other fossil Xyelini as well. Within the species group, there are no other species described with a symmetrical ovipositor apex. Moreover, species with a sheath as wide (*X. bakeri* Konow, *X. menelaus* Benson) have an ovipositor that is not downcurved.

Xyela (Xyela) angustipennis

Statz, 1936

Figures 9, 10, 17–19

Xyela angustipennis Statz, 1936: 264, Abb. 3; Burdick, 1959: 121 (as possibly conspecific with *Xyela latipennis*); Sphon, 1973: 60.

Xyela (Xyela e.g. magna) latipennis: Rasnitsyn, 1965: 491.

MATERIAL EXAMINED. LACMIP lectotype 4011 [specimen described and figured by Statz (1936); designated (as holotype) by Sphon (1973)] and LACMIP paralectotypes 4012, 4014 [designated as paratypes by Sphon (1973)]; Rott Formation, Rott near Bonn, Germany, Latest Oligocene. Note: One further paralectotype ("paratype" of Sphon, 1973) proved to belong to a different species of *Xyela* (see below).

DESCRIPTION. This description is based mostly on paralectotypes because the lectotype is faded and has been partly destroyed and its ovipositor is seen only from above. As a result, the lectotype shows no important characters except the color pattern and sheath length which are similar to those of paralectotypes.

Structure generally similar to that figured by Statz (1936). Color dark, including mesonotum, with antennal segment 3 and probably legs light-colored. Antennal funicle not preserved. Ovipositor flat (saw-like), wide, gently downcurved, sheath not downcurved, parallel-sided basally, almost rectilinear tapering from somewhat between midlength and last third toward subacute, asymmetrically placed apex, with lower margin practically straight. Small, widely spaced denticles seen on the lower sheath margin of one paralectotype probably belong to lower ovipositor stylet. Basal sheath truncation subvertical. Wing: ovipositor ratio in lectotype (with wing length calculated from Statz's drawing) 1.6:1, sheath: basal plate ratio 1.9 (lectotype)–2.1:1. Length of body with ovipositor, as preserved, 4.3–4.9 mm (lectotype 4.8 mm), forewing length 2.8 mm (lectotype), ovipositor 1.6–1.7 mm (lectotype), sheath 1.0–1.1 (lectotype) mm.

TAXONOMIC POSITION. Assignment of this species to the *X. (X.) julii* group is based on similar grounds as the assignment of the previous species. Within the group there are no other species described with a similar sheath contour. In addition, the wing size is among the smallest in the genus.

cf. *Xyela (Xyela) menelaus*

Benson, 1960

Figures 11, 12, 20, 21

Xyela latipennis Statz, 1936: 263 (p.p.); Sphon, 1973: 60 (p.p.).

MATERIAL EXAMINED. LACMIP 4017–4016 [paralectotypes of *Xyela latipennis* Statz, designated as paratypes by Sphon (1973)]; Rott Formation, Rott near Bonn, Germany, Latest Oligocene.

DESCRIPTION. LACMIP 4017. Color pattern generally typical for the genus (Fig. 2), though rather dark. Third antennal segment dark dorsally. Ovipositor short, slightly downcurved, with sheath straight, weakly tapering toward subacute, slightly beak-like downward directed apex, obliquely truncated basally. Wing: ovipositor ratio about 2.8:1, sheath: basal plate ratio 1.1:1. Length of body with ovipositor, as preserved, 4.5 mm, wing about 2.8 mm, ovipositor 1.6 mm, sheath 0.9 mm.

LACMIP 4016. Color comparatively light (possibly faded), possibly with typical pattern (Fig. 2), although less developed. Ovipositor as above, except sheath narrow, possibly because of some deformation. Length of body with ovipositor, as preserved, 4.9 mm, ovipositor about 1.7 mm, sheath 0.9 mm.

