

First amber fossil Rhysipolini (Hymenoptera: Braconidae): a new genus and species in Early Eocene Cambay amber

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Abstract. A new genus and species of fossil braconid wasps (Ichneumonoidea: Braconidae) are described and figured from Early Eocene (Ypresian) Cambay amber (Gujarat, India). *Trichelyon tadkeshwarensis* Ortega-Blanco & Engel gen. et sp. nov. is described from two females belonging to the Rhysipolini (Exothecinae), a tribe of considerable complexity and debatable classificatory placement, and representing the first, definitive fossils for this lineage of Braconidae. The fossils are compared with modern rhysipoline diversity and the complexity of the tribe is briefly discussed.

Key words. Hymenoptera, Ichneumonoidea, amber, Eocene, fossil, taxonomy, India

Introduction

Wasps of the cyclostome tribe Rhysipolini are solitary ectoparasitoid koinobionts of leaf-mining Lepidoptera (TOWNSEND & SHAW 2009). While the tribe is moderately well characterized, its rank and position among cyclostome braconids remains in flux, with a lack of consensus regarding the phylogenetic placement and appropriate classificatory treatment of the clade (e.g., WHITFIELD & WAGNER 1991; SHARKEY 1993; VAN ACHTERBERG 1993, 1995; WHITFIELD & WHARTON 1997; SCATOLINI et al. 2002; SHAW 2006; BELOKOBYSKIJ & ŽIKIĆ 2009; TOWNSEND & SHAW 2009; SHARANOWSKI et al. 2011) (Table 1). Rhysipolines have been included or conveniently treated under various subfamilies, such as Exothecinae (VAN ACHTERBERG 1993, BELOKOBYSKIJ & ŽIKIĆ 2009), Rogadinae (SHARKEY 1993, WHITFIELD & WAGNER 1991), Hormiinae (WHITFIELD & WHARTON 1997), or as their own subfamily (VAN ACHTERBERG 1995,

Table 1. Representative concepts of Rhysipolini/Rhysipolinae over the last 20 years, indicating advocated classification and genera included (where specified).

WHITFIELD & WAGNER (1991)	Rogadinae: including Hormiini, <u>Rhysipolini</u> , Rhysalini, and Rogadini	<i>Cantharoctonus</i> , <i>Cerophanes</i> , <i>Neurocrassus</i> Šnoflák, 1945, <i>Noserus</i> Förster, 1863 [= <i>Pachystigmus</i>], <i>Pseudavga</i> Tobias, 1964, and <i>Rhysipolis</i>
SHARKEY (1993)	Rogadinae: including Exothecini, Hormiini, Lysterimini, Pambolini, Rhysipolini, Rhysalini, and Rogadini (very broad concept)	Not specified, but indicated as worldwide with seven genera
VAN ACHTERBERG (1993)	Exothecinae: including Exothecini and Rhysipolini	Not specified (small Holarctic tribe, infrequently collected)
WHITFIELD & WHARTON (1997)	Hormiinae: included therein for convenience	<i>Cantharoctonus</i> and <i>Rhysipolis</i> (probably more, not specified)
SCATOLINI et al. (2002)	Rhysipolinae: equivalent to Rhysipolini	<i>Cantharoctonus</i> , <i>Pseudorhysipolis</i> , <i>Rhysipolis</i>
SHAW (2006)	Rhysipolinae: keyed as “similar to Rogadinae but the lateral carina on the anterior part of 1 st tergum not fused”	Three genera (two from the Neotropical region)
TOWNSEND & SHAW (2009)	Rhysipolinae: <i>Andesipolis</i> reclassified from Mesostoinae	Not specified apart from <i>Rhysipolis</i> and the new <i>Andesipolis</i>
BELOKOBYLSKIJ & ŽIKIĆ (2009)	Exothecinae: including Clinocentrini, Hormiini, and Rhysipolini	Only <i>Cerophanes</i> and <i>Rhysipolis</i> explicitly specified
SHARANOWSKI et al. (2011)	Rhysipolinae	Not specified

SCATOLINI et al. 2002, HANSON & GAULD 2006, TOWNSEND & SHAW 2009, SHARANOWSKI et al. 2011). Indeed, the general classification of cyclostome braconids as a whole remains controversial and needing of continued investigation. Several genera do not fit within any of the subfamilies and tribes as currently circumscribed, furthering the need for critical phylogenetic and revisionary studies (WHITFIELD et al. 2004).

