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## A New Moustache Wasp in Dominican Amber, with an Account of Apoid Wasp Evolution Emphasizing Crabroninae (Hymenoptera: Crabronidae)

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### ABSTRACT

A new, extinct species of the wasp genus *Lindenius* (Crabroninae: Crabronini: Crabronina) is described and figured from two exquisitely preserved specimens discovered in Early Miocene Dominican amber. *Lindenius paleomystax*, new species, represents the first record for the tribe Crabronini in Dominican amber and the southernmost record for the genus in the New World. The unique locality and habitat data begin to reveal a more complicated natural history for the genus than that suggested by Recent taxa alone. A checklist of fossil apoid wasps in amber is provided and the new species is discussed within the context of an overview of apoid wasp origins and evolution.

### INTRODUCTION

Apoid wasps of the subtribe Crabronina, or “moustache wasps”, are rarely discovered as amber inclusions, despite the worldwide occurrence of numerous wood- or twig-nesting species. Most species occur in more xeric environments, areas outside of the tropical or subtropical forests producing amber, and many nest in soil. As such, the rarity of

moustache wasps in amber can be at least partially explained by habitat preferences. Nonetheless, a significant variety of forest-loving groups that nest in various plant materials in tropical and temperate areas exists, and thus the problem of fully understanding why these wasps are rare in amber remains. In the search for an explanation, note that ground-nesting is the primitive condition for the subtribe (Bohart and Menke, 1976)

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and that to a large extent wood- and twig-nesting habits are found among the most diverse genera, such as *Ectemnius*, *Rhopalum*, and *Crossocerus*. If these are derived groups representing recent radiations into niches formerly unused by moustache wasps, then the paucity of these wasps in fossiliferous resins could be explained by habitat preferences in combination with fundamental nesting differences between modern and prehistoric faunas. Whether such speculation can be developed into a supported hypothesis awaits a formal cladistic analysis of the Crabronina (under way by D.J.B.) and a more precise understanding of the evolution of nesting behavior in the subtribe.

Prior to this report, two species of the genus *Tracheliodes* described by Cockerell (1909) from Baltic amber were the only representatives of the subtribe known from fossiliferous resin (table 1). However, given that Cockerell did not describe the relative position of the eyes in these specimens (note that an important character of *Tracheliodes* is widely separated eyes ventrally), his generic assignments must be treated with caution (W.J. Pulawski, personal commun.). Compression fossils of Crabronina are equally rare, with the only species being another *Tracheliodes* and an *Ectemnius* from Colorado's Eocene-Oligocene Florissant Shale (Cockerell, 1906, 1910) and a putative species of *Ectemnius* from the Early Miocene of Germany (Meunier, 1911). Interestingly, putative species of *Tracheliodes* should represent half of the Crabronina known as fossils, as this group is likely basal within the subtribe. Today the genus is composed of about a dozen species occurring in the western United States, Central Europe, and Mediterranean region. The fossil record and modern distribution of *Tracheliodes* hint at a formerly more diverse and widespread distribution. We herein report on the occurrence of two specimens of the closely related crabronine genus *Lindenius* recently discovered in Dominican amber (figs. 1–3). This is the first record of a crabronine in Dominican amber and the first fossil of *Lindenius*.

*Lindenius* is a moderately large genus presently comprised of 60 extant species distributed throughout the Holarctic region

(Pulawski, 2006). Most of these are Palearctic, with the highest diversity occurring in Mediterranean countries (Bohart and Menke, 1976). The handful of species studied construct relatively shallow nests in soil and predominantly prey on small flies or Heteroptera, though prey records also include various Hymenoptera, including Chalcidoidea, Braconidae, and ants (Hamm and Richards, 1926; Leclercq, 1954; Court, 1961; Evans, 1970; Bohart and Menke, 1976). North American species were treated in an unpublished Master's thesis (Court, 1961); Palearctic taxa were treated by de Beaumont (1956) and later by Leclercq (1989).

