



First record of anaxyelid woodwasps (Hymenoptera: Anaxyelidae) in Lower Cretaceous Spanish amber

J. ORTEGA-BLANCO¹, A.P. RASNITSYN² & X. DELCLÒS¹

¹Dep. d'Estratigrafia, Paleontologia I Geociències Marines, Facultat de Geologia, Universitat de Barcelona, 08071 Barcelona, Spain. E-mail: j.ortega.blanco@ub.edu, xdelclos@ub.edu

²Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya Str. 123, 117997, Moscow, Russia, and Natural History Museum, Cromwell Road SW7 5BD, London, England. E-mail: rasna_us2002@yahoo.com

Abstract

A new species of the family Anaxyelidae (*Eosyntexis parva* n. sp.) is described. This is the first record of the family from Lower Cretaceous Spanish amber. The specimen is mostly well preserved, except for dorsally. This makes it possible to identify several important details rarely or never observed in compression fossils. *Eosyntexis* spp. and the closely related genus *Cretosyntexis* are confined to the Eurasian Lower Cretaceous, whereas the extant monotypic genus *Syntexis* is restricted to western North America. The morphology of this new species suggests xylophagous habitus, and its relation with *Syntexis libocedrii* implies a possible relationship with burned wood, apparently a frequently available resource in northern Spanish forests of the Lower Cretaceous.

Key words: “Symphyta”, Albian, Peñacerrada, Basque Country, Spain

Introduction

The new species is placed into the Anaxyelidae that was defined by Martynov (1925) for fossil specimens from the Jurassic of Turkestan within the “Symphyta”.

To date, 12 genera and 27 species of the family Anaxyelidae have been described. Of these, there is only one extant species, the incense cedar wood wasp *Syntexis libocedrii* Rohwer, 1915, recorded from southwestern USA (California, Idaho, Oregon). All previous extinct taxa were found as compression fossils in sedimentary rock, mainly carbonate deposits, but also tuffaceous siltstones and mudstones in Daohugou (China) (Rasnitsyn & Zhang 2004a), and detritic siltstones in Yixian (China) and Kempenday (Russia) (Sinitshenkova, 1992). This is the first species of Anaxyelidae to be found as an amber inclusion and, together with a few orussid fossils (*sensu* Vilhelmsen 2004; Engel 2008), it is the only non-apocritan fossil found in Mesozoic amber (Rasnitsyn 1977; Zhang & Rasnitsyn 2006).

Syntexis libocedrii can be found in the northwestern USA (California, Idaho, Oregon) (Rohwer 1915; Benson 1935). The incense cedar wood wasp has very unusual ovipositing behaviour: it lays its eggs into recently burnt or even still burning wood of some cupressacean conifers, such as *Libocedrus decurrens*, *Juniperus occidentalis*, and *Thuja plicata* (Middlekauff 1964). The male was first described, the host plants identified and the life cycle found to be annual, only much later (Middlekauff 1964, 1974).

Rohwer (1915) described *Syntexis libocedrii* based on two female individuals and initially placed the species in the Cephidae, but also noted some similarities with the Xiphydriidae. *Syntexis* resembles Cephidae in the morphology of the thorax and the basal part of the abdomen, but is more like Xiphydriidae in the structure of the palpi, the antennae, long malar space, ventral elongation of the cheek, wing venation, elongate female

eighth tergum, and its ovipositor morphology. He proposed that *Syntexis* should be placed within the Cephidae because the characters they shared were less subject to modifications by adaptation, and he considered that Cephidae were ancestors of the Xiphydriidae. Benson (1935) did not agree with the placing of *Syntexis* within the Cephidae, concluding that there were more similarities with the Xiphydriidae. Ross (1937) pointed out that *Syntexis* differs from Xiphydriidae in not having a transscutal articulation, and in the wide groove between the mesoscutellum and metanotum. For this reason Benson proposed the new family Syntexidae, which was later placed as a subfamily within Anaxyelidae by Rasnitsyn (1969).

Modern hymenopteran phylogenetic analyses were initiated by Rasnitsyn (1988). Some of his clades are upheld by more recent cladistic analyses. The major dichotomies of the non-apocritan Hymenoptera (non monophyletic “Symphyta”) have been resolved since Rasnitsyn’s (1988) and Vilhelmsen’s (1997) studies. In 1997 Vilhelmsen proposed a cladistic analysis of “symphytan” relationships based on morphological characters. He obtained the same results as Rasnitsyn (1988) with the Anaxyelidae in the “Symphyta”, as a sister-group of the [Siricidae + Xiphydriidae + (Orussoidea + Apocrita)]. Rasnitsyn (2002) and Rasnitsyn *et al.* (2004) proposed the same hypothesis. Ronquist (1999) and Ronquist *et al.* (1999) proposed a phylogeny of the symphytans that shows a trichotomy at the base of Anaxyelidae + Siricidae + [Xiphydriidae + (Orussidae + Apocrita)]. Rasnitsyn (2000a) reviewed different previous proposals and combined some figures drawn by Ronquist *et al.* (1999), showing Anaxyelidae as the sister-group of the Jurassic Gigasiricidae. This family has recently been included as a subfamily within the Siricidae leaving Protosiricidae as the sister of Anaxyelidae (Rasnitsyn & Zhang, 2004a). In 2001, Vilhelmsen proposed a new cladistic analysis of the Hymenoptera with the same unresolved trichotomy, and considered Siricoidea non monophyletic. Sharkey & Roy (2002) re-analysed the data of of Ronquist *et al.* (1999), emphasizing wing venation; the proposal included a basal tetrachotomy of Anaxyelidae + Siricidae + Xyphydriidae + parasitic Hymenoptera. Schulmeister *et al.* (2002) and Schulmeister (2003 a, b) combined molecular and morphological data and differed from Vilhelmsen’s results in a sister-group relationship between Anaxyelidae and Siricidae, included in Siricoidea. To date, the placement of the Anaxyelidae is controversial; morphological data suggest it as the sister of Siricidae + Xiphydriidae + Vespina (= Orussoidea + Apocrita), whereas the molecular data support its being a sister-group of Siricidae. Recent synthesis (Sharkey 2007) does not favour either of these proposals.