The tribe presently includes seven extant genera – *Afrorhysipolis* Belokobylskij, 1999 (Afrotropical), *Cantharoctonus* Viereck, 1912 (Holarctic, Neotropical), *Cerophanes* Tobias, 1971 (Palearctic), *Neoavga* Belokobylskij, 1989 (Australasian), *Pachystigmus* Hellén, 1927 (Afrotropical, Palearctic), *Pseudorhysipolis* Scatolini, Pentead-Dias & van Achterberg, 2002 (Neotropical), and *Rhysipolis* Förster, 1862 (Holarctic, Neotropical, Oriental, and Oceania). TOWNSEND & SHAW (2009) also include the Andean *Andesipolis* Whitfield & Choi, 2004 (WHITFIELD et al. 2004), contrary to ZALDIVAR-RIVERON et al. (2006) who placed the genus in Mesostoinae.

Despite the plethora of described Tertiary species of Braconidae (e.g., BRUES 1910, 1923, 1933, 1939; COCKERELL 1913, 1919, 1920, 1921, 1927; STATZ 1936, 1938), the only fossil rhysipoline that has been documented is *Rhysipolis distinctus* Théobald, 1937 from the Oligocene of Aix-en-Provence, France. THÉOBALD’S (1937) specimen is a compression that is apparently cyclostome (difficult to determine) and with an antenna and forewing venation superficially

similar to Rhysipolini, but definitive placement therein is not possible based on his description and figures. Herein we provide an account of the first, definitive fossils for the tribe, recently discovered in Early Eocene (Ypresian) amber from Gujarat, India. While the general body size of braconids is optimal for fossilization (MARTÍNEZ-DELCLÒS et al. 2004) and their history assuredly extends well into the Early Cretaceous (RASNITSYN & QUICKE 2002; GRIMALDI & ENGEL 2005; MURPHY et al. 2008; PERRICHOT et al. 2009; ORTEGA-BLANCO et al. 2009, 2011; BELOKOBYSKIJ 2012), their Cretaceous record is meagre. The diversity of Cretaceous genera has been summarized by ORTEGA-BLANCO et al. (2009, 2011), PERRICHOT et al. (2009), and BELOKOBYSKIJ (2012). To date there has been no comprehensive overview of the Tertiary diversity, many species of which have been described from mid-Eocene Baltic amber (e.g., BRUES 1923, 1933, 1939; VAN ACHTERBERG 1982, 1988) or the Eocene-Oligocene boundary of Florissant, Colorado (e.g., BRUES 1910; COCKERELL 1913, 1919, 1927), and although only a few have been documented in Early Miocene amber of the Dominican Republic (e.g., ZUPARKO & POINAR 1997, VAN ACHTERBERG 2001, ENGEL & BENNETT 2008), numerous new species representing several subfamilies await description (ENGEL, pers. observ.). The fossil history of Braconidae has been very briefly considered by RASNITSYN & QUICKE (2002), GRIMALDI & ENGEL (2005), and PERRICHOT et al. (2009).

Herein we follow BELOKOBYSKIJ & ŽIKIĆ (2009) and VAN ACHTERBERG (1993) in considering Rhysipolini as a tribe of Exothecinae, recognizing that its isolation as a separate subfamily in its own right may be warranted but deserving of more critical consideration well outside the scope of the present contribution. Our material fits perfectly the definition of Rhysipolini/ae as recognized by VAN ACHTERBERG (1993), although the species differ clearly from all of the extant genera.

Material and methods

Two complete females were discovered during preparation of amber inclusions excavated from the Tarkeshwar (sometimes written Tadkeshwar) lignite mine in Gujarat, India. The amber is of Early Eocene (Ypresian) origin, with RUST et al. (2010) providing a detailed overview of the age of the deposits and origin of the amber. Excavations for Cambay amber were carried out by M.S.E. and colleagues during the years 2009–2012, while the current piece was located by P. C. Nascimbene from work by D. A. Grimaldi, K. Luzzi, and P. C. Nascimbene on the 2012 trip. Both specimens are in the same piece of clear amber, with some fractures and many bubbles, and well preserved except for partial collapse of the compound eyes and portions of the mesosoma and metasoma due to degradation and/or moderate compression. The amber was polished and embedded in epoxy resin following the method of NASCIBENE & SILVERSTEIN (2000).