The age of Dominican amber has been unnecessarily confused in recent years, with age estimates ranging from the Miocene through the Eocene. In fact, critical analysis of multiple lines of evidence indicates a Neogene age, and all valid evidence supports an Early Miocene (Burdigalian) origin (e.g., Iturralde-Vinent and MacPhee, 1996). Furthermore, the inclusions themselves attest to a relatively recent age for Dominican amber in comparison with definitively more ancient resins (e.g., refer to comparisons of Dominican and Baltic amber faunas of flies and bees by Grimaldi, 1994 and Engel, 2001, respectively). Morphological terminology generally follows that of Bohart and Menke (1976).

## SYSTEMATIC PALEONTOLOGY

### *Lindenius paleomystax*, new species

Figures 1–5

**DIAGNOSIS:** The new species is immediately recognizable as a member of the Crabroninae owing to large cuboidal head, single submarginal cell, elongate scape, and nonemarginate eyes. It is further distinguished as a member of the subtribe Crabronina by ventrally convergent eyes, toruli positioned very low and close together on face, and ventral margin of mandibles entire (Bohart and Menke, 1976). It is placed in *Lindenius* by mandible with apex simple, ventral margin entire (figs. 1, 2, 4), ocellar triangle broader than high, scapal basin ecarinate, and hind wing longer than second cubital cell (submedian cell) (Bohart and Menke, 1976). With



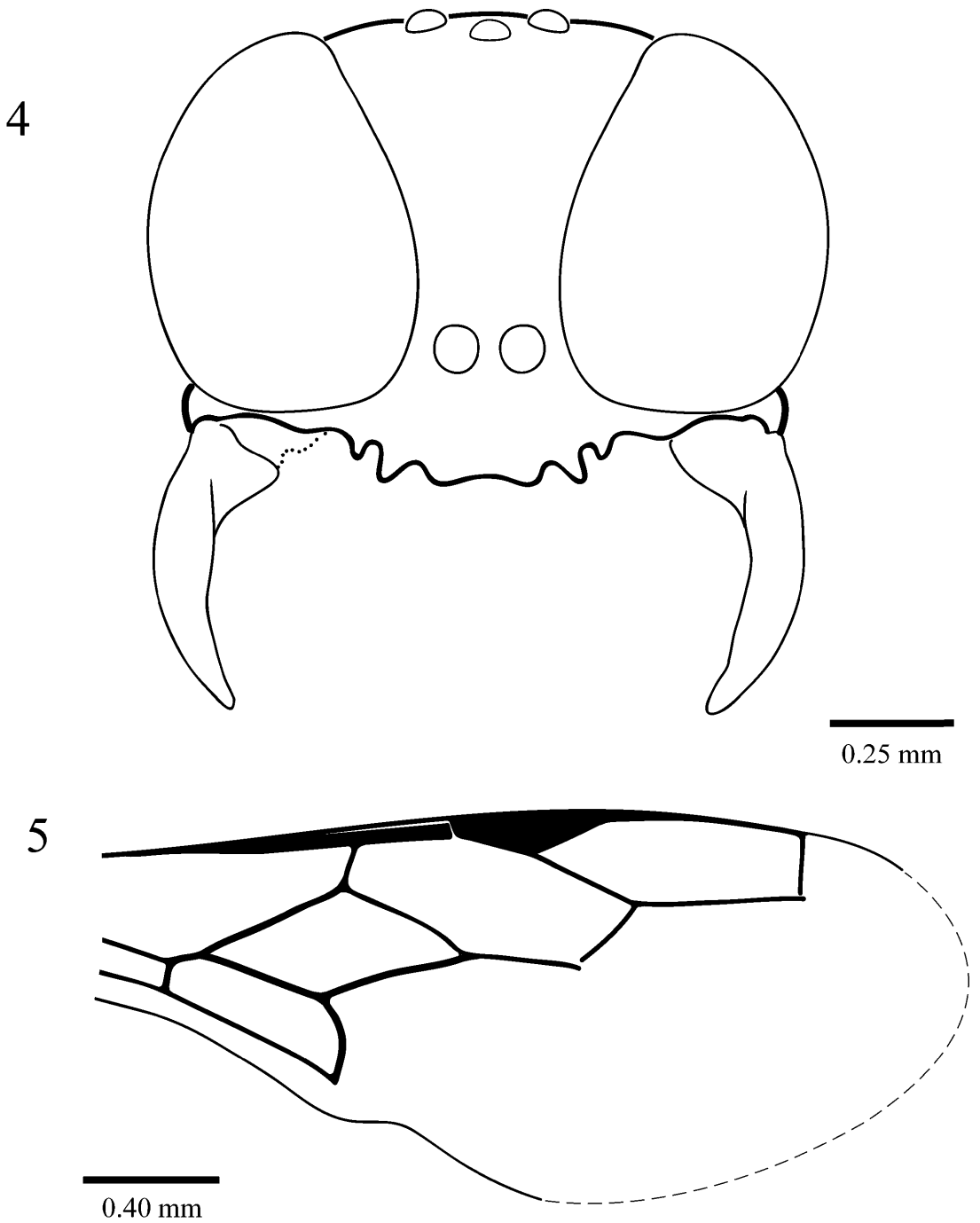
Figs. 1–3. Photomicrographs of holotype female of *Lindenius paleomystax*, new species (AMNH DR-14-1091). 1. Oblique lateral habitus. 2. Facial aspect. 3. Dorsal aspect.

