

# New ambrosia beetles (Coleoptera: Curculionidae: Platypodinae) from Miocene Mexican and Dominican ambers and their paleobiogeographical implications

David Peris<sup>1</sup> · Mónica M. Solórzano Kraemer<sup>2</sup> · Enrique Peñalver<sup>3</sup> · Xavier Delclòs<sup>1</sup>

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**Abstract** Two new species are described from Mexican amber (15–20 Ma): *Cenocephalus tenuis* Peris and Solórzano Kraemer sp. nov. and *Tesserocerus simojovelensis* Peris and Solórzano Kraemer sp. nov. *Cenocephalus*, originally described as living in Central and South America and then as fossils from Early to Middle Miocene amber, is noted as morphologically indistinguishable from *Mitosoma*, and originally described as endemic from Madagascar. Thus, we consider that a close taxonomic relationship exists, even if they are not the same genus. New evidence of the species already described in Platypodinae (Tesserocerini) from Mexican and Dominican ambers (15–20 Ma) and the differences between those species are discussed, complementing the original descriptions. The paleobiogeography of *Cenocephalus* and *Mitosoma* is analyzed, which strongly supports the hypothesis of colonization from Afrotropical Madagascar to America prior to Early to Middle Miocene (15–20 Ma) via sea currents. *Hymenaea* was interpreted as the Mexican and Dominican

resin producers. Based on the analysis of fossil and current distribution of such plants, our hypothesis considers that the beetle dispersion occurred with *Hymenaea*, which was possibly its host plant.

**Keywords** Platypodinae · *Cenocephalus* · *Mitosoma* · *Hymenaea* · Paleobiogeography · Madagascar

## Introduction

Ambrosia beetles is the common name for the beetle subfamily Platypodinae, which contains more than 1,400 species (Kuschel et al. 2000; Oberprieler et al. 2007; Kirkendall et al. 2015) that cultivate fungi in tunnels excavated in wood. Although Platypodinae was traditionally considered an independent family within Curculionoidea (Wood 1986, 1993; Wood and Bright 1992), it is now considered within the family Curculionidae (Kuschel et al. 2000; Oberprieler et al. 2007; Alonso-Zarazaga and Lyal 2009; Bouchard et al. 2011; Jordal et al. 2011, 2014). Extensive analyses by Kuschel et al. (2000) and Farrell et al. (2001) suggested that platypodines should be better classed as a group of scolytines (Jordal and Cognato 2012); however, other researchers, namely Marvaldi (1997) and Marvaldi et al. (2002, 2008), concluded they were more suitably described as being independent subfamilies within Curculionidae.

Jordal et al. (2011) carried out an extensive phylogenetic study on the most prominent wood-boring taxa, within which they suggested that Scolytinae and Platypodinae were sister lineages within Curculionidae and that early diversification made them as advanced weevils. More recently, with the analysis of higher-level phylogenetic relationships in weevils, the polyphyly of wood-boring lineages remains open. However, it is possible that the Platypodinae may not be closely related to

✉ David Peris  
daperce@gmail.com; david.peris@ub.edu  
Mónica M. Solórzano Kraemer  
monica.solorzano-kraemer@senckenberg.de  
Enrique Peñalver  
e.penalver@igme.es  
Xavier Delclòs  
xdelclos@ub.edu

<sup>1</sup> Departament d'Estratigrafia, Paleontologia i Geociències Marines; and Institut de Recerca de la Biodiversitat (IRBio), Facultat de Geologia, Universitat de Barcelona (UB), Martí i Franquès s/n, 08028 Barcelona, Spain

<sup>2</sup> Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

<sup>3</sup> Museo Geominero, Instituto Geológico y Minero de España, Ríos Rosas 23, 28003 Madrid, Spain

Scolytinae, and so the position of Platypodinae remains ambiguous (Guillett et al. 2014; Hulcr et al. 2015), and the debate is ongoing (Bright 2014; Jordal et al. 2014).

Ambrosia beetles embedded in Mexican and Dominican Early to Middle Miocene ambers are extremely diverse (see Schedl 1962; Schawaller 1981; Bright and Poinar 1994; Davis and Engel 2007) and often include several specimens not yet described. Platypodine involvement in Miocene resin production, together with scolytines, has been suggested by some authors (Bright and Poinar 1994; Grimaldi and Engel 2005; McKellar et al. 2011). The Mexican and Dominican ambers were formed by resiniferous angiosperms (*Hymenaea* spp.) and their scolytine and platypodine fauna probably used these plant species as hosts, which would have damaged the trees and induced the resin production (Poinar and Poinar 1999; Cognato and Grimaldi 2009).

*Hymenaea* (Fabaceae (=Leguminosae): Detarieae) is a resin-producing angiosperm tree. It currently comprises 14 species, which are generally well distributed in the tropical and subtropical forests of Central America, the West Indies, and most of South America. *Hymenaea verrucosa* is a unique species that is found in East Africa and Madagascar and is considered the most primitive species of the genus (Lee and Langenheim 1975; Langenheim 2003; Fougère-Danezan et al. 2010). Nevertheless, a complete phylogenetic and molecular study of the whole species has not been carried out until now.

The species *Hymenaea mexicana* and *H. allendis* have been found in Mexican amber (Poinar and Brown 2002; Calvillo-Canadell et al. 2010) while *H. protera* has been found in Dominican amber (Poinar 1991). These findings may have been made possible through the analysis of flowers and leaves preserved as bioinclusions. These fossil species are thought to be the producers of both Mexican and Dominican fossil resins, respectively. Furthermore, a morphological study of *H. protera* and *H. mexicana* indicated a close relationship with the Afrotropical species *H. verrucosa* (Poinar and Brown 2002). Given the lack of a molecular phylogenetic study that includes all *Hymenaea* species and the absence of *Hymenaea* spp. in the macro-remains and pollen fossil records of Africa and South America before the Middle Miocene, there are varying ways to interpret the evolutionary history of this tree genus (see below).

Davis and Engel (2007) and Kirejtshuk et al. (2014) carried out studies in which they summarized all the fossil species known in Platypodinae. They reported a total of 14 species in one fossil and three extant genera, plus a highly dubious assignment to an extant species. The first fossil containing ambrosia beetle was described from Miocene Mexican amber as *Cenocephalus* by Schedl (1962), while the earliest evidence was reported from Cretaceous Myanmar amber and then from Eocene Baltic amber (Larsson 1978; Poinar 1992; Cognato comm. pers.). Platypodinae were occasionally listed among the beetles from Baltic amber; however, reliable evidence of

their occurrence has not yet been presented (Weitschat and Wichard 2002), and no description of these findings has been made to date (Alekseev 2013; see Cognato 2015). However, the authors of the present study will be analyzing a sample of platypodine in Baltic amber in the near future.

In this study, a description of two new platypodine species in Mexican amber is presented as well as new evidence relating to several species already described from Mexican and Dominican ambers (Table 1). Based on the analysis of this new evidence, some taxonomic changes related to *Mitosoma* (Malagasy distribution) and *Cenocephalus* (Neotropical distribution) will be required following Schedl's work (1972). The morphological similitude, at generic level, of *Cenocephalus* with living *Mitosoma* is discussed. Additionally, we will analyze a hypothesis that attempts to explain the current distribution of *Mitosoma* and *Cenocephalus*. This hypothesis takes into account the fossil record and ecology of living representatives, as well as the analysis of data related to the Miocene resin-producing trees in the Neotropics.

## Materials and methods

Samples with bioinclusions described in this paper are from Dominican and Mexican ambers. They are housed at three different institutions: “EPGM-RD” Dominican amber collection of the Laboratori de Paleontologia, Department of Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona (Barcelona, Spain); “MCAM” Museu de la Ciència Ambre, CosmoCaixa Barcelona (Barcelona, Spain); and “Mx” Staatliches Museum für Naturkunde, Schloss Rosenstein (SMNS) (Stuttgart, Germany).

The Dominican amber pieces are from La Toca mine, located at Cordillera Septentrional in northern Dominican Republic (Fig. 1a). The Dominican amber was reviewed by several authors, and following discussions regarding the age and origin of the specimen, it was concluded that it dated back to the late Early to early Middle Miocene (15–20 Ma) (Grimaldi 1994; Iturralde-Vinent and MacPhee 1996; Iturralde-Vinent 2001; Grimaldi and Engel 2005; Penney 2010). The Mexican amber pieces are from Simojovel de Allende in the state of Chiapas, Mexico (Fig. 1b). This amber is considered to be of Early to Middle Miocene in age (15–20 Ma) and was therefore correlated with the Dominican amber deposits (Solórzano Kraemer 2007, 2010).