Fossil Hymenoptera from the Spanish Lower Cretaceous

With the exception of Peñacerrada amber, Lower Cretaceous Hymenoptera are found in Spain in the lithographic limestones (Barremian in age) partly from Las Hoyas (Cuenca Province) and mainly from El Montsec (Lleida Province) (Rasnitsyn 2000b; Rasnitsyn & Ansorge 2000a, b; Rasnitsyn & Martínez-Delclòs 2000). The following families have been recorded: Xyelotomidae Rasnitsyn, 1968, Sepulcidae Rasnitsyn, 1968, Anaxyelidae Martynov, 1925, Ephialtitidae Handlirsch, 1906, Praeaulacidae Rasnitsyn, 1972, Gasteruptiidae Ashmead, 1900, Andreneliidae Rasnitsyn & Martínez-Delclòs, 2000, Mesoserphidae Kozlov, 1970, Bethylo-nymidae Rasnitsyn, 1975, Sphecidae Latreille, 1802, Scoliidae Latreille, 1802, and possibly Bethylidae Haliday, 1833. La Cabrera outcrop in the Montsec is the type locality of two species of the Anaxyelidae: *Eosyntexis catalonicus* [*recte: catalonica*] Rasnitsyn & Martínez-Delclòs, 2000, and *Cretosyntexis montse-censis* Rasnitsyn & Martínez-Delclòs, 2000.

In the Spanish ambers, hymenopteran individuals are frequently found, and Hymenoptera is the second most diverse and abundant group of insects (Delclòs *et al.* 2007). The majority of specimens belong to the suborder Apocrita. Eight families of non-aculeate parasitic wasps are represented: Trigonalidae, Evaniidae, Megaspilidae, Scelionidae, Stigmaphronidae, Serphitidae, Mymaromatidae, and Braconidae. The specimen previously cited as a member of the Orussidae (Delclòs *et al.* 2007) is not an orussid (Vilhelmsen pers. com.). Aculeata make up 4% of the Hymenoptera and belong to the Sphecidae, Chrysididae and Bethylidae families.

Álava amber is found in several outcrops of the Basque-Cantabrian Basin (Delclòs et al. 2007). The palynological assemblage suggests an Upper Aptian-Lower Albian age for the deposit that contains the amber included in the Escucha Formation, and the presence of *Inaperturopollenites dubius* pollen is related to the conifer family Cupressaceae (Barrón et al. 2001). In the Basque-Cantabrian Basin, the Escucha Formation is divided into three sub-units which represent the regression-transgression vertical evolution of a deltaic system. Amber levels are associated with coal layers that are abundant in the middle member of the formation, coinciding with the period of maximum regression of the deltaic system (Salas et al. 2001; Martínez-Torres et al. 2003), related to inter-distributary deltaic bay sequences, associated with the top of abandoned channels or on crevasse splay facies.

Hymenopterans included in this amber lived between a high number of anemophilous and hydrophilous plants and a low proportion of entomophilous ones. The palynological associations suggest the presence of a dense low-land wet coniferous forest (mainly of araucariaceans and cupressaceans, and with lesser presence of pinaceans and podocarpaceans) on alluvial plains, with an important under-forest of lycophytes and schizaeacean ferns, and coastal areas under xeromorphic conditions, dominated by cheirolepidiacean conifers and cyathacean and matoniacean ferns, under a wet and cold climate (Barrón et al. 2001).

Material and methods

The type locality for the new species is Peñacerrada I (Moraza, Spain). The specimen is an inclusion in a small piece of amber (9.0 x 2.5 x 3.3 mm), now embedded in an epoxy resin EPO-TEK 301 (9.3 x 2.8 x 3.4 mm). The technique for its preparation is explained in Corral *et al.* (1999). It is housed in the Museo de las Ciencias Naturales de Álava, in Vitoria-Gasteiz (Province of Álava, Spain), reference number MCNA 8756.

The specimen was examined with a Leica MZ 9.5 stereomicroscope using both reflected and transmitted light. Drawings were made using a *camera lucida* attached to the stereomicroscope. The fossil was photographed by the above microscope and a Nikon D70 camera, and measurements established with the Leica IM1000 image manager.

Body morphology and wing nomenclature (Fig. 1) are slightly modified after Rasnitsyn (1980). Nomenclature of the surface sculpture of integuments is after Harris (1979).

