

## A new belytine wasp in Cretaceous amber from France (Hymenoptera: Diapriidae)

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### ABSTRACT

*Gaugainia electrogallica* gen. and sp. nov., a new genus and species of belytine wasp (Diapriidae: Belytinae), is described from a female preserved in middle Cretaceous (Late Albian) amber from south-western France. The new fossil is the first Cretaceous and oldest known Belytinae, providing evidence for the antiquity of modern diapriid lineages. The Berriasian genus *Coramia* Rasnitsyn & Jarzembowksy 1998, is removed from Diapriidae and considered herein as a Proctotrupoidea *incertae sedis* stat. nov. The geological history of Diapriidae is briefly reviewed and a list of all known fossils of the family is given.

**KEY WORDS:** Hymenoptera. Diapriidae. Belytinae. Cretaceous amber. Albian. France.

### INTRODUCTION

Diapriidae is a quite diverse family of small wasps endoparasitic mainly on Diptera, but also on ants and beetles (Loiacono 1987, Masner 1993). Only about half of the estimated extant species ( $\approx 4500$ ) have been described to date (Johnson 1992). They are found worldwide, although most abundantly in the southern hemisphere, and live in wet forests and marshes near water or in the soil. Diapriids are usually sexually dimorphic, with most notable differences in the antennae. No clear diagnostic trait exists for distinguishing the family which is merely defined on the absence of characters of related families within Proctotrupoidea (Masner 1993).

Phylogenetic relationships of the family are controversial, as proctotrupoids appear to be a paraphyletic group (Königsmann 1978; Downton *et al.* 1997; Downton & Austin 2001; Rasnitsyn 2002). Sister-group relationships with Cynipoidea, as suggested by morphological analysis (Rasnitsyn 1988; Sharkey & Roy 2002), or with Chalcidoidea + Platygastroidea as suggested by molecular analysis (Downton *et al.* 1997; Castro & Downton 2006), are still not confidently supported (Ronquist *et al.* 1999, Early *et al.* 2001). Together with the Cynipoidea, diapriids have two unique synapomorphies, viz. the concave/convex vein M(+Cu) on hind wing and the male basal flagellomere modified to accommodate the gland secretion releaser (Rasnitsyn 1988, 2002). Even though the diapriid autapomorphies in respect to the cynipoids are not unique (scape elongate, and metasomal apex tight at rest, with ovipositor internalized), they are suitable enough to help positioning diapriids on a cladogram, however. Within proctotrupoids, diapriids are likely closely related to Monomachidae and the recently described Maamingidae (Downton & Austin 2001; Early *et al.* 2001).

Four subfamilies are currently recognized within diapriids: the Ambositrinae, Belytinae, Diapriinae, and Ismarinae. Belytinae is hypothesized as the most basal subfamily (Masner 1993), though relationships with ambositrines and ismarines remain unclear. So far however, the fossil record of belytines contradicted this hypothesis, being significant in the Cenozoic but not older than Eocene, when that of diapriines and ismarines extends to the Late Mesozoic (Appendix 1). Indeed, one undetermined diapriine has been mentioned from Cretaceous amber of Taimyr (Zherikhin & Sukatcheva 1973), and two ismarines have been described in Cretaceous ambers from France and Japan (Schlüter 1978, Fujiyama 1994). The fossil record of ambositrines is very scant, with only a few undescribed species of the extant genus *Ambositra* Masner 1961 being mentioned in Eocene Baltic amber (Masner 1969; Naumann 1982). According to Kozlov (1968), the oldest diapriids would occur in the middle Jurassic of Karatau in Kazakhstan (in Königsmann 1978), but we failed to find this mention in the reference he cited and this appears to be a misidentification (Rasnitsyn, pers. comm.). Additional diapriids of unknown subfamily are mentioned from Cretaceous and Cenozoic ambers but are still undescribed.

Here we describe a new genus and a new species of diapriid wasp belonging to the subfamily Belytinae, from Late Albian amber of south-western France. The new fossil is the first Cretaceous and oldest known representative of the subfamily, demonstrating the only previously supposed antiquity of this lineage. The terminology of Huber & Sharkey (1993) is employed throughout for morphological features of the body and wing venation.

## SYSTEMATIC PALAEOONTOLOGY

Order: Hymenoptera Linnaeus 1758

Family: Diapriidae Haliday 1833

Subfamily: Belytinae Förster 1856

GENUS: *Gaugainia* gen. nov.Type species: *Gaugainia electrogallica* sp. nov.

**Etymology.** Dedicated to Mr Arnaud Gaugain who collected and kindly gave us the piece of amber containing the type specimen.