Dominican pieces have the following accession numbers: EPGM-RD-0106, EPGM-RD-0107, EPGM-RD-0108, EPGM-RD-0110, EPGM-RD-0111, MCAM-0034, MCAM-0530, MCAM-0590, and MCAM-0623. The accession numbers of the Mexican pieces are as follows: Mx-213, Mx-214, Mx-238, Mx-275, Mx-347, Mx-354, and Mx-379. All

**Table 1** List of already described species of *Cenocephalus* from Mexican or Dominican ambers that have been found and analyzed in the pieces studied from the (1) Dominican amber collection of the Laboratori de Paleontologia de la Universitat de Barcelona (Barcelona, Spain), (2) Museu de la Ciència Ambre, CosmoCaixa Barcelona (Barcelona, Spain), and (3) Staatliches Museum für Naturkunde, Schloss Rosenstein (Stuttgart, Germany)

Amber	Species	Original description	New samples	Depository
Mexican	<i>C. succinicaptus</i> Schedl, 1962	1962 <i>C. succinicaptus</i> Schedl: Figures 1–4 and Text-Fig. 1	Mx-214, Mx-275	3
Mexican	<i>C. hurdi</i> Schedl, 1962	1962 <i>C. hurdi</i> Schedl: Figures 5–8 and Text-Fig. 1	Mx-213, Mx-347	3
Dominican	<i>C. rhinoceroide</i> (Schwaller, 1981)	1981 <i>Mitosoma rhinoceroide</i> Schwaller: Figures Abb. 1–3 and 14–20	EPGM-RD-0106, EPGM-RD-0107, EPGM-RD-0108, MCAM-0530	1, 2
Dominican	<i>C. exquisitus</i> Bright and Poinar, 1994	1994 <i>C. exquisitus</i> Bright and Poinar: Figures 5–6 and 18–19	EPGM-RD-0106, MCAM-0034, MCAM-0623	1, 2
Dominican	<i>C. quasitexquisitus</i> Davis and Engel, 2007	2007 <i>C. quasitexquisitus</i> Davis and Engel: Figures 1–5	EPGM-RD-0110	1
Dominican	<i>C. spinatus</i> Bright and Poinar, 1994	1994 <i>C. spinatus</i> Bright and Poinar: Figures 9–10 and 22–23	MCAM-0590	2

See “Materials and Methods” to find information related to the geology of these ambers and “References” to find the complete references where the original species were described

samples were cut and polished, and the EPGM-RD pieces were also embedded in a transparent epoxy resin (see Nascimbene and Silverstein 2000).

Specimens were examined under a Leica MS5 stereomicroscope and an Olympus BX41 compound microscope. General photographs were taken using a Leica DFC 420 camera attached to the Leica MS5 stereomicroscope, using the software Leica IM1000. Drawings were made using a camera lucida attached to the Leica stereomicroscope. Photographs were merged using the software Combine ZP edited with Photoshop Elements 10 and CorelDraw X6. All measurements in the descriptions are in millimeters.

We used the key from Wood (1993), but the taxonomic arrangement follows Alonso-Zarazaga and Lyal (2009). Table 2 summarizes the author and year of each species.

## Systematic paleontology

Order: Coleoptera Linnaeus, 1758

Suborder: Polyphaga Emery, 1886

Superfamily: Curculionoidea Latreille, 1802

Family: Curculionidae Latreille, 1802

Subfamily: Platypodinae Shuckard, 1840

Tribe: Tesserocerini Strohmeyer, 1914

## New species from Mexican amber

Genus: *Cenocephalus* Chapuis, 1865

Type species: *Cenocephalus thoracicus* Chapuis, 1865

*Cenocephalus tenuis* Peris and Solórzano Kraemer sp. nov.

Figure 2

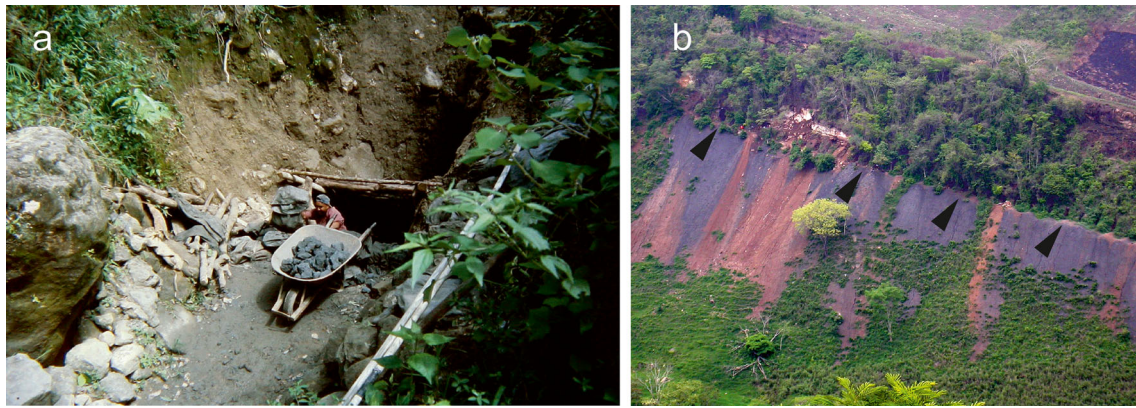
Etymology: Specific name *tenuis* is the Latin word for ‘slender’.

Holotype: Mx-379, Miocene amber from Simojovel de Allende, Chiapas, Mexico; housed at the SMNS (Stuttgart, Germany). The holotype is a complete specimen clearly collapsed internally by taphonomic processes but with all the necessary characters clearly visible. It is female by its frons strongly flattened covered with long setae.

Allotype: Mx-354, the locality and depository are the same as the holotype, as syninclusion with one Arachnida, three Diptera: (Ceratopegonidae, Cecidomyiidae, and Psychodidae) and one Psocoptera.

Paratype: Mx-213, the locality and depository are the same as the holotype, as syninclusion with one specimen of *Cenocephalus hurdi* and one possibly Anthribidae (Coleoptera: Curculionoidea). It is a female.

Diagnosis: Female with slim body, elytral declivity very short, it is margin-armed by small spiniform protrusions, apical margin extending into a short, acute process, face of declivity very convex with a pair of acute spiniform protrusions into the interstriae



**Fig. 1** Miocene amber mines; **a** La Toca, Cordillera Septentrional, northern Dominican Republic; **b** Simojovel de Allende, Chiapas, Mexico; *arrows* indicate pitheads

3, protibiae armed with two transverse rugae and outer face of metatibiae armed by four transverse rugae.

**Description:** Female. Body length 3.64 without mandibles, maximum width 0.59 at the elytral apex, 6.2 times longer than wide. Body completely collapsed. Pubescence present dorsally in the head (long hairs) and elytra (short hairs), pronotum glabrous.

Head distinctly longer than wide, approximately two times longer than eye diameter, slightly constricted behind the eyes, marked dorsally. Eyes lateral, small, round, easily visible in dorsal view, very finely faceted. Frons as wide as head, strongly concave transversely, surface with long, straight setae, which are curved on periphery. Limit between the frons and the rostrum unidentifiable. Antennae insertion basal, antennae length very short, not extending to cephalic insertion. Scape straight, only slightly curved at the insertion with the head, extending until the fore margin of the eyes; funicle four-segmented; very little pedicel inserted at the scape apex, as wide as long; antennomere 3 conical, narrower at base and wider at apex, as long as the apical diameter; antennomeres 4 and 5 strongly transverse; club compressed, almost round. Mandibles large, with one large tooth at the apex and one tooth at the apical third of the biting edge, smooth and convex on upper face. Submentum separated on each side from margin of oral fossa by deep cleft.

Pronotum 2.1 times longer than wide, wider at apical fifth, narrower towards the base; pronotal disk smooth. Posterior margin of prothorax strongly procurved in pleural area. Scutellum small, slender, apically pointed. Procoxae contiguous, precoxal piece on prosternum obtusely pointed.