TAXONOMIC POSITION. LACMIP 4017. The ovipositor form is typical for the *X. julii* group and similar to *X. (X.) menelaus* Benson. The precise relationship to *X. (X.) menelaus* cannot be determined, however, because its description mentions length of neither wing nor ovipositor (Benson, 1960). LACMIP 4016 and 4017 probably are conspecific, unless the difference in ground color and sheath width is real and not due to postmortem changes.

cf. *Xyela (Xyela) julii*

(Brébisson, 1818)

Figures 13, 22

Xyela latipennis Statz, 1936: 263 (p.p.); Sphon, 1973: 60 (p.p.).

MATERIAL EXAMINED. LACMIP 4018, paralectotype of *Xyela latipennis* Statz [designated as paratype by Sphon (1973)]; Rott Formation, Rott near Bonn, Germany, Latest Oligocene.

DESCRIPTION. Color pattern generally typical for the genus (Fig. 2), head possibly light (what appears to be a dark orbit is probably the internal eye apodeme). Ovipositor moderately long, gently downcurved, with sheath straight, weakly tapering toward subacute, slightly beak-like downward directed apex, obliquely truncated basally. Wing: ovipositor ratio about 1.8:1, sheath: basal plate ratio 1.9:1. Length of body with ovipositor, as preserved, 5.5 mm, wing 3.8 mm, ovipositor 2.1 mm, sheath 1.5 mm.

TAXONOMIC POSITION. The shape of the ovipositor is typical for the subgenus *Xyela* and



Figures 20–22. 20, 21. *Xyela (Xyela) cf. menelaus* Benson, 1960, photographs of LACMIP 4017 (20) and LACMIP 4016 (21). 22. *Xyela (Xyela) cf. julii* (Brébisson, 1818), photograph of LACMIP 4018.

similar to that of *X. (X.) julii* (Brébisson, 1818), differing only in that the sheath is narrower subapically. In addition, head is possibly lighter in color. Both of these differences are rather subtle and might be preservational. Assignment of the fossil to *X. (X.) julii* cannot be rejected at present, although additional material is necessary for certain identification.

Xyela (Xyela) florissantensis

sp. nov.

Figures 23, 24

MATERIAL EXAMINED. NMNH holotype 127677; Early Oligocene, Florissant, Colorado.

DESCRIPTION. Color pattern not preserved. Head with maxillary palp large, leg-like, though less developed than in ordinary *X. (Xyela)* species. Fore femur short and thick, especially apically (due to discoloration of femoral apex). Forewing venation unusual in having short first abscissa of RS combining with short RS+M, otherwise ordinary. Ovipositor long, flat, gently downcurved, sheath tapering from beyond middle toward subacute apex situated at dorsal sheath margin. Wing: ovipositor ratio 1.4:1, sheath: basal plate ratio 2.2:1. Length of body with ovipositor, as preserved, 6.7 mm, wing 3.8 mm, ovipositor 2.7 mm, sheath 1.9 mm.

DIAGNOSIS. The new species differs from all other *Xyela* in having a forewing with the first abscissa of RS short. It possibly also differs by having a short and thick fore femur, unless this is due to diagenetic discoloration as a result of the seeming loss of the femoral apex. It is similar to, and can be tentatively assigned to, the *X. (X.) julii* group because of its flat, gently curved ovipositor. Within the group it differs from all other species by the dorsal position of the ovipositor apex. In its sheath: basal plate ratio, the species is similar to *X. (X.) julii* but differs in the wing: ovipositor ratio.

ETYMOLOGY. The species is named after the type locality.

Xyela (Xyela) micrura sp. nov.

Figures 14, 25

Xyela angustipennis Statz, 1936: 264 (p.p.); Sphon, 1973: 60.

MATERIAL EXAMINED. LACMIP holotype 4013 [paralectotype of *Xyela angustipennis* Statz, 1936, designated as paratype by Sphon (1973)]; Rott Formation, Rott near Bonn, Germany, Latest Oligocene.

