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A new enigmatic ant genus from late Eocene Danish Amber and its evolutionary and zoogeographic significance

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Usomyrma mirabilis gen. et sp. nov., belonging to the tribe Leptomyrmecini of the subfamily Dolichoderinae, are described based on two males from the late Eocene Danish Amber. *Usomyrma* differs from *Leptomyrmex* by a set of plesiomorphic and autapomorphic features. Distinctly plesiomorphic characters include the fore wing venation, i.e., the presence of the well developed pterostigma, the wide closed cell 3r and the big central closed cell that formed by the fusion of the cells (1+2r)+mcu, and the structure of mandibles, which are elongate-triangular, with a well developed masticatory margin that, unlike *Leptomyrmex*, possesses a set of well developed, relatively long and sharp teeth. The most distinctive autapomorphy of *Usomyrma* is the structure of the antennae: although it remains 13-segmented, its second funicular segment is extremely elongate, much longer than any other segment, including the apical one. The generic composition of the tribe Leptomyrmecini is partly reassessed compared to the previously published data. We propose to establish a new informal *Leptomyrmex* genus-group within tribe Leptomyrmecini, including in it the extant genus *Leptomyrmex*, two fossil (*Usomyrma* gen. nov., *Leptomyrmula*) and a “*Leptomyrmex*” male from the Dominican Amber that probably represents a third extinct genus. Finally, a new, alternative evolutionary and zoogeographic scenario for the *Leptomyrmex* genus-group is proposed. We suggest that fore wing venation of *Usomyrma* is ancestral to other genera of this group. The next evolutionary step was the complete reduction of the closed central cell in *Leptomyrmula*, while conserving the pterostigma and a wide closed cell 3r. Then, in the modern *Leptomyrmex* males the pterostigma was reduced and the cell 3r became very narrow. Finally, the most apomorphic condition is illustrated by the venation of “*Leptomyrmex*” male from the Dominican Amber, which has no pterostigma and pterostigmal appendages, combined with the absence of the closed cell 3r. As a result, we suppose that the ancestor of *Leptomyrmex* might penetrate from Eurasia to Australia via South-East Asia, and then *Leptomyrmex* penetrated to South America, where the most advanced morphologically form (i.e., “*Leptomyrmex*” male from the Dominican Amber) arose, but extinct in Miocene.

Key words: Hymenoptera, Formicidae, Dolichoderinae, Leptomyrmecini, evolution, amber, Eocene.

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Introduction

The subfamily Dolichoderinae represents one of the oldest evolutionary stocks of the modern ant subfamilies: the oldest palaeontological records for a member of this subfamily belong to the Late Cretaceous (Canadian amber, Campanian, ca. 80 Ma) (Dlussky 1999), though the modern genera are known first from the middle Eocene deposits (ca. 45 Ma) (Wilson 1985a; Dlussky and Rasnitsyn 2002). The dolichoderine ants dominated numerically in the Eocene taphocenosis

of Europe, but from the start of the Oligocene their proportion strongly decreased compared to the members of other modern subfamilies—Myrmicinae and Formicinae (Dlussky 2002, 2008; Dlussky and Rasnitsyn 2002, 2007). Now Dolichoderinae has worldwide distribution, but the highest generic and species diversity occurs in the Neotropical, Australasian, and Oriental Regions.

The genus *Leptomyrmex* Mayr, 1862 is highly specialized morphologically and is one of the most enigmatic genera among Dolichoderinae ants. Most probably, it forms a sister group for the rest of dolichoderines (Shattuck 1995; see also

discussion below). Discovery of the fossil *Usomyrma* gen. nov. not only strongly support the uniqueness of the *Leptomyrme* genus-group, but helps to throw light on questions concerning the evolution and zoogeography of the tribe Leptomyrmeini as a whole, that are not yet fully resolved.

Institutional abbreviations.—ZMUC, Zoological Museum of the University of Copenhagen, Denmark.

Other abbreviations.—AH, height of mesosoma seen in profile, measured from the upper level of scutum perpendicularly to the level of lower margin of mesopleuron; AL, diagonal length of mesosoma seen in profile, measured from the anterior-upper margin of pronotum to the posterior margin of propodeal lobes; HL, length of head in full-face view, measured in a straight line from the anterior point of median clypeal margin to mid-point of the posterior margin; HW, maximum width of head in full-face view behind the eyes; HTL, length of tibia of hind leg; OL₁, maximum diameter of eye; OL₂, minimal diameter of eye, PH, maximum height of petiole in profile; PL, maximum length of petiole seen from above from the posterodorsal margin of petiole to the articulation with propodeum; SCL, maximum length of scutum + scutellum seen from above; SCW, maximum width of scutum seen from above; SL, maximum straight-line length of antennal scape seen in profile.

Indices.—AI, AL/AH; CI, HL/HW; HTI, HTL/HL; OI₁, OL₁/HL; OI₂, OL₂/HW; OI₃, OL₃/OL₂; PI, PL/PH; SCI, SCL/SCW; SI₁, SL/HL; SI₂, SL/HW.

Material and methods

We investigated two pieces of amber, each containing one male; both preserved in ZMUC (Danish [= Scandinavian] Amber). The figures are based on the original drawings of the specimens and photographs made using a Canon A640 digital camera fitted to an Olympus SZX9 stereomicroscope in conjunction with the computer software Corel Draw 8 program.

The specimens were measured (accurate to 0.01 mm) using a stereomicroscope Leica S6E, and the measurements were used to calculate the various indices (see Other abbreviations section). We measured as many features as possible on each specimen, given that not all were properly visible and measurable.