Elytra subparallel, becoming wider apically, base of elytra as wide as base of pronotum. Elytra 2.9 times longer than wide (measured from the base to the declivity and the wider, apical portion); 1.5 times longer than pronotum. Elytral disk shallow punctured, deeply striate, total number of striae and interstriae not discernible. Bases of interstriae 3 and 5 transversely rugose; interstriae 3 carinate along the basal third, interstriae 5 subcarinate close to the base. Elytral declivity beginning near apical fourth, convex, lateral margin evenly arcuate and armed

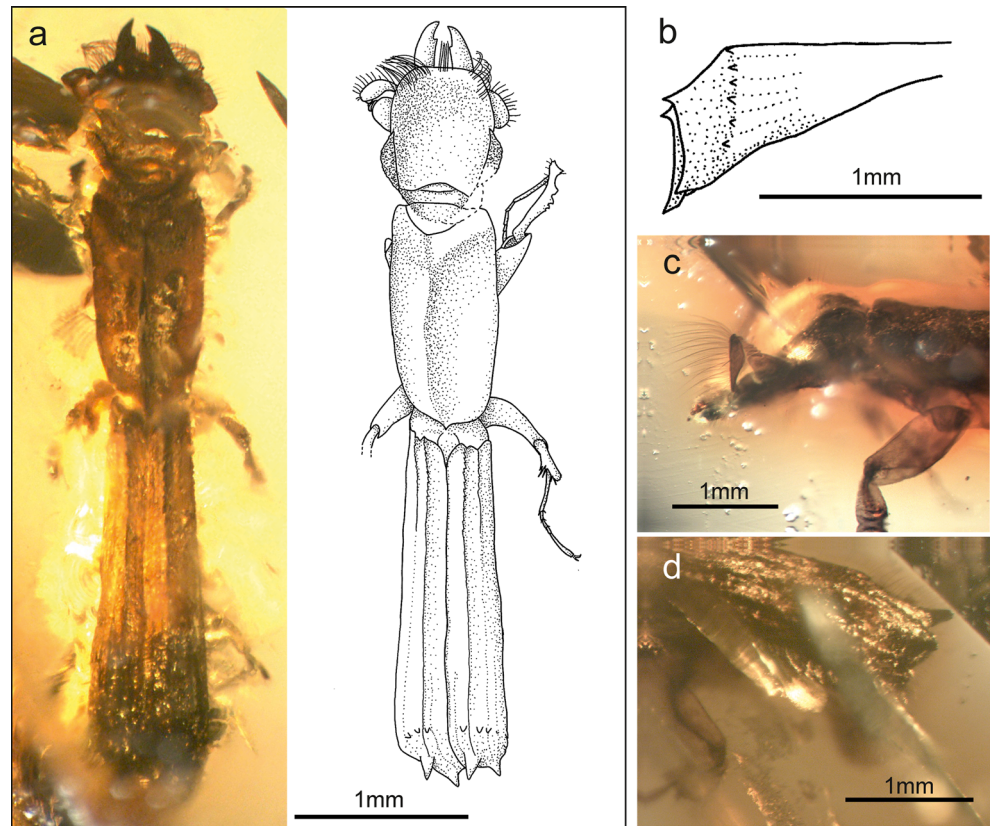
by short spiniform protrusions, a pair of acute spiniform protrusions into the face of the declivity, interstriae 3; apical margin extending into a short, acute process.

**Table 2** Taxa and author named along the text (with the exception of the already named taxa in Table 1)

Plant		
<i>Hymenaea</i>	Linnaeus	1753
<i>H. allendis</i>	Calvillo-Canadell, Cevallos-Ferriz and Rico-Arce	2010
<i>H. courbaril</i>	Linnaeus	1753
<i>H. mexicana</i>	Poinar and Brown	2002
<i>H. protera</i>	Poinar	1991
<i>H. verrucosa</i>	(Gaertner) Oliver	1791
Animal		
<i>Acanthotomicus</i>	Blandford	1894
<i>A. hymenaeae</i>	Eggers	1933
<i>Batrachorhina</i>	Chevrolat	1842
<i>Chaetastus</i>	Numberg	1953
<i>Cladoctonus</i>	Strohmeier	1911
<i>C. ruber</i>	Bright and Poinar	1994
<i>Coccotrypes</i>	Eichhoff	1878
<i>Coecephalophonus</i>	(Schedl)	1965
<i>Cryptocarenus</i>	Eggers	1937
<i>Electroborus</i>	Cognato	2013
<i>Hypothenemus</i>	Westwood	1836
<i>Mitosoma antiquus</i>	Bright and Poinar	1994
<i>Mitosoma biconicus</i>	Bright and Poinar	1994
<i>Nesanoplium puberulum</i>	(Fleutiaux and Sallé)	1889
<i>Platypicerus</i>	(Nunberg)	1953
<i>Scolytogenes</i>	Eichhoff	1878
<i>Tesserocerus primus</i>	Bright and Poinar	1994
<i>T. retusus</i>	Guérin-Méneville	1838
<i>Wendilgarda</i>	Keyserling	1886

Differences between plants and animals are presented here, ordered alphabetically

**Fig. 2** *C. tenuis* sp. nov. from Miocene amber from Simojovel de Allende, Chiapas, Mexico; **a** holotype Mx-379, female, illustration and camera lucida drawing of the dorsal habitus; **b** holotype, detailed camera lucida drawing of the elytral declivity; **c** allotype Mx-354, male, detailed illustration of the head and the antennae; **d** paratype Mx-213, detailed illustration of the elytral declivity



Mesosternum with mesepisternum convex, unarmed. Metasternum long, with distinct femoral impression; metacoxae contiguous. Legs long; femora wide, compressed; protibiae with two transverse rugae and a long weakly hooked inner mucro; outer face of metatibiae armed by four transverse rugae. Tarsi slender, longer than tibia; tarsomere 1 as long as the following tarsomeres combined; tarsomeres 2 and 3 equal in length; tarsomere 4 the shortest, 0.5 times the length of tarsomere 3, tarsomere 5 as long as the previous three combined, slender, with long, slender claws.

Male. Of similar size, proportions, and general sculpture. It differs from the female in frons feeble depressed, glabrous, and elytral declivity with spiniform protusions on the interstriae 3 more strongly developed.

Comments: The specimens fit within *Cenocephalus* by the posterior margin of prothorax strongly procurved in pleural area, submentum separated on each side from margin of oral fossa by deep cleft, procoxae contiguous, scutellum small, slender, pointed, antennal funicle four-segmented (counting the pedicel), eye with circular profile in lateral view, mesepisternum convex, unarmed, precoxal piece on prosternum obtusely pointed, second segment on antennal funicle longer than wide, outer face of metatibiae armed by four transverse rugae, elytral declivity convex, base of declivity armed by spiniform protusions, and Central American distribution (Browne 1971; Schedl 1972; Wood 1993).

The unique character that differentiates this genus from the Magalasy *Mitosoma* is the current distribution, which is a relatively weak piece of evidence when describing fossils (see “Discussion”). *C. tenuis* sp. nov. has several similarities with the African genus *Chaetastus*, but they differ in the antennae type and elytral disk (see also “Discussion” about taxonomic remarks). These characters were highlighted by Browne (1971), who described them as essential in differentiating *Chaetastus* from *Mitosoma* and *Cenocephalus*. However, several other characters in *C. tenuis* sp. nov. warrant a more correct assignment of the new species in *Cenocephalus* (although see also “Discussion” about taxonomic remarks); these include dimensions and proportions of the body parts, which lack an apparent transverse band of fine pores along basal portion of the pronotal disk, number of transverse rugae at the pro- and metatibiae outer surface, position and size of spines along the declivity face and margins, and American distribution.

*C. tenuis* sp. nov. is not as stout as members of this genus tend to be, and the pronotum is slender; however, the set of characters are concordant with *Cenocephalus*. The fossil species *Cenocephalus exquisitus*, *Cenocephalus antiquus*, and *Cenocephalus spinatus* also have a slender pronotum. Although *C. tenuis* sp. nov. has a similar spine distribution along the declivity to the fossil *C. biconicus*, the new species is more slender, with the declivity margin armed with short

spiniform protrusions and face of declivity convex; *C. biconicus* is more robust, with the declivity margin unarmed and its face obliquely truncated.

Genus: *Tesserocerus* Saunders, 1837

Type species: *Platypus insignis* Saunders, 1837

*Tesserocerus simojovelensis* Peris and Solórzano Kraemer  
sp. nov.

### Figure 3

Etymology: Specific name *simojovelensis* after Simojovel de Allende (Mexico), locality where new species was found.