**Diagnosis.** Mandibles short, not forming a beak; eyes pilose; antennae 15-segmented, inserted high above clypeus on a distinct shelf; scape long, fully equal to head height as seen from the side; pedicel and first flagellomere cylindrical, other flagellomeres broadened distally; fore wing with radial cell [2R1] longer than pterostigma, entirely closed at apex; hind wing with basal cell well defined; deep and long notauli on mesoscutum; scutellum with a row of posterior foveae; a well defined epomia present; metanotum with two small dorso-lateral teeth; no false spur on fore tibia; petiole less than twice as long as broad; metasoma ellipsoidal, not narrowly pointed at apex; second metasomal sternite the longest.

*Gaugainia electrogallica* sp. nov.

Figures 1-2

**Etymology.** Combination of *electro-*, from the Greek *elektron* meaning amber, and *Gallica*, the Latin name for France, referring to the French amber containing the holotype.

**Holotype.** Specimen MNHN ARC 263.1 (a complete female in amber, partly covered by a 'milky coat' on right side and by mycelial strands on left side), deposited in the Earth History Department, Muséum National d'Histoire Naturelle, Paris, France.

**Type locality and horizon.** Archingeay/Les-Nouillers, Charente-Maritime, SW France. Lower Cretaceous, Uppermost Albian (Néraudeau *et al.* 2002).

**Diagnosis.** As for the genus.

**Description.** Head: hypognathous, transversely ovoid; eyes large, with sparse setae; ocelli equidistant; several long hairs on front; mandibles short, endodont, not forming a beak, with outer side curved. Antenna with 13 flagellomeres, not clubbed, inserted high above clypeus on a distinct transverse shelf; antennal sockets facing upwards; scape five times longer than wide and fully equal to head height as seen laterally; pedicel and first flagellomere nearly equal in length, cylindrical, about twice as long as wide; following flagellomeres shorter but increasing gradually in length and width, broadened distally, about as long as broad; apical one ovoid; flagellum bearing numerous curved trichoid sensilla but no long hair.

Mesosoma: a well defined epomia present (*sensu* Nixon 1957), notauli deep and long, scutellum without tooth, with a row of posterior foveae; metanotum with two small dorso-lateral teeth. Fore wing vein Rs not forked; pterostigma small, almost linear; radial cell [2R1] closed, much longer than pterostigma; veins Sc + R, M + Cu, M, distal parts of Rs, M and Cu well visible, other veins spectral. Hind wing narrow elongate, basal cell [R] closed. Hind coxa much thicker than fore and mid ones; fore and mid legs thin, hind leg thicker; tibiae broadened at about fourth-fifths of length; tibial spur formula 1-2-2, no false spur on fore tibia.

Metasoma: ellipsoidal, not narrowly pointed at apex; petiole short, less than twice as long as broad; second metasomal tergite the longest, tergum 2 about 17 times longer than tergum 3, a longitudinal ridge between sternum 2 and lateral margin of tergum 2; ovipositor internalized, not visible.

**Measurements (in mm).** Head length 0.30, height 0.20; mesosomal length 0.46, height ca. 0.20; fore wing length 1.10, width 3.80; hind wing length 0.60, width 0.08; legs: fore femur length 0.20, tibia 0.18, tarsi 0.28, mid femur 0.20, tibia 0.20, tarsi 0.24, hind femur 0.26, tibia 0.30, tarsi 0.32; metasomal length 0.60, width ca. 0.25; petiole length 0.08; metasomal tergum 2 length 0.34.