Taxonomy

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Superfamily “Siricoidea” Billberg, 1820

Family Anaxyelidae Martynov, 1925

Subfamily Syntexinae Benson, 1935

Remarks: The family Anaxyelidae is included in the Siricoidea [= Anaxyelidae + “Gigasiricidae” + Siricidae (*sensu* Grimaldi & Engel 2005); = Anaxyelidae + Protosiricidae + Daohugoidae + Siricidae + Xiphydriidae (*sensu* Rasnitsyn & Zhang 2004a, b, Rasnitsyn 2006)] and comprises four subfamilies: the Late Jurassic Anaxyelinae Martynov, 1925, the Late Jurassic or Lower Cretaceous Kempendajinae Rasnitsyn, 1980, the Lower Cretaceous Dolichostigmatinae, Rasnitsyn 1968 and the Lower Cretaceous – Recent Syntexinae Benson, 1935. The palaeogeographical range of the family is extensive, specimens being known from Central

Asia, England, Spain and Brazil. The Syntexinae includes three genera: the extant *Syntexis* Rohwer, 1915 and two Lower Cretaceous genera, *Eosyntexis* Rasnitsyn, 1990 (Neocomian of East Siberia, Berriasian of England and Barremian of Spain) and *Cretosyntexis* Rasnitsyn & Martínez-Delclòs, 2000 (Barremian of Spain) (see Fig. 5).

New diagnosis of Syntexinae. Pedicel as long as scape (known only for *Syntexis* and *Eosyntexis parva* n. sp.) (Figs. 2G and 4B). Pronotum with dorsal face well developed and crossed by medial suture or impressed line (Fig. 2C). Mesonotum with distinct transverse rugae (known for *Syntexis* and *Cretosyntexis*, although in *E. parva* similar rugae are present on the pronotum) (Figs. 2A, C and 3E). Fore wing with SC completely lost, 1r-rs either longer than 2r-rs or lost. Hind wing with r-m placed near RS bending and with m-cu lost (known only for *Syntexis* and *Eosyntexis senilis*).

Remarks. The Syntexinae show an important simplification and reduction of the wing venation (Fig. 1): fore wing with SC completely lost, RS more or less straightened between cells 1mcu and 2r due to 1r-rs crossvein either long or lost, distal R and RS sometimes lost; hind wing when known with distal venation somewhat reduced, with r-m crossvein displaced basally and m-cu lost. Also the long pedicel, furrowed pronotum and mesonotum with marked sculpture distinguish Syntexinae from the three other subfamilies.

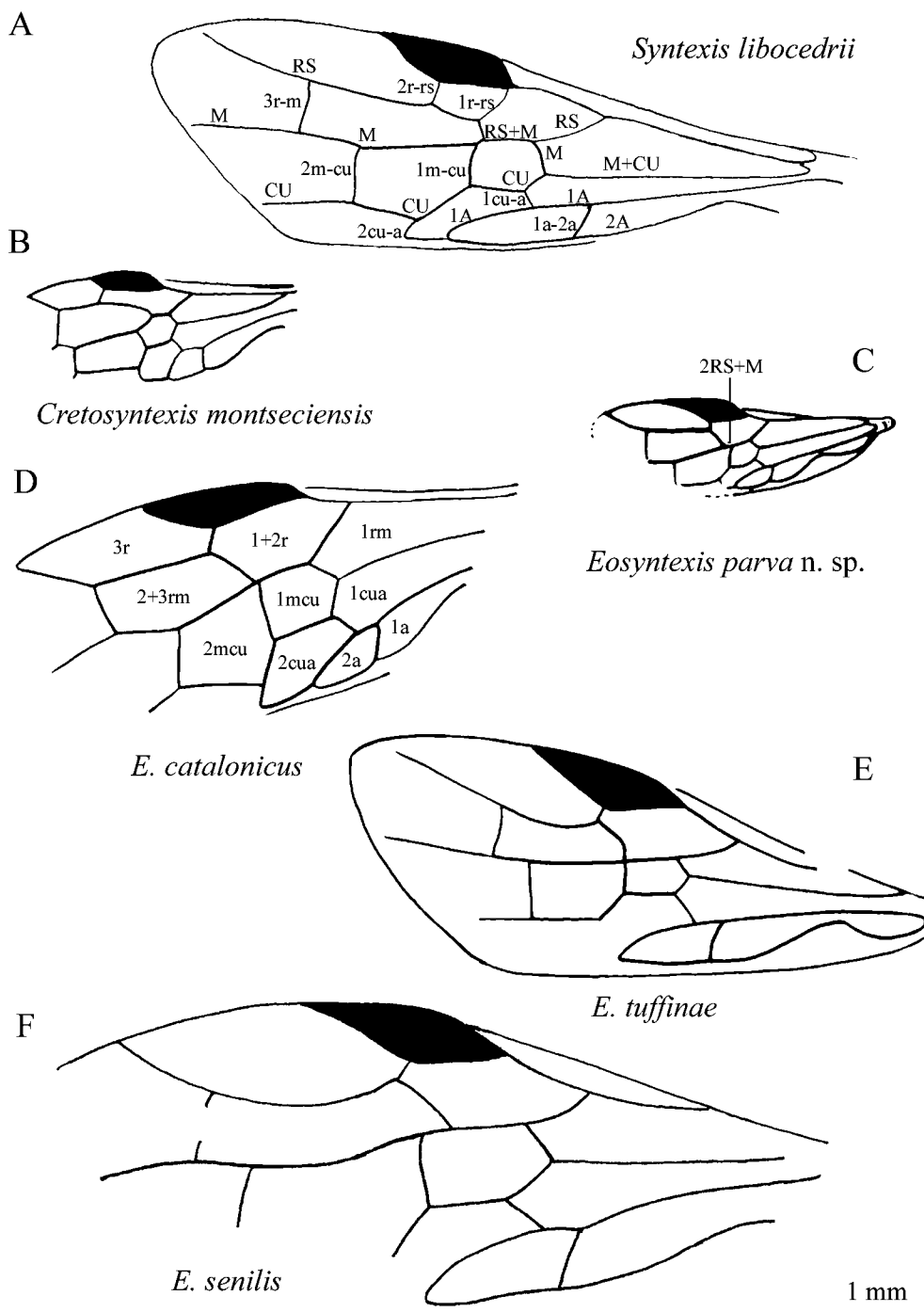
Genus *Eosyntexis* Rasnitsyn, 1990

Type species: *Eosyntexis senilis* Rasnitsyn, 1990.