Holotype: Mx-238, Miocene amber from Simojovel de Allende, Chiapas, Mexico; housed at the SMNS (Stuttgart, Germany). The holotype is a complete specimen, the entire habitus visible and well preserved. It is a female by its frons flattened with surface covered by long setae and rounded base of the declivity, something explanate but without protrusions.

Diagnosis: Female. Body 5.5 times longer than wide; head distinctly longer than wide, about two times longer than eye length; scape, mandible insertion, and prosternum strongly pubescent, with long and stout hairs; elytral declivity with three spiniform protrusions on anterior border; protrusions becoming sequentially shorter from the first to the third; metasternum long, impressed near metacoxa for reception of femur, anterior margin of impression armed by one pointed spine.

Description: Body length 5.35, maximum width 0.97 at the elytral apex, 5.5 times longer than wide. Pubescence present along the entire body, very conspicuous on the head, frons, scape, mandibles, and prosternum; elytral disk almost glabrous.

Head distinctly longer than wide, about two times longer than eye length. Eyes lateral, elongate, big, approximately 1.5

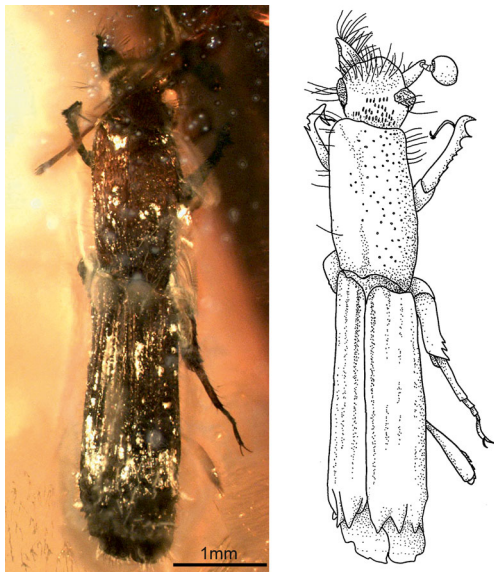
times longer than wide, almost flat, slightly visible in dorsal view, subtriangular in outline, anterior margin entire; posterior border delimited by some long and stout setae, as similarly occur along mandible insertions. Vertex coarsely punctured, punctures two times longer than wide. Frons slightly concave transversely, surface with relatively long, fine, erected setae. Antennal insertion basal, closer to mandibles than to the eyes; antennae short extending to cephalic insertion; scape large, slender, extending until the fore margin of the eyes, completely covered by long and stout setae, being longer toward apex; funicle four-segmented; pedicel inserted at the pedicel apex, rounded in shape; antennomere 3 conical, narrower at base and wider apically, as long as the apical diameter; antennomeres 4 and 5 strongly transverse; club compressed, almost round. Mandibles are large, with one large tooth at the apex and one tooth at the apical third of the biting edge, smooth and convex on upper face. Submentum separated on each side from margin of oral fossa by deep cleft.

Pronotum 1.8 times longer than wide, narrower towards the base; pronotal disk of rough appearance, completely covered by rounded punctures; pronotal lateral margins thickened, with a set of long and stout setae along the margins. Scutellum very small, apically pointed. Prosternum long, covered by short and stout setae, precoxal piece on prosternum acutely pointed. Procoxae contiguous.

Elytra subparallel, becoming wider apically, base of elytra slightly wider than base of pronotum. Elytra 2.9 times longer than wide; 1.7 times longer than pronotum. Elytral disk strongly punctured, deeply striate; interstriae 3 carinate along the basal third, interstriae 5 remarked with small tubercles close to the base. Elytral declivity beginning near apical fourth, steep, with three spiniform protrusions on anterior margin of elytral declivity and arising from elytral striae 3, 5, and 7; protrusions become sequentially shorter from the first to the third, although the first and the second are much bigger than the third. Declivity face covered by short and fine hairs and apical margins extending into a short, rounded lobe in each elytron.

Metasternum long, impressed near metacoxa for reception of femur, anterior margin of impression armed by one pointed spine; metacoxae contiguous. Legs short, robust; femora wide, compressed; profemora wider than the rest; protibiae armed with two transverse rugae on the posterior face and a long weakly hooked inner mucro; becoming wider from protibiae to metatibiae; outer face of metatibiae armed by three transverse rugae. Tarsi stout, longer than tibiae in all the legs; tarsomere 1 as long as tarsomeres 4 and 5 combined, protarsomeres 2 and 3 equal in length, protarsomere 4 the shortest, 0.5 times the length of tarsomere 3, tarsomere 5 slightly longer than the previous three combined, slender, with long, slender claws.

Comments: The specimen fits within *Tesserocerus* by the posterior margin of prothorax strongly procurved in pleural area, submentum separated on each side from margin of oral fossa by deep cleft, procoxae contiguous, scutellum small,



**Fig. 3** *T. simojovelensis* sp. nov. from Miocene amber from Simojovel de Allende, Chiapas, Mexico; holotype Mx-238, female, illustration and camera lucida drawing of the dorsal habitus

slender, pointed, antennal funicle four-segmented (counting the pedicel), eye elongate, 1.5 times longer than wide, anterior margin entire, pronotum 1.8 times longer than wide, precoxal piece on prosternum acutely pointed, and pedicel attached near its apex (Wood 1993). All *Tesserocerus* spp. are between 3.0 and 4.5 times longer than wide, including the unique fossil species (Wood 1993; Bright and Poinar 1994), while *T. simojovelensis* sp. nov. is 5.5 times longer than wide. Except for this morphological feature, we have decided to keep it in *Tesserocerus* because all the characters in the new species are consistent with those for this genus in the key to world platypodine genera from Wood (1993).

*T. simojovelensis* sp. nov. is clearly different from *Tesserocerus primus*, which is currently a unique fossil species of this genus, described from Dominican amber (Bright and Poinar 1994). The new species is larger, with two rugae on the posterior face of the protibiae and with three spiniform protrusions on anterior margin of elytral declivity, while *T. primus* is smaller, with one ruga on the posterior face of protibiae, and four spiniform protrusions on the elytral declivity, also with different proportions between them. *T. simojovelensis* sp. nov. is similar to *Tesserocerus retusus* in number and position of spiniform protrusions, but the first pair of protrusions in the new species is longer than the second pair, while in *T. retusus* all the spines are of similar length.

#### Species already known from Mexican and Dominican ambers

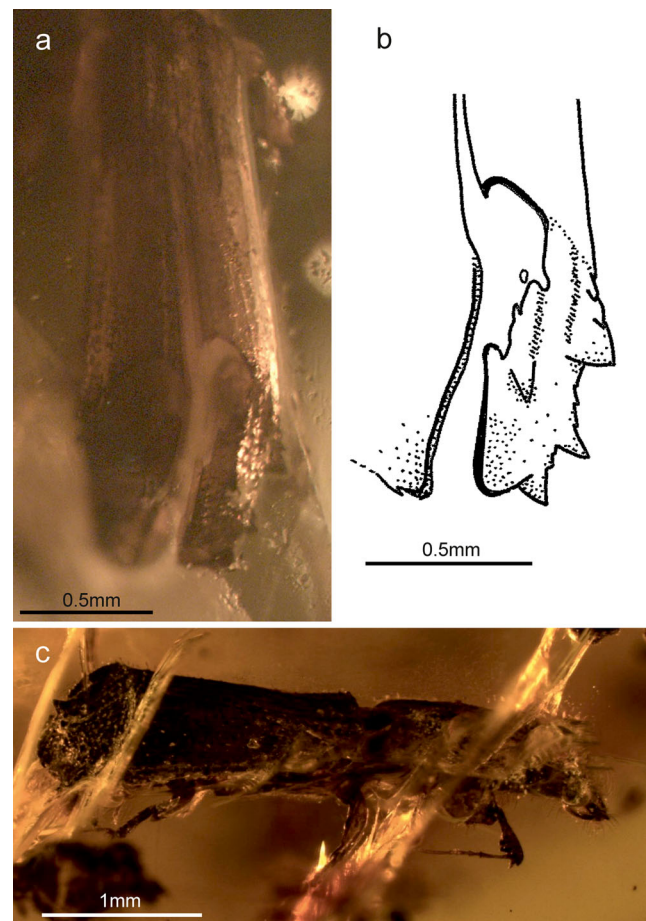
Several species already described from Mexican and Dominican ambers were observed in the amber pieces studied. The difficulty in differentiating between some of these species using the published data justifies the following review, which includes comments on certain aspects of the species (see Table 1 for details).

