

## The ant genus *Tapinoma* Förster (Formicidae: Dolichoderinae) in Miocene amber of Peru

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On the 17 extant subfamilies of ants, Dolichoderinae is one of the four major species-rich clades (with Formicinae, Ponerinae, and Myrmicinae), and a cosmopolitan group including some of the world's most invasive species such as the Argentine ant and white-footed ant. It comprises currently 846 species in 28 extant and 20 extinct genera (Bolton, 2019). Most of the fossils are Cenozoic in age, which accords with the timeline of the Dolichoderinae as proposed by molecular phylogenetic studies (Ward *et al.*, 2010; Moreau & Bell, 2013; Borowiec *et al.*, 2019). According to these studies, crown-group dolichoderines arose sometime between 66 and 53 million years ago. Thus, around or after the Cretaceous–Paleogene transition, although this would have been preceded by approximately 30 million years of stem group evolution. Cretaceous dolichoderines are exceedingly rare indeed, and the only two known genera—*Eotapinoma* Dlussky, and *Chronomyrmex* McKellar, Glasier & Engel, from Canadian Campanian amber (79–78 Ma)—although originally placed in the Tapinomini and Leptomyrmecini, respectively, have been suggested to be stem dolichoderines (Dlussky, 1999; McKellar *et al.*, 2013; Boudinot *et al.*, 2016). Another fossil dolichoderine was reported from “Cretaceous amber” of Ethiopia (LaPolla *et al.*, 2013: suppl. fig. 5) but this amber is now known to be much younger in age, likely Miocene (Perrichot *et al.*, 2016, 2018). The first definitive crown-group dolichoderines are thus currently from the middle Eocene (50–45 Ma) of Europe and North America, belonging to various extinct species of the genera *Dolichoderus*, *Iridomyrmex*, *Liometopum*, and *Tapinoma* (see Barden, 2017). Some earlier crown-group dolichoderines may be present in early Eocene (55–52 Ma) ambers from France, India, and China (Perrichot, pers. observ.), but these have yet to be formally described.

Here we describe the first fossil ant from Miocene amber of Peru, which is assignable to the genus *Tapinoma*.

Among extant dolichoderines, *Tapinoma* is a cosmopolitan genus known from 71 species, but with a low diversity in South America (five species and two subspecies). This genus has not been previously recorded from Peru. It is also known from five fossil species, all Cenozoic in age: *T. aberrans* Dlussky (junior secondary homonym of *T. aberrans* (Santschi, 1911)—but see proposed replacement name below) and *T. electrinum* Dlussky from Eocene Rovno amber of Ukraine; *T. baculum* Zhang from an impression fossil of the Miocene Shanwang Formation of China; *T. minutissimum* Emery in Sicilian amber (unknown age between late Eocene and middle Miocene, see Ragazzi & Roghi, 2014); and *T. troche* Wilson in Miocene Dominican amber (Emery, 1891; Wilson, 1985; Zhang, 1989; Dlussky & Perkovsky, 2002). The new fossil is the first ant described from an amber inclusion of South America.

### Material and methods

The piece of amber that contains the newly discovered ant comes from amber-rich grey lignitic clays exposed on the eastern bank of the Amazon River in the Tamshiyacu locality, 30 km upstream of Iquitos in northeastern Peru (Antoine *et al.*, 2006), assigned to the Pebas Formation (*Crassoretitritiletes* zone, middle Miocene, 15–12 Ma; Hoorn, 1994). These clays are typical of the Pebas Mega-wetland System that existed before the onset of the modern Amazon River basin (Wesselingh *et al.*, 2002; Hoorn *et al.*, 2010). The Pebas System consisted of interconnected shallow lakes and swamps, under a marine influence, covering over 1 million km<sup>2</sup> in Western Amazonia, and it formed a cradle of speciation for both invertebrates (Hoorn & Vonhof, 2006; Wesselingh *et al.*, 2006; Boonstra *et al.*, 2015) and vertebrates (*e.g.*, Salas-Gismondi *et al.*, 2015; Antoine *et al.*,

2016, 2017). Its unique situation in the Western Amazonia provides the record of an intertropical entomofauna prior to the land connection with Central and North America which occurred in the latest Miocene–Pliocene (Gingras *et al.*, 2002; Coates *et al.*, 2004; Antoine *et al.*, 2006; Petrulėvičius *et al.*, 2011; Perrichot *et al.*, 2014). Miocene fossil insects are otherwise unknown in South America.