Systematic palaeontology

Family Formicidae Latreille, 1809

Subfamily Dolichoderinae Forel, 1878

Tribe Leptomyrmeini Emery, 1913

Genus *Usomyrma* nov.

Type species: *Usomyrma mirabilis* sp. nov., by monotypy; see below.

Etymology: From Russian *us*, moustache (that often means antennae of insects in Russian) combined with the Greek *myrmecos*, ant, to indicate the peculiar structure of antennae of the genus.

Diagnosis.—Body slender, with long appendages. Antennae 13-segmented, second funicular segment is extremely long and curved, longer than any other antennal segments, including scape and terminal segment. Eyes big, reniform (i.e., their inner margin distinctly concave anteriorly). Mandibles elongate-triangular, masticatory margin quite long, with long and pointed apical tooth and at least five smaller though sharp following teeth (exact number of teeth is not properly visible), apices of mandibles crossed. Maxillary palps 6-segmented, labial palps 4-segmented. Fore wing with well developed pterostigma and closed cells (1+2r)+mcu and 3r; cell 3r wide. Middle and hind tibiae with very big, but not pectinate spur.

Remarks.—By the main morphological features, i.e., 13-segmented antennae, long and slender body and appendages, shape of mandibles, 6-segmented maxillary and 4-segmented labial palps, and especially by the structure of antennae and character of wing venation, *Usomyrma* certainly belong to the tribe Leptomyrmeini (for more details see discussion, below).

Stratigraphic and geographic range.—Late Eocene Amber, Denmark.

Usomyrma mirabilis sp. nov.

Figs. 1–3.

Etymology: From Latin *mirabilis*, wonderful, marvellous, miraculous, to indicate the peculiar morphology of this species.

Type material: Holotype: ZMUC, the label says “Børge Mortensen, 28.2.1965, no. 380”, male, complete specimen. Paratype: ZMUC, the label says “Børge Mortensen, 1.11.1964, no. 398”, male, complete specimen.

Type locality: Unknown locality in Denmark.

Type horizon: Danish (= Scandinavian) Amber, late Eocene.

Diagnosis.—As for genus.

Description.—Total length ca. 3.5 mm. Head ca. 1.3 times longer than broad, with distinct, quite long temples, narrowly rounded occipital corners and straight posterior margin. Occiput strongly elevated above the level of frons, and very big ocelli situated on the top of this elevated portion. Eyes very big, their maximal diameter ca. 0.6 of head length; genae very short. Shape of clypeus rather peculiar: it is quite long, its median portion swollen and forms subtriangular elevation narrowed anteriorly, lateral portions of clypeus flattened, subrectangular, with narrowly rounded anterio-lateral corners; posterior clypeal margin widely inserted between frontal lobes. Frontal triangle well developed, clearly separated by sutures from the head surface. Antennae extremely unusual (see generic diagnosis); 2nd to 12th funicular segments very long and narrow, cylindrical; length of funicular segments starting from third decreasing to the apex of antenna, except for terminal one; length of funicular segments 1:2:3:4:5:6:7:8:9:10:11:12 are 0.09:0.40:0.20:0.20:0.18:0.18:0.16:0.16:0.13:0.13:0.13:0.25 mm (holotype) and 0.15:0.37:0.21:0.21:0.18:0.18:0.16:0.16:0.16:0.16:0.18:0.26 mm (para-