Observations were made using Olympus SZ-60 and SZX-12 stereomicroscopes and an Olympus BX-41 compound microscope with reflected and transmitted light. Photomicrographs were made with a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens, arranged and sharpened with CombineZ and edited with Photoshop CS3, while illustrations were prepared with the aid of a camera lucida attached to an Olympus BX41 compound microscope.

Systematic paleontology

Superfamily Ichneumonoidea Latreille, 1802
Family Braconidae Nees von Esenbeck, 1811
Subfamily Exothecinae Förster, 1862
Tribe Rhysipolini Belokobylskij, 1984

Trichelyon Ortega-Blanco & Engel, gen. nov.

Type species. *Trichelyon tadkeshwarensis* Ortega-Blanco & Engel, sp. nov.

Diagnosis. Cyclostome wasps with 26 antennomeres, antenna much longer than forewing; scape relatively robust, about twice as long as wide, pedicel about $0.75\times$ scape length. Malar suture apparently absent (difficult to discern though). Clypeus concave, not protruding outward in profile; labrum set in ovoid hypoclypeal depression. Maxillary palpus 6-segmented. Compound eyes large, not emarginate. Occipital carina complete. Pronope absent. Notauli short, distinct only in anterior part of mesoscutum, shallow and faint from midpoint posteriorly. Epicnemial carina present. Sternaulus apparently absent. Forewing 2a vein absent; 1Rs long, more than one-half length 1M; vein 1r-rs arising just distad middle of pterostigma; 1cu-a postfurcal; 1rs-m sclerotized but faintly pigmented (Fig. 1); distal abscissa M sclerotized at base then becoming nebulous; 3Rs shorter than 2M, making second submarginal cell narrower anteriorly. Metatibia without fringe stiff setae or spines on inner apex; metatibial spurs slightly curved; pretarsal claws simple, with basal area swollen; arolium large. Propodeum with small, medial areola, anteriorly integument smooth. First metasomal tergum with exceedingly faint dorsope, apparently acarinate; integument of first through third terga longitudinally striate except apical half of third tergum apparently imbricate; remaining terga largely membranous. Ovipositor sheaths slightly shorter than metatibia, asetose; ovipositor relatively straight.

Etymology. The new genus-group name is a combination of the Greek words *trion* (“three”) and *chelyon* (“tortoise shell”), and is a reference to the three-segmented carapace of the metasoma. The name is neuter.

Trichelyon tadkeshwarensis Ortega-Blanco & Engel, sp. nov.

(Figs. 1–2)

Type material. HOLOTYPE: ♀, Tad-420, India: Gujarat, Tarkeshwar lignite mine, Cambay Formation (Palaeo-Eocene), 21°21.400'N, 73°4.532'E, 11–16 January 2012; deposited in the Birbal Sahni Institute of Paleobotany, Lucknow, India. PARATYPE: 1 ♀, same amber piece as holotype and same repository.

Diagnosis. As for the genus (see above).

Description. Female. Body length 1.98 mm; forewing length 1.8 mm. Head hypognathous, covered by scattered, thin setae, most numerous in and around hypoclypeal depression; occipital carina present but low, ventrally running to base of mandibles. Compound eyes large, occupying entire lateral side of head, not emarginate. Ocelli present but difficult to discern as preserved (portions of head collapsed and fractures prevent a clear view), but distinctly far from occipital carina. Clypeus mid-ventral margin apparently placed well above level of mandibular base, with a distinct hypoclypeal depression (cyclostome). Mandibles curved