Included species: *E. senilis* Rasnitsyn, 1990 from the Lower Cretaceous of Transbaikalia, *E. tuffinae* Rasnitsyn & Jarzembowski in Rasnitsyn *et al.*, 1998 from the Lower Cretaceous (Berriasian in age) of England, *E. catalonica* Rasnitsyn & Martínez-Delclòs, 2000 and *E. parva* sp. n. from the Lower Cretaceous (Barremian and Albian in age, respectively) of Spain.

New diagnosis of the genus. Forewing (Fig. 1C-F, 2D) with pterostigma sclerotized; crossvein 1r-rs lost; cell 1mcu pentagonal or, if hexagonal, with one side very short; crossvein 2r-rs arising from the mid-part of pterostigma (not from near apex); M+Cu vein straight or slightly arched only very basally; section 3Cu shorter than 4Cu. Flagellomeres of the antenna less than twice as long as wide (Figs. 4A, C). Pronotum with distinct fore and upper faces meeting at angle (Fig. 3E). Propleura not elongated to form a distinct neck (Figs. 2B, 3A).

Remarks. Within Syntexinae, *Syntexis* is the most distinct because of its flat pronotum, transparent (unsclerotized) pterostigma, R lost beyond pterostigma, 1r-rs retained, section 3Cu and cell 2a very long (longer than half of 1a). These characters are difficult to evaluate without a cladistic analysis, although they suggest that *Eosyntexis* is more closely related to *Cretosyntexis* than to *Syntexis* (except for the form of pronotum which is not known in sufficient detail for *Cretosyntexis*). Nevertheless, *Eosyntexis* is more like *Syntexis* than *Cretosyntexis* in some wing characters, such as having 2r-rs placed at pterostigmal mid-length (correlating with this, RS before it very long and arched near 1mcu), M+Cu straight and 1mcu pentagonal or almost so. *Eosyntexis* differs from the other genera in having flagellomeres comparatively short. The main similarity between *Eosyntexis* and *Cretosyntexis* lies in loss of 1r-rs and pronotum differentiated into fore and upper faces meeting at angle. Similarities between *Syntexis* and *Eosyntexis* are the straight M+Cu, the pentagonal 1mcu and the proximal position of 2r-rs. Finally, *Syntexis* and *Cretosyntexis* resemble each other in having long, narrow antennomeres. The exact relationships between the different genera are impossible to decide without a cladistic analysis.



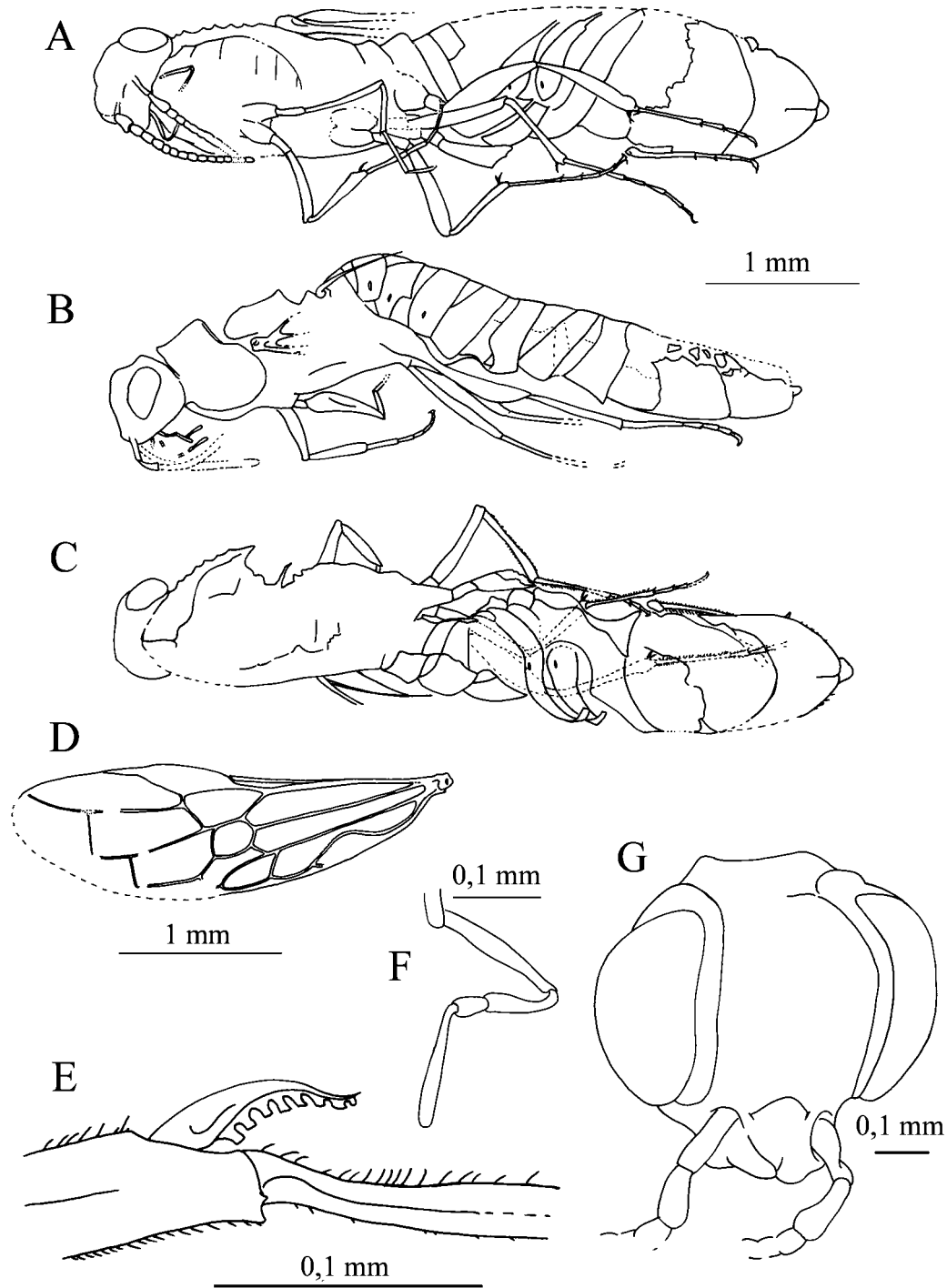
FIGURES 1. Forewings of members of the subfamily Syntexinae at the same scale, showing venation (A and C) and cell nomenclature (D).