DESCRIPTION. Color pattern of metanotum typical of genus (Fig. 2). Ovipositor flat (saw-like), wide, short, more or less straight, sheath probably parallel-sided basally, almost rectilinear tapering toward dorsally situated apex, with lower margin convex and dorsal margin apparently straight, basal sheath truncation possibly oblique. Wing: ovipositor ratio about 2.6:1, sheath: basal plate ratio about 1.5:1. Length of body with ovipositor, as preserved,

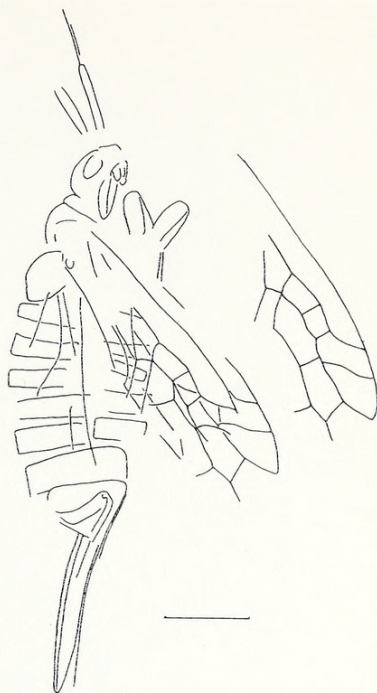


Figure 23. *Xyela (Xyela) florissantensis* Rasnitsyn sp. nov., line drawing of holotype.

4.2 mm, forewing length about 3.5 mm, ovipositor about 1.3 mm, sheath about 0.7 mm.

DIAGNOSIS. The new species is similar to, and can be tentatively assigned to, the *X. (X.) julii* group because it has a flat, straight ovipositor. Within the group it is similar to *X. (X.) bakeri* and *X. (x.) menelaus* in having a short ovipositor but differs in the dorsal position of apex. Additionally, the new species differs from *X. (X.) bakeri* in having the sheath relatively short and from *X. (X.) menelaus* in having the sheath longer.

ETYMOLOGY. The species epithet is Greek for "short tail" and refers to the short ovipositor.

cf. *Xyela (Xyela) minor* Group

Xyela (Xyela) magna Statz, 1936

Figures 15, 26

Xyela magna Statz, 1936: 264, Abb. 4; Burdick, 1959: 121; Sphon, 1973: 61.

Xyela (Xyela e.g. magna) magna: Rasnitsyn, 1965: 498, fig. 5.

Xyela (Xyela) magna: Rasnitsyn, 1969: 38, fig. 63.

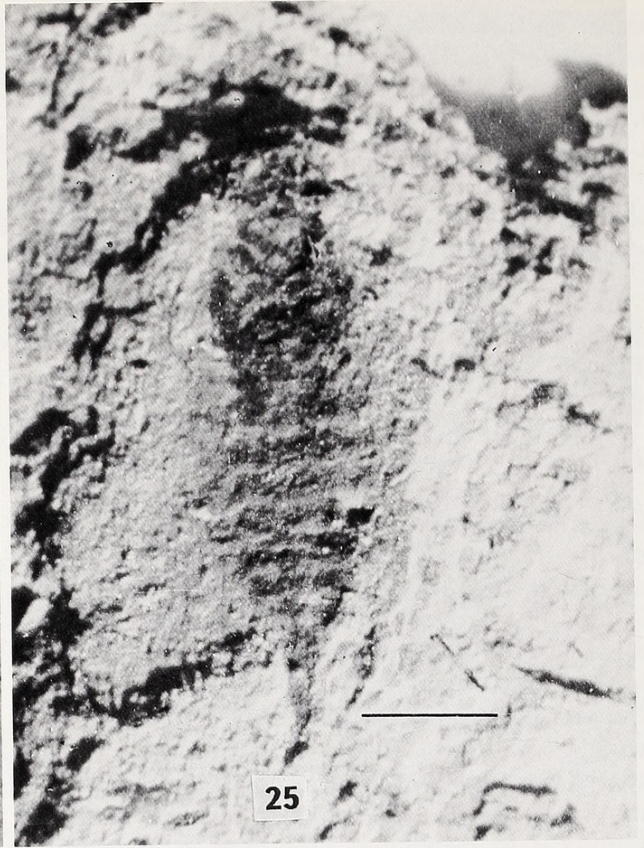
Xyela (Xyela: Sect. Magnixyela) magna: Rasnitsyn, 1971: 193.