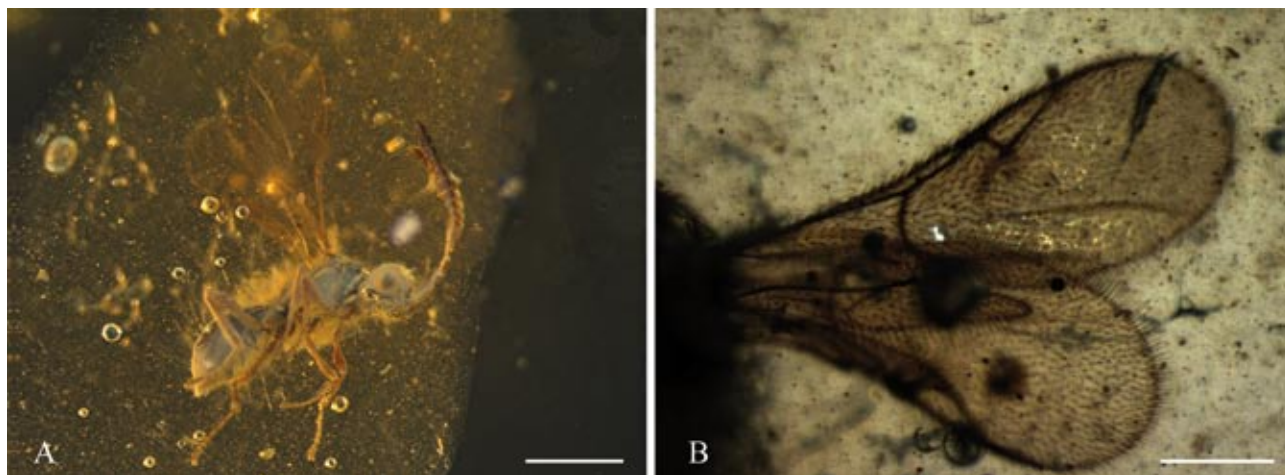


Figure 1. *Gaugainia electrogallica* gen. nov., sp. nov., holotype specimen MNHN ARC 263.1. A. General habitus in right lateral view, scale bar = 0.5 mm; B. Detail of wings, scale bar = 0.25 mm.

## DISCUSSION

The new genus shows characteristic features of the Diapriidae in its elongate scape inserted high above the clypeus on a prominent transverse ledge, its fore wing with a short linear pterostigma, and its petiolate metasoma with tergum 2 the longest (Masner 1993). It shares with the Maamingidae the character ‘flagellomeres bearing numerous curved trichoid sensilla’, a putative synapomorphy of the Diapriidae and Maamingidae according to Early *et al.* (2001). Maamingids also have the antennae inserted on a prominent frontal shelf, but diapriids differ from them by the long metasomal tergum 2, as observed in *Gaugainia*.

The rather complete venation displayed by the new genus, with radial cell of fore wing and basal cell of hind wing well defined, is present in Belytinae. This relatively plesiomorphic condition as well as the presence of 15 segments in the antennae exclude affinities with Diapriinae but not necessarily with Ambositrinae (in *Scianomas* Naumann 1982: fig. 85). According to Masner (1961, 1976, 1993) and Naumann (1988) however, *Gaugainia* can be excluded from ambositrines because of its second metasomal sternite being the longest. Ismarinae can be also excluded because *Gaugainia* has no false spur on the fore tibia, its antennae are inserted high above the clypeus on a very distinct shelf with the sockets opening upwards, and its notauli are distinct (Nixon 1957, Masner 1976). According to Masner (1993), the belytines are characterized by the unique synapomorphy “two longitudinal grooves on metasomal sternum 2 in which the lateral margin of tergum 2 fits, and which sometimes is supplemented by a ridge”. However Notton (2004) indicated that these grooves are

also present in “the diapriid subfamily Ismarinae, and in a more derived form in Ambositrinae, and there is only one subfamily, the albeit heterogeneous Diapriinae, where it does not occur universally”. A ridge is visible in *Gaugainia* but the grooves cannot be seen. Nevertheless, we include *Gaugainia* in Belytinae, mainly because it clearly does not belong to the three other subfamilies for the reasons stated above.

Among the belytine world genera keyed by Kieffer (1910), the new genus would fall near *Lyteba* Thomson 1858 (= *Oxylabis* Förster 1856 = *Cinetus* Jurine 1807) in many characters but differs from it in its distinctly longer scape. Based on the key to Palaearctic genera of Nixon (1957), it would fall near the extant *Paroxylabis* Kieffer 1907 but differs from it in its metasoma being distinctly broader. It would fall near *Belyta* Jurine 1807, *Pantoclis* Förster 1856, and *Aprestes* Nixon 1957 in its posterior foveae on scutellum, but differs from them in its longer scape and its fore wing cell [R] closed. Other genera not keyed in Nixon (1957) or Kieffer (1910) but listed in Johnson (1992) or described later differ from the new genus as follows: *Styloclista* Dodd 1915, *Aclistoides* Dodd 1916, and *Gladicauda* Early 1980 have a petiole several times longer than wide and a hind wing without a closed cell (Dodd 1915, 1916; Early 1980); *Probetyla* Brues 1922 has wings just reaching the tip of the metasoma (Brues 1922); *Ctenopria* Ogloblin 1966 has no ocelli (Ogloblin 1966); *Masnerosema* Sundholm 1970 lacks the hind wing basal cell (Sundholm 1970); *Panbelista* Chambers 1985 has very long hairs on the flagellomeres (Chambers 1985); *Psilomacra* Macek 1990 has its cell [2R1] open and an elongate metasoma (Macek 1990: fig. 5); *Masneretus* Buhl 1997 has