***Eosyntexis parva* sp. nov.**

Figure 1C and Figures 2-4.

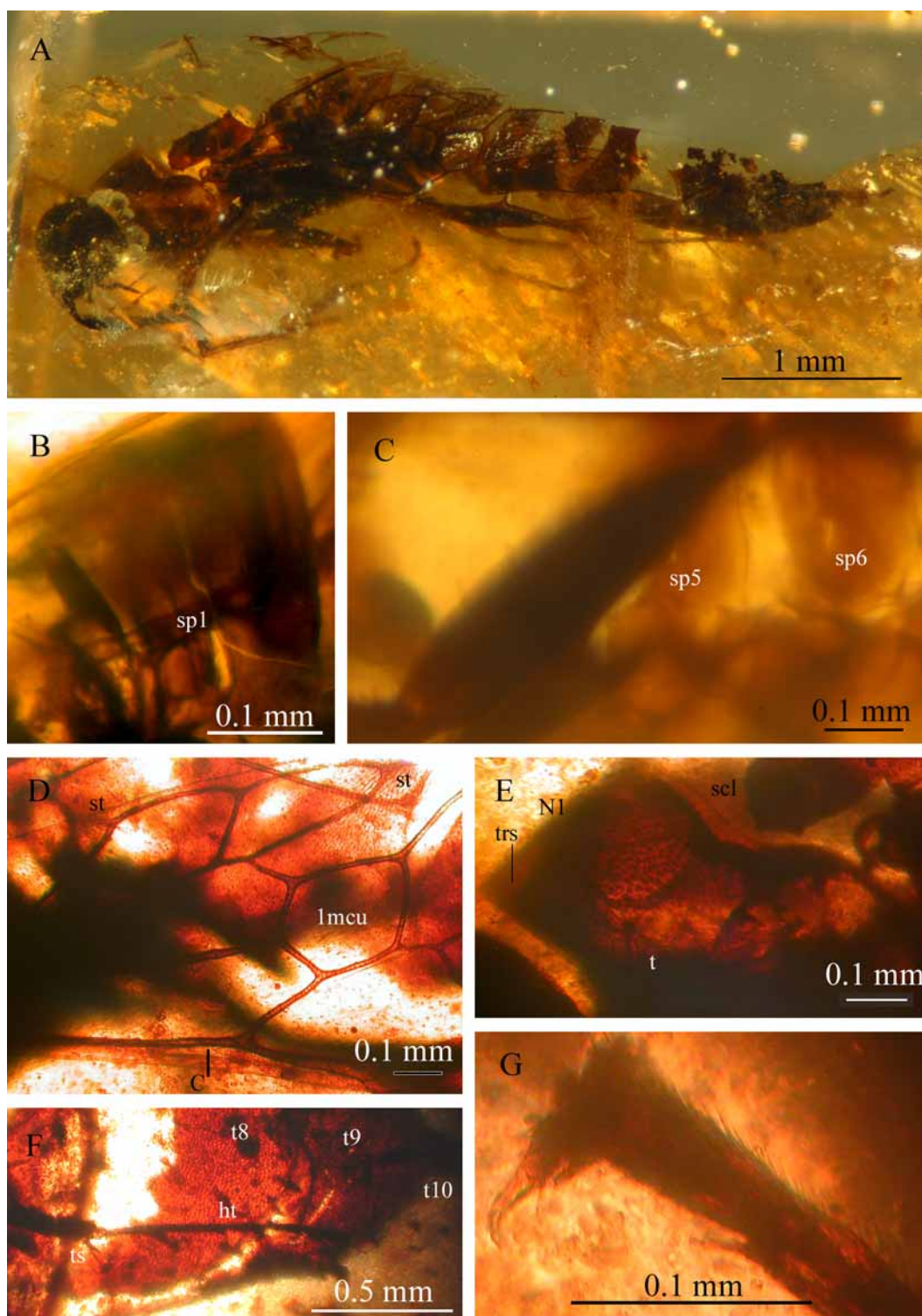
Etymology. The species name is derived from the Latin “little”, due to its small size.