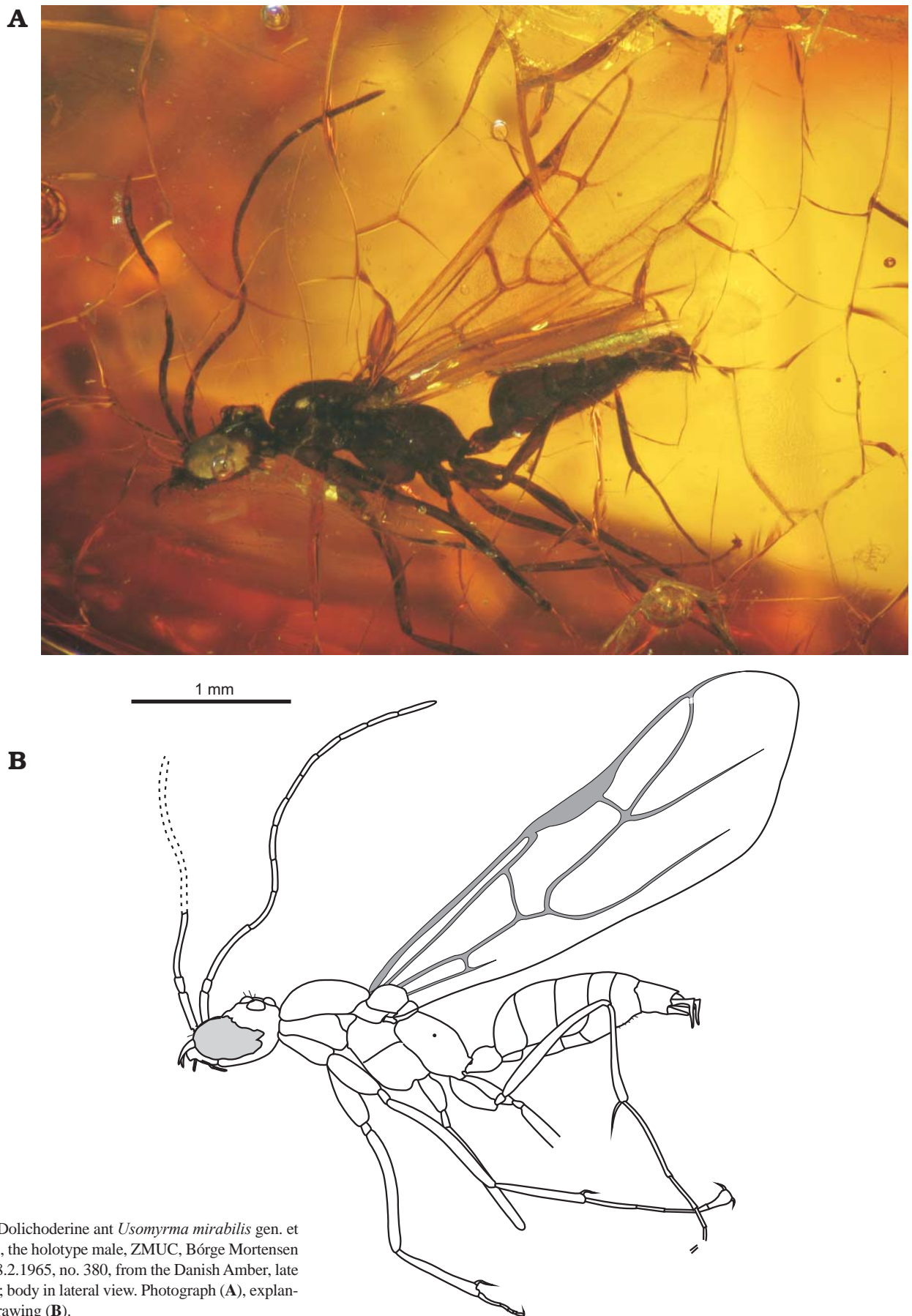


Fig. 1. Dolichoderine ant *Usomyrma mirabilis* gen. et sp. nov., the holotype male, ZMUC, Børge Mortensen coll., 28.2.1965, no. 380, from the Danish Amber, late Eocene; body in lateral view. Photograph (**A**), explanatory drawing (**B**).

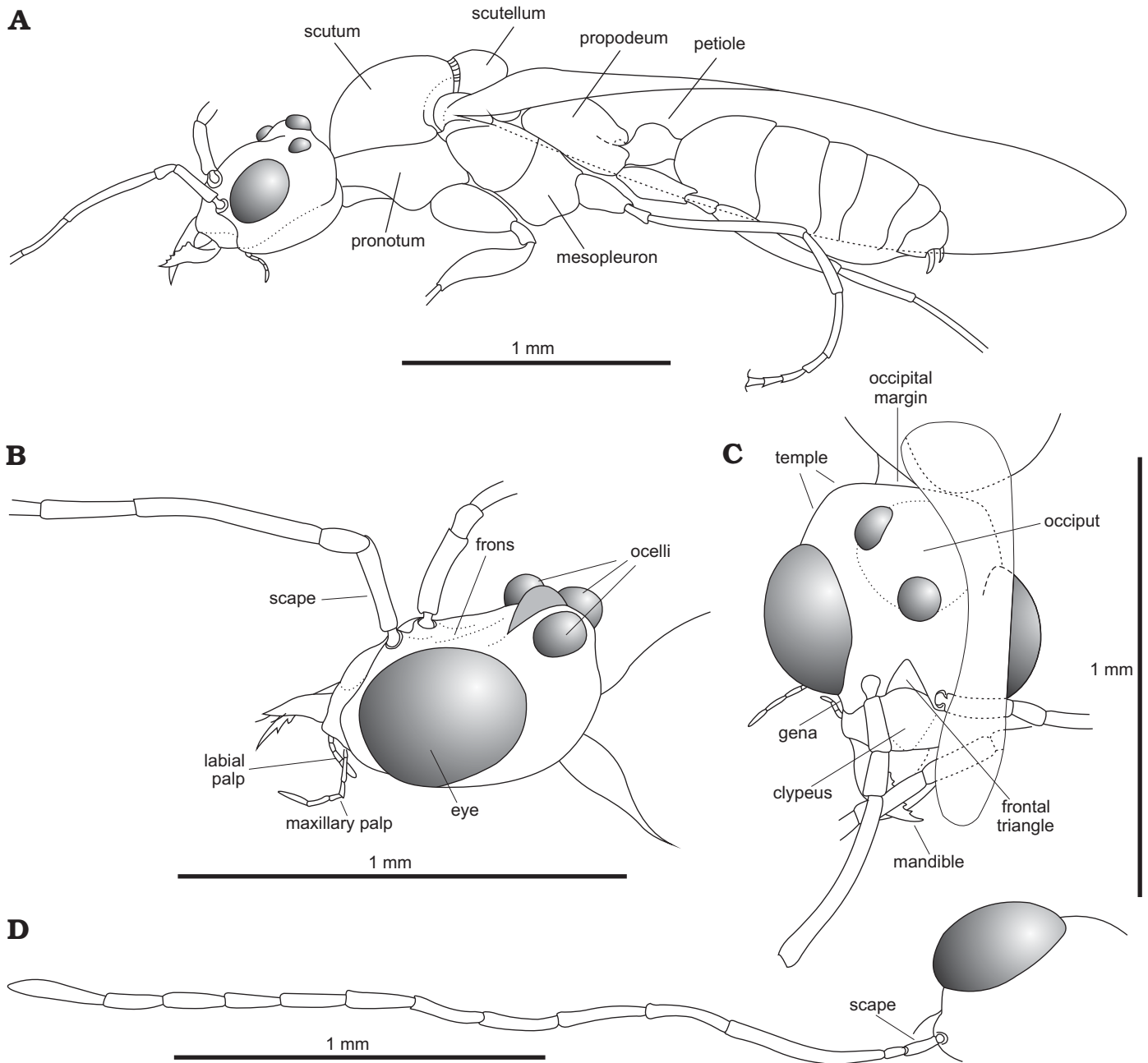


Fig. 2. Dolichoderine ant *Usomyrma mirabilis* gen. et sp. nov., the paratype male, ZMUC, Børge Mortensen coll., 1.11.1964, no. 398, from the Danish Amber, late Eocene; explanatory drawings based on the original photographs, body in lateral view (A), head in lateral view (B), head in dorsal view (C), antenna (D).