MATERIAL EXAMINED. LACMIP holotype 4020; Rott Formation, Rott near Bonn, Germany, Latest Oligocene.

DESCRIPTION. Visible structure similar to that figured by Statz, but many details are indiscernible because of fading. Antenna light, head and mesonotum with characteristic color pattern (Fig. 2). Forewing venation poorly preserved, differing from Statz's (1936) drawing in lacking proximal (super-



24



25



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Figures 24–26. 24. *Xyela (Xyela) florissantensis* sp. nov., photograph of holotype. 25. *Xyela (Xyela) micrura* sp. nov., photograph of holotype. 26. *Xyela (Xyela) magna* Statz, 1936, photograph of holotype.

numery) vein between RS and M+Cu and in free SC branch situated near RS base (more distally than figured). Ovipositor long, flat (saw-like), down-curved, with sheath:basal plate ratio 2:1, wing: ovipositor ratio 1.5:1. Length of body with ovipositor, as preserved, 7 mm, forewing length 4.5 mm, ovipositor 3.1 mm, sheath 2.1 mm.

TAXONOMIC POSITION. In Rasnitsyn's (1965) key, this fossil keys to the *X. minor* group and particularly to *X. minor* Norton, 1868, and *X. pini* Rohwer, 1913. It differs from both in having a widely rounded sheath apex and an intermediate sheath: basal plate ratio. Additionally, it differs from the latter species in having a shorter ovipositor and sheath. *Xyela magna* is most similar to North American species.

Genus cf. *Enneoxyela*
Rasnitsyn, 1966
? *Enneoxyela cenozoica*
(Zhang, 1989) comb. nov.
Figure 27

Xyela cenozoica Zhang, 1989: 211, figs. 205, 206, pl. 57, fig. 1.

MATERIAL EXAMINED. Photograph of LPM holotype 820138; Shanwang Formation, 22 km east of Linq, Shandong Province, China; Middle Miocene.

DESCRIPTION. Color dark. Head narrow. Antenna with 3rd segment and funicle both short, subequal in length, funicle figured originally as about 8-segmented. Forewing with SC free, meeting R well before RS base, meeting C clearly beyond RS base. R almost straight, gently curved at (not before) RS base. First abscissa of RS much longer than that of M, RS+M shorter than the latter. Pterostigma narrow, with 2r-rs at its midlength. Ovipositor long, upcurved, tapering caudally, sheath probably half as long as forewing or a little longer. Length of body with ovipositor, as preserved, 9.3 mm, forewing length 5.3 mm, sheath more than 2.3 mm.

TAXONOMIC POSITION. Characters seen on the photograph of the holotype basically are diagnostic of *Enneoxyela*, which is known from three species from the Late Jurassic of the Karatau Range in Southern Kazakhstan (northern central Asia) (Rasnitsyn, 1966, 1969). There are differences, however, particularly in the relatively short SC and in the ovipositor which is upcurved and tapering rather than being straight and parallel-sided. These differences warrant separation of the fossil in a new, closely related genus. I prefer to postpone this until study of the actual holotype is possible.