Material. Holotype: MCNA 8756, from Peñacerrada I amber fossil site, Escucha Formation, Moraza village (Spain) (Alonso *et al.* 2000; Delclòs *et al.* 2007). Specimen housed in the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Basque Country, Spain).



FIGURES 2. Drawings of general habitus of the holotype of *Eosyntexis parva* n. sp. MCNA 8756. A) in ventral view, B) in left view and C) in dorsal view. D) Left fore wing reconstructed from left and ventral views. E) Right fore tibial calcar. F) Maxillary palp. First and second segments seen in left view. G) Frontal view (note the pedicel as long as the scape).

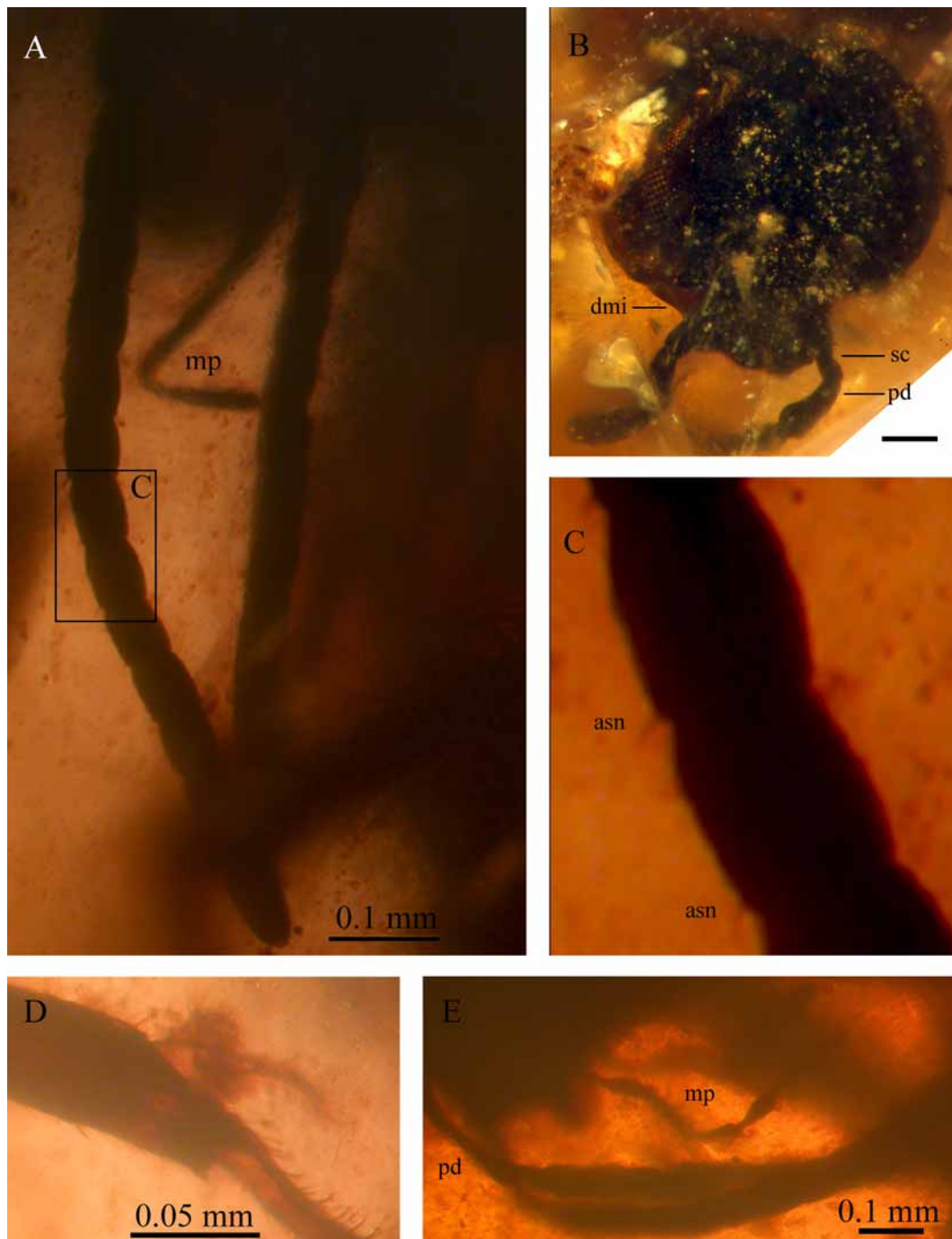
Description. Head roughly as wide as thorax, widest at temples, in side view only slightly longer than high (Figs. 2A-C). Eyes moderately large, subovoid, distant from mandibular base for ca. 0.3 of its length. Ocelli not visible. Vertex somewhat elevated above eyes. Temples inflated, as wide as eye in side view. Genae excavated to form a channel to accommodate scape at rest. Clypeus narrow, somewhat protruding. Mandibles short and apparently wide, teeth and precise form not discernible. Antennal base near clypeal sides below eye (Figs. 2B, G, and 4B). Antenna apparently 16 segmented with scape and pedicel sub-equal in



FIGURES 3. Photographed habitus and details of *Eosyntexis parva* n. sp. MCNA 8756. A) Left view. B) Spiracle in tergum 1 (sp1). C) Spiracles in terga 5 (sp5) and 6 (sp6). D) Detail of 1mcu cell and vein stubs (st) (see also the transverse striation in mid terga in second plane). E) Pronotum (N1) showing the transversal suture (trs) with both faces meeting at right angle, punctuated sculpturation and teeth (t), and support of the dorsal mesonotal sclerite (scl). F) Left hind tarsus (ht), and habitus and sculpturation of terga 8, 9 and 10 (t8, t9, t10, respectively). G) Simple tarsal claw of right mid leg.