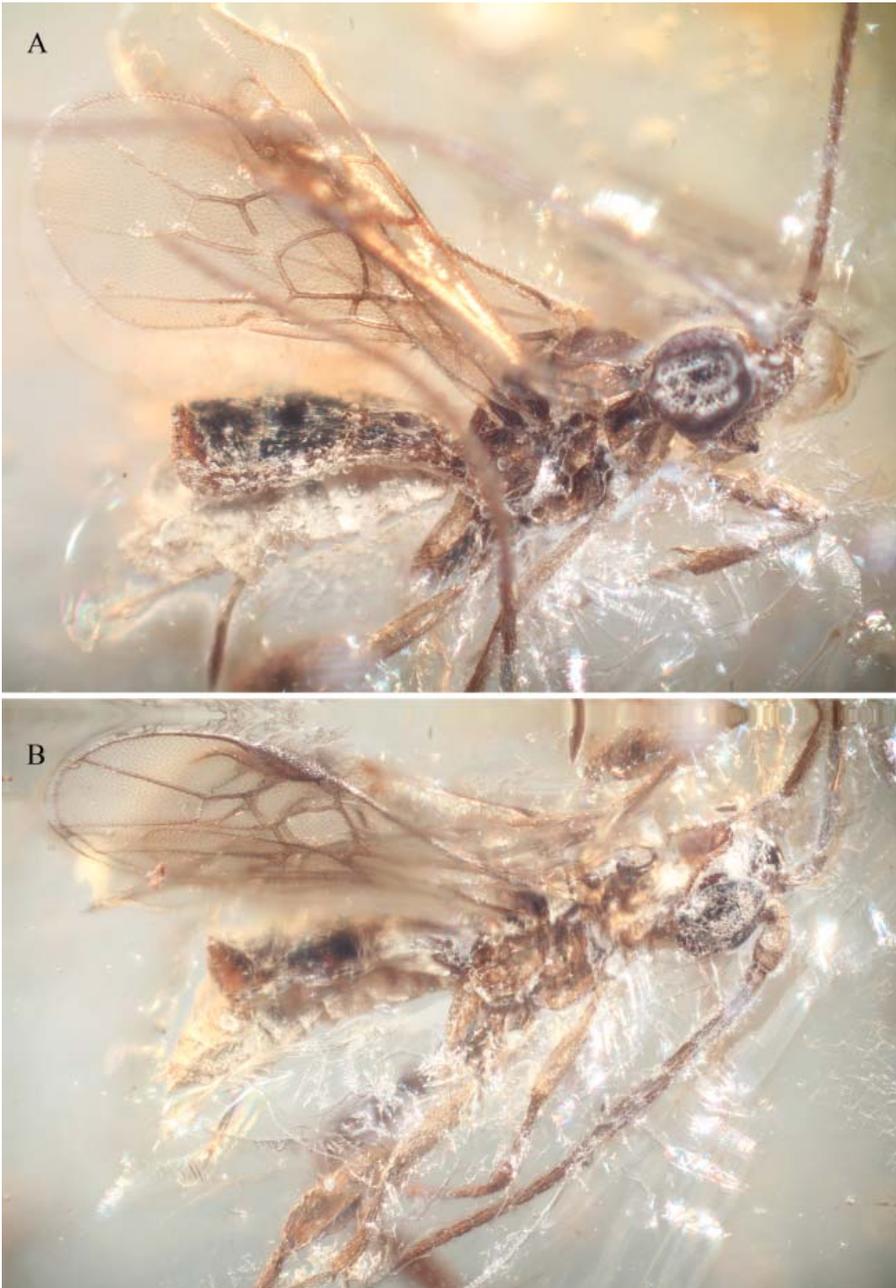


Fig. 1. Photomicrographs of holotype (A) and paratype (B) females of *Trichelyon tadkeshwarensis* Ortega-Blanco & Engel, gen. & sp. nov. (Tad-420) in Early Eocene Cambay amber.