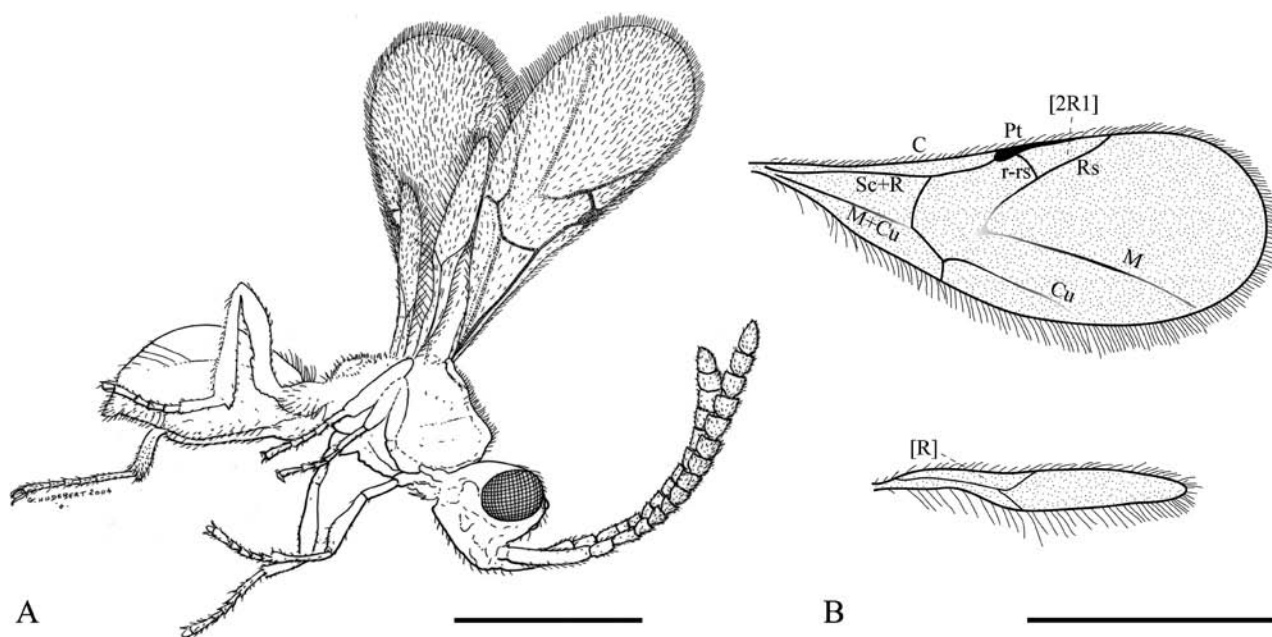


Figure 2. *Gaugainia electrogallica* gen. nov., sp. nov., holotype specimen MNHN ARC 263.1. A. Reconstruction of the general habitus in right lateral view; B. Reconstruction of wings. Scale bars = 0.5 mm.

a very short cell [2R1]; *Masnerolyta* Buhl 1997 has an elongate metasoma and a long petiole (Buhl 1997); *Eccinetus* Muesebeck & Walkley 1965 has an elongate metasoma.

Among the fossil diapiiid genera listed in the appendix, *Archaebelyta* (Oligocene of Rott, Germany) differs from

the new genus in its elongate metasoma and the absence of a defined cell [2R1] (Meunier 1923). *Lithobelyta* (Late Eocene, Isle of Wight, UK) also differs in the absence of [2R1] (Cockerell 1921). *Galesimorpha* (Eocene of Florissant) differs in its comparatively longer petiole and its