length, about twice as long as first flagellomere, both flattened dorso-ventrally (scape particularly so), pedicel quite broadened at apex. Flagellomeres slightly longer than wide, all similar in size and shape except for the first slightly narrowing toward base, middle ones slightly wider than the rest, and apical flagellomere dis-

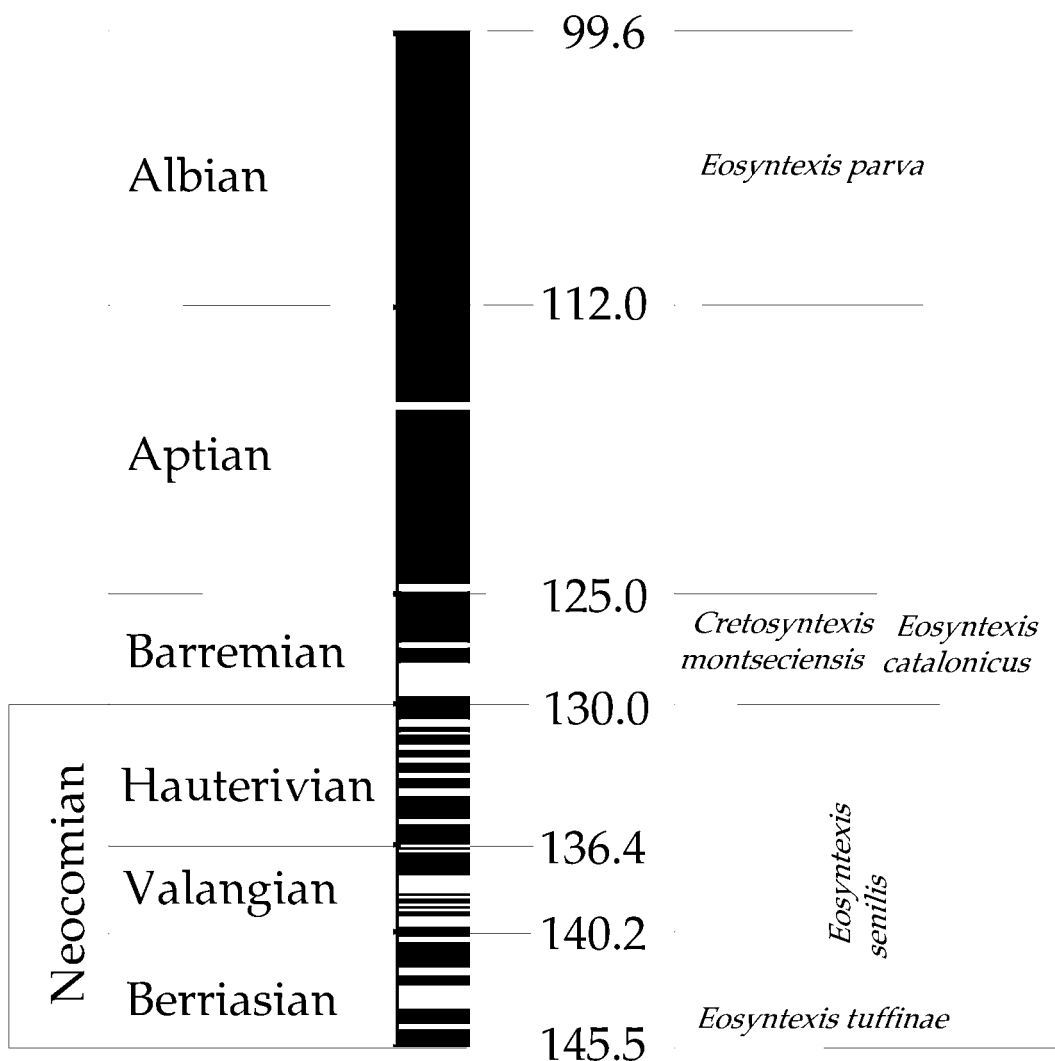
tinctly longer and rounded apically. Trichoid sensilla present at apex of flagellomeres, possibly except several basal and apical ones (Figs. 2A, G, 4A, B, C, E). Maxillary palps six-segmented, third and sixth segments longest, sixth segment thickened in apical half (Figs. 2F, 4A, E).



FIGURES 4. Photographed details of *Eosyntexis parva* n. sp. MCNA 8756. A) Antenna and 3rd and 4th segments of maxillary palp (mp) in frontal view. B) Habitus in frontal view showing the deep malar impression (dmi), and the long pedicel (pd) and scape (sc) (scale bar 0.1 mm). C) Detail of 7th and 8th flagellomeres showing apical sensilla (asn). D) Calcar on the right fore tibia with velum deeply incised in several (apparently 8) lamellae; E) Left view of the maxillary palpi (mp) and the pedicel (pd) strongly compressed dorso-ventrally.