##### *Mexican species of Platypodinae*

##### *Cenocephalus succinicaptus* Schedl, 1962

In Fig. 4a–b, the overall habitus of the new ambrosia beetles Mx-214 and Mx-275 is indicative of *C. succinicaptus* based on its original description and the figures 1–4 in Schedl (1962). However, the original description was also accompanied by the Text-Fig. 1, which contains an error in the figure legend: the male declivity illustrations presented by Schedl corresponding to *C. succinicaptus* (left) and *C. hurdi* (right) were referenced on the contrary in the legend, according to the original description. Taking into account this modification, the original illustration for the male declivity in *C. succinicaptus* (Schedl 1962) is consistent with Fig. 4b herein, which illustrates the male declivity of *C. succinicaptus*.

The original line drawing in Schedl (1962) is lacking detail and differs in some ways from the picture. Figure 4b herein



**Fig. 4** Diverse illustrations of two species of *Cenocephalus* from Miocene amber from Simojovel de Allende, Chiapas, Mexico; **a** *C. succinicaptus*, Mx-275, dorsal illustration of the elytral declivity; **b** detailed camera lucida drawing of the elytral declivity; **c** *C. hurdi*, Mx-347, lateral habitus

illustrates more clearly the male declivity of *C. succinicaptus*. Bright and Poinar (1994) noted that the holotype of this species is a completely distorted and broken specimen and that the allotype (male) is also distorted except for the elytral apex; the new specimens found herein will be very helpful in the identification of the species. We know that both specimens are males due to the well-developed spiniform protrusions along the elytral declivity margins and interstriae 3, the feebly depressed frons, and the lack of notable pubescence (Schedl 1962). The declivity margin in Mx-275 was partially polished, and the illustration is based only in part on one elytron. Mx-275 was found in syninclusion with a possible Ceratopogonidae (Diptera) specimen. Mx-214 was found in syninclusion with other probable Platypodinae specimens, but its preservation is not sufficient to enable us to identify this specimen in any more detail.

##### *C. hurdi* Schedl, 1962

In Fig. 4c, there are two specimens consistent with the description and illustration of the declivity that Schedl

(1962) described in *C. hurdi*. Mx-213 and Mx-347 are probably males due to their flat frons (Schedl 1962). Mx-213 was found in syninclusion with *C. tenuis* sp. nov. and one possible Anthribidae specimen (Coleoptera: Curculionoidea). Unfortunately, the new material cannot be compared with the holotype because it is lost; Bright and Poinar (1994) were unable to locate the specimen described by Schedl (1962) during their search in the Museum of Paleontology of the University of California and the Naturhistorisches Museum (Wien). Furthermore, the authors of the present study were unable to locate the holotype of *C. hurdi* in the Naturhistorisches Museum collection. No paratypes were designated in the original description.

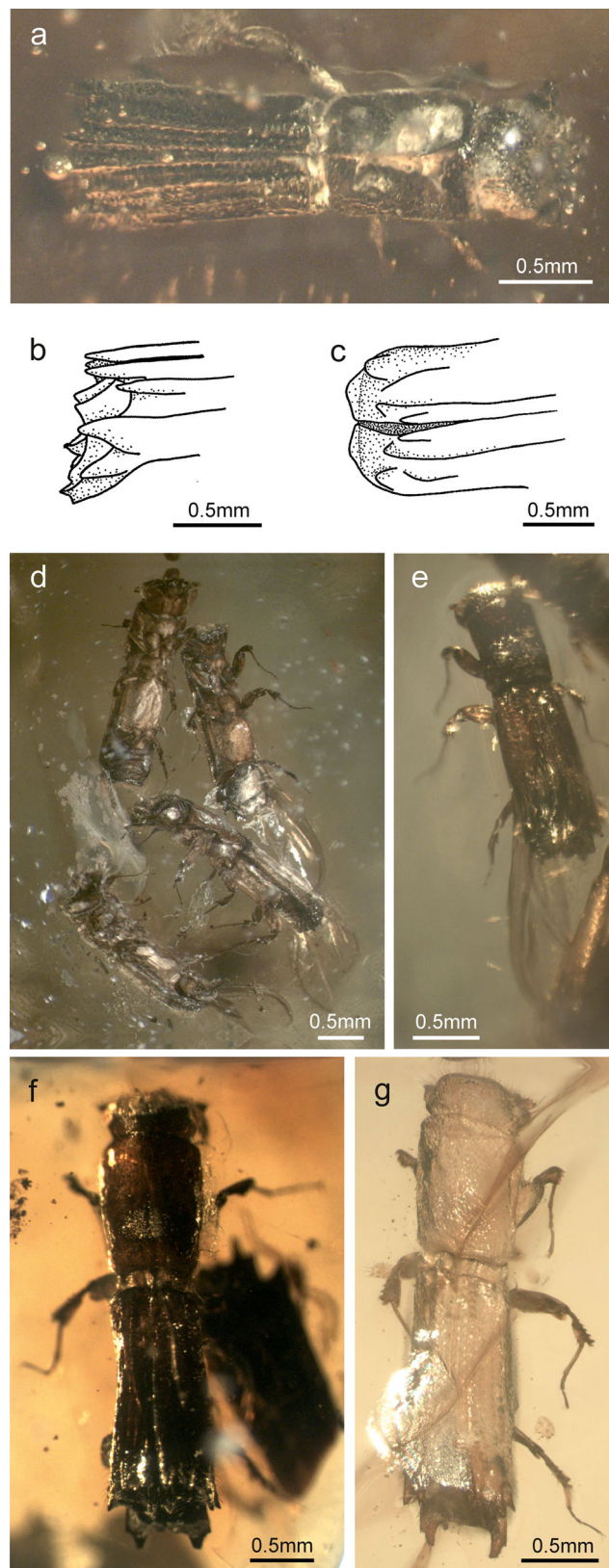
#### Dominican species of *Platypodinae*

##### *C. exquisitus* Bright and Poinar, 1994

Shown in Fig. 5a–c, there are two specimens (one male and one female, both in EPGM-RD-0106) which are consistent with the general description of *C. exquisitus* (Bright and Poinar 1994). The male has a particular set of spiniform protrusions along elytral declivity that is described by Bright and Poinar (1994) and later by Davis and Engel (2007). The original illustration for the male declivity in Bright and Poinar (1994) has a mistake: The length of the spiniform protrusions on the anterior margin of the elytral declivity in the dorsal aspect does not reflect the similar proportion as the same spiniform protrusions in the lateral aspect (Figures 5 and 6 in Bright and Poinar 1994). This, combined with the conclusions of Davis and Engel (2007), leads us to believe that the second pair of spiniform protrusions on the anterior margin of the elytral declivity should be shorter than the first pair. Indeed, this characteristic is typically used to differentiate between *C. exquisitus* and *C. quasiexquisitus*. As such, the present study offers new illustrations of male elytral declivity (Fig. 5a–b).

Although the species is only described based on the male form, this study located a possible female specimen in syninclusion with the male. Due to its proximity with the male, it has been tentatively interpreted as a female of *C. exquisitus*. Sexual dimorphism is a very common characteristic in nearly all Platypodinae, mainly in structures that include the frons, elytral declivity, abdominal ventrites, and

the presence of mycangia (Knizek and Beaver 2004). Females of *C. exquisitus* can be differentiated from the male by their longer and stouter bodies, frons broadly flattened, covered



**Fig. 5** Diverse illustrations of four species of *Cenoccephalus* from Miocene amber from La Toca, Cordillera Septentrional, Dominican Republic; **a** *C. exquisitus*, MCAM-0623, illustration of the dorsal habitus; **b** EPGM-RD-0106, male, detailed camera lucida drawing of the elytral declivity in lateral view; **c** female, detailed camera lucida drawing of the elytral declivity in dorsal view; **d** *C. rhinoceroide*, EPGM-RD-0106, illustration of the habitus of three females and one male; **e** male from the same piece, illustration of the dorsal habitus; **f** *C. quasiexquisitus*, EPGM-RD-0110, male, illustration of the dorsal habitus; **g** *C. spinatus*, MCAM-0590, male, illustration of the dorsal habitus



with long erect hairs, and elytral declination convex, with two poorly developed spiniform protrusions in each elytron (Fig. 5c).