Taxa	Age	Deposit	Reference
<b>Ambositrinae Masner 1961</b>			
<i>Ambositra</i> sp.	Eocene	Baltic amber	Masner 1969
<b>Belytinae Förster 1856</b>			
<i>Belyta</i> sp.	Quaternary	African copal	Dalman 1825
Belytinae indet.	Oligocene	Saxonian amber	Perrichot, pers. obs.
† <i>Lithobelyta reducta</i>	Oligocene	Isle of Wight, England	Cockerell 1921
<i>Miota strigata</i>	Oligocene	Isle of Wight, England	Cockerell 1921
<i>Zygota filicornis</i>	Oligocene	Isle of Wight, England	Cockerell 1921
<i>Pantoclis manevali</i>	Oligocene	Aix-en-Provence, France	Théobald 1937
<i>Pantoclis margeritaceus</i>	Oligocene	Rott, Germany	Statz 1938
† <i>Archaebelyta superba</i>	Oligocene	Rott, Germany	Meunier 1923
<i>Psilomma pulchellus</i>	Oligocene	Rott, Germany	Statz 1938
<i>Aclista</i> sp.	Eocene	Baltic amber	Buhl 2002
<i>Acropiesta janzeni</i>	Eocene	Baltic amber	Buhl 2002
<i>Acropiesta macrocera</i>	Eocene	Baltic amber	Buhl 2002
<i>Acropiesta</i> spp.	Eocene	Baltic amber	Buhl 1999
<i>Belyta</i> sp.	Eocene	Baltic amber	Buhl 2002
<i>Belyta mortuella</i>	Eocene	Florissant, USA	Brues 1910
<i>Cinetus inclusus</i>	Eocene	Baltic amber	Maneval 1938
<i>Cinetus balticus</i>	Eocene	Baltic amber	Szabó & Oehlke 1986
<i>Miota</i> sp.	Eocene	Baltic amber	Buhl 2002
<i>Pantoclis</i> sp.	Eocene	Baltic amber	Buhl 2002
<i>Pantoclis deperdita</i>	Eocene	Florissant, USA	Brues 1910
<i>Pantolyta somnulentata</i>	Eocene	Baltic amber	Maneval 1938
<i>Pantolyta antiqua</i>	Eocene	Baltic amber	Buhl 1999
<i>Pantolyta</i> spp.	Eocene	Baltic amber	Buhl 2002
<i>Synacra microptera</i>	Eocene	Baltic amber	Buhl 2002
<i>Zygota</i> sp.	Eocene	Baltic amber	Buhl 2002
† <i>Gaugainia electrogallica</i> gen. et sp. nov.	Albian	SW French amber	this paper
<b>Diapriinae Haliday 1833</b>			
<i>Diapria</i> sp.	Quaternary	African copal	Dalman 1825
<i>Basalys</i> sp.	Miocene	Dominican amber	Poinar & Poinar 1999
<i>Monelata</i> (= <i>Corynopria</i> )	Miocene	Dominican amber	Poinar & Poinar 1999
<i>Trichopria</i> sp.	Miocene	Dominican amber	Poinar & Poinar 1999
Diapriinae indet.	Oligocene	Saxonian amber	Perrichot, pers. obs.
<i>Aneurhynchus conservatus</i>	Oligocene	Isle of Wight	Cockerell 1916
<i>Diapriites insignicornis</i>	Oligocene	Rott, Germany	Statz 1938
<i>Paramesius defectus</i>	Eocene	Florissant, USA	Brues 1910
Diapriinae indet.	Eocene	Baltic amber	Buhl 1999, 2002
Diapriinae indet.	Cenomanian	Taimyr amber	Zherikhin & Sukatcheva 1973
<b>Ismarinae Thomson 1858</b>			
Ismarinae indet.	Cenomanian	NW French amber	Schlüter 1978
† <i>Cretapria tsukadai</i>	Aptian	Choshi amber, Japan	Fujiyama 1994
<b>Subfamily unknown</b>			
Diapriidae indet.	Miocene	Mexican amber	Hurd <i>et al.</i> 1962
† <i>Galesimorpha wheeleri</i>	Eocene	Florissant, USA	Brues 1910
Diapriidae indet.	Eocene	Rovno amber	Perkovsky <i>et al.</i> 2007
Diapriidae indet.?	Campanian	Canadian amber	in Schlüter 1978
Diapriidae indet.	Turonian	Timmerdyakh amber, Russia	Rasnitsyn 1980
Diapriidae indet.	Albian	Burmese amber	Grimaldi <i>et al.</i> 2002

metasoma as long as the combined length of head and mesosoma (Brues 1910). An unnamed Ismarinae described by Schlüter (1978: fig. 51) from the Cenomanian amber of Bezonnois (NW France) differs in its short scape and the absence of cell [R] in the hind wing. *Cretapria* (Aptian Choshi amber, Japan) was tentatively assigned to Ismarinae based on the absence of a frontal shelf, however Fujiyama (1994) noted that other features such as the 14-segmented female antennae do not correspond with those of the ismarines; it differs from the new genus in the absence of notauli and fore wing cell [2R1].

The enigmatic genus *Cretacoformica* (Early Cretaceous of Australia) was originally considered as in Formicidae (Jell & Duncan 1986) but later was transferred into the Diapriidae (Ross & Jarzembowski 1993, Rasnitsyn *et al.* 1998). However Naumann (1993) considered it as a hymenopteran of uncertain relationship but with possible affinities with Proctotrupoidea. Indeed, he identified it as being distinct from the Diapriidae by only a few characters of plesiomorphic condition, the wing venation being particularly similar except for a more developed pterostigma. *Cretacoformica* mainly differs from the new genus in its frons without an antennal shelf (Naumann 1993). Similarly, the genus *Coramia* (Berriasian of Dorset, UK) is currently included in the Diapriidae (Rasnitsyn *et al.* 1998) but is an incomplete specimen lacking the basal segments of the antennae, the apical part of the mesosoma, and the entire metasoma, essential diagnostic features of the Diapriidae. Moreover, in the diagnosis of *Coramia* (see Rasnitsyn *et al.* 1998: p. 358), *Cretacoformica* is stated as its most similar genus. As mentioned above however, *Cretacoformica* must be preferably referred as a proctotrupoid of uncertain affinities. Therefore, *Coramia* cannot confidently be assigned to Diapriidae and the genus is now transferred to Proctotrupoidea *incertae sedis* stat. nov.