type). Scape short, ca. 2.5 times shorter than head length. Fore wing with an extraordinary venation (see also generic diagnosis). Vein section 2M+Cu more than twice longer than cross-vein cu-a. Vein sections 4Cu and 5M well developed, almost reaching wing margin. Vein A short. Cross-vein cua displaced proximally to the base of wing. Length of fore wing ca. 2.9 mm. Venation of hind wing is invisible. Mesosoma long, more than 1.6 times longer than height, scutum and scutellum slightly convex, propodeum rounded, its dorsal surface somewhat convex, subequal to declivity; mesopleural suture presents. Scutum quite narrow, nearly twice narrower than total length of scutum and scutellum; pronotum com-

pletely overlapped by scutum, invisible from above. Petiole with relatively short peduncle and well-developed, rounded node, narrowly attached to first gastral segment. Its ventral surface convex, without tooth or lobe (seen in profile). Tarsal claws simple. Genitalia: pygidium convex, without any additional structures, pointed at the apex. Pygostyles well developed. Stipites long and narrow. Volsellae long and narrow, with basal finger-shaped process that almost reach midlength of volsella. Distal part of volsella with long and pointed ventral and blunt dorsal processes. Sagittae of aedeagus long and straight, ventral denticles invisible. Integument of whole body with very fine superficial microsculpture, appears dull.

Body and legs seem to be without standing hairs, only funicular segments with very short subdecumbent pilosity.

Dimensions and indices.—Holotype: HL = 0.64, SL = 0.24, AL = 1.12, AH = 0.61, PL = 0.20, PH = 0.15, HTL = 0.58 mm; SI₁ = 0.38, PI = 1.33, AI = 1.83, HTI = 0.91; paratype: HL = 0.60, HW = 0.45, SL = 0.25, OL₁ = 0.35, OL₂ = 0.28, AL = 1.00, AH = 0.62, SCW = 0.38, SCL = 0.68, HTL = 0.75 mm; CI = 1.33, SI₁ = 0.42, SI₂ = 0.56, OI₁ = 0.58, OI₂ = 0.78, OI₃ = 1.27, AI = 1.61, SCI = 1.78, HTI = 1.25.

Remarks.—The wing venation, the antennal structure and the general appearance of the *Usomyrma* males are so amazing and unusual for any other ants, that when we first investigated the holotype and paratype specimens, we supposed that they may represent a new ant subfamily. Nevertheless, on further study we recognized that in many respects this genus resembles and most probably related to the peculiar dolichoderine genus *Leptomyrmex* by the general body shape, by the structure of antennae, and by the wing venation. For these reasons we place it to the tribe Leptomyrmecini.

Nevertheless, *Usomyrma* well differs from *Leptomyrmex* by a set of important features, that we consider either as plesiomorphic or as autapomorphies (compared to *Leptomyrmex*). One of the distinct plesiomorphies of *Usomyrma* is the peculiarities on the fore wing venation: the wings having the well developed pterostigma, the much wider closed cell 3r, and the big central closed cell that formed by the fusion of the cells (1+2r)+mcu that forms based on the loss of the vein section Rs+M (the latter also can be considered as a unique autapomorphy compare to all other known ants) (for details of the putative reconstructions of evolution of the wing venation in *Leptomyrmex* see Emery 1913; Wheeler 1934). Another plesiomorphy is the structure of mandibles: they are elongate-triangular, with a well developed masticatory margin, similar to that in *Leptomyrmex*, but except that in *Usomyrma* the masticatory margin possesses a set of the well developed, relatively long and sharp teeth.

The most distinctive autapomorphy of *Usomyrma* is the structure of antennae: the second funicular segment is extremely elongate, much longer than any other segment, including the apical one, while antennae remain 13-segmented. An analogous structure of the antennae is known only in two New Guinean species (*Leptomyrmex puberulus* Wheeler, 1934 and *L. flavitarsus* [Smith, 1859]), where the second funicular segment is similarly elongate, but the antennae have become 12-segmented! In other words, the second funicular segment in *Usomyrma* is elongated itself, but in the two *Leptomyrmex* species it represents the fusion of the second and third segments. The depressed frons, the peculiar shape of clypeus, the reniform eyes also may be considered as autapomorphies in *Usomyrma* (for details see description, above).

Stratigraphic and geographic range.—Late Eocene Amber, Denmark.

Discussion and conclusions

The majority of *Leptomyrmex* workers are quite large, up to 10 mm, and slender, with very long antennae and legs; their bodies are often a quite bright orange colour or markedly bicoloured.

Nowadays, the distribution of *Leptomyrmex* is restricted to the eastern Australia, New Guinea (and in the adjacent Aru Islands and Ceram Island), and New Caledonia (with Loyalty Islands) (Wheeler 1934; Shattuck 1992; Smith and Shattuck 2009; Lucky and Ward 2010). They inhabit sclerophyll or rainforests in mountains or sea coasts, nesting mainly in soil or in wood remnants, and foraging predominately on the ground surface. Interestingly, when moving, the workers, which forage solitarily, fold their gaster vertically or somewhat forward, over the mesosomal dorsum (similar to many specialized members of *Cataglyphis* Foerster, 1850 or *Oecophylla* Smith, 1860 species). *Leptomyrmex* has sub-caste of plerergates, which make honey-storing role, like in American honey-ants *Myrmecocystus* Wesmael, 1838 or Palearctic *Proformica* Ruzsky, 1902 (Formicinae), but such lifestyle is unknown among all other Dolichoderinae genera. Lastly, *Leptomyrmex* queens are ergatoid (except for a single known exception, see below) and differ from their workers mainly by the somewhat larger size, by the presence of ocelli and by the somewhat enlarged mesosoma (Wheeler 1934; Shattuck 1992; Lucky and Ward 2010); it should be noted that queens have been described only for seven “macro” *Leptomyrmex* species (Lucky and Ward 2010).