Less than 30 amber chunks have been collected from this deposit; thus the diversity of the fossil arthropod fauna is quite low although significant already (Antoine *et al.*, 2006). Two ants have been found among the hexapods identified. One is only fragmentary, preserved by the head capsule without mouthparts and antennae, and represents an undetermined genus; the other one, complete, is described herein in the subfamily Dolichoderinae.

The ant was originally preserved in a piece of translucent yellow amber but partly concealed by other insect inclusions, a fairy wasp (Mymaridae) and a biting midge (Ceratopogonidae), so the amber piece was cut in three parts and each fragment (A-2005-5a to A-2005-5c) was polished to optimize the view of the inclusions. Photomicrographs of the ant were taken using a Canon 5D camera attached to a Leica MZ APO stereomicroscope, and Helicon Focus software (Helicon Soft, Ltd.) was used to stack multiple pictures taken at different focal planes. High resolution images of the type material will be made available on AntWeb ([www.antweb.org/fossil.jsp](http://www.antweb.org/fossil.jsp)).

Measurements (all in mm) were taken using an ocular micrometer. Morphological terminology employed throughout and indices listed below follow those used by Bolton (1994, 2007). The first four measurements were taken in the same plane, i.e. with the head in full-face view.

HL	Head length, in a straight line from the mid-point of anterior clypeal margin to the mid-point of the occipital margin.
HW	Maximum head width measured behind the eyes.
SL	Scape length: maximum straight-line length of the scape, excluding radicle.
ED	Maximum diameter of eye as measured in lateral view of the head to show full surface of eye.
ML	Mesosomal length in dorsal view, from juncture with the petiole to anterior border of pronotum.
PW	Maximum width of pronotum.
PtL	Length of petiole in dorsal view.
PtW	Width of petiole in dorsal view.
nAL	Length of abdominal tergite n in dorsal view.
nAW	Width of abdominal tergite n in dorsal view.
CI	Cephalic index ( $HW/HL \times 100$ ).
SI	Scape index ( $SL/HW \times 100$ ).
OI	Ocular index ( $ED/HW \times 100$ ).
PtI	Petiolar index ( $PtL/PtW \times 100$ ).
EPI	Eye position index. In full-face view, longitudinal length from the anteriormost point of the eye to the anterior clypeal margin, divided by longitudinal length from the posteriormost point of the eye to the posterior head margin $\times 100$ .

## Systematic palaeontology

### Family Formicidae Latreille, 1809

### Subfamily Dolichoderinae Forel, 1878

### Genus *Tapinoma* Förster, 1850

#### *Tapinoma glaesaria* **nom. nov.**

*Tapinoma aberrans* Dlussky in Dlussky & Perkovsky, 2002: 8. Secondary junior homonym of *Tapinoma aberrans* (Santschi, 1911).

**Etymology.** From the Latin *glaesarius*, meaning “of amber”.

**Remarks.** The specific epithet *aberrans* was initially introduced by Santschi (1911) with the original combination *Technomyrmex aberrans* Santschi, 1911, from Madagascar. Fisher (in Bolton, 2007: 120) transferred it to the genus *Tapinoma*, making the extinct *Tapinoma aberrans* Dlussky, 2002 from Eocene Rovno amber (Dlussky & Perkovsky, 2002) a secondary junior homonym of *Tapinoma aberrans* (Santschi, 1911). According to article 60.3 of the ICZN (1999), the specific epithet *aberrans* Dlussky, 2002 must be rejected and replaced by a new substitute name, proposed here as *glaesaria* **nom. nov.**

#### *Tapinoma neli* **sp. nov.**

(Fig. 1)

**Holotype.** Specimen MUSM-A-2005-5a, a worker preserved in Peruvian amber; deposited in the Paleontology Department of the Museo de Historia Natural, Universidad Nacional Mayor San Marcos, Lima, Peru (MUSM).

**Etymology.** The specific epithet is a patronym honoring Prof. André Nel, a friend and palaeoentomologist extraordinaire, in celebration of his 60<sup>th</sup> anniversary and for his invaluable contribution to the knowledge of insect history.