In addition to the two specimens of *C. exquisitus* in EPGM-RD-0106, there were initially seven specimens of *C. rhinoceroide*, one Scolytinae (*Cladoctonus ruber*), and one Acari. Following preparation of the amber, only two specimens of *C. exquisitus* and five specimens of *C. rhinoceroide* remained. The fact that both species were found in the same piece of amber confirms their coexistence in the past.

The male specimens of *C. exquisitus* resemble males of *C. rhinoceroide*, *C. quasiexquisitus* (both from Dominican amber), and *C. succinicaptus* (from Mexican amber). However, *C. exquisitus* differs from *C. rhinoceroide* by the longer spiniform protrusions on the declivity margin and declivity face and by the second pair of spiniform protrusions on the anterior margin of the elytral declivity, which is shorter than the first pair. In contrast, in *C. rhinoceroide*, the spiniform protrusions are shorter and the two first pairs of spiniform protrusions on the anterior margin of the elytral declivity are equally long.

The male specimens of *C. exquisitus* differ from *C. quasiexquisitus* firstly by the second pair of spiniform protrusions on the anterior margin of the elytral declivity, which is shorter than the first pair, and secondly by the protrusions at the base of the declivity, which are shorter and situated further apart. *C. quasiexquisitus* differs from the second pair of spiniform protrusions on the anterior margin of the elytral declivity as they are slightly longer than the first pair, and the protrusions at the base of the declivity are very long and are situated closer together. Males of *C. exquisitus* differ from *C. succinicaptus* by the much longer spine on the lower outer apical margin of the declivity and by the different configuration of the spiniform protrusions on the lateral margin of the elytral apex (Schedl 1962; Schawaller 1981; Bright and Poinar 1994; Davis and Engel 2007).

As with the amber piece described above, MCAM-0623 also contains two males and one female of *C. exquisitus* as syninclusions. By contrast, in MCAM-0034, there are 23 specimens of *C. exquisitus*, which are mainly males, although there are possibly some females visible. In this last case, the piece also contains seven specimens of the scolytine *Cladoctonus ruber*, which is very commonly seen as syninclusion with platypodines (Bright and Poinar 1994).

*C. rhinoceroide* (Schwaller, 1981) Wood and Bright 1992

Shown in Fig. 5d–e, there are four new pieces of amber containing specimens of this species; however, EPGM-RD-0106 and EPGM-RD-0107 constituted the same piece of amber prior to preparation. EPGM-RD-0106 contains only one entire male, three entire females, and one very spoiled female lacking the posterior half of the body. EPGM-RD-0107 contains one male and one female. EPGM-RD-0108 contains one

entire male. MCAM-0530 contains one female of *C. rhinoceroide* in syninclusion with one Curculionoidea (Coleoptera), one Diptera, one Psocoptera, one Hymenoptera, one Trichoptera, one Arachnida, and one *Hymenaea* flower.

This species was defined originally within the genus *Mitosoma* by Schwaller (1981). It has already been described and carefully illustrated, so it is unnecessary to give a new illustration herein. The existing description notes the differences between males and females, which is also seen in the new pieces of Dominican amber. Although the frons of the females in EPGM-RD-0106 and EPGM-RD-0107 are covered by hairs in a more compact fashion than those of both the female in MCAM-0530 and the original illustration (Schawaller 1981), all other characters are consistent with the original female description. Thus, this character was not considered sufficient to divide them into two species, as it could be a preservational effect.

*C. rhinoceroide* is very similar to *C. exquisitus*, but, given the features commented on in the previous species and the comparison of both species in EPGM-RD-0106 (Fig. 5a and 5e, elytral declination in both species), it is possible to differentiate them.

*C. quasiexquisitus* Davis and Engel, 2007

Shown in Fig. 5f, the species was initially described by Davis and Engel (2007) from an isolated fossil specimen from Dominican amber, who noted its resemblance with *C. exquisitus*. However, some comments in their paper allow for the possible separation of the two species (see comments of *C. exquisitus* herein and in Davis and Engel 2007). EPGM-RD-0110 contains one entire male, which can be clearly aligned with the description of *C. quasiexquisitus*, and a posterior half of another specimen. The remains of the latter are also consistent with the elytral declivity of *C. quasiexquisitus*; however, it is impossible to make a definitive taxonomical determination. In the same piece, there are syninclusions of three Acari: two specimens associated with its metasternum and one free specimen, which is very close to the metasternum.

*C. spinatus* Bright and Poinar, 1994

Shown in Fig. 5g, one isolated male (MCAM-0590) is present in a completely transparent piece of amber. This species is clearly different to the species previously discussed due to its elytral declivity in males, which is armed by a peculiar set of large spiniform protrusions.

*Unnamed sample*

EPGM-RD-0111: The fossil is the posterior half of a Platypodinae. By the elytral declivity, it is possible to infer

its resemblance to males of *C. quasiexquisitus*, but its preservation precludes any definite determination.

## Discussion

### Taxonomic remarks on *Cenocephalus* and *Mitosoma*

After the author's observation of extant platypodines from the MNHN (Paris, France) and NHMW (Wien, Austria), the morphological confusion between the genera *Mitosoma* and *Cenocephalus* in current entomological collections was noted.

Chapuis (1865) described both genera. However, after some new descriptions of living and fossil species, Schedl (1972) decided to synonymize *Cenocephalus* (Neotropical), *Chaetastus* (Afrotropical: Africa), *Platypicerus*, and *Coecephalophonus* (Afrotropical: Madagascar) with *Mitosoma* (Afrotropical: Madagascar). The reasons for this are based on previous research by Browne (1971), who reviewed the genus *Chaetastus* and noted the clearly defined group comprised *Mitosoma*, *Cenocephalus*, and *Chaetastus*, and a possible similarity to *Coecephalophonus*. The author was only able to distinguish *Chaetastus* from the other similar genera by the second segment of the antennal funicle as it was longer than it was wide (third antennomere), a general sculpture of the elytra drawn in his work, and its African distribution (Browne 1971). Schedl (1972) did not consider the characters described by Browne (1971) sufficient to maintain the diversity and synonymized all the genera cited previously with *Mitosoma*.

This proposal was maintained for 30 years and *Cenocephalus rhinoceroides* was the first fossil platypodine described from Dominican amber in *Mitosoma* (Schawaller 1981). The situation changed when Wood and Bright (1992) considered *Mitosoma*, *Cenocephalus*, and *Chaetastus* as different genera in their catalogue with no explanations about their generic names. Later, Wood (1993) specified the restoration of all three names to full generic status and proposed a key to differentiate the diverse genera in Platypodinae (Platypodidae *sensu* Wood 1993). In that key, *Chaetastus* was clearly separate from the other two genera by the following: posterior one third of pronotum with a transverse band of mycetangia pores instead of mycetangia pores not discernible; anterior face of metatibiae with only one transverse ruga instead of anterior face of metatibiae armed by three or more transverse rugae; African instead of Malagasy or Central and South American distribution; and some additional less visible characters. Wood (1993) did not consider one of the characters used by Browne (1971) important in differentiating between *Chaetastus* and its two related genera. This characteristic was the third segment of the antenna, which was longer than it was wide. Furthermore, although Wood (op.cit.) decided to separate *Mitosoma* and *Cenocephalus* again, he could only

separate them morphologically by certain features on the elytral declivity treated as "usual" and by the difference in the geographic distribution of the living species, i.e., *Mitosoma* is endemic to Madagascar and *Cenocephalus* to Central and South America.

*C. succinicaptus*, a fossil from Mexican amber, has a very oblique elytral declivity (Schedl 1962). In several fossils described as *Cenocephalus* from Dominican amber, the base of the male declivity has large spiniform protrusions (Bright and Poinar 1994). The last two characters were treated as "usual" for *Mitosoma* by Wood (1993). Based on the observed variability, the unique argument to separate both genera is biogeographic.

Although it is not the objective of this study to review the current genera, it is necessary to consider some close relationships between *Cenocephalus* and *Mitosoma*. The use of current distribution as a definitive character to separate two genera is not suitable and even less so when considering fossil forms. Thus, consistent with the approach by Browne (1971) and Schedl (1972), it is necessary to critically assess the relationship between these genera, particularly the group comprising *Cenocephalus*, *Mitosoma*, and *Chaetastus* (clade with a possible category of subtribe Mitosomatina *sensu* Jordal comm. pers.). In the present work, the synonymy between *Mitosoma* and *Cenocephalus* is not formally established. This is firstly because it is not the focus of the study and secondly because this would require an analysis of their phylogeny and morphological features (including fossil and living species). However, it is considered that they are closely related through a common ancestor and are morphologically indistinguishable from each other.