The preceding taxonomic revisions of *Leptomyrmex* were made by Wheeler (1915, 1934) and it was need of a modern revision. Then Smith and Shattuck (2009) described six so-called “micro” *Leptomyrmex* species from Australia, that at first were identified as members of the genus *Iridomyrmex* Mayr, 1862. Superficially, these species quite well differed from the “typical”, previously known *Leptomyrmex* species by their much smaller size, by their brownish body colour and by their less slender body and shorter appendages, etc. Shattuck (1992: 112) noted that “...several species (as yet undescribed) ...have fully winged queens...”. Surprisingly, when they (Smith and Shattuck 2009) described the new “micro” *Leptomyrmex* species, they recorded a gyne (called by them a queen) and male only for the newly described *L. burwelli*. Except for the measurements and indices for one gyne and two males they provided no formal description of them, noting only: “Queen description. As described in Shattuck (1992). Male description. As described in Shattuck (1992), except the antenna lacks the distinctive bend between funicular segments 3 and 4” (Shattuck 1992: 61). Unfortunately, such a “description” tells us very little. Finally, a modern comprehensive revision of the “macro” *Leptomyrmex* species were made by Lucky and Ward (2010) who recognized 27 species in this genus.

As we describe a new genus based on males and obviously the most important information for our discussion are the characteristics of *Leptomyrmex* males. The male of this

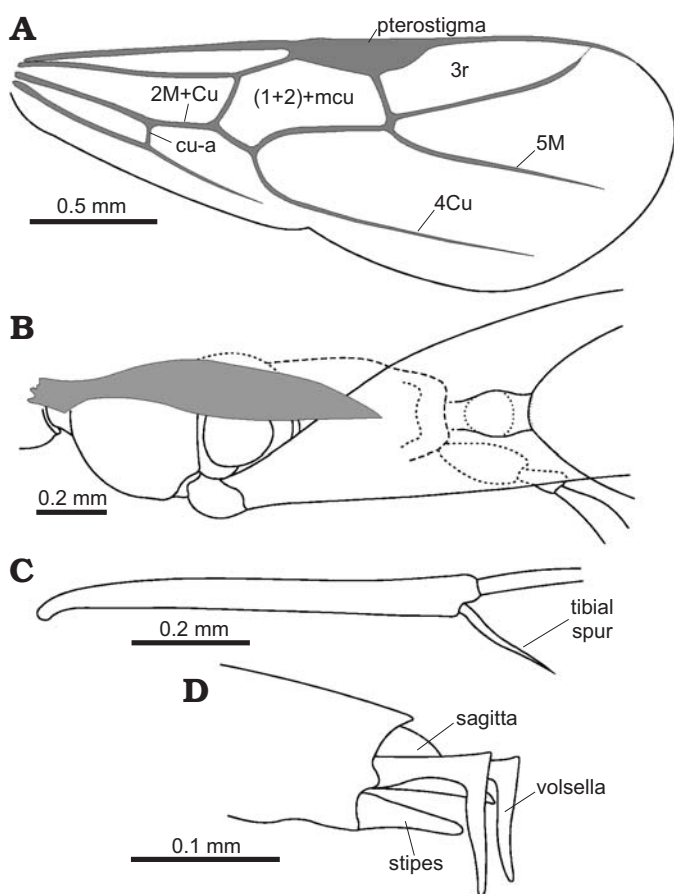


Fig. 3. Dolichoderine ant *Usomyrma mirabilis* gen. et sp. nov., the paratype male, ZMUC, Børge Mortensen coll., 1.11.1964, no. 398, from the Danish Amber, late Eocene; explanatory drawings based on the original photographs, fore wing (A), mesosoma and petiole in dorsal view (B), hind tibia (C), genitalia in lateral view (D).

genus was described first by Emery (1891), and males of 18 “macro” *Leptomyrmex* and one “micro” *Leptomyrmex* species are known now (Lucky and Ward 2010). Emery (1913: 16) stressed that in *Leptomyrmex* males “La nervulation de l’aile antérieure présente une disposition qui ne se retrouve chez aucune fourmi”, and Wheeler (1934: 76) emphasized that “Unquestionably, the most singular and intriguing feature of the male is its wing venation”. The most peculiar in the fore wing venation are absence of the pterostigma and, in many species, the presence of a pterostigmal appendage—a short, often curved or twisted vein, arising from the costal vein in the area where there should normally be the pterostigma. Secondly, the closed cell 3r is very long, and most importantly, it is very narrow; all other closed cells are absent. Although Shattuck (1992) noted that rarely two “cubital” and one “discoidal” cells may be present (according to the nomenclature used by us, these are cells 1+2r and mCu, respectively), Lucky and Ward (2010) did not mention such features. Additionally, as discussed by Wheeler (1934), the frenal apparatus is vestigial and quite functionless. Such degeneration of the frenal apparatus combining with the reduction of the wing venation in the “macro-”*Leptomyrmex* males

may be caused by the absence of true nuptial flight, because gynes are ergatoid and mating, probably, takes place inside the maternal nests or at most close to them on a ground.