**Diagnosis.** Small species (total length 1.65 mm) with coxae, tarsomeres and mandibles paler than remaining body, with large compound eyes (OI 33), long antennal scape (SI 143) surpassing the occipital margin by about one-third its length, and masticatory margin of mandibles with 5 teeth (t) and 11–12 denticles (d) arranged as follows from apex to basal angle: 2t-3d-1t-3d-1t-3d-1t-2(3?)d; apical tooth largest, third to fifth teeth subequal, smallest.

**Type locality and horizon.** Tamshiyacu, IQ26 locality, 30 km upstream of Iquitos, northeastern Peru (Antoine *et al.*, 2006); amber from the Pebas Formation (Mollusc Zone MZ7, late Middle Miocene, ~12 Ma; Wesselingh *et al.*, 2006; Salas-Gismondi *et al.*, 2015).

**Measurements.** BL 1.65, HL 0.55, HW 0.43, SL 0.62, ED 0.15, ML 0.77, PW 0.29, PtL 0.13, PtW 0.09, IIIAL 0.26,





**FIGURE 1.** *Tapinoma neli* **sp. nov.** (Formicidae, Dolichoderinae), holotype worker. IQ26 locality (late middle Miocene; Tamshiyacu, Loreto, Peruvian Amazonia). **A**, Habitus in lateral view. **B**, Head in full-face view. **C**, Habitus in dorsal view. Scale bars = 0.25 mm.

III<sub>AW</sub> 0.40, I<sub>VAL</sub> 0.19, IV<sub>AW</sub> 0.39. *Indices*: CI 79, SI 143, OI 33, EPI 98–100, Pti 150.

**Description.** Integument coriaceous, shiny, mostly reddish brown except coxae, tarsi, petiole, and mandibles more yellowish, and posterior borders of gastral terga with more transparent outlines; body generally covered with very short appressed pubescence, and additionally with short decumbent setae dorsally and ventrally on third and fourth gastral segments and sparse, longer suberect setae on clypeus, coxae, and gastral sternites.

**Head.** In full-face view, posterior margin (vertex) straight, posterior corners rounded, sides faintly convex. Compound eyes oval, moderately large (OI 33), situated

around midlength of head (EPI 98–100), and comprising numerous ommatidia; eye surface only slightly elevated over surrounding integument, the outer margin in full-face view aligned with outline of the sides of head. Frontal carinae present, well separated from each other, ending around midlength of eyes, without frontal lobe such that antennal sockets are entirely exposed. Antenna 12-segmented, filiform, with relatively long scape surpassing vertex for slightly more than one-third its length; funicular segments cylindrical, shortening and only slightly broadening toward apex, first funicular segment 5 × shorter than scape, apicalmost segment longest, terminating with rounded acute point. Clypeus with anteromedian region situated anteriorly to anterolateral

margins, anterior median margin with a shallow concavity; two thin anterior clypeal setae, and two stiff median clypeal setae. Posterior clypeal margin located slightly posterior to the line connecting the posteriormost surfaces of the antennal socket cavities. Mandible with 5 teeth and 11–12 denticles, each tooth separated by a series of three denticles except apical and subapical teeth contiguous; apical tooth largest, third to fifth teeth subequal, smallest; basal angle indistinct, continuously arched between masticatory and basal margins, with 2–3 denticles. Maxillary palp with six subequal segments, labial palp not visible.

**Mesosoma.** In profile pronotum continuously convex, with posteroventral corners rounded; promesonotal suture distinct, mesonotal outline feebly convex and strongly inclined in its anterior half, subhorizontal and distinctly higher than propodeum in its posterior half; metanotal groove distinctly impressed; propodeal dorsum approximately 3× shorter than declivitous face, their junction distinctly angled, without spine; declivitous face flat. Propodeal spiracle around middle of margin between lateral and declivitous faces. Legs elongate and slender, glabrous except one stiff seta on inner surface of all coxae; femora, particularly profemur, swollen in the basal one-third; protibia with two apical spurs, a long pectinate one (calcar) and a very small simple one, mesotibia and metatibia each with one long simple spur; all legs with basitarsomere as long as combined length of following tarsi, tarsomeres I–IV with two short apical setae, pretarsal claws simple, arolium small.

**Petiole.** In profile a scale strongly reduced and inclined anteriorly, the anterior face extremely short, the posterior face a long flat strip; apparently entirely concealed in dorsal view when gaster is in line with alitrunk, overhung by the anteriorly projecting first gastral tergite.