## CONCLUSION

Modern Belytinae are found worldwide but are most abundant and diversified in moist temperate forests of the southern hemisphere (Masner 1993). During the Cenozoic, belytines lived in a range of climates from warm temperate (Eocene of Florissant – Moe & Smith 2005) to moist subtropical or tropical (Eocene Baltic – Weitshat & Wichard 1998). The mid-Cretaceous amber forest from southwestern France likely grew in a mesohaline habitat of an estuarine or mangrove-like tropical environment (Perrichot 2005; Perrichot *et al.* 2007). Therefore the known fossil record of belytines, including the new Cretaceous genus from French amber, provides evidence for an early occupation of various habitats by the subfamily. It is notable that no fossil belytine older than Quaternary (i. e., from African copal) is known from the southern hemisphere yet, which certainly is due to a bias in the fossil record as the modern belytines are rather widespread and diversified through the old Gondwana. While the modern distribution of Ambositrinae in the southern hemisphere is likely relictual, as emphasized by its fossil occurrence in Baltic

amber, modern Belytinae, Diapriinae, and Ismarinae are found worldwide. At least three of the four extant diapriid subfamilies were already present in the Early Cretaceous, demonstrating the antiquity and early diversification of this group of parasitoid wasps.

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## REFERENCES

- BRUES, C.T. 1910. The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. Bulletin of the Museum of Comparative Zoology at Harvard College, 54 (1): 4-125.
- BRUES, C.T. 1922. Some parasitic Hymenoptera from New Zealand. Psyche, 29 (5-6): 216-225.
- BUHL, P.N. 1997. Two new genera of Belytinae from Argentina (Hymenoptera, Diapriidae). Entomofauna, 18 (10): 89-92.
- BUHL, P.N. 1999. On a collection of Hymenoptera in Baltic amber, with the description of a new species of *Pantolyta* Foerster, 1856 (Hymenoptera, Diapriidae). Entomologica Fennica, 10: 187-189.
- BUHL, P.N. 2002. On a Baltic amber collection of Platygasteridae and Diapriidae (Hymenoptera). Entomologiske Meddelelser, 70 (1): 57-61.
- CASTRO, L.R. & DOWTON, M. 2006. Molecular analyses of the Apocrita (Insecta: Hymenoptera) suggest that the Chalcidoidea are sister to the diaprioid complex. Invertebrate Systematics, 20 (5): 603-614.
- CHAMBERS, V.H. 1985. A new genus of the Belytinae (Hym., Proctotrupoidea, Diapriidae). Entomologist's Monthly Magazine, 121 (1456-1459): 207-209.
- COCKERELL, T.D.A. 1916. British fossil insects. Proceedings of the United States National Museum, 49: 469-499.
- COCKERELL, T.D.A. 1921. Fossil arthropods in the British Museum. 5. Oligocene Hymenoptera from the Isle of Wight. Annals and Magazine of Natural History, (9)7: 1-25.
- DALMAN, J. 1825. Om Insekter inneslutna i copal, jeinte beskrifning pa nagra, deribland förekommande nya