The antennae in *Leptomyrmex* males (except for two New Guinean species, see Lucky and Ward 2010) are 13-segmented with a rather short scape, but they are very long, subequal to or sometimes longer than body. The funicular segments, starting from the third one, are very long and thin, the third and fourth funicular segments are curved and forming an angle between them (except for *L. burwelli* from the “micro” *Leptomyrmex* group), the second funicular segment is straight (not curved) and varying in the length, but always it is shorter than the third one (Wheeler 1934; Shattuck 1992; Lucky and Ward 2010). The mandibles of *Leptomyrmex* males are well developed, elongate-triangular, with a distinct masticatory margin that has no teeth (except in some species an apical one) but in some cases has minute denticles. Generally, the body is long and slender, with a nodiform peduncle, and the legs are very long.

Based on the set of plesiomorphies and autapomorphies (see Remarks, above), we conclude that *Usomyrma* has in general, more archaic features and *Leptomyrmex* has the evolutionary derived morphology.

Our next question was: what is the limit of the tribe Leptomyrmecini? Emery (1913) included two genera—*Leptomyrmex* and *Leptomyrmula* Emery, 1913—when he first established the tribe (*Leptomyrmula* was established to accommodate the a fossil species from the Sicilian Amber, previously described as *Leptomyrmex maravignae* Emery, 1891). Until the early 1990’s all subsequent authors considered Leptomyrmecini as the tribe sensu Emery, 1913. Then Shattuck (1992) reduced all tribes in the Dolichoderinae but his reasons for doing this were not clear and do not seem to be well supported. Ward et al. (2010) re-established tribe Leptomyrmecini, although their treatment of its generic composition cardinally differed from the earlier one (see below).

Baroni Urbani (1980) described *Leptomyrmex neotropicus* based on workers found in the Dominican Amber (Central America, Miocene) and in the same paper he recorded another fossil specimen (male) found in the same deposit, ascribing this very interesting specimen to the genus *Leptomyrmex*. Wilson (1985b) cast doubt on the taxonomic position of *L. neotropicus*, but in a subsequent paper Baroni Urbani and Wilson (1987) studied a second worker specimen and confirmed the attribution of this species to *Leptomyrmex*. In the same paper they also discussed the morphological peculiarities and possible taxonomic position of the “*Leptomyrmex*” male mentioned above; they wrote that *L. neotropicus* by the general appearance most resembles the extant *L. fragilis* (Smith, 1859), which is distributed in New Guinea, Ceram Island, and Aru Island, but differs from the latter by its smaller body size and some other morphological features (for details see Baroni Urbani and Wilson 1987: 2, 4, 5).

The characteristics of the “*Leptomyrmex*” male from the Dominican Amber, as given by Baroni Urbani and Wilson (1987), are most relevant to this discussion. The most import-

ant feature is again the fore wing venation: the pterostigma, pterostigmal appendages, and closed cells, including the cell 3r, are completely absent! In our opinion, this character of fore wing venation is probably sufficient to consider that this male belongs to a separate new genus. A similar suggestion was also made by Baroni Urbani and Wilson (1987: 5): “The leptomyrmecine male, whether *Leptomyrmex neotropicus* or not, may be sufficiently different from the living *Leptomyrmex* and Sicilian amber *Leptomyrmula* to warrant separation as a distinct genus”; but they went on to say “However, we do not believe it prudent to take this step until enough material has accumulated to make the worker-male association more probable, and to better estimate the extent of variation in both cases”, an opinion with which we agree.

So, how do we see the modern generic composition of the tribe Leptomyrmecini? Ward et al. (2010) in their very interesting and useful paper included 16 genera to the tribe Leptomyrmecini; six genera are distributed exclusively or chiefly in the Neotropics, and the other 10—in the Australasian and Oriental Regions. Concurrently, they excluded from this tribe the genus *Leptomyrmula*, even though relatedness of this genus to *Leptomyrmex* was never doubted by any of the preceding authors. Ward et al. (2010: 352) also stated that the earlier (e.g., Shattuck 1995) “morphological studies suggested that *Leptomyrmex* is sister to the rest of the Dolichoderinae, an arrangement not supported by our results”. It is quite obvious that Ward et al. (2010: 361) reached this conclusion based almost exclusively on molecular-genetic analysis and that morphological features were not taken into account in the phylograms. Moreover, somewhat inconsistently with their own molecular results, they have written in the diagnosis of the tribe Leptomyrmecini: “Morphologically heterogeneous assemblage, recognized primarily by disagreement with the 3 preceding diagnoses (i.e., diagnosis of the tribes Dolichoderini, Tapinomini, and Bothriomyrmecini—our remark)”. In our opinion, the Ward and co-authors’ treatment of the tribe Leptomyrmecini is too wide and should be reassessed based on morphological analysis or perhaps combined morphological and molecular-genetic analysis.

The complete revision of the subfamily Dolichoderinae at the suprageneric level lies far outside the main task of this paper and at the moment we do not have sufficient data to reassess formally the generic composition of the Leptomyrmecini sensu Ward et al. (2010). Nevertheless, based on morphological evidence (obviously there is no molecular genetic data for fossil amber specimens) we propose as a first step towards such a revision, to group together the extant genus *Leptomyrmex* and the fossil genera *Usomyrma*, *Leptomyrmula*, and “*Leptomyrmex*” male specimen from the Dominican Amber, to establish informal *Leptomyrmex* genus-group within the tribe Leptomyrmecini. The main synapomorphies for this genus-group (based on the males morphology) are the peculiarities of the fore wing venation, particularly loss of the vein section Rs+M (which led to the fusion of the cells [1+2r]+mcu in *Usomyrma*) with the further reduction of the central vein sections and cells in the other genera. Such wing