Pronotum with high vertical (forward) and long horizontal (upper) faces meeting at about right angle and carinated there, with carina low medially. Dorsal pronotal face 2/3 as long as lateral face, with medial impressed line, rather punctate except laterally, smooth band at junction of dorsal and lateral face with six low

teeth placed longitudinally (better seen in upper view) (Figs. 2B, C, 3E). Lateral pronotal face forming wide rounded lobes lateroventrally. Fine imbricate sculpturation over most of pronotum. Propleura not elongated to form distinct neck (Figs. 2B, 3A, E). Mesonotum not preserved. Mesopostnotum short, not well preserved but apparently laterally slightly constricted. Legs moderately short, looking flattened as preserved. Coxae small, trochanter rather thin, sub-cylindrical. No trochantellus seen with any certainty. Fore and mid femora narrow, slightly curved and almost parallel-sided; hind femur elongate fusiform, roughly four times as long as wide. Tibiae thin, somewhat widened apically, hind tibia wider (Figs. 2A, B, C, 3A). Fore tibia with one apical spur, and mid and hind tibia with two. No sub-apical spurs found. Fore tibia with distinct dorso-apical spine. Fore tibial spur (calcar) thick basally, otherwise thin, slightly S-shaped, inner surface with deeply incised velum with several (possibly 8) indentations, with free, possibly bifid apex (Fig. 4D) (cf. Basibuyuk & Quicke 1995). Proportion of tarsomeres in fore leg (first tarsomere is 1) 1: 0.5: 0.3: 0.2: 0.27, mid leg 1: 0.55: 0.50: 0.4: ?, hind leg 1: 0.35: 0.3: 0.22: ca. 0.22. Fore basitarsus with inner surface slightly concave in basal 0.45 bearing protocomb here composed of not very regular row of slightly curved setae of varying length. Tarsal claws simple (Fig. 3G).



FIGURES 5. Time scale showing the age of each fossil Syntexinae.

Fore wing with pterostigma large (sub equal in area to 1+2r cell), R lost beyond pterostigma, 1RS straight, as long as 1RS+M, 1r-rs lost, 2r-rs very short, 2RS+M slightly longer than 2r-rs, 3RS straight in basal half and gently arching beyond, reaching very near wing fore margin. Crossvein 2r-m not preserved (might be lost).

Crossvein 2cu-a levelled with pterostigmal apex. Anal loop with distal vein stub (Figs. 2D, 3D).

Abdomen long, much damaged (especially the dorsal part), with ten segments, without laterotergites, the last segment very small and rounded apically. Abdominal spiracles slit-like, small except larger one on tergum 1 (seen on terga 1, 2, 3, 5 and 6) (Figs. 2A, B, C, 3B, C). No genitalia preserved, but ninth tergum strongly convex in rear half (decreasing toward 10th tergum) and with lower basal corners somewhat elongate cephalad indicating female sex. Fore and mid terga with fine transverse striation at least laterally, eighth and ninth terga looking darker than the previous, with imbricate sculpture (Figs. 3D, F).

Body length ca. 4.4 mm, fore wing length 2.7 mm.

Comparison. Unlike other *Eosyntexis* species, *E. parva* has cells 2+3rm and 1m_{cu} are separated by distinct 2RS+M, R is lost shortly beyond pterostigma and, unlike all except *E. tuffinae*, 2r-rs is very short. Additionally, unlike *E. senilis* and *E. tuffinae*, 1RS is straight. Unlike *E. senilis*, cell 1m_{cu} is pentagonal. Unlike *E. catalonica*, cell 2m_{cu} is longer than high. Unlike *E. tuffinae*, 2RS is straight and RS practically reaches wing margin. In non-venational characters, it differs from all other species in smaller body and wing size and also from *E. catalonica* in more narrow body and legs, large eyes, fewer antennomeres (15 or 16 against 17 or more) and longer dorsal face of pronotum.

Discussion

The new species can be confidently assumed to develop in wood, probably a conifer. This inference is based both on its taxonomic position within the superfamily Siricoidea, whose extant species are all xylophagous when this feature is known, and on its own functional morphology. In particular, its inflated temples indicate hypertrophied mandibular occlusor muscles for the eclosed adult wasp to get out. The series of “teeth” or spines on the lateral side of pronotum, as well as apical teeth of the fore tibia, are adaptations widespread among wood-living wasps to brace the body within the tunnel in wood, and so support mandibles reliably when they are active. The long and impressed malar space is equally a common insect adaptation to xylophagy which helps to accommodate and protect antennae when escaping from the wood.

Females of *Syntexis libocedrii* lay eggs in recently burnt cupressacean trees (Middlekauff 1964, 1974). Probably the host tree for *E. parva* was a gymnosperm conifer. Conifer pollen and wood is common in Álava amber, as pointed out in Alonso *et al.* (2000) and Barrón *et al.* (2001), and evidence of fossilized burnt wood also exists (Suárez-Ruiz 2003). Furthermore in the Spanish Barremian limestones, where other species of Anaxyelidae have been found, fusinized wood is present, suggesting that forest fires were common at the time of deposition. Unfortunately, we have no direct evidence of the oviposition behaviour of *E. parva*. Like *S. libocedrii*, it may have been attracted to fires.

A woodwasp infesting conifers did have a good chance of being trapped in resin and eventually being preserved as an amber inclusion. Nevertheless, the paucity of this highly specialised group of Hymenoptera in any amber around the world may be because of their body size, which is larger than the average size of the Cretaceous amber pieces (larger pieces are more common in Cenozoic amber deposits, but at that time siri-coids might have been much rarer than in the Mesozoic) (Middlekauff 1974). The very small body size of the present fossil, which is one of the smallest of all woodwasps, is probably the reason it was preserved in amber (Martínez-Delclòs *et al.* 2004). Perhaps the specimen was an unusually small one for the species (the extant *Syntexis libocedrii* ranges from 4.6 to 13.3 mm; Middlekauff 1964). The absence in Cretaceous amber of any other Anaxyelidae suggests that they were big enough to not be trapped in resins or that they laid eggs in freshly burnt wood before the resin was exuded.

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