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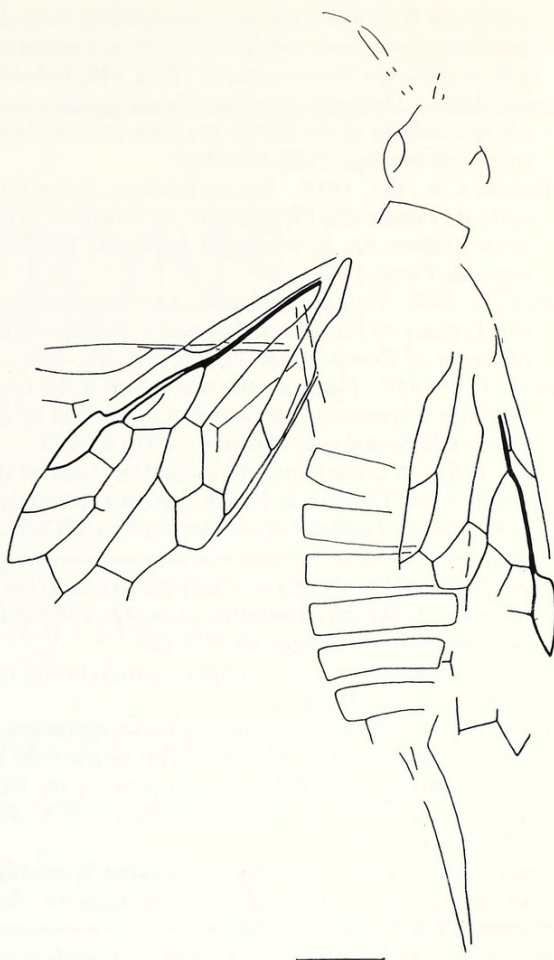


Figure 27. ?*Enneoxyela cenozoica* (Zhang, 1989), line drawing traced after the photograph of holotype.

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LITERATURE CITED

- Ashmead, W.H. 1898. Classification of the horntails and sawflies, of the suborder Phytophaga. *Canadian Entomologist* 30:205-213.
Benson, R.B. 1960. Two new European species of *Xyela* Dalman (Hymenoptera: Xyelidae). *Proceedings of the Royal Entomological Society of London B* 29(7-8):110-112.
———. 1961. The sawflies (Hymenoptera Symphyta) of