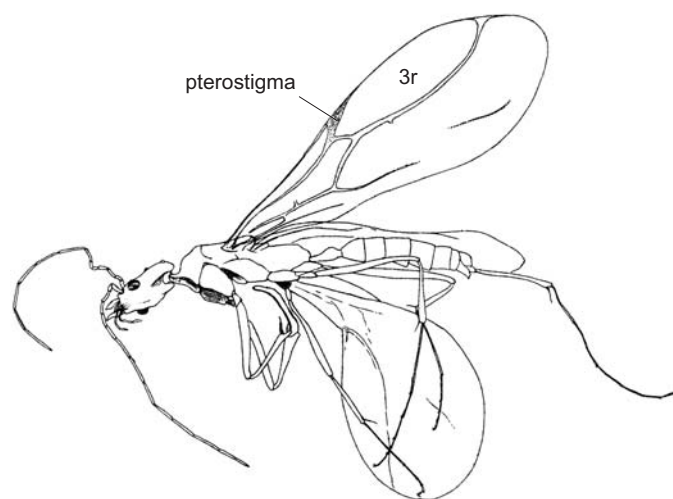


Fig. 4. Dolichoderine ant *Leptomyrmula maravignae* (Emery, 1891), the holotype male, from the Sicilian Amber, body in lateral view (after Emery 1891).

venation is unique not only for the subfamily Dolichoderinae, but for all known ants at all.

We suggest the following evolutionary trend in the fore wing venation within this group. The most plesiomorphic, i.e., putatively ancestral to other genera of this genus-group, is the venation of *Usomyrma* that has the well developed pterostigma, the closed central cell and the relatively wide cell 3r (Figs. 1A, B, 3A). We suggest that the next evolutionary step was the complete reduction of the closed central cell in *Leptomyrmula* while conserving the pterostigma (though it is somewhat smaller than that in *Usomyrma*) and a wide closed cell 3r (Fig. 4). Then, in the modern *Leptomyrmex* males the pterostigma was reduced and the cell 3r became very narrow (see Lucky and Ward 2010). Finally, the most apomorphic condition is illustrated by the venation of “*Leptomyrmex*” male from the Dominican Amber, which has no pterostigma and pterostigmal appendages combined with the absence of the closed cell 3r (see Baroni Urbani and Wilson 1987; Fig. 2).

Ward et al. (2010) proposed the following scenario for the origin and further spread and diversification of the tribe Leptomyrmecini (“s.l.”): the tribe arose in the Neotropics about 50 Ma, and two subgroups of leptomyrmecines (including *Leptomyrmex*) later colonized Australia. The older of these, *Leptomyrmex*, is a sister to the New World clade of (*Forelius* Emery, 1888 + *Dorymyrmex* Mayr, 1866). Based on the latter, they supposed that “*Leptomyrmex*” from the Dominican Amber (15–20 Ma) represents an extinct stem lineage of (*Forelius* + *Dorymyrmex*) in America. Their data also suggested the average time of the origin of the *Leptomyrmex* stock ca. 37 Ma, with the oldest possible age being somewhat more than 40 Ma. Our finding of *Usomyrma* in the late Eocene amber (ca. 37 Ma), and the modern dating of the Sicilian Amber (where *Leptomyrmula* was found) as not the Miocene but the early Oligocene (Skalski and Veggiani