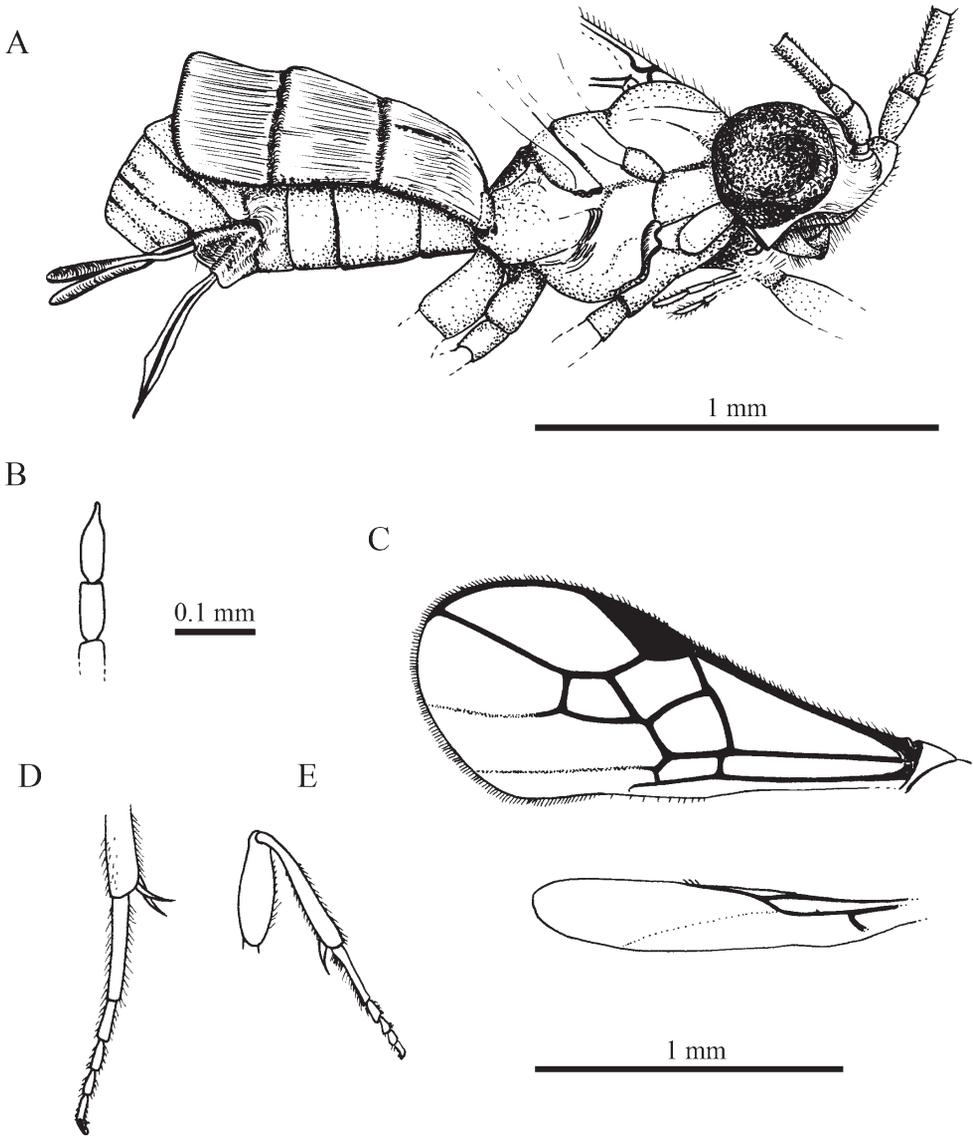


Fig. 2. Camera lucida drawings of *Trichelyon tadkeshwarensis* Ortega-Blanco & Engel, gen. & sp. nov. showing important diagnostic characters. A – lateral habitus of holotype showing propleural flange, epicnemial carina, propodeum areola, and metasomal carapace, among other characters. B – apicalmost part of antennae showing prominent acute tip of last flagellomere (most easily visible in holotype). C – forewing of holotype and hind wing of paratype, showing pattern of venation. D – hind leg of paratype showing apical part of metatibia and spurs, and metatarsus with telotarsus not enlarged. E – protibia without pegs or spines (as viewed from holotype). C, D, E to the same scale.

inwards, facing each other, overlapping when closed, with two teeth. Maxillary palpus 6-segmented; palpomeres 3 and 4 distinctly longer than palpomeres 1, 2, 5, and 6. Labial palpus not discernible as preserved. Antenna 26-segmented, with flagellomeres cylindrical and not flattened; toruli facing upwards, inserted in a low frontal shelf; scape short and robust, about twice as long as apically wide; pedicel shorter than scape, about as wide as long; flagellomeres 1–3 longest, about three times longer than wide; flagellomeres 4 and 5 slightly longer than succeeding flagellomeres; flagellomeres 6–24 less than two times as long as wide; all flagellomeres sparsely covered with minute setae, with at least two apical, longer setae; last flagellomere tapered but with distinct elongate thin tip.