- slågten och arter. Kongliga Svenska Vetenskaps-Akademiens Handlingar, 46: 375-410.
- DODD, A.P. 1915. Australian Hymenoptera Proctotrypoidea. N° 3. Transactions of the Royal Society of South Australia, 39: 384-454.
- DODD, A.P. 1916. Australian Hymenoptera Proctotrypoidea. N° 4. Transactions of the Royal Society of South Australia, 40: 9-32.
- DOWTON, M. & AUSTIN, A.D. 2001. Simultaneous analysis of 16S, 28S, COI and morphology in the Hymenoptera: Apocrita – evolutionary transitions among parasitic wasps. *Biological Journal of the Linnean Society*, 74 (1): 87-111.
- DOWTON, M., AUSTIN, A.D., DILLON, N. & BARTOWSKY, E. 1997. Molecular phylogeny of the apocritan wasps: the Proctotrupomorpha and Evaniomorpha. *Systematic Entomology*, 22 (3): 245-255.
- EARLY, J.W. 1980. The Diapriidae (Hymenoptera) of the southern islands of New Zealand. *Journal of the Royal Society of New Zealand*, 10 (2): 153-171.
- EARLY, J.W., MASNER, L., NAUMANN, I.D. & AUSTIN, A.D. 2001. Maamingidae, a new family of proctotrupoid wasp (Insecta: Hymenoptera) from New Zealand. *Invertebrate Taxonomy*, 15 (3): 341-352.
- FUJIYAMA, I. 1994. Two parasitic wasps from Aptian (Lower Cretaceous) Choshi amber, Chiba, Japan. *Natural History Research*, 3 (1): 1-5.
- GRIMALDI, D.A., ENGEL, M.S. & NASCIMBENE, P.C. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, 3361: 1-71.
- HEDQVIST, K.J. 1975. Notes on the genus *Prosynacra* Kieffer (Hymenoptera: Proctotrupeoidea: Diapriidae). *Entomologisk Tidskrift*, 96: 51-54.
- HUBER, J.T. & SHARKEY, M.J. 1993. Structure. In: *Hymenoptera of the world: an identification guide to families*, GOULET H. & HUBER J.T. (eds), Research Branch Agriculture Canada Publication, Ottawa: 13-59.
- HURD, P.D.JR., SMITH, R.F. & DURHAM, J.W. 1962. The fossiliferous amber of Chiapas, Mexico. *Ciencia*, 21: 107-118.
- JELL, P.A. & DUNCAN, P.M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra fossil bed, (Korumburra Group), South Gippsland, Victoria. In: *Plants and invertebrates from the Lower Cretaceous Koonwarra fossil bed, South Gippsland, Victoria*, JELL, P.W. & ROBERTS, J. (eds), *Memoirs of the Association of Australasian Palaeontologists*, Sydney, 3: 111-205.
- JOHNSON, N.F. 1992. Catalog of the world species of Proctotrupeoidea excluding Platygasteridae (Hymenoptera). *Memoirs of the American Entomological Institute*, 51: 825 pp.
- KIEFFER, J.J. 1910. Hymenoptera fam. Belytidae. *Genera Insectorum*, 107: 1-47.
- KÖNIGSMANN, E. 1978. Das phylogenetische System der Hymenoptera. Teil 3: "Terebrantes" (Unterordnung Apocrita). *Deutsche Entomologische Zeitschrift*, 25: 1-55.
- KOZLOV, M.A. 1968. Jurassic Proctotrupeoidea (Hymenoptera). In: *Jurassic insects of Karatau*, ROHDENDORF, B.B. (ed.), *Akademiya Nauk SSSR, Otdelenie Obshchej Biologii, Moscow*: 237-240. [in Russian]
- LOIACONO, M.S. 1987. Un nuevo diaprido (Hymenoptera) parasitoide de larvas de *Acromyrmex ambiguus* (Emery) (Hymenoptera, Formicidae) en el Uruguay. *Revista de la Sociedad Entomologica Argentina*, 44: 129-136.
- MACEK, J. 1990. Revision of European Psilommina (Hymenoptera, Diapriidae). 1. *Psilomma* and *Acanosema* complex. *Acta Entomologica Musei Nationalis Pragae*, 43: 335-360.
- MANEVAL, H. 1938. Trois serphoïdes de l'ambre de la Baltique. *Revue française d'Entomologie*, 5 (2): 107-116.
- MASNER, L. 1961. Ambositrinae, a new subfamily of Diapriidae from Madagascar and Central Africa (Hymenoptera: Proctotrupeoidea). *Mémoires de l'Institut Scientifique de Madagascar (E)*, 12: 289-295.
- MASNER, L. 1969. The geographic distribution of recent and fossil Ambositrinae (Hymenoptera: Proctotrupeoidea: Diapriidae). *Berichte über die 10. Wanderversammlung Deutscher Entomologen, 1965, Dresden*, 1. *Tagungsberichte Deutsches Akademie Landwirtschaftswissen Berlin*, 80 (1): 105-109.
- MASNER, L. 1976. A revision of the Ismarinae of the New World (Proctotrupeoidea: Diapriidae). *The Canadian Entomologist*, 108: 1243-1266.
- MASNER, L. 1993. Superfamily Proctotrupeoidea. In: *Hymenoptera of the world: an identification guide to families*, GOULET, H. & HUBER, J.T. (eds), Research Branch Agriculture Canada Publication, Ottawa, 1894/E: 537-557.
- MEUNIER, F. 1923. Sur quelques insectes de l'Aquitainien de Rott. *Miscellanea Entomologica*, 26: 82-88.
- MOE, A.P. & SMITH, D.M. 2005. Using pre-Quaternary Diptera as indicators of palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 221: 203-214.
- NAUMANN, I.D. 1982. Systematics of the Australian Ambositrinae (Diapriidae, Hymenoptera), with a synopsis of non-Australian genera of the subfamily. *Australian Journal of Zoology, Supplementary Series*, 30 (85): 1-239.
- NAUMANN, I.D. 1988. Ambositrinae (Insecta: Hymenoptera: Diapriidae). *Fauna of New Zealand*, 15: 168 p.