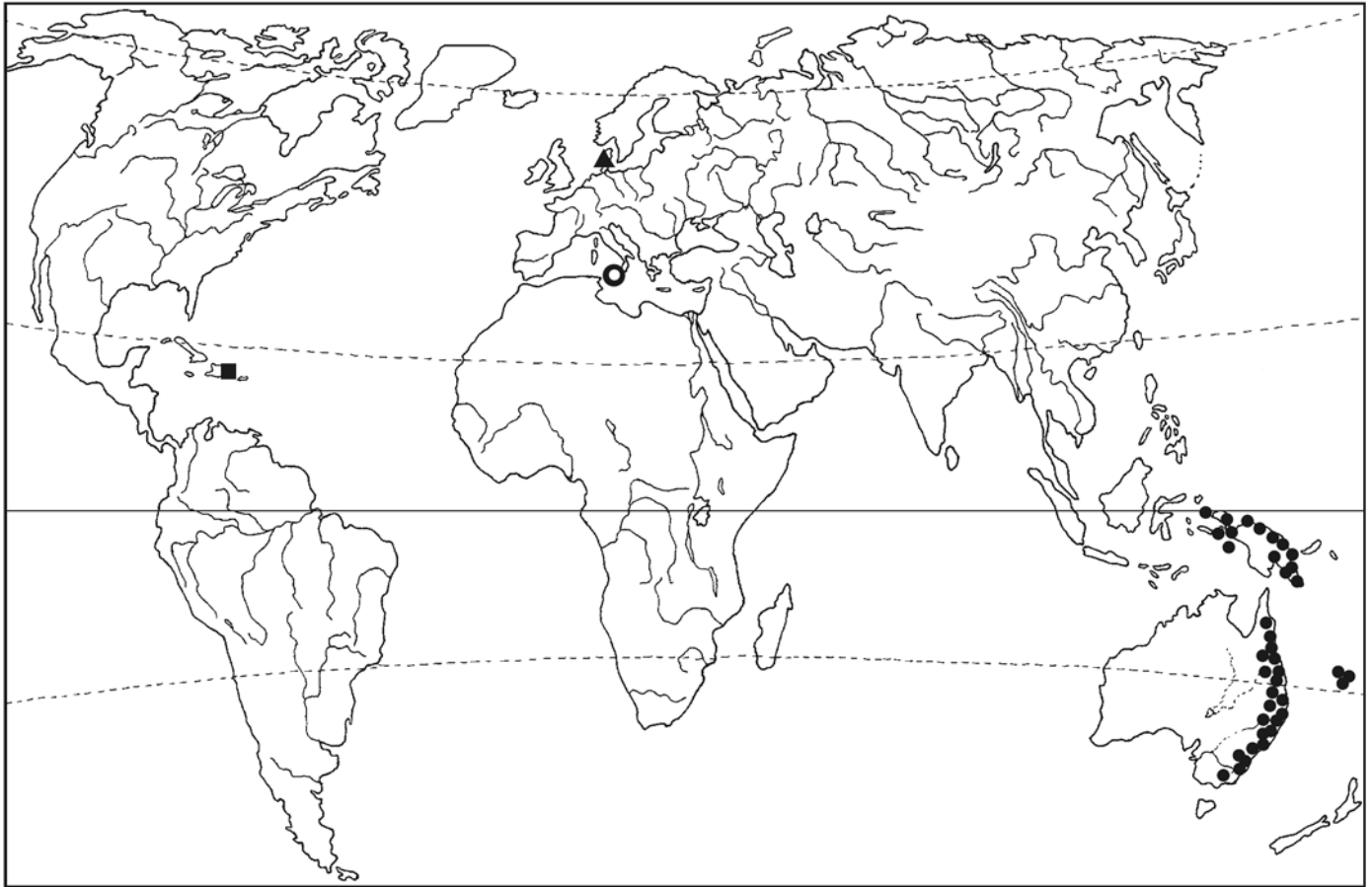


Fig. 5. Map of distribution of fossil species *Usomyrma* gen. nov. (triangle), *Leptomyrmula* Emery, 1913 (circle), “*Leptomyrmex*” male (square) and of extant species *Leptomyrmex* Mayr, 1862 (dots).

1990; 29–34 Ma), does not contradict the timing proposed by Ward et al. (2010).

On the other hand, if one accepts our treatment of the *Leptomyrmex* genus-group (above), then this group probably does not have an American origin (see also Fig. 5). The main reasons are: the representative of the oldest stem and most primitive morphologically, is the genus *Usomyrma* (Danish Amber, late Eocene, ca. 37 Ma), the representative of the next evolutionary step, *Leptomyrmula*, was found in Sicilian Amber (early Oligocene, 29–34 Ma) while modern *Leptomyrmex* (Australasian Region) is more derived. The only known “*Leptomyrmex*” male from the America (Dominican Amber, Miocene, 15–20 Ma) is, in our opinion, the most derived. Under this scenario, Ward et al.’s (2010) supposition that South America was a possible place of the origin of Leptomyrmecini (and modern *Leptomyrmex*) with their later dispersion to Australia seems unlikely. We think it more probable that the ancestor of *Leptomyrmex* penetrated from the Europe during the Eocene (or even earlier) to Australia.

If so, what was the way of dispersion of this ancestor? As there are no strict evidences for a such way, one may propose two alternative scenarios.

The first one claims that the ancestor of *Leptomyrmex* might penetrate to Australia via South-East Asia. We are

well aware that there were no direct land connections between South-East Asia and Australia (e.g., see Sinitsyn 1962, 1965), but species might cross the relatively narrow straits between Soenda Isles, New Guinea, and Australia. The argument that the ergatoid queens observed in modern *Leptomyrmex* species might indicate poor dispersion among ancestral species is very doubtful: ergatoid queens might evolve much later after *Leptomyrmex* reached Australia. Furthermore, the indirect evidence of Aenictinae species distribution supports our suggestion: all species of *Aenictus* Shuckard, 1840 have wingless gynes and highly specialized physogastric queens, but there is no doubt the genus has an Asian origin but occurs also in Australia and New Guinea. Then *Leptomyrmex* penetrated to South America, where the most advanced morphologically form (i.e., “*Leptomyrmex*” male from the Dominican Amber) arose, following the mode suggested by Ward et al. (2010), but in the reverse direction: i.e., *Leptomyrmex* species may have migrated from Australia to South America via Antarctica, which was connected by land masses until the late Oligocene (Sanmartín and Ronquist 2004).

On the other hand, there are several facts that at least partly contradict such scenario. Perhaps the most important is that there are no any known either modern or fossil rep-

representatives of the *Leptomymex* genus-group in South and South-East Asia, despite the habitat conditions in these regions both in a past and present seem quite suitable for them. Moreover, despite we have no evidence to positively answer the question where genus *Leptomymex* arose: in Asia, New Guinea or in Australia, most probably the place of its origin was Australia. This may be supported by the fact that in New Guinea lives more derived morphologically species than in Australia (see also Lucky and Ward 2010). Hence, the alternative way of dispersion of the ancestor of *Leptomymex* might be from Europe to America via so-called De Geer's Land Bridge in the late Eocene (see McKenna 1983; Tiffney 1985), and then—to Australia (by the way from America via Antarctica as proposed by Ward et al. 2010). In such a case, the Dominican Amber "*Leptomymex*" might evolve later, but extinct after Miocene.

Whichever, the species radiation and diversification of the genus took place in Australia.

In conclusion, one can find many examples when the modern distribution of extant groups of animals does not correspond with the paleontological evidence of distribution. One example among ants may be the "bulldog ants", subfamily Myrmeciinae. Their modern distribution is restricted to Australia and New Caledonia but fossils suggest a much wider distribution in the past: a couple of fossil genera were found in the middle and late Eocene deposits of the North (USA and Canada) and South America (Argentina), and Europe (Denmark, Germany) (Dlussky and Perfilieva 2003; Archibald et al. 2006; Dlussky 2012).

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