possible exception of the latter trait (which is not visible in the type material), the new species can be diagnosed by these characters in combination with the lack of an inner basal mandibular tooth (figs. 2, 4) and a clypeal margin as figured (figs. 2, 4) and described below.

**DESCRIPTION:** *Female:* Body length excluding antenna approximately 4.2 mm; head width 1.5 mm, height 0.8 mm; forewing length 3.4 mm. Color dark brown to black with brown maculations on pronotal lobe, antenna, tegula, and mandible, mandibular apex black; wing veins dark brown to black, membrane hyaline. Integument apparently imbricate. Antennal scape elongate, length approximately equal to three-fourths mandibular length, ecarinate; medial flagellomeres about as long as wide, becoming more compact apically and slightly longer basally. Clypeus short and narrow; apical margin denticulate, with three teeth lateral of medial concavity, submedial tooth broad, middle tooth longer and pointed, lateral tooth shorter and pointed (figs. 2, 4). Toruli narrowly separated, positioned low on face, meeting epistomal sulcus, scapal basin shallow and ecarinate, without medial tubercle. Gena broad behind compound eye, orbital fovea weakly present, not margined by carina (observable only in paratype), ocellar triangle broader than high, ocelli apparently all of similar size. Occipital carina present dorsally and laterally, not observable ventrally. Compound eyes large, bare, strongly convergent below, reaching clypeal margin laterally; separated from toruli by slightly less than torular diameter. Mandible simple and apically acuminate, ventral margin entire. Three segments of labial palpus visible (in paratype); three relatively long maxillary palpal segments visible (in paratype), apical segment nearly twice as long as subapical segment; pronotal collar rounded, medial notch weak (especially in paratype), strongly notched laterally. Mesoscutum simple, admedian lines, notauli, and parapsidial lines not apparent. Mesoscutellum and metanotum simple, prescutellar sulcus foveate. Postspiracular carina and epicnemial carina present, continuous; acetabular carina apparently absent, verticulus, sternaulus, and mesopleuralus absent; hypersternaulus present, episternal groove