- NAUMANN, I.D. 1993. The supposed Cretaceous ant *Cretacoformica explicata* Jell and Duncan. *Journal of Australian Entomological Society*, 32 (4): 353-356.
- NÉRAUDEAU, D., PERRICHOT, V., DEJAX, J., MASURE, E., NEL, A., PHILIPPE, M., MOREAU, P., GUILLOCHEAU, F. & GUYOT, T. 2002. Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). *Geobios*, 35 (2): 233-240.
- NIXON, G.E.J. 1957. Hymenoptera, Proctotrupeoidea, Diapriidae, subfamily Belytinae. *Handbooks for the Identification of British Insects*, 8: 1-107.
- NOTTON, D.G. 2004. A catalogue of types of Diapriinae (Hymenoptera, Diapriidae) at the National Museum of Natural History, Paris, with notes on the classification of Diapriinae and a brief history of the types of Jean-Jacques Kieffer (1856-1925). *Zoosystema*, 26 (2): 315-352.
- OGLOBLIN, A.A. 1966. *Ctenopria* un género nuevo de la familia Diapriidae (Hymenoptera). *Revista de la Sociedad Entomologica Argentina*, 28: 61-64.
- PERKOVSKY, E.E., RASNITSYN, A.P., VLASKIN, A.P. & TARASCHUK, M.V. 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates*, 48 (1): 229-245.
- PERRICHOT, V. 2005. Environnements paraliques à ambre et à végétaux du Crétacé nord-aquitain (Charentes, Sud-Ouest de la France). *Mémoires de Géosciences Rennes*, 118: 310 pp.
- PERRICHOT, V., NEL, A. & NÉRAUDEAU, D. 2007. Schizopterid bugs (Insecta: Heteroptera) in mid-Cretaceous ambers from France and Myanmar. *Palaeontology*, 50 (6): 1367-1374.
- POINAR, G.O.JR. & POINAR, R. 1999. *The amber forest: a reconstruction of a vanished world*. Princeton University Press, Princeton: 239 pp.
- RASNITSYN, A.P. 1980. Origin and evolution of Hymenoptera. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR*, 174: 1-192 [in Russian].
- RASNITSYN, A.P. 1988. An outline of evolution of the hymenopterous insects (Order Vespida). *Oriental Insects*, 22: 115-145.
- RASNITSYN, A.P. 2002. Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linné, 1758 (= Vespida Laicharting, 1781). In: *History of insects*, RASNITSYN, A.P. & QUICKE, D.L.J. (eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 242-254.
- RASNITSYN, A.P., JARZEMBOWSKI, E.A. & ROSS, A.J. 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. *Cretaceous Research*, 19 (3-4): 329-391.
- ROSS, A.J. & JARZEMBOWSKI, E.A. 1993. Arthropoda (Hexapoda; Insecta). In: *The fossil record 2*, BENTON, M. J. (ed.), Chapman & Hall, London: 363-426.
- SCHLÜTER, T. 1978. Zur Systematik und Palökologie harzkonserverter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. *Berliner Geowissenschaftliche Abhandlungen (A)*, 9: 150 pp.
- SHARKEY, M.J. & ROY, A. 2002. Phylogeny of the Hymenoptera: a reanalysis of the Ronquist et al. (1999) reanalysis, emphasizing wing venation and apocritan relationships. *Zoologica Scripta*, 31 (1): 57-66.
- STATZ, G. 1938. Neue funde parasitischer Hymenopteren aus dem Tertiär von Rott am Siebengebirge. *Decheniana (A)*, 98 (1): 71-154.
- SUNDHOLM, A. 1970. Hymenoptera: Proctotrupeoidea. *South African Animal Life*, 14: 306-401.
- SZABÓ, J.B. & OEHLKE, J. 1986. Neue Proctotrupeoidea aus dem Baltischen Bernstein. *Beiträge zur Entomologie*, 36: 99-106.
- THÉOBALD, N. 1937. Les insectes fossiles des terrains oligocènes de France. *Mémoires de la Société des Sciences de Nancy*, 2: 1-473.
- WEITSCHAT, W. & WICHARD, W. 2002. *Atlas of plants and animals in Baltic amber*. Verlag Dr. Friedrich Pfeil, München: 256 pp.
- ZHERIKHIN, V.V. & SUKATSHEVA, I.D. 1973. On the Cretaceous insect-bearing „ambers“ (retinites) from North Siberia. In: *Problems in Insect Palaeontology: XXIV annual lectures in memory of N. A. Kholodovsky (1-2 April 1971)*, NARCHUK, E.P. (ed.), Nauka, Leningrad: 3-48. (in Russian)

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