### *Hymenaea* dispersal

*Hymenaea* currently includes 14 species. *H. verrucosa*, from Madagascar and Eastern Africa, is considered the most ancient representative of the genus. The other 13 species have Neotropical distribution (Lee and Langenheim 1975; Langenheim 2003; Fougère-Danezan et al. 2010). There are various hypotheses that attempt to explain the historic distribution of the genus, which are proposed and discussed as follows:

1. Poinar (Poinar 1991) and Poinar and Brown (2002) argued that the recent distribution of *Hymenaea* spp. is the result of a vicariance process.

Based on the presence of fossil caesalpinoid pollen in Late Cretaceous of South America (Muller 1981), they suggested that *Hymenaea* existed in Gondwana during the Cretaceous period before the rifting of South America and Africa (at about 100 Ma). However, vicariance in *Hymenaea* is difficult to

sustain as the ancient records found to date of the genus are from Early to Middle Miocene ambers.

- In contrast, Langenheim and Lee (1974), Lee and Langenheim (1975), and Fougère-Danezan et al. (2010) defend an African origin of the tree.

According to these authors, *Hymenaea* may have reached Central and South America through two pathways: (1) via the boreotropical corridor proposed by Wolfe (1985) and supported by Lavin and Luckow (1991, 1993); or (2) via sea currents (Langenheim and Lee 1974). In the first situation, *Hymenaea* could have firstly dispersed to North America and later to Central America and Antilles during the Paleocene–Eocene Thermal Maximum (PETM, an episode of intense global warming at about 55 Ma, lasting 100 thousand years, Magioncalda et al. 2004; Secord et al. 2010). Following this, it would have dispersed to South America via land bridges between Greater Antilles and South America (Iturralde-Vinent and MacPhee 1999, but see Ali 2012).

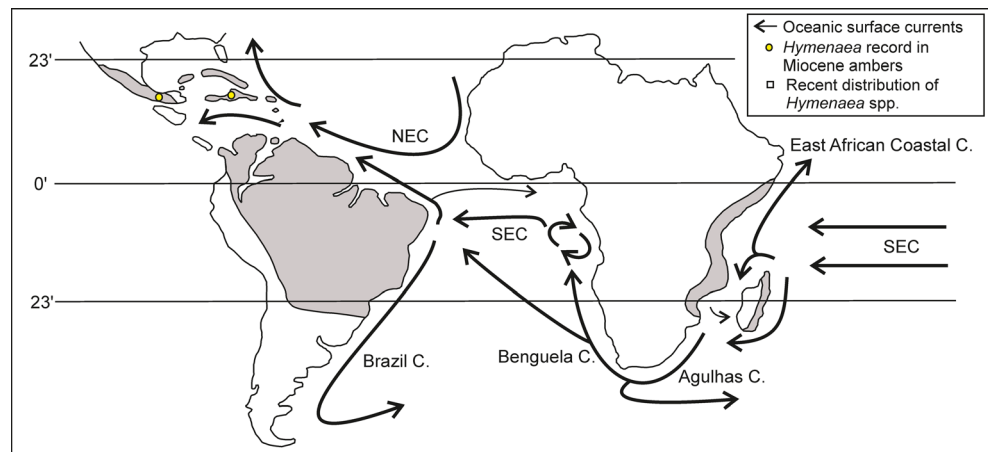
Some examples of Leguminosae are cited in Calvillo-Canadell et al. (2010), who suggest their distribution expanded through “boreotropical flora” patterns and the migration of certain Afrotropical lowland plants to South America via Europe (Erkens et al. 2009). Nevertheless, the fossil record supports the cited examples. By contrast, there are no fossil records (neither macro-remains nor pollen record) of *Hymenaea* in Laurasia or South America until the Middle Miocene, and therefore this alternative pathway cannot be considered. Furthermore, certain authors (Morley 2003; Graham 2011) doubt that megathermal plants from the African tropical rainforest crossed land areas of the boreotropical region and dispersed to North America during the PETM. It seems that the majority of megathermal and mesothermal taxa that would have made this crossing developed in the boreotropical region (30–45° N) at the precise time.

The other possibility is that the genus originated in Africa and dispersed from West Africa to America via sea currents (Langenheim and Lee 1974). The authors proposed that the African stock was transported from West African coasts to South America or Antilles via the oceanic South Equatorial Current (SEC) (Fig. 6), considering that the evergreen forests were more widespread in Africa during the Paleogene (see also Feakins and Demenocal 2010; Jacobs et al. 2010). A similar colonization was proposed for other examples involving plants (Thorne 1973; Chanderbali et al. 2001; Dick et al. 2003; Gottschling et al. 2004; Lavin et al. 2004; Renner 2004; Antonelli 2008) and insects (see below), and was also demonstrated with diverse groups of vertebrates (Fleagle 1999; Houle 1999).

Nonetheless, it is not necessary to explain the distribution of *Hymenaea* stock from Western Africa to the New World. Oceanic currents in the South Atlantic are similar nowadays since the Late Oligocene (Fig. 6). Shortly after the Late Oligocene the Antarctic Circumpolar Current (ACC) was established (Kennett et al. 1975; Lawver and Gahagan 2003; Pfuhl and McCave 2004). The only area of the surface circulation that is assumed to be particularly different from today’s circulation occurred in the Caribbean, prior to the closure of the Panama isthmus (Lawver and Gahagan 2003; Renner 2004). Therefore, *Hymenaea* might have reached the New World from the Eastern Africa (East coast and Madagascar), where *H. verrucosa* is currently distributed.

Madagascar is surrounded by several important oceanic currents (Lutjeharms et al. 1981). When in contact with Madagascar, the SEC is divided between the Tanzanian and Kenyan coasts and the Agulhas Current, which is located along the Eastern South African coast (Ali and Huber 2010). The South Atlantic currents comprise a gyre: the Benguela current north and westward and the Brazil current south and eastward (Stramma and England 1999). The Benguela current has two branches, one that crosses the Atlantic to the region of Bahia (Brazil), and the other parallel to the West African coast

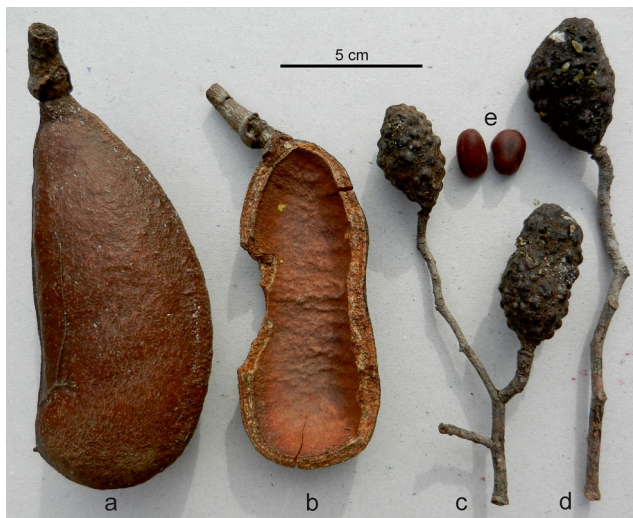
**Fig. 6** Paleogeographic map of the Oligocene showing simplified oceanic circulation system proposed as responsible for current distribution of *Hymenaea* spp. in the Antilles and fossil records for the genus. The map has been modified after Langenheim and Lee (1974), Stramma and England (1999), Ali and Huber (2010), and Beal et al. (2011)



towards to the tropics. Both branches link with the westward SEC and reach the regions of Paraíba and Rio Grande do Norte (Brazil) (Séranne and Nzé Abeigne 1999). The SEC then runs through the coasts of north Brazil, Guyana (where it mixes with the westward North Equatorial Current (NEC)), Venezuela, Lesser Antilles, and reaches the Caribbean Sea (Fig. 6).