**Gaster.** First gastral tergite longest, anterior projection ventrally with a groove accommodating the petiole. In dorsal view four visible tergites, each with posterior margin bordered by a row of short suberect setae barely surpassing the margin. Fourth tergite small, with posterior border straight. Fifth tergite, although weakly discernable, is placed anteroventrally of tergite 4.

**Remarks.** The new fossil is placed in *Tapinoma* owing to the petiole with a highly reduced scale, the first gastral tergite projecting over the petiole and with a ventral groove for the reception of the entire petiole, and the gaster with only four tergites visible dorsally (Shattuck, 1992). The petiolar scale is absent in most species of *Tapinoma*, but present in few extant species with exactly the same shape as in our fossil: reduced, ridged and with a distinct angle dorsally, strongly inclined anteriorly and with the anterior face much shorter than the posterior face (see for example photographs of *T. demissum*, *T. epinotale*, *T. lugubrum* or *T. sinense* on [www.antweb.org](http://www.antweb.org)). *Aptinoma* Fisher, another representative of Tapinomini from Madagascar, is very similar to *Tapinoma* but it has a more developed petiolar scale not ridged between

anterior and posterior faces, the propodeum has no distinct angle, and the antennal scape does not surpass the occipital margin (Fisher, 2009).

## Discussion

Among the five extinct species of *Tapinoma* previously described, *T. glaesaria* and *T. minutissimum* are known from the male caste only and they thus cannot be compared with the new worker documented here. Among the species known by workers, *Tapinoma electrinum*, from Eocene Rovno amber, is not considerably larger (length ca. 2 mm instead of 1.65 mm in *T. neli*), but it is figured as having a short scape not reaching the vertex (SI approximately 74; Dlussky & Perkovsky, 2002: fig. 3a), while the new species has a relatively long scape surpassing the vertex for one-third its length (SI 143). *Tapinoma electrinum* apparently has the eyes entirely situated below the level of midlength of head, while these are centered with midlength of head in *T. neli*. *Tapinoma baculum*, from an impression fossil of the middle Miocene of Shanwang (China), is hardly comparable based on the drawing of the dorsal view alone (Zhang, 1989: fig. 284). It is an alate, apparently a gyne, but the scape is not clearly visible and the petiole concealed. The only visible differences with *T. neli* are a larger size (3.25 mm, but useless since it is a gyne) and the anterior clypeal margin apparently broadly convex. Last, *T. troche*, from Miocene Dominican amber, differs by its shorter scape not reaching the vertex (SI 31) and its smaller eyes (OI 16 in *T. troche*, 33 in *T. neli*). *Tapinoma* has not been recorded from Peru so far, either as a living or fossil organism, and only five extant species are known from South America, from which the new fossil can be distinguished by its size, scape length, eye position, and mandibular teeth, among others. *Tapinoma amazonae* Wheeler, from Brazil, is larger (2.5–3.0 mm), bears fewer mandibular teeth and denticles (3 large teeth and 7–8 denticles), and the scapes extend for one fourth its length beyond the posterior head margin. *Tapinoma antarcticum* Forel from Chile is only slightly larger (1.8–2.0 mm) but its scapes barely surpass the posterior margin of head (by 1/6 their length) and the mandible bears 5 contiguous teeth and no denticles. *Tapinoma atriceps* Emery, known from Brazil and Paraguay, has a different coloration, smaller eyes, the scapes surpassing the posterior head margin by nearly one fifth their length, and at least 5 contiguous teeth on mandibles. *Tapinoma litorale* Wheeler from Venezuela is smaller (1.25–1.50 mm), with a pale colouration, shorter scapes not reaching the posterior head margin, smaller eyes situated more anteriorly, and mandibles with numerous teeth gradually increasing in size to the apex. Finally, *T. ramulorum* Emery from Brazil has the scapes surpassing the posterior head margin by nearly one fifth their length, and



at least 6 mandibular teeth not separated by denticles and gradually increasing in size to the apex.

The discovery of *Tapinoma* in amber of Peru provides a first hint of the South American ant composition during the early Neogene and before the land connection between Central and North America. The chemical characterization of Peruvian amber indicates it is a class Ic amber (*sensu* Anderson *et al.*, 1992) that was probably produced by legume trees of the genus *Hymenaea* (Perrichot, unpublished pers. data), thus similarly to the slightly older, highly fossiliferous amber from Mexico and the Dominican Republic. It is hoped that more Peruvian amber will be accessed in the near future to further reveal the ancient South American ant diversity as well as possible biogeographic patterns.

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