- the Swiss National Park and surrounding area. *Ergebnisse der wissenschaftlichen Untersuchungen des schweizerischen Nationalparks* 7(N.F.)(44):163–191.
- . 1962. Holarctic sawflies (Hymenoptera: Symphyta). *Bulletin of the British Museum (Natural History) Entomology* 12(8):381–409.
- Brébisson, L.A., de. 1818. Sur un nouveau genre d'insecte de l'ordre des Hyménoptères (Pinicola). *Nouveau Bulletin des Sciences par la Société Philomatique de Paris*, 116–117.
- Brues, C.T. 1908. New phytophagous Hymenoptera from the Tertiary of Florissant, Colorado. *Bulletin of the Museum of Comparative Zoology* 51:257–276.
- Burdick, D.J. 1959. Notes on the taxonomy of the fossil Xyelidae (Hymenoptera: Symphyta). *Journal of the Kansas Entomological Society* 32(3):120–122.
- . 1961. A taxonomic and biological study of the genus *Xyela* Dalman in North America. *University of California Publications in Entomology* 17(3):285–356.
- Dalman, J.W. 1819. Några nya Genera och Species af Insekter, beskrifna. *Kunglige Svenska Vetenskapsakademiens Handlingar* 40:117–127.
- Farris, J.S. 1988. Hennig86. Computer program and reference manual. 18 pp.
- Fridolin, W.Yu. 1936. The animal-plant community of the mountain region Khibiny. The biocenotic research during 1930–1935. *Transactions of the Kola Station, Academy of Sciences of the U.S.S.R.* 3:3–295 (in Russian).
- Königsmann, E. 1976. Das phylogenetische System der Hymenoptera. I. *Deutsche Entomologische Zeitschrift*, N.F. 23(4/5):253–279.
- Konow, F.W. 1897. Über die Xyelini. *Entomologische Nachrichten* 23:55–58.
- Krassilov, V.A., and A.P. Rasnitsyn. 1982. Unique finding: Pollens in gut of the Early Cretaceous sawflies. *Paleontologicheskii Zhurnal* 4:83–96 (in Russian).
- Linné, C., von. 1753. *Systema Naturae systema Regna tria Naturae, in Classes et Ordines, Genera et Species redacta tabulisque aeneis illustrata*. Editio 8. Holmiae, 136 pp.
- Meunier, F. 1920. Quelques insectes de l'Aquitaine de Rott, Sept.-Monts (Prusse rhénane). *Koninklijke Academie van Wetenschappen te Amsterdam, Proceedings, Section of Science* 22(2):891–898.
- Newman, E. 1834. Attempted division of British insects into natural orders. *Entomological Magazine* 2:379–431.
- Norton, E. 1868. Catalogue of the described Tenthredinidae and Uroceridae of North America. *Transactions of the American Entomological Society* 2:321–368.
- Patterson, C., and D.E. Rosen. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* 158:81–172.
- Rasnitsyn, A.P. 1964. New Triassic Hymenoptera from Middle Asia. *Paleontologicheskii Zhurnal* 1:88–96 (in Russian).
- . 1965. Notes on the biology, systematics and phylogeny of Xyelinae (Hymenoptera, Xyelidae). *Polskie Pismo Entomologiczne* 35(12):483–519 (in Russian, with English summary).
- . 1966. New Xyelidae (Hymenoptera) from the Mesozoic of Asia. *Paleontologicheskii Zhurnal* 4:69–85 (in Russian; translated into English in *International Geological Review*, 1967, 9:723–737).
- . 1969. Origin and evolution of Lower Hymenoptera. *Transactions of the Paleontological Institute, Academy of Sciences of the U.S.S.R.* 123:1–196 (in Russian; translated into English in 1979 by Amerind Co., New Delhi).
- . 1971. Evolution of Xyelidae (Hymenoptera). In *Current problems in paleontology. Transactions of the Paleontological Institute, Academy of Sciences of the U.S.S.R.* 130:187–196 (in Russian).
- . 1980. Origin and evolution of Hymenoptera. *Transactions of the Paleontological Institute, Academy of Sciences of the U.S.S.R.* 174:1–192 (in Russian).
- . 1987. The importance of [not] being a cladist. *Sphecos* 14:23–25.
- . 1988. Outline of evolution of the hymenopterous insects (order Vespida). *Oriental Insects* 22:115–145.
- Rohwer, S.A. 1913. A synopsis, and description of the Nearctic species of sawflies of the genus *Xyela*, with descriptions of other new species of sawflies. *Proceedings of the U.S. National Museum* 45:265–281.
- Ross, H.H. 1932. The hymenopterous family Xyelidae in North America. *Annals of the Entomological Society of America* 25:153–169.
- Smith, D.R. 1978. Suborder Symphyta. In *Hymenopterorum Catalogus*, Pars 14, ed. J. Van der Vecht and R.D. Shenefeldt, Hague: Dr. W. Junk, 193 pp.
- Sphon, G.G. 1973. Additional type specimens of fossil invertebrata in the collections of the Natural History Museum of Los Angeles County. *Contributions in Science, Natural History Museum of Los Angeles County* 250:1–75.
- Statz, G. 1936. Über alte und neue fossile Hymenopterenfunde aus den tertiären Ablagerungen von Rott am Siebengebirge. *Decheniana* 93:256–312.
- Weyland, H. 1937. Beiträge zur Kenntnis der rheinische Tertiärfloora. II. *Palaeontographica Abt. B* 83:67–122.
- . 1948. Beiträge zur Kenntnis der rheinische Tertiärfloora. VII. *Palaeontographica Abt. B* 88:113–188.
- Zhang, Jun feng. 1989. *Fossil insects from Shanwang, Shandong, China*. Jinan: Shandong Science and Technology Publishing House, 459 pp. (in Chinese, with English summary).
- Zhelochovtzev, A.N., and A.P. Rasnitsyn. 1972. On some Tertiary sawflies (Hymenoptera: Symphyta) from Colorado. *Psyche* 79(4):315–327.
- Zherikhin, V.V., and I.D. Sukacheva. 1989. Patterns of insect burial in resins. In *Sedimentary cover of the earth in time and space. Stratigraphy and paleontology*, ed. B.S. Sokolov, 84–92. Moscow: Nauka Press (in Russian, with English summary).

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yn, A. P. 1995. "Tertiary sawflies of the tribe Xyelini (Insecta: Vespida = Hymenoptera: Xyelidae) and their relationship to the Mesozoic and modern faunas." *Contributions in science* 450, 1–14. <https://doi.org/10.5962/p.208084>.

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