Mesosoma moderately high, not setose. Pronotum dorsally short but distinct. Posterior flange of propleuron present, placed more posteriorly than in dorsal position. Epicnemial carina present. Notauli faintly present, anteriorly more distinct. Mesoscutellum small, rhomboid. Metanotum much wider than long, almost obscured. Propodeum without spines or protuberances, with a long median carina and a small medial areola, anteriorly integument smooth. Legs with numerous setae; metacoxa elongate, slightly flattened, antero-marginally rounded (without angle or tubercle); trochanter short and flattened; trochantellus small and rounded; femora and tibiae slightly flattened; tibiae noticeably more setose, with a longitudinal row of stiffer setae or spicules along anterior surface; tibial spur formula 1-2-2; calcar simple, curved inwards, without inner lamella; remaining spurs slightly curved outward; basitarsi densely setose, with a longitudinal row of stiffened setae, slightly shorter than remainder of tarsus; last tarsomere (telotarsus) not enlarged, with length similar to individual lengths of tarsomeres 2–4; pretarsal claws simple, with basal area swollen; arolium large but not surpassing pretarsal claws in length. Forewing membrane with sparse microtrichia, more distinct and slightly thicker on margins, particularly anterior margin; pterostigma large and semioval; tubular veins include C+Sc+R, R beyond pterostigma; all abscissae Rs; M+Cu, 1M, 2M, base of distal abscissa M, all abscissae Rs+M, Cu, 1rs-m, 1m-cu, 1cu-a, and 2cu-a (Fig. 2C); hind wing with three hamuli, a single closed cell (Fig. 2C).

Metasoma about as long as remainder of body, proximally constrained, without petiole, with eight visible terga, overall largely membranous except first three terga which are heavily sclerotized and fused to form metasomal carapace; first metasomal segment proximally constrained, apparently without medial longitudinal carina, basal carinae, or distinct lateral carinae, apparently though with faint dorsope; spiracles not visible given preservation; terga of carapace with longitudinal striae except apically on third tergum imbricate; second metasomal tergum without smooth, triangular, mediobasal area; terga laterally short such that sterna are well visible laterally. Ovipositor and valves exposed, shorter than metatibia.

Etymology. The specific epithet refers to the lignite mine in Gujarat, India and from where the amber bearing the type material was collected.

Comments. As noted, where known, species of Rhyssipolini are parasitoids of leaf-mining Lepidoptera. In connection with this there are small, unidentified Lepidoptera occurring in Cambay amber (D. A. Grimaldi, pers. comm.), which might have served as potential hosts. However, leaf-mining Lepidoptera extend back to the Jurassic (GRIMALDI & ENGEL 2005) and suitable hosts were clearly abundant during the time of this fossil species.

Discussion

Despite the significant interest in braconids owing to their exceptional value as biological control agents, the systematics of this complex clade remains challenging and there remains disagreement over the higher relationships and subfamilial-tribal organization of the family. This is particularly highlighted by the complex classificatory history and challenges of determining definitive relationships of the rhysipolines (Table 1). Using the concept of the group as advocated by VAN ACHTERBERG (1983), the fossils described herein fit perfectly within tribe Rhysipolini, and as included in the subfamily Exothecinae. Exothecinae is differentiated from Rogadinae by the ventral third of the occipital carina (straight in Rhysipolini, curved towards the hypostomal carina or absent in rogadines) and absence of m-cu in the hind wing (variable in rogadines), among other features. However, SHARKEY (1993) took a more conservative approach, highlighting the lack of conclusive evidence for relationships and considered Rogadinae in a much broader sense, comprising most cyclostome braconids and with diverse tribes such as Exothecini, Hormiini, Lysterimini, Pambolini, Rhyssalini, Rhysipolini (including Hydrangiocolini), and Rogadini (including Ypsistoceratini). At the other extreme, SHAW (2006) considered the rhysipolines as a subfamily, independent of Exothecinae and Rogadinae (noting also that Rhysipolinae differs from rogadines in the structure of the first tergal carina). Regardless of the rank recognized, among all of the currently employed cyclostome lineages, the Cambay fossils share the most characters with rhysipolines. Naturally, a cladistic treatment of the tribe, including *Trichelyon* Ortega-Blanco & Engel, gen. nov., is desperately needed in order to ascertain relationships among the various rhysipoline genera and determine biogeographic patterns. It will be of considerable interest to see if the fossil genus is most closely related to Oriental or Australasian lineages, or whether there is a tighter affinity between *Trichelyon* and groups which are today found in the Afrotropics.

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