foveate, scrobe distinct. Anteromedial section of propodeal spiracle meeting upper arm of sideways Y-shaped carina, lower arm of carina bounds spiracle ventrally and intersects with dorsal end of weak lateral carina of propodeum; propodeal enclosure defined by transverse carina (observable in dorsal view of holotype, challenging to discern in posterior view but present), posterior longitudinal depression apparent below enclosure. Forewing basal vein distad cu-a by distance approximately equal to length of cu-a; Rs separating from Sc+R at point anterior to pterostigmal base approximately equal to length of posterior border of pterostigma within submarginal cell; marginal cell about as long as submarginal cell; apical margin of truncate marginal cell approximately equal to apical margin of submarginal cell; 1m-cu (recurrent vein) meeting posterior margin of submarginal cell near cell midpoint (fig. 5). Protochanter widest apically, about 2.6 times as long as wide; protochantellus narrow and ringlike; profemur widest medially, about 3.5 times longer than wide; protibia widest slightly distad middle, about 4.4 times longer than wide, lightly spinose, with spur as long or nearly as long as antenna cleaner. Mesofemur expanded medially, about 2.2 times longer than wide; mesotibia somewhat expanded distad middle, about 3.7 times longer than wide, rather strongly spinose with anterior spur about twice length of posterior spur. Metafemur widest medially, about 2.7 times longer than wide; metatibia widest subapically, about 3.4 times longer than wide, spinose, with anterior spur roughly two-thirds length of posterior spur. Basitarsus about as long as combined lengths of tarsomeres II-V; tarsomeres progressively shorter except for distitarsi, which are longer than preceding tarsomeres. Pretarsal claws simple, arolia distinct. Metasoma sessile, relatively compact, roughly two-thirds as wide as mesosoma; second through fourth metasomal sterna subequal in length except third apparently slightly longer; pygidial plate flat, triangular, longer than broad, evenly narrowed, with apex truncate and punctuate throughout, somewhat more strongly so apically.

**HOLOTYPE:** Female (AMNH DR-14-1091), Dominican Republic: Early Miocene (Burdi-



Figs. 4-5. Line drawings of *Lindenius paleomystax*, new species, as preserved. 4. Face depicting clypeal margin. 5. Apical two-thirds of forewing.

galian) amber, specific mine unknown. Deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History.

PARATYPE: Female (AMNH DR-14-236), Dominican Republic: Early Miocene (Burdigalian) amber, northern mines. Deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History.

ETYMOLOGY: The specific epithet is a combination of the Greek words for “ancient” (*palaios*) and “moustache” (*mystax*), a reference to the common name for the subtribe *Crabronina*.

COMMENTS: One major difference between the fossil and its modern relatives is the lack of an inner basal mandibular tooth in the former. Although a cladistic analysis of the *Crabronina* is needed to be certain of its polarity, the tooth is likely a feature derived within *Lindenius*. It occurs in other moustache wasps (e.g., *Huavea*, *Moniacera*, some *Crossocerus*, and most *Ectemnius*) but not in any obviously closely related group. Based on this character alone, the species could plausibly be interpreted to represent an extinct lineage basal within *Lindenius*, outside of modern species groups as outlined by de Beaumont (1956) (see also summary in Bohart and Menke, 1976). However, such an interpretation is not congruent with the presence of a hypersternaulus, a character that suggests placement in the *mesopleuralis* species group of *Lindenius*. The correct placement of the fossil within the genus must await a broader analysis of additional characters.

## DISCUSSION

Like their more intensely studied relatives, the bees (Anthophila), apoid wasps are uncommon as fossils. Both have relatively comparable numbers of fossil species documented as both compressions and amber inclusions (the bees have slightly more species, but this is a bias resulting from the fact that their geological history has been the focus of work by one of us [M.S.E.] during the last decade). Unlike the bees, however, the apoid wasps have a far better representation in the Cretaceous, thereby providing greater insight

into the earliest history of the Apoidea. The earliest apoid wasps are a series of plesiomorphic species classified in the family Angarosphecidae. Unfortunately, angarosphecids are defined only by plesiomorphies and thereby likely represent a grade leading to all other apoid families. This also strongly suggests that the assertion that this artificial family persisted into the Paleogene (based on *Eosphecium* from the Eocene of Quilchena, British Columbia; Pulawski et al., 2000) is erroneous since it is based solely on a forewing compression that preserves no derived features of any apoid family. As such, *Eosphecium* could just as likely represent a plesiomorphic species of Sphecidae (highly probable) or Crabronidae (less likely). This grade of plesiomorphic wasps is recorded from as long ago as the Early Cretaceous of Brazil, Europe, and Central Asia (Grimaldi and Engel, 2005). By the early epochs of the mid-Cretaceous, the families Ampulicidae and Crabronidae are definitively recorded from the Mesozoic, as evidenced by the exquisitely preserved Burmese amber fauna (Antropov, 2000b; Engel, personal obs.). Perhaps most importantly, the presence of crabronids, the most derived family of apoid wasps, immediately indicates that prior cladogenetic events in the superfamily (i.e., diversification of the families of apoid wasps) had taken place earlier in the Cretaceous. Furthermore, the occurrence of crabronids indicates that the bees, their sister group (Lomholdt, 1982; Alexander, 1992; Prentice, 1998; Melo, 1999; Grimaldi and Engel, 2005), had also already diverged by this time (Engel, 2001, 2004; Grimaldi and Engel, 2005).

Within the Crabronidae the nominate subfamily is presently documented only from the Tertiary, with most species in amber and most being of the tribe Trypoxylini (e.g., table 1). Nel (2005) enigmatically asserted that the Trypoxylini described by him from Parisian amber (Eocene) were the earliest records of Sphecidae. Aside from the attribution to the wrong family (prior to 1993 all apoid wasps were classified as one family “Sphecidae”), these are not older than fossils of Sphecidae (in the modern strict sense) or other fossils of Crabronidae, the family to which these actually belong (see table 1).



TABLE 1  
Amber Fossil Apoidea, Exclusive of Anthophila

Taxon	Resin	Age
Family AMPULICIDAE Shuckard		
<i>Apodolichurus diaphanus</i> Antropov, 2000b	Burmese amber	Albian
<i>Apodolichurus sphaerocephalus</i> Antropov, 2000b	Burmese amber	Albian
<i>Cretampulex gracilis</i> Antropov, 2000b	Burmese amber	Albian
<i>Mendampulex monilicularis</i> Antropov, 2000b	Burmese amber	Albian
<i>Dolichurus heevansi</i> Ohl, 2003	Baltic amber	Eocene
<i>Protodolichurus sucinus</i> Nemkov, 1988	Baltic amber	Eocene
Family CRABRONIDAE Latreille		
—Subfamily Burmastatinae Antropov		
<i>Burmastatus triangularis</i> Antropov, 2000b	Burmese amber	Albian
—Subfamily Pemphredoninae Dahlbom		
<i>Cretoecus spinicoxa</i> Budrys, 1993	Siberian amber	Santonian
<i>Cretopilomena familiaris</i> Antropov, 2000b	Burmese amber	Albian
<i>Eomimesa rasnitsyni</i> Budrys, 1993	Baltic amber	Eocene
<i>Eopinoecus samogiticus</i> Budrys, 1993	Baltic amber	Eocene
<i>Eopinoecus truncifrons</i> Budrys, 1993	Baltic amber	Eocene
<i>Eoxyloecus albipalpis</i> Budrys, 1993	Baltic amber	Eocene
<i>Eoxyloecus palionisi</i> Budrys, 1993	Baltic amber	Eocene
<i>Eoxyloecus seticeps</i> Budrys, 1993	Baltic amber	Eocene
<i>Eoxyloecus succinicola</i> Budrys, 1993	Baltic amber	Eocene
<i>Lisponema singularis</i> Evans, 1969	Canadian amber	Campanian
<i>Palanga succinea</i> Budrys, 1993	Baltic amber	Eocene
<i>Passaloecus electrobis</i> Budrys, 1993	Baltic amber	Eocene
<i>Passaloecus microceras</i> Sorg, 1986	Baltic amber	Eocene
<i>Passaloecus munax</i> Sorg, 1986 <sup>a</sup>	Baltic amber	Eocene
<i>Passaloecus piletskisi</i> Budrys, 1993	Baltic amber	Eocene
<i>Passaloecus zherichini</i> Budrys, 1993	Baltic amber	Eocene
<i>Pittoecus pauper</i> Evans, 1973	Siberian amber	Santonian
<i>Prollemistus apiformis</i> Antropov, 2000b	Burmese amber	Albian
<i>Psilomena electra</i> Antropov, 2000a	New Jersey amber	Turonian
<i>Succinoecus lituanicus</i> Budrys, 1993	Baltic amber	Eocene
—Subfamily Crabroninae Latreille		
<i>Eopison menieri</i> Nel, 2005 <sup>b</sup>	Parisian amber	Eocene
<i>Lindenius paleomystax</i> , n.sp.	Dominican amber	Miocene
<i>Pison antiquum</i> Antropov & Pulawski, 1996	Dominican amber	Miocene
<i>Pison electrum</i> Antropov & Pulawski, 1989	Baltic amber	Eocene
<i>Pison eocenicum</i> Nel, 2005 <sup>b</sup>	Parisian amber	Eocene
<i>Pison oligocaenum</i> Cockerell, 1909	Baltic amber	Eocene
<i>Tracheliodes succinalis</i> (Cockerell, 1909)	Baltic amber	Eocene
<i>Tracheliodes tornquisti</i> (Cockerell, 1909)	Baltic amber	Eocene
<i>Trypoxylon dominicanum</i> Prentice & Poinar, 1993	Dominican amber	Miocene
<i>Trypoxylon electrum</i> Antropov, 1995	Dominican amber	Miocene
<i>Trypoxylon eucharis</i> Prentice & Poinar, 1993	Dominican amber	Miocene
<i>Trypoxylon pallidiventre</i> Prentice & Poinar, 1993	Dominican amber	Miocene
Family Incertae Sedis		
<i>Gallosphex cretaceus</i> Schlüter, 1978 <sup>c</sup>	French amber	Cenomanian
<i>Trigampulex pervetus</i> (Cockerell, 1917)	Burmese amber	Albian
—Subfamily Cirrosphecinae Antropov		
<i>Cirrosphex admirabilis</i> Antropov, 2000b	Burmese amber	Albian

<sup>a</sup>This species was described from “Bitterfeld” amber and attributed to the Early Miocene. Amber from the Bitterfeld site is merely redeposited Baltic amber and is of middle Eocene age (vide Weitschat, 1997; Engel, 2001, 2004).

<sup>b</sup>The paper describing these species was enigmatically titled as the oldest record of the Sphecidae. The taxa described therein do not belong to the Sphecidae at all, but instead to the Crabronidae. Furthermore, these are not the oldest records for their family since crabronids, and pemphredonines in particular, have been long known from the Cretaceous (e.g., Evans, 1969, 1973; Budrys, 1993; Antropov, 2000a, 2000b).

<sup>c</sup>Ohl (2003) provided a thorough discussion on possible affinities of *Gallosphex*, as well as other fossil Ampulicidae.

As mentioned previously, the moustache wasps (subtribe Crabronina) are known, like Trypoxylini, only from the Tertiary, ranging from the middle Eocene (i.e., Baltic amber species) through the Miocene (species documented herein). Prior associations of *Lindenius* with genera such as *Entomognathus*, *Encopognathus*, and *Oxybelus* (taxa outside of the Crabronina) indicate that *Lindenius* is likely basal or relatively basal within the subtribe, as is *Tracheliodes*. It is therefore interesting that species from these groups should make up most of the fossil record for the subtribe. The records of *Ectemnius* from Colorado and Germany are more intriguing, as the genus is apparently derived among the moustache wasps. However, characters defining *Ectemnius* were not preserved in these compression fossils, and attribution to the genus is exceedingly speculative, based almost entirely on general habitus (Cockerell, 1906, 1910; Meunier, 1911). As such, these records must be considered tentative and the types should be restudied before further conclusions based on these records are proposed. Overall, the sparse available records and their apparent phylogenetic position suggest an Early Tertiary (perhaps Paleocene?) origin of the Crabronina.

With regard to *Lindenius* in particular, extant species of the genus are nearly restricted to the Holarctic region; one species, *Lindenius montezuma* (Cameron), reaches Neotropical portions of southern Mexico (Amarante, 2002). It is notable that an extinct and perhaps basal member of the genus should be found outside of its modern range and amid exceptional habitat, which allows speculation that the modern diversity in the Mediterranean region may not be attributable to an origin there. Like its relative *Tracheliodes*, *L. paleomystax* suggests a relict aspect to the distribution and habitat preference of modern *Lindenius*. Clearly, the natural history of *Lindenius* is more complicated than that revealed by Recent taxa alone. Once cladistic work on the Crabronina has been completed, more insight on questions of moustache wasp origins and historical biogeography, particularly that of *Lindenius*, can be gained.

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