The *Hymenaea* tree can produce more than 7,000 pods/year (Vaca et al. 2002) (Fig. 7). Pods are considered tropical drift seeds because they are very buoyant and impervious to salt water; seeds (Fig. 7e) of some species can remain in good condition inside the pod for several months (Gunn and Dennis 1976; Roth 1987). It is possible that pods of the *Hymenaea* African stock, or partially incomplete tree individuals as well, arrived by sea currents to the Caribbean islands and/or to South America during the Late Oligocene to Early Miocene (Walker 1990; Gonzoli and Gordon 1996; Bryden et al. 2005; Beal et al. 2011; Simon et al. 2013). Indeed, pods of *Hymenaea courbaril* (Fig. 7a–b) are often washed ashore on the beaches of the Caribbean islands, the Gulf of Mexico, and Florida (Perry and Dennis 2003).

As well as pods, tangled plant parts, also called “floating islands”, are constantly carried out into the tropical Atlantic from the major African and South American deltas, e.g., Congo, Niger, Senegal, and Amazon rivers. Nevertheless, although eastward currents also exist, the currents may not be ideal for transporting plant remains from South America to West Africa (Fratantoni et al. 2000; Renner 2004).



**Fig. 7** Pods and seeds of *Hymenaea* spp. Pods of *H. courbaril*, Simojovel de Allende, Mexico; (a) complete pod; (b) pod cut in half, note the thickness of the wall. Pods and seeds of *H. verrucosa*, Ambahy (Nosy Varika), Madagascar; (c) complete pods in a bifurcated branch; (d) complete pods in a single branch; (e) sample of two seeds contained inside a pod

## Nexus between Caribbean and African insect faunas

Cognato (2013) noted the similarities between the fossil genus *Electroborus* (Curculionidae: Scolytinae) from Dominican amber and some African Hylesinini genera. One possible explanation for this resemblance is the worldwide distribution of extant Hylesinini genera, which indicates that the origin of this tribe was before the separation of Africa and South America (120–90 Ma) (Cognato 2013, and references therein). It is not the first time that a connection between Caribbean and Afrotropical insect taxa has been suggested (Liebherr 1988), but, in the case of scolytines, the explanation was the vicariance, with early origin and spread previous to the Gondwana break up. Based on the ancient record of Scolytinae (Cognato and Grimaldi 2009; Kirejtshuk et al. 2009), which is older than other curculionid groups, the proposal is possible. Despite this, some authors do not believe that vicariance can explain the biota from Caribbean islands (Iturralde-Vinent and MacPhee 1999; Penney 2008). The present study notes a strong resemblance between fossil *Cenocephalus*, described in Miocene Central American ambers, and *Mitosoma*, from Madagascar, and concludes they are morphologically indistinguishable.

Darlington (1938) was the first author to discuss Antillean animal colonization through over-water dispersal. He argued that this type of dispersal was not an accidental or random process but considered the directions of storms and currents and biological attributes of potential colonizers as important factors, among others. However, Darlington (1957) only considered the possibility of Antillean colonization by relatively short distances. Subsequently, Rosen (1975) expanded the list of possible currents and noted a West African to Caribbean route from the Gulf of Guinea via the South Equatorial Current.

Some examples of arthropod groups have been noted, which highlight faunal ties between the Caribbean islands and the Afrotropical region. For example, Bright (1972) reviewed platypodines and scolytines beetles from Jamaica and demonstrated that almost 19 genera are also found in Africa. *Acanthotomicus*, *Cladoctonus*, *Scolytogenes*, *Cryptocarenus*, *Coccotrypes*, and *Hypothenemus* are other bark-boring beetles with several species living in Central America and Africa; the last one was associated with *Hymenaea* as referenced by Wood and Bright (1992). Some other examples are spiders of the genus *Wendilgarda* (Theridiosomatidae), with four species, three of which are found in Central and South America, and one in Gabon (Coddington 1986). Other examples include Scarabaeidae and Carabidae beetles (Matthews 1966; Howden 1970; Erwin 1979; Liebherr 1986; Nichols 1988; Peck and Perez-Gelabert 2012), dragonflies and caddisflies (Flint 1978), Chironomidae and Drosophilidae flies (Grimaldi 1988), Lygaeidae bugs (Slater 1988), and certain butterflies (Shields and Dvorak 1979).

### Biogeography and insects related to *Hymenaea* spp.

Previous studies have focused on direct insect–*Hymenaea* relationships. For example, after a study in Guyana, Gombauld (1991) proposed that *H. courbaril* is usually attacked by diverse groups of insects, mainly in primary forests, such as Coleoptera: 14 species of Curculionidae, which include two species of Platypodinae and one Scolytinae; one Anthribidae, nine Cerambycidae; two Heteroptera: one Aradidae and one Reduviidae; one Hymenoptera, and some termites. Seeds are also infested by diverse groups of insects, mainly Coleoptera and Hymenoptera. Bright (1972) and Peck (2010) recognized Scolytinae *Araptus hymenaeae* and the Cerambycidae *Nesanoplium puberulum* in Jamaican associated with *Hymenaea*, which have close affinities with African fauna.

Following an expedition in October 2013 to gather data, the authors of this study are currently analyzing insects related to *H. verrucosa* from Madagascar. We have observed Hymenoptera: Formicidae and Coleoptera: Curculionidae: Scolytinae (*Hypothenemus* sp.) inside *H. verrucosa* pods (Fig. 7c–d). The presence of abundant *Mitosoma* specimens in the Malagasy copal of *H. verrucosa* and the abundant *Cenocephalus* presence in Mexican and Dominican Miocene ambers originated by other *Hymenaea* spp. indicates that the clade *Mitosoma*–*Cenocephalus* has a powerful interaction with *Hymenaea*. It also indicates that it was established after the Miocene, at least. Furthermore, if these platypodines are not considered of the same genus, the relationship with the plant should have already been strong regardless of the ancestor. In such a scenario, it is possible it moved from Africa with the plant itself and colonized in the New World.

### Conclusions

Based on the literature referring to the platypodine genera *Mitosoma* and *Cenocephalus*, our analysis of the historical classification, and taking into account data extracted from the fossil record, we conclude that both genera are morphologically indistinguishable; differentiation is only supported biogeographically. A formal synonym should await a more detailed study including *Chaetastus* spp.

Given past and Recent distributions, we felt an explanation was required to better understand the connection between the Afrotropical (Madagascar) and Neotropical (Central and South America) fauna (*Mitosoma* and *Cenocephalus* respectively) and plants (*Hymenaea*). There were two hypotheses proposed to explain different examples of paleobiota colonization from Africa to Eurasia and America (i.e., the vicariance hypothesis and the boreotropical corridor hypothesis); however, neither of them are well supported by the data analyzed. The arguments are: (1) the fossil record only shows Cenozoic evidence for ambrosia beetles up today, and no record of

*Hymenaea* has been found that is older than Early to Middle Miocene Central American ambers, and (2) the alignment between recent *Hymenaea* plants and *Mitosoma* beetles from Madagascar is also observed between the resin-producing plants of the Miocene Central America (*Hymenaea* spp.) and the platypodines preserved in the amber originated from that resin.

Thus, we firmly support the need for a third proposal involving the platypodine *Cenocephalus*–*Mitosoma* clade. The group lived in Africa and was closely interacting with *Hymenaea*. Their current morphological pattern and biogeographic distribution is indicative of a dispersal process via sea currents to the Neotropical region. It is likely to have occurred following the colonization of *Hymenaea* during the Late Oligocene to Early Miocene. Due to the biology of platypodines, which live during their ontogeny inside the wood of their host tree, they could be dispersed together to South America or Central America more easily than other insects or animals that live related but not inside the plants. As this hypothesis is a proposal, some other scenarios can arise if new living or fossil specimens are found in other geographical areas or older fossils of these insects and plants appear.

We support the hypothesis that pods and other remains of *Hymenaea* spp. trees could be dispersed from Eastern Africa to the New World instead of Western Africa as argued by Langenheim and Lee (1974). Along with wood and pods, their related insects were also transported in either one or several seasons, probably during their pupal and larval stages. This process was possible after the Late Oligocene (about 25 Ma), due to the establishment of the ACC and other sea currents previously discussed (Fig. 6).

Nevertheless, conclusive evidence of the Central or South American areas that were first colonized is lacking given the lack of phylogenetic analysis of the *Hymenaea* species and its fossil record.

Finally, it is therefore possible that the hypothesis of colonization by sea current from Africa to South and Central America could also be extended to other examples either living or fossil taxa embedded in amber (e.g., Schneider et al. 2015).

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**Ethical approval** This work complies with the current laws of the countries where